PARTITIONING HETEROTROPHIC AND RHIZOSPHERIC SOIL RESPIRATION IN A MATURE DOUGLAS-FIR FOREST

by

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Abstract

Total belowground respiration (R_s) was partitioned into heterotrophic (R_h) and rhizospheric (R_r) respiration to determine the amount of CO_2 originating from each component. The 15-month experiment took place in a 55-year-old coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) France) forest on Vancouver Island, Canada (49°51'N, 125°19'W). R_s was measured within cylinders (10 cm in diameter and 7 cm long) installed 2 cm into the soil. R_h was measured within longer cylinders (10 cm in diameter and 55 cm long) from which roots, hyphae, and associated rhizosphere organisms where excluded by a 0.5-micron nylon mesh. These cylinders were installed 50 cm into the soil. R_r was calculated as the difference between the two measured respiration rates (R_s and R_h)

R_s was 12 Mg C ha^{-1} yr^{-1} and ranged from 0.71 to 6.57 g C m^{-2} day^{-1} over the 15-month experiment. R_h was 7.8 Mg C ha^{-1} yr^{-1}, which contributed 65% of R_s mostly between May and August. R_r was 4.2 Mg C ha^{-1} yr^{-1} (35% of R_s) and peaked in spring and fall. Soil temperature could describe the variability in R_s ($p=0.0004$) better than soil moisture ($p=0.6156$) and Q_{10} values for R_s and R_h were 1.7 and 2.2, respectively. Also measured were potential sources of error associated with using this sampling technique such as: respiration resulting from decaying severed roots inside meshed cylinders, disturbance of cylinder installation, and lateral diffusion of CO_2 through the mesh.

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List of Abbreviations

Variable	Units	Description
C		Carbon
CO_2		Carbon dioxide
SOC		Soil organic carbon
SIC		Soil inorganic carbon
O_2		Oxygen
L		Liter
NPP		Net primary productivity
R_s		Total soil respiration: $R_s = R_h + R_r$
R_h		Heterotrophic respiration
R_r		Rhizospheric respiration
CWHxm2		Coastal western hemlock biogeoclimatic zone
IRGA		Infrared gas analyzer
PVC		Polyvinyl chloride
CSI		Campbell Scientific Inc.
Kg	10^3 grams	Kilograms
Mg	10^6 grams	Megagram
J	mg m^{-2} s^{-1}	Diffusive flux density of gas: $J = -D (d_c/d_z)$
D	m^{-2} s^{-1}	Diffusion coefficient
c	mg m^{-3}	Concentration of gas in the soil air
z	m	Distance air traveled
Pg	10^{15} grams	Petagram
ha	10,000 m^2	Hectare
µm	10^{-6} moles	Micromole
V_e	m^3	Effective volume for each cylinder
P	pascals	Partial pressure of dry air
R	J mol^{-1} K^{-1}	Universal gas constant (8.31)
T	K	Air temperature in Kelvin
s_v	mol H_2O mol^{-1} dry air	Mean water vapour-mixing ratio
Δs_c	mol CO_2 mol^{-1} dry air	CO_2 mole-mixing ratio
A	m^2	Soil surface area
ρ_b	kg m^{-3}	Bulk density: $\rho_b = W_d/V_c$
V_c	m^3	Volume of soil within each cylinder
W_d	kg	Dry weight of soil
W_c	%	Water content: $W_c = ((W_w-W_d)/W_d)*100$
W_w	grams	Wet weight
r^2		Correlation coefficient
y		Carbon flux
β_o		Fitted constants
β_1		Fitted constants
T	^0C	Temperature in degrees Celsius
Q_{10}		Factor by which soil respiration increases for an increase of 10°C in temperature

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1. Literature Review

1.1. Soil and the carbon cycle

Through the carbon (C) cycle (Figure 1), C is continuously recycled in various chemical forms and dispersed between atmospheric, vegetation, soil, oceanic, lake, and sedimentary reservoirs. Weathering and biological processes such as photosynthesis and respiration in the terrestrial component, propel C in and out of these reservoirs.

