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Radiocarbon-Based Partitioning of Soil Respiration in an Old-Growth Coniferous Forest

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Abstract

Temperate forests play an important role in the global carbon cycle, and are thought to currently be a sink for atmospheric CO_2. However, we lack understanding of the drivers of forest carbon accumulation and loss, hampering our ability to predict carbon cycle responses to global change. In this study, we used CO_2 flux and radiocarbon (^{14}C) measurements to investigate the role of seasonal drivers on soil respiration. Radiocarbon measurements of CO_2 evolved during incubation of fine roots and root-free soils at the beginning and end of the growing season (April and August) showed that these two soil respiration sources (fine roots vis-à-vis soils) have different mean residence times that stayed constant between seasons. Radiocarbon measurements show that root respiration was made up of carbon fixed 3–5 years prior to sampling, and that heterotrophic respiration was made up of carbon fixed 7–10 years prior. The difference in radiocarbon signature between the two sources allowed us to partition autotrophic and heterotrophic respiration sources for soil respiration measurements in the field. We observed a small but significant increase in $\Delta^{14}C$ of soil respiration between April and August, suggesting an increase in heterotrophic respiration sources over the growing season. Using a two end-member mixing model, we estimate that $55 \pm 22\%$ of soil respiration originated from autotrophic (root) sources in April, but their contribution dropped to $38 \pm 21\%$ in August. These findings suggest that the contribution of root respiration increases at a time of high productivity and/or as a result of relatively low microbial respiration in the early spring in this old-growth coniferous forest.

Key words: soil CO_2 flux; radiocarbon; root respiration; residence time of soil carbon; stored carbon; photosynthates.

Introduction

Forest ecosystems are currently thought to be a carbon sink (Pan and others 2011), but how long this sink will persist is poorly known. Large stocks of organic substrates accumulate in the surface soils of old-growth forests, yet these stores may be lost to the atmosphere at an increasing rate as the climate warms. Considerable uncertainties persist in

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modeling soil C storage because the sensitivity of processes governing carbon accumulation and loss to phenology and environmental drivers (temperature, moisture) remains poorly quantified. The rate of soil respiration differs between autotrophic and heterotrophic controls, and the rate change varies seasonally (Cisneros-Dozal and others 2005). Separating soil respiration, defined as the sum of autotrophic and heterotrophic respiration, into autotrophic and heterotrophic sources helps us understand the environmental sensitivities of these processes to make better predictions about potential feedbacks between climate and soil respiration.

Characterizing turnover rates of soil C of old-growth forests in the Pacific Northwest of the USA is important because these forests have the greatest storage of belowground C in the contiguous USA (Kern 1994; Turner and others 1995). The radiocarbon (^{14}C) signature of CO_2 has been used to determine the residence time of atmospheric C in terrestrial ecosystems since its fixation by plant photosynthesis after 1960 to an uncertainty of ±1–3 years (Trumbore 2009). The annual rate of decline of $^{14}CO_2$ caused by the legacy from the aboveground testing of nuclear weapons in the 1950's and 60's and by the ongoing fossil fuel emissions has been about 5‰ per year in the last decade (Levin and others 2010). Changes in the atmosphere's ^{14}C signature allow us to distinguish carbon fixed from the atmosphere from 1 year to the next. For example, recently fixed C has ^{14}C values close to that of current atmospheric CO_2. Whereas, stored C, such as is found in litter, SOM, and plant C pools, has greater ^{14}C values because C fixed for these components was from the atmosphere at a time closer to the bomb-testing period (Schuur and Trumbore 2006).

There is a growing body of evidence showing recent photosynthates as a major driver of root and soil respiration (Horwath and others, 1994; Högberg and others 2001; Scott-Denton and others 2006; Kuzyakov 2006, 2011; Hopkins and others 2013). Phillips and others (2013) measured ^{14}C of soil-respired CO_2 in a mixed hardwood forest in Wisconsin, U.S.A. They found that recent photosynthates are the major C source supporting root growth in spring and early summer. They also found ^{14}C of soil-respired CO_2 continues to decline in late summer after root activity decreases. They attribute this later-summer ^{14}C decline to continued microbial turnover of root-derived C. They conclude that inputs of new photosynthates through roots are an important C source of soil respiration.

Plants also store a portion of assimilated C for future use (Chapin and others 1990; Cisneros-Dozal and others 2005). The importance of C storage in plants is illustrated by the fact that C storage directly competes with growth. Hoch and others (2003) found non-structural carbohydrate reserves present in ten temperate deciduous and coniferous tree species throughout the growing season. Cisneros-Dozal and others (2005) show the residence time of C respired by tree roots varied significantly from early to late spring, suggesting a shift in consumed substrates from stored non-structural carbohydrates to recent photosynthates. Richardson and others (2013) demonstrate a two-pool (fast and slow turnover of C) model can reasonably predict the interannual variability in woody biomass increment. Besides fueling root respiration in the early growing season, C reserves are an important resource for mature trees recovering from environmental stress (Chapin and others 1990; Vargas and others 2009; Gaudinski and others 2009). Carbone and Trumbore (2007) suggested three C pools are involved in plant metabolism rates: a fast pool, an intermediate pool, and a long-term storage pool. The latter tend to be used during periods of stress or to meet early season growth demands. Gaudinski and others (2009) suggest as stress conditions become more extreme, the contribution of stored C reserve would be expected to increase. Despite these advances, the role of temporal and environmental drivers in the use of stored C as a constant source of respired CO_2 is poorly characterized, and to our best knowledge, has never been investigated in an old-growth forest in which the age of many trees exceed 500 years.

The objectives of this study are to determine (1) the mean residence time (MRT) of respired CO_2 from autotrophs and heterotrophs and (2) the proportional contribution from these two respiration sources to soil CO_2 flux at the beginning and the end of a growing season. We used radiocarbon measurements at the beginning and end of the growing season (April and August) over 2 years to determine the seasonal variation of C sources in plant and soil respiration at Wind River Field Station (WRFS), where strong seasonality in ecosystem C fluxes has been demonstrated by eddy covariance (EC) and soil chamber measurements. Our ^{14}C measurement campaigns coincide with periods of seasonally high (low) and low (high) soil moisture content (soil temperature) conditions between which considerable differences in gross C fluxes also are present. This seasonal difference in gross C fluxes could potentially have large impacts on the interpretation of the ^{14}C measurements.

Materials and Methods

Study Site

Wind River Field Station is located in the Gifford Pinchot National Forest, Washington, USA in a

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preserved 478 hectare section of old-growth forest known as the Thorton T. Munger Research Natural Area (45°49′13.76″N, 121°57′06.88″W). Canopy leaf area index estimates range from 8 to 9 m^2 (Thomas and Winner 2000; Roberts and others 2004; Parker and others 2002). The local climate is classified as a temperate winter-wet, summer-dry climate. The dominant tree species are *Tsuga heterophylla* and *P. menziesii*. The average height of dominant overstory trees is 55 m. Soils include a large amount of coarse and fine roots. Mature root systems extend up to 2 m deep, though most of the root biomass is found in the first 0.5 m of the soil (Shaw and others 2004). Soils are described as medial, mesic, Entic Vitrands, and are 2–3 m deep, primarily made of volcanic material, and well drained (Shaw and others 2004). Annual precipitation had a mean of 2,223 mm y^{-1} during 1978–1998, with less than 10% occurring in the summer months. Annual average temperature was 8.7°C during 1978–1998. More site information can be found in Shaw and others (2004), Harmon and others (2004), Falk and others (2008), and Wharton and others (2012).

Radiocarbon Definition and Partitioning Methods

Radiocarbon data are expressed as $\Delta^{14}C$ in parts per thousand or per mil (‰), which is the deviation of a sample $^{14}C/^{12}C$ ratio relative to the OxI standard in 1950:

$$^{14}C = \left[\frac{\left[\frac{^{14}C}{^{12}C}\right]_{sample,-25}}{0.95 \times \left[\frac{^{14}C}{^{12}C}\right]_{oxl,-19} \times \exp\left(\frac{(y-1950)}{8267}\right)} - 1 \right] \times 1000, \quad (1)$$

where y is the year of sample measurement. All measurements are corrected for the effect of mass-dependent isotope fractionation using AMS on-line $^{13}C/^{12}C$ and normalizing it to a common $\delta^{13}C$ value of $-25‰$, assuming ^{14}C is fractionated twice as much as ^{13}C (Stuiver and Polach 1977; Reimer and others 2004).

Using ^{14}C signatures, soil respiration can be partitioned following isotopic mass balance (for example, Hanson and others 2000; Czimczik and others 2006; Gomez-Casanovas and others 2012), given by

$$\%R_A = \frac{S-H}{A-H} \times 100, \quad (2)$$

where Δ represents measured $\Delta^{14}C$ values from respiratory fluxes (R), and subscripts S, H, and A represent soil, heterotrophic, and autotrophic respiration, respectively. Using average Δ_A and Δ_H values measured in each campaign as end members, we estimated the proportional contribution of autotrophic versus heterotrophic sources to total soil efflux for each of the two study periods.

The ^{14}C signature of carbon reservoirs or fluxes can be used to estimate the mean residence time of carbon moving through different ecosystem processes. Carbon fixed in ecosystem reservoirs carries the ^{14}C signature of that year's atmosphere, which decreases measurably year to year (4–5.5‰ y^{-1} decline in recent decades; Levin and others 2010; Graven and others 2012). Thus, the ^{14}C signature of respiratory flux should be equivalent to the residence time of carbon in a well-mixed reservoir at steady state (Gaudinski and others 2009). We used a single pool, homogeneous steady state model (Trumbore 2000) with the atmospheric history of ^{14}C to calculate the mean residence time of respired CO_2.

Long-Term Ecosystem Fluxes

In addition to the radiocarbon measurements, we analyzed long-term NEE and unpublished soil respiration data from 2005 to 2011. These long-term flux datasets were aggregated to reveal the seasonal pattern in the observed net ecosystem and soil respiration fluxes at our study site. We interpreted the ^{14}C measurements in the context of the seasonal variation revealed by meteorological and CO_2 flux data.

Automated Soil Chambers

The WRFS long-term soil CO_2 flux monitoring system follows the design of Goulden and Crill (1997) and is briefly summarized here. In 2005, seven automated chambers, each constructed of a clear Lexan cylinder (25 l), were installed on top of the soil organic layer equidistant in a circular pattern of approximately 10 m radius with a chamber control and air sample measurement system located at circle center. Chamber lids were actuated pneumatically. Soil temperature near each chamber site was measured continuously with a thermocouple buried to 15 cm. Two dual prong time-domain reflectometry probes, and one air temperature probe located 5-m north of circle center, provided site-specific volumetric soil moisture content and near-surface air temperature. The sampling cycle was continuous during snow-free months (April to October), when chamber lids can open freely. The chambers ran in order (1–7) over a 9-min cycle. The chambers were flushed using

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CO_2-free air during the first 3 min after a chamber closes. During minutes 4–9, the chamber remained closed and soil CO_2 was allowed to accumulate. Measurements were taken during minutes 5–7. The last cycle of each day had a standard of 2% CO_2 added to check chamber volume.