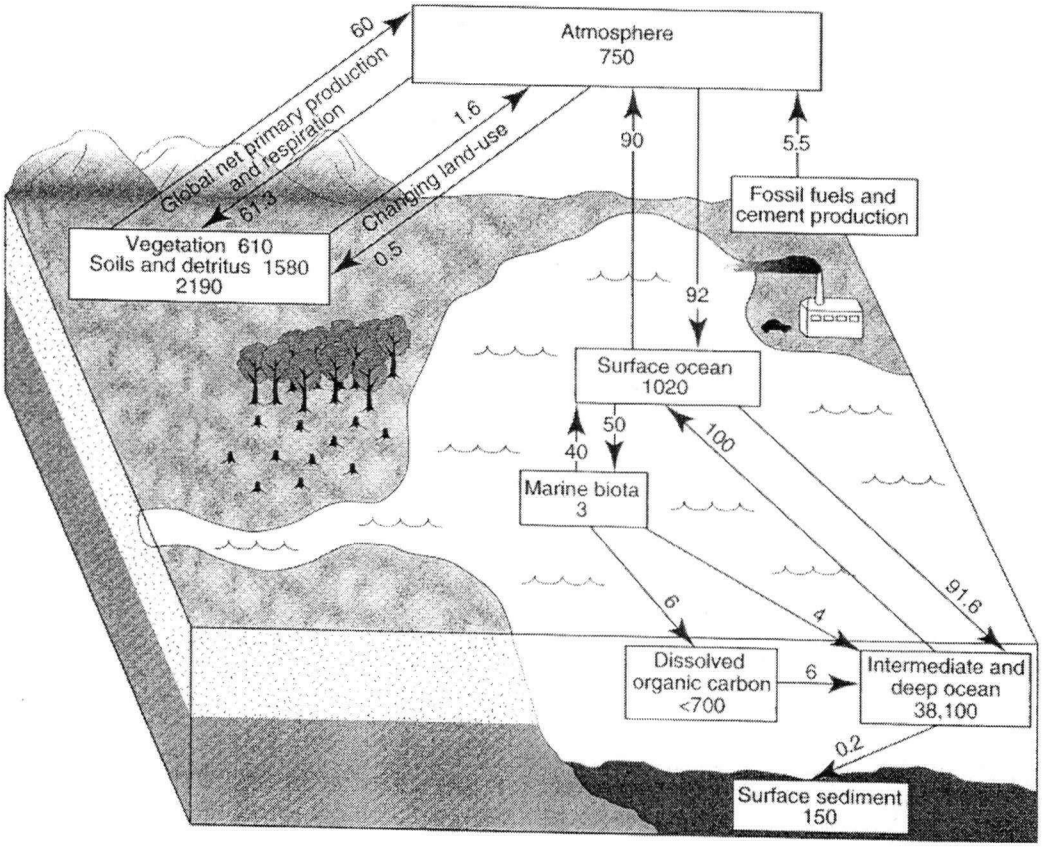

Figure 1. The global carbon cycle, showing reservoirs (Petagrams (Pg) of C) and fluxes (Pg C yr^{-1}) (Schimel et al. 2000).

Since the end of the last glacial period, 17,000 years ago, carbon dioxide (CO_2) levels in the atmosphere have remained relatively balanced (Schlesinger 1997). However, additional CO_2 emitted into the atmosphere from fossil fuel burning since the industrial revolution (Figure 2) has shifted this balance and has been identified as the primary cause for the 0.6°C warming that the earth has experienced in the last century (Sarmiento and Gruber 2002). Natural C reservoirs may be able to compensate for this additional anthropogenic C (Sarmiento and Gruber 2002) but their ability to act as a C sink depends on the reservoirs C fluxes and the residence time of the C. Small reservoirs that adjust quickly