Tower eddy Covariance System

Continuous, half-hourly measurements of ecosystem CO_2 flux exchange have been measured with the eddy covariance technique at the Wind River AmeriFlux tower since 1998. The most recent system consists of a 3-D sonic anemometer/thermometer (CSAT3, Campbell Scientific, Logan, Utah) and a closed-path infrared gas analyzer (LI-7000, Li-Cor, Lincoln, Nebraska). The EC system is located approximately 15 m above the canopy at a height of 67 m. Half-hourly NEE fluxes were calculated to include the storage CO_2 flux as well as the direct EC measurement. Half-hourly NEE was partitioned into GPP, and ecosystem respiration (R_e) following methodology found in Falk and others (2008). In brief, half-hourly R_e fluxes were modeled using the ustar threshold approach which estimates respiration as a function of 2 m air temperature and soil moisture. Half-hourly GPP was calculated from the difference between NEE and R_e. Full details on instrumentation, flux post-processing, and flux partitioning are found in Paw U and others (2004), Falk and others (2005, 2008), and Wharton and others (2009, 2012).

Plant and Soil OM Sample Collection and $\Delta^{14}C$ Analyses

Bulk samples were collected from the forest floor and later separated into individual components from three locations within 5 m of the automated soil chamber system. At each location, roughly 5 g of bulk samples were placed in separate paper envelopes. Soil samples (without litters) were collected at two depths (0–5 and 5–10 cm). These organic samples were oven-dried at 60°C within an hour from the time of collection.

Plant and soil bulk samples were further separated in the laboratory following the procedure described by Gaudinski and others (2000). All radiocarbon sample preparation and analyses were performed in the W.M. Keck Carbon Cycle AMS facility at the University of California, Irvine. Bulk samples were separated using a three-tiered sieve into the following components: (1) coarse organic materials, including recognizable leaf litter, mosses, woody materials, and roots, were separated individually before ^{14}C analysis, (2) mid-level fine organic material, including low-density humified materials and, (3) finer organic materials mixed with mineral soils. Materials from each of the latter 2 components were lumped together for ^{14}C analysis. Separated bulk samples were combusted into CO_2 gas in sealed quartz tubes with CuO at 900°C, which was extracted and converted to graphite, and then analyzed by accelerator mass spectroscopy (NEC 0.5MV 1.5SDH-2 AMS system) to obtain the radiocarbon signature of the original sample per the method described by Xu and others (2007). These $\Delta^{14}C$ values of bulk components were presented in Table 1 for comparison with those in CO_2 respired from root/soil incubation experiments.

Root and Soil Incubation Experiments

On-Site Root Incubation

In-situ root incubation was conducted three times at the WRFS, in August 2012 and April and August 2013. Root samples were excavated from 3 *T. heterophylla* and 3 *P. menziesii* trees in a manner consistent with the protocol described by Carbone and others (2008). The trees were selected for relative uniformity in height, diameter, and ground cover. Root samples were initially separated into two size classes: fine roots (<2 mm), and coarse roots (2 mm to 10 mm). All roots were rinsed with distilled water and placed into 1 L Mason jars sealed with airtight lids equipped with sampling ports. Jars were flushed with CO_2 free air, sealed, and allowed to sit in a shaded, cool spot for 24 h. After the 24 h incubation, 0.5 l evacuated steel flasks were connected to the incubation jars to remove air from the headspace. The root incubation experiment was repeated in April and again in August 2013 to examine potential effects of seasonality on the $\Delta^{14}C$ of root-respired CO_2. Because no difference in fine versus coarse roots was observed in the initial root respiration data, only fine roots were collected in the later two campaigns.

On-Site Soil Incubation

Soil incubations were conducted in August 2012, April 2013, and August 2013. Similar to the root incubation experiment, root-free *soils* were placed in jars and allowed to incubate for 24 h before being transferred to evacuated flasks. Roots and other living plant material were carefully removed from the soil samples to isolate heterotrophic components. In August 2013, two types of soils were collected. Soil from the top 5 cm (O horizon) was collected and roots were carefully removed. In

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Table 1. Monthly Sum of CO_2 Fluxes and Monthly Average of Environmental Variables and Radiocarbon Contents ($\Delta^{14}C$) of Soil Components in the Old-Growth Forest at Wind River Field Station

	April	August
Radiocarbon data		
$\Delta^{14}C$ measured in 2012		
Leaf litter	n/a	87.7 (±0.8); n = 3
Woody debris	n/a	126.3 (n/a); n = 3
Mosses	n/a	52.9 (±6.6); n = 3
Mid-level fine organic material	n/a	81.3 (±5.7); n = 6
Finer organic materials mixed with mineral soils	n/a	122.3 (n/a); n = 3
Roots (0–10 cm depth)	n/a	108.0 (±12.3); n = 3
Root incubation (Δ_A)	n/a	39.3 (±4.7); n = 11
Atmospheric $\Delta^{14}CO_2$ obs. in Barrow	29.2 (±0.5); n = 4	30.3 (±1.5); n = 5
$\Delta^{14}C$ of respired CO_2 measured in 2013		
Root incubation (Δ_A)	33.9 (±4.1); n = 12	38.3 (±7.0); n = 12
Root-free soil incubation (Δ_H)	53.0 (±8.5); n = 4	60.0 (±8.6); n = 10
Soil chamber (Δ_S)	45.3 (±5.6); n = 6	51.6 (±5.3); n = 12
Atmospheric $\Delta^{14}CO_2$ obs. in Barrow	23.3 (±0.8); n = 4	24.3 (±1.4); n = 4
Environmental variables		
T_a (°C)	6.1 (±1.6)	16.6 (±0.9)
	6.9 (±4.0) in 2013	18.4 (±4.3) in 2013
T_s @ 15 cm depth (°C)	6.5 (±1.1)	15.6 (±0.5)
	6.9 (±1.0) in 2013	16.3 (±0.4) in 2013
SMC @ 20 cm depth (%)	21.0 (±0.01)	9.0 (±0.00)
	26.7 (±2.5) in 2013	15.3 (±1.2) in 2013
GPP (g C m^{-2} $month^{-1}$)	161	164
R_e (g C m^{-2} $month^{-1}$)	88	180
NEE (g C m^{-2} $month^{-1}$)	−73	16
Chamber soil CO_2 efflux (g C m^{-2} $month^{-1}$)	85	174

Air temperature (T_a), soil temperature (T_s), volumetric soil moisture content (SMC), gross primary production (GPP), ecosystem respiration (R_e), and net ecosystem exchange (NEE) of CO_2 fluxes represent multi-year averages (2005–2011). Ancillary measurements from 2013 are presented for comparison where possible. Radiocarbon measurements were made only in 2012/2013. Values in parentheses are 1 SD

addition, mineral soils from approximately 10 cm below the surface were collected. Mineral soils and SOM were both incubated for 24 h and respired CO_2 was transferred to evacuated steel flasks at the site. Flask samples were then shipped to the AMS facility at the University of California, Irvine for laboratory processing.

In-Situ Soil Chambers

In April 2013, two existing soil collars were connected to a soil chamber flow-through system to collect air samples of total soil-respired CO_2. The soil chamber experiment was repeated in August 2013 to examine how seasonality may affect the proportions of autotrophic and heterotrophic CO_2 respiration to total soil efflux.

Soil chamber systems were designed per the method described in Gaudinski and others (2000). The two soil collars have been established on top of the soil organic layer for several years as part of a previous experiment. Therefore, no disturbance was introduced during our chamber air sample collection. The two soil collars are located within 10 m of each other in a relatively homogeneous area of ground cover and sunlight exposure. A pair of air samples was simultaneously collected from the two collars twice per day, on three different days in each campaign. Lids were placed on each of the collars to create a seal. Air was first circulated through soda-lime traps in the system for 30 min to completely remove atmospheric CO_2. The chambers were left sealed for 45 min, allowing soil-respired CO_2 to accumulate. A valve was then switched to divert the air flowing through steel u-traps packed with a molecular sieve to trap CO_2. Trapped samples were then shipped back to the laboratory for radiocarbon analysis.

Of the three field campaigns we collected a total of 82 samples for radiocarbon analysis, including 20 flask samples of total soil respiration (R_S), 24 flask samples of autotrophic (root) respiration (R_A), and 16 flask samples of heterotrophic (root-free SOM)

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respiration (R_H). Fine roots were collected from two tree species (*P. menziesii* and *T. heterophylla*), but we did not observe significant differences in Δ_A values between the two species ($P > 0.05$). Therefore, all the Δ_A values collected in each campaign were grouped together for further analysis.

Results

$\Delta^{14}C$ of Bulk Samples and Respiratory Fluxes

Average $\Delta^{14}C$ values produced from the combustion of bulk samples in the laboratory and from on-site respiratory fluxes are summarized in Table 1. Woody debris and mineral soils had the highest $\Delta^{14}C$ values of all measured components. Bulk samples, with an average $\Delta^{14}C = 96‰$, approximately equivalent to a mean age of 15 years old, have $\Delta^{14}C$ signatures in general substantially higher than those measured from respired CO_2. $\Delta^{14}C$ values produced from combusted bulk roots in the laboratory were 70‰ higher than fine root-respired CO_2 ($\Delta^{14}C = 39.3 \pm 4.7‰$) collected from on-site incubation in August 2012. This information obtained from the pilot study was confirmed by additional on-site root incubation measurements in 2013.

The average $\Delta^{14}C$ values measured for R_A, R_H, and R_S are shown in Table 1. The $\Delta^{14}C$ of background atmospheric CO_2 was approximately 24‰ in 2013 (Xu and others unpublished data). Notice that Δ_S values fall between those of Δ_A and Δ_H for both study periods in 2013. In terms of residence time, C released by R_A was about 3–5 years old, 7–10 years old for R_H, and 5–7 years old for R_S.

Seasonal Variation in Temperature, Moisture, and Ecosystem Fluxes

The pronounced precipitation seasonality in the Pacific Northwest strongly influences carbon flux dynamics of forest ecosystems in the region. Our ^{14}C measurements were made in early spring when soil moisture content (SMC) was close to its maximum, and at the end of summer when SMC approached the lowest values (Figure 1A). To interpret ^{14}C observations in the context of seasonal C flux dynamics, we averaged multi-year ecosystem flux data from 2005 to 2011 and show the mean seasonal pattern in Figure 1B (also see monthly averages in Table 1). The largest net CO_2 uptake by this coniferous forest (that is, seasonal NEE peak) occurs in early spring. The strength of NEE starts to decrease after May corresponding to