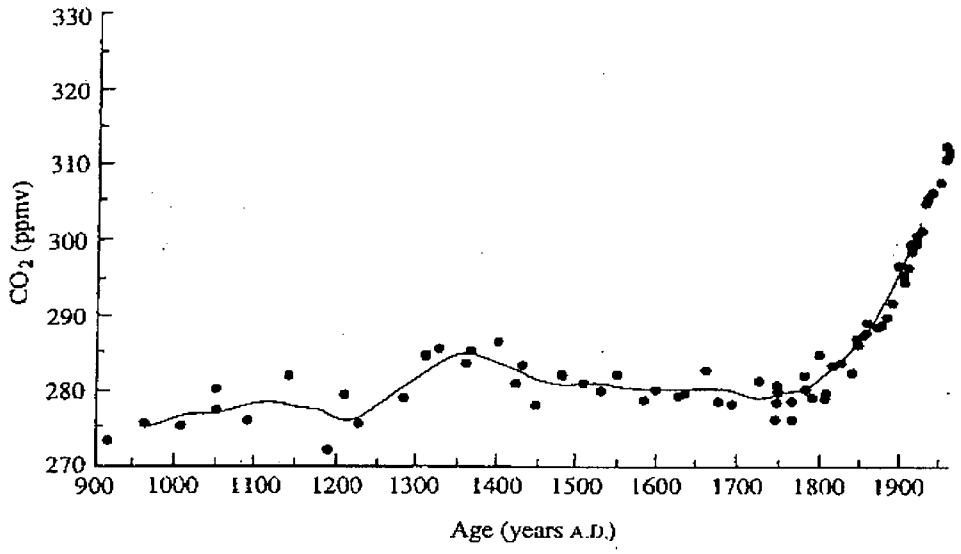

Figure 2. Atmospheric CO_2 concentrations from bubbles of gas trapped in ice cores from Antarctica (Schlesinger 1997).

to enhanced C inputs are not good long-term sinks for storing C, but large pools that turn over more slowly may remain C sinks long enough to partially offset fossil fuel additions to the atmosphere for a decade or two (Trumbore 2000).

Soils are one of the largest C reservoirs in the global C cycle despite global emissions of 80-81 Pg C yr^{-1} (Raich et al. 2002). Thus, fluxes of C from soils have substantial influence on atmospheric CO_2 concentrations. It has been suggested that increased atmospheric CO_2 levels will enhance soil C efflux, further escalating temperatures (Cox et al. 2000, Fang et al. 2005, Jones et al. 2005, Knorr et al. 2005, Schlesinger and Lichter 2001, Trumbore et al. 1996). However, Giardina and Ryan (2000) suggested that this may not occur because soil organic matter is too recalcitrant to respond to temperature increases. Valentini et al.'s (2000) finding that ecosystem respiration increased with latitude despite decreasing air temperature also suggests that respiration and temperature are not as closely related as previously assumed.

Soil carbon occurs in both organic and inorganic forms. Soil organic carbon (SOC) is mostly concentrated at the surface. Global estimates of SOC are around 1550 Pg, which is 2.8 times the global biotic pool of organic carbon. SOC has a mean residence time of 32 years but because it quickly decomposes the accumulation rate is only about 0.4 Pg yr^{-1} (Schleshinger 1997). Surface SOC is susceptible to degradation from anthropogenic activities such as deforestation, plowing and drainage, and natural causes such as leaching,

mineralization and oxidation. Soil inorganic carbon (SIC) is mostly below 1 m and in carbonate form ($CaCO_3$), with global estimates of about 750 Pg (Trumbore 2000).

Since 40% of the global belowground (soils, litter, and roots) C stores are contained in forests (Dixon et al. 1994) and soil respiration represents 40-80% of forest ecosystem respiration (Janssens et al. 2001), the response of forest soils to increasing atmospheric CO_2 levels and temperatures could have a large effect on the global C cycle. Canada's forests cover about 420 million ha, or 10% of the earth's forested area and contain more than 2.25 Pg of C (Natural Resources Canada 1999). Canadian forest soils (45-65° latitude) contain more C than mid and low latitude forests and have relatively high soil respiration effluxes (Dixon et al. 1994, Goodale et al. 2002, Raich and Schlesinger 1992, Raich et al. 2002, Schlesinger 1997, Van Cleve and Powers 1995).

Predictions from the Canadian Carbon Budget Model (Figure 3) estimate that Canadian forests were a C sink from 1920-1980, with a large amount (10.7 Pg) of C being sequestered into soil and detritus pools during this time (Kurz et al. 1995). However, insect outbreaks in the 1970's followed by large fires in the late 1980's, resulted in Canadian forests becoming a C source (Kurz and Apps 1999, Goodale et al. 2002). This reduction in C sequestration was associated with the increasing age of boreal forests, as growth rates began to level and the susceptibility to disturbance increased (Kurz and Apps 1999).