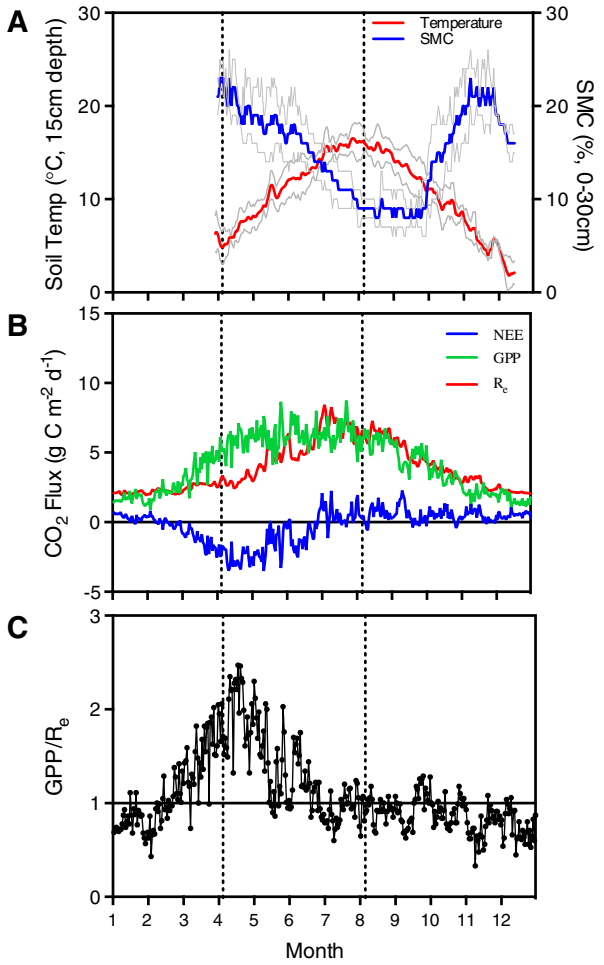

Figure 1. **A** Ensemble seasonal averages of soil temperature and moisture (SMC) at the Wind River Field Station (2005–2011). *Error bars* (1 SD) are represented by gray lines around the mean due to interannual variability. **B** Ensemble seasonal variation of canopy CO_2 fluxes (2005–2011). Notice that net ecosystem exchange (NEE) is shown as $-1 \times$ NEE for clarify. **C** Ensemble seasonal variability in the GPP/R_e ratio. *Vertical dotted lines* show sampling times for ^{14}C measurements in 2012 and 2013

decreasing SMC into the summer. By mid July, NEE turns slightly positive and stays so for the rest of the year. The early spring NEE peak results from a combined effect of high GPP and low R_e values at this time. GPP reaches its maximum by April and remains relatively constant between our two sampling periods (depicted by vertical lines in Figure 1). This seasonal mismatch between maximum GPP and peak temperature differs from the pattern found in temperate deciduous forests in which peak growing season generally coincides with the warmest time of the year. By contrast, R_e, closely tracking temperature, was relatively low in April but steadily increases to a summer maximum. The

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seasonal dynamic of the two gross C fluxes is clearly illustrated by the GPP/R_e ratio (Figure 1C). Our two ^{14}C sampling periods took place during the portion of the growing season that coincides with highest GPP/R_e in April and when GPP/$R_e \approx 1$ in August. This seasonal difference in GPP/R_e informs the interpretation of the ^{14}C measurements.

Seasonal Variation of Soil CO_2 Fluxes

Figure 2 shows the seasonally averaged soil CO_2 efflux (R_s) from 2005 to 2011 measured by automated soil chambers. The average R_s during snow-free months (April to October) was 1,085 g C m^{-2} y^{-1}, compared to the annual R_s estimate 1,194 g C m^{-2} y^{-1} (Klopatek 2002) for this site. Consistent with the seasonal pattern in derived R_e (Figure 1B), R_s was highly correlated with the seasonal variation of soil temperature (Figure 3). On the seasonal time scale, soil temperature and moisture content are negatively correlated (Figure 1A). This leads to an apparent negative correlation between SMC and R_s when SMC was not limiting. At low SMC (<0.15), R_s began to attenuate from the temperature response. Estimating R_s by soil temperature without considering SMC limitation would result in an overestimation during summer months at this site. This is in agreement with findings made by understory EC measurements in which R_s was found to decline by 25–50% under relatively high soil temperature but low SMC conditions (Falk and others 2005). Our two ^{14}C sampling periods coincide with times of lowest and highest R_s, with the monthly average R_s value in April being 50% lower than that in August; whereas, monthly average GPP remains equal between the two periods (Table 1).

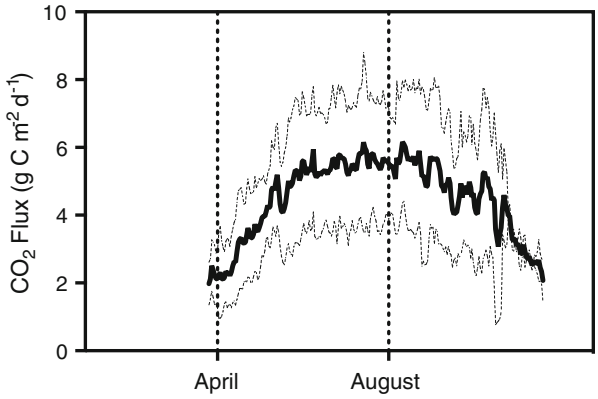

Figure 2. Ensemble seasonal average soil CO_2 efflux (2005–2011) measured by automated soil chambers. Dashed lines surrounding the mean (*bold line*) denote error bars resulting from the combined effect of year-to-year and chamber-to-chamber variability

Seasonal Comparison of Δ^{14}C in Respired CO_2

The three measured sources of respiration (R_S, R_A, R_H) showed small seasonal Δ^{14}C differences in this old-growth coniferous forest (Figure 4). The average Δ_S value measured in August was significantly higher ($P = 0.02$, Student's t test) than that in April, but those pairs were not significantly different for either R_A or R_H, despite the large seasonal fluctuation in soil temperature, moisture content, and the contrast between the magnitudes in both GPP and R_e fluxes between the two study periods. Within each period, Δ_H was statistically significant ($P < 0.01$) from Δ_A with the Δ_S value falling between the two end-members.

Comparison of Δ^{14}C in Respired CO_2 and Background Atmosphere

Figure 5 shows our ^{14}C measurements made in this forest relative to the background atmospheric ^{14}C content, represented by observations made in

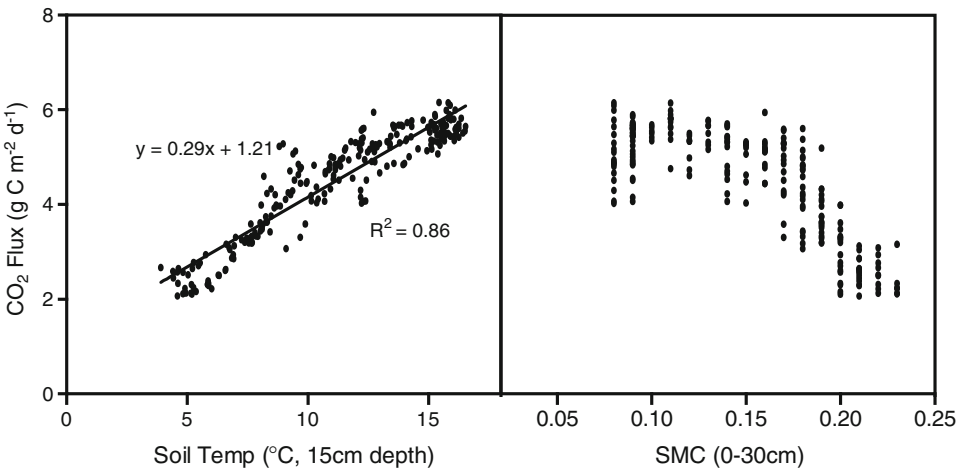

Figure 3. Soil CO_2 efflux versus soil temperature and soil moisture content (SMC). Both data sets are daily averages from 2005 to 2011

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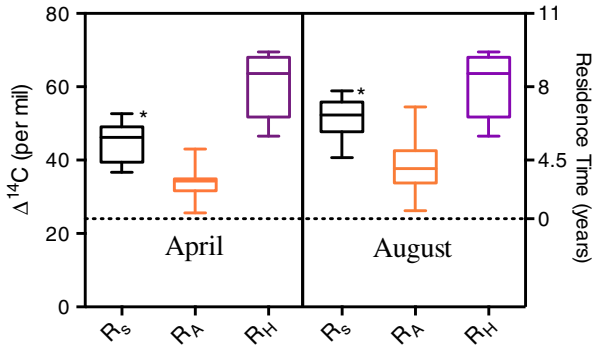

Figure 4. Comparison between $\Delta^{14}C$ values from soil respiration (R_S), autotrophic respiration (R_A), and heterotrophic respiration (R_H) measured in April and August 2013. Equivalent mean residences times calculated using a one-pool model are shown on the *right axis*. *Horizontal dotted line* represents background atmospheric $\Delta^{14}CO_2$ value at the time of our measurements (2013). *Asterisks* indicate statistical difference ($P < 0.05$ at 95% confidence interval)

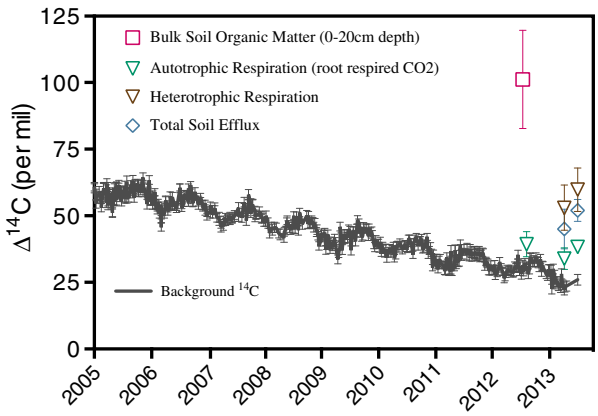

Figure 5. Background atmospheric $^{14}CO_2$ measured in Point Barrow, Alaska, shown with averaged $\Delta^{14}C$ of soil and its component fluxes measured at WRFS in 2012 and 2013. *Error bars* represent 1 S.D

Barrow, AK. There is a much smaller difference in average values or seasonal trends in the atmospheric $\Delta^{14}CO_2$ at the latitude of our study site compared to observations made in Barrow (Levin and others 2010). Interestingly, we observed elevated $\Delta^{14}C$ values from root-respired CO_2 for all three sampling periods, suggesting a contribution of carbon substrates fixed prior to the sampling year in root respiration.

Autotrophic and Heterotrophic Contributions to Total Soil Efflux

Using equation 2, we calculated the relative contribution of R_A to total soil respiration as 55 ± 22%

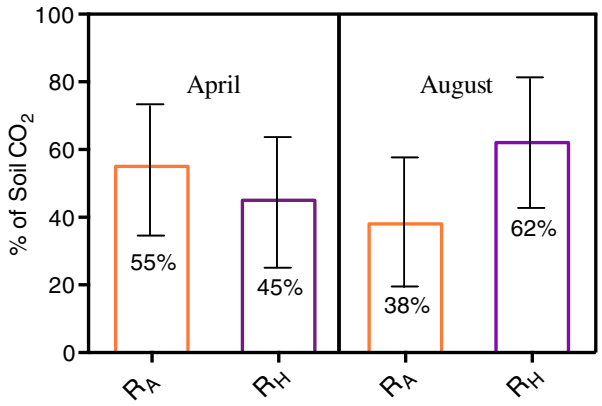

Figure 6. Estimates of proportional contribution from autotrophic (R_A) and heterotrophic (R_H) sources to total soil CO_2 efflux

in April 2013 and 38 ± 21% in August 2013 (Figure 6). The contribution of autotrophic components was found to vary between periods of peak NEE, in April, and late summer. The relatively high R_A contribution in April is thought to be the result of the combined effect of increasing root respiration at a time of high GPP and relatively low microbial activities in early spring (that is, high GPP/R_e). Even though we did not detect a clear ^{14}C signal, indicating root respiration depends strictly on current year photosynthates for these very old trees, it is plausible that high GPP stimulated root activities in the early spring. Relatively low R_H rates also contribute to the apparent high R_A/R_H ratio at this time of the year. These seasonal patterns are consistent with findings by Phillips and others (2013) in which higher R_A contribution was shown to occur at the time of high productivity.

Our late-summer sampling period occurred at a time when GPP and R_e were about equal, in contrast to the spring growing season when monthly mean GPP/R_e was greater than 1 (Figure 1B). Seasonal variation of GPP/R_e largely reflects seasonal increase in R_e as GPP remains roughly constant over the course of the growing season. Variation in R_A/R_H coincides with that of GPP/R_e. That is, the magnitude of root respiration stays about the same in relation to a constant GPP from April to August. Meanwhile, the magnitude of heterotrophic respiration increases over time primarily following a temperature response. These changes lead to an apparent decline of R_A contribution between the two study periods. To demonstrate this, we applied the fractional percentage from the partitioning calculation to multi-year, ensemble averages of seasonal soil efflux to estimate the R_A and R_H fluxes representing the two

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study periods. Figure 7 shows the peak rate of R_A stays roughly constant at 2 mg C m^{-2} s^{-1}, but the rate of R_H drastically increases from 1 to over 3 mg C m^{-2} s^{-1} from early spring to late summer.

Discussion

Our results show that the contribution from autotrophic sources to soil respiration was higher during the time of high GPP/R_e ratio. We also found that there was no seasonal difference in the MRT for either autotrophic or heterotrophic C sources. In contrast to studies conducted in broadleaf, deciduous forests, we did not observe a marked seasonal ^{14}C difference in root or soil respiration. Phillips and others (2013) observed a 40‰ (77–37‰ between March and October) seasonal decrease in Δ^{14}C of soil-respired CO_2 in a temperate deciduous forest in Wisconsin, USA. Such a seasonal decline is also reported by ^{14}C studies in soil-respired CO_2 (Gaudinski and others 2000), ecosystem respired CO_2 (Hicks Pries and others 2013), and root-respired CO_2 (Hopkins and others 2013). These seasonal patterns result from the combined effect of soil respiration having an elevated ^{14}C level at the onset of a growing season, followed by a gradual decrease in Δ^{14}C from spring to late summer. The general explanation for the seasonal Δ^{14}C decline in soil respiration can be described by two stages of belowground processes: (1) a greater contribution of Δ^{14}C-depleted root respiration associated with enhanced rooting activity in the first half of a growing season; and (2) a continued microbial turnover of root-derived C after root activities had ceased through late summer (Phillips and others 2013). On the other hand, Schuur and Trumbore (2006) observed an increase in ^{14}C values of soil respiration over the growing season in a spruce forest in Alaska.

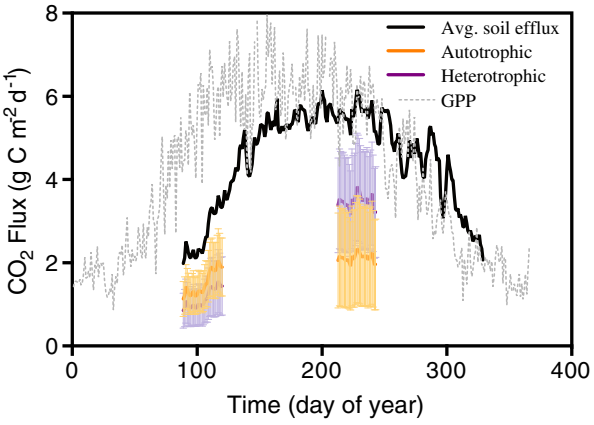

Figure 7. Autotrophic and heterotrophic flux components of soil respiration estimated from the product of ^{14}C-based component contribution (Figure 6) and the ensemble average total soil efflux (Figure 2). Errors were propagated to account for uncertainties in both fluxes and ^{14}C estimates. Ensemble-average GPP (*gray dotted line*) is also shown

We did not observe a marked seasonal Δ^{14}C difference in root-respired CO_2. Despite the fact that we only conducted experiments twice during the growing season, our measurements coincide with the two periods of greatest contrast with respect to physical conditions of the soil and gross C fluxes at this site. We therefore expect our observations to be representative of the seasonal variability between the beginning and the end of the growing season. Lack of seasonality can be largely attributed to the low Δ^{14}C values observed in April, which did not reflect a large proportion of stored C in root respiration as has been seen in the early growing season in other ecosystems. To our knowledge, there has not been a study that reports Δ^{14}C seasonal variation in old-growth coniferous forests. Little is known regarding whether these sites would display a seasonal Δ^{14}C trend similar to those found in deciduous forests. Our data suggest that evergreen trees differ from deciduous trees in their reliance on stored C reserves in early growing season.

All our radiocarbon field data were elevated above background atmosphere ^{14}C values (Figure 5), including root respiration. The interpretation of these elevated Δ^{14}C values requires careful attention. The Δ^{14}C value of a bulk sample was measured after combusting the sample to produce CO_2. Thus, all C molecules, including labile, nonstructural carbohydrates and those found in structural tissues, all contribute to the measured value. C molecules are locked in structural tissues for their entire life span and are much older than the labile C that most likely fuels respiration (Trumbore 2000). Using Δ^{14}C values from bulk samples as end members in flux partitioning therefore leads to large bias.

At WRFS, net C uptake begins in early March, peaking in April, and begins to decline after spring. This forest turns into a small net C source to the atmosphere after June, and continues to be so throughout the rest of the year (Figure 1B). Dang and others (2011) compared seasonal patterns of NEE fluxes in coniferous and deciduous forests in the US. They show that coniferous forests reach the highest monthly mean NEE in early spring (April/May). By contrast, monthly mean NEE in deciduous forests tend to peak in mid-summer (July). Unlike their deciduous counterparts, conifers have

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intact green needles that allow them to photosynthesize under favorable conditions throughout the year. Our spring sampling period occurred at the time when this forest had reached maximum NEE and the highest GPP/R_e ratio (Figure 2, also see Falk and others 2008). The co-occurrence between a seasonal low $\Delta^{14}C$ value in root/soil respiration and high GPP is not a coincidence. Hopkins and others (2013) suggest global C models should incorporate GPP as a main driver for predicting soil respiration. If GPP is a main driver and recent photosynthates, in part, contribute to root and soil respiration, then a relatively low $\Delta^{14}C$ in respiration can be expected at this time.

The timing for the onset of a growing season for this forest site is not as clear-cut as that typically determined for deciduous forests. Nevertheless, we cannot rule out the possibility that we may have missed the timing to capture the ''early-season'' signal of an elevated $\Delta^{14}C$ value, which has been postulated as an indicator on the remark that trees relying on older, stored C assimilated in previous years at the onset of a growing season (Gaudinski and others 2009). Using stable isotope labeling, Kuptz and others (2011) compared seasonal patterns of C allocation to respiration between deciduous (beech) and coniferous (spruce) trees, each from a single species. Their results showed a pronounced seasonal shift in trunk growth respiration, but only of deciduous trees, from relying on a greater proportion of stored C in early spring to recent photosynthates at a later time of high GPP. By contrast, respiration of coniferous trees constantly uses a mixture of stored and recent C throughout the growing season. A constant use of combined storage and recent C also has been reported for fueling fine-root respiration in deciduous (American sweetgum) trees (Lynch and others 2013). Our results are in agreement with these findings, suggesting C turnover of root respiration is highly dynamic, and is better described by a two-pool model (Lynch and others 2013; Richardson and others 2013).

We observed a small but significant increase in Δ_S from April to August ($P < 0.05$), in comparison to a large seasonal variation found in temperate deciduous forests (Gaudinski and others 2000; Phillips and others 2013), Arctic tundra (Hicks Pries and others 2013) and boreal forests (Schuur and Trumbore 2006). Atmospheric $\Delta^{14}CO_2$ values observed at high latitudinal locations in the Northern Hemisphere generally increase by 5–6‰ from spring to late summer (Figure 5; also see Levin and others 2010 and Graven and others 2012), although monthly $\Delta^{14}CO_2$ averages observed in Barrow were not significantly different between April and August in 2012 and 2013 (Table 1). Such seasonal variation is much smaller (1–2‰) in temperate regions, which cannot explain the greater seasonal difference in Δ_S and Δ_A observed in this study. We did not find a seasonal difference in Δ_H. Our results are consistent with previous studies in which high spatial variability has been reported, but no consistent seasonal variation was found in Δ_H (Carbone and others 2011; Phillips and others 2013). This site typically experiences a summer drought causing the upper soil layers to dry out. Although the 2013 summer season had higher SMC than the average summer season (but still dry), it remains inconclusive how soil moisture may affect vertical CO_2 production in the soil (Phillips and others 2013).

We found that, on average, Δ_H is 25‰ higher than Δ_A. This difference is at the low end of literature values. For instance, Phillips and others (2013) reported a mean difference between Δ_A and Δ_H of 46‰ in a hardwood forest, and Carbone and others (2011) reported a mean difference of 35‰ in a chaparral ecosystem. Two factors may have contributed to the relatively small difference in our observations. First, our Δ_A was consistently 10–15‰ higher than background atmospheric values. This is in contrast with previous studies showing $\Delta^{14}C$ of root-respired CO_2 near the ambient air level during the peak growing season (Phillips and others 2013; Hopkins and others 2013). Secondly, our R_H measurements were more enriched in ^{14}C than soil respiration by an average of 12‰, which is much lower than 34‰ found by soil gas well measurements that include contributions from older C in deep soils (Phillips and others 2013). In this study, we used on-site incubation of root-free soils excavated from the top 10 cm to estimate Δ_H. We incubated only surface soils because they likely have the largest contribution to fluxes measured at the surface, and soil respiration rates have been shown to decline exponentially with depth (Phillips and others 2013). One of the limitations in our approach is we were unable to account for the contribution of older C in deep soils to Δ_H. Furthermore, measured Δ_H include contributions from root exudates and other root-derived labile substrates from the rhizosphere, which isotopically are similar to Δ_A. These factors could have contributed to the discrepancy between Δ_H and $\Delta^{14}C$ of bulk soil material.

We determined values of Δ_A, Δ_H, and Δ_S by measuring CO_2 sampled in different ways, ranging from removed and rinsed roots, excavated soils, and undisturbed soil surface, respectively. This discrepancy in sample acquisition methods likely introduces other types of uncertainty in addition to

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those discussed above. For example, Δ_H values could potentially be affected by enhanced decomposition of old organic material in disturbed soils (Ewing and others 2006; Phillips and others 2013), partly due to the priming effect. Another source of uncertainty comes from the effect of collar-insertion depth on the contribution of root respiration to total soil CO_2 efflux. Heinemeyer and others (2011) showed that collar insertion by only a few centimeters cuts off fine roots and reduces total CO_2 respiration by an average of 15% in three ecosystems. Similarly, shallow collar insertion could cut off contributions by ectomycorrhizal fungal mats, commonly found in forest soils in this region, reducing total soil respiration (Phillips and others 2012). Overall, reducing errors associated with sample acquisition remains a challenge in the interpretation of ^{14}C data for soil C studies.

The mean residence time of root-respired CO_2 was found to be 2–3 years old from the two dominant overstory species. The 2–3 years MRT of root-respired CO_2 likely results from use of a mixture of older and recently fixed C substrate in the roots. It is increasingly recognized that starch pools that supply roots with C are a mixture of different ages (Richardson and others 2013). Our data support this finding. Lack of seasonality in root-respired Δ^{14}C at this site suggests that the balance between older and younger root respiration substrates stays constant across the growing season, or at least while GPP is constant. It is conceivable to hypothesize that these coniferous trees continuously incorporate assimilated C at varying rates into a mixed C pool throughout the growing season. In a broader context, this conceptual mixing pool incorporates recent photosynthates at varying rates that depend on species, age, and time of year. A future experiment incorporating measurements outside the growing season would be valuable for testing this hypothesis.

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