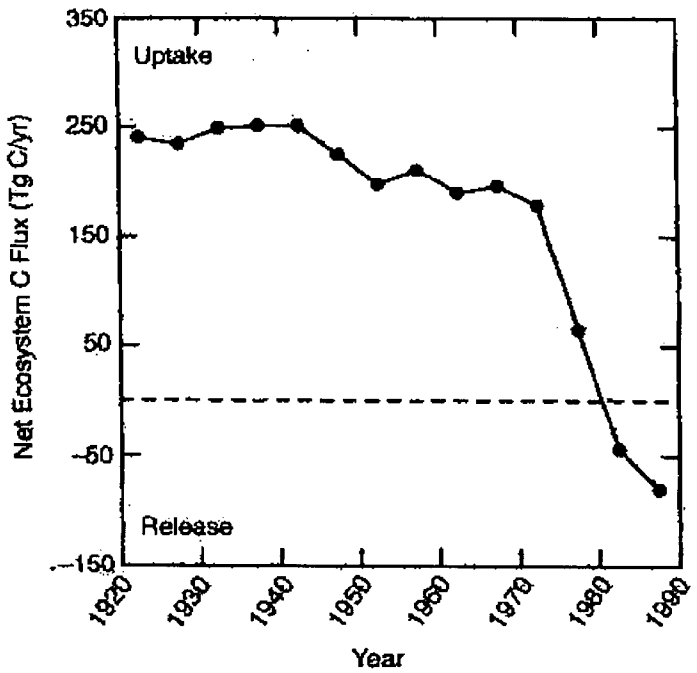

Figure 3. Annual net ecosystem C flux from Canadian forests between 1920 and1989 estimated with the Canadian Carbon Budget Model (Kurz and Apps 1999).

Advances in technology have increased our ability to estimate fluxes of CO_2 from soil surfaces using chamber systems. But unresolved debate over chamber design, length of measurement, spatial variability, and effect the chamber has over the natural concentration gradient of soil allows for the use of non-standardized chamber techniques (Davidson et al. 2002, Hutchinson and Livingston 2001) (Table 1). Dynamic chambers are considered to be more accurate than static chambers (Lund 1999), thus a non-steady state dynamic chamber system was used for this study.

Table 1. Different types of chambers to measure soil CO_2 efflux (Davidson et al. 2002, Hutchinson and Livingston 2001, Drewitt et al. 2002, Lund et al. 1999).

Chamber Type	Description		Advantage	Disadvantage
Static Chambers	CO_2 diffuses from soil and is absorbed inside a closed chamber using either an alkali solution (NaOH, KOH) or soda lime.		Relatively inexpensive	Underestimates CO_2 flux at high flux rates.
			Easy to employ	Overestimates CO_2 flux at low flux rates.
				Difficult to capture spatial variability and compare with other chamber measurements.
Dynamic Chambers	Open system, Steady-state mode	Ambient air is passed continuously through the chamber head space. Soil CO_2 efflux is calculated as the difference between CO_2 concentration between air entering and leaving the chamber.	Preferred when doing continuous measurements ranging from hours to days.	This method requires accurate measurement of flow rate and two air-stream concentrations (requiring two gas analyzers).
			Able to transmit natural pressure fluctuations which can contribute to the transport of gas from porous surfaces.	Difficult to capture spatial variability and compare with other chamber measurements.
	Closed system, Non-steady-state mode	Air is circulated in a closed loop between the chamber head space and an IRGA. Soil CO_2 efflux is calculated as the difference between the beginning and end of the measurement period.	A measurement can be obtained relatively quickly (5 minutes).	If measurements are too long disturbance to the natural fluxes of CO_2 from the soil surface will result.
			Considered more accurate than static method.	Difficult to capture spatial variability and compare with other chamber measurements.

1.2. Soil aeration

Soil aeration is controlled by mass flow and diffusion. Both aid in buffering the soil air from the large volume of the earth's atmosphere. Mass flow results because of a difference in total pressure in the soil, resulting in a transfer of mass from one point to another. Factors such as soil air temperature, barometric pressure, and wind movements will determine the extent of mass flow. Diffusion results because of a difference in concentration gradients, or partial pressure, of a gaseous mixture with no difference in total pressure. Both processes

may exist simultaneously but diffusion is the primary mechanism in the interchange of gases between the soil and the atmosphere (Evans 1965).

Kinetics of gas diffusion dictates the movement of gas from an area of high to low concentration in order for equilibrium to be reached. Thus, even though the total pressure of soil-air is the same as that of the atmosphere, a general inverse relationship exists between oxygen (O_2) and CO_2. The higher concentration of CO_2 in the soil results in an upward movement of CO_2 into the atmosphere and a downward movement of O_2 from the atmosphere (Brady, 1974).

The rate of diffusion depends upon concentration gradients, temperature, molecular weight of diffusing gas, and the cross-sectional area through which diffusion may occur (Evans 1965). Fick's first law of diffusion for gas exchange in a soil system can be used to describe gas flux when the primary form of CO_2 transport is gas diffusion:

$$J = - D (d_c/d_z) \qquad (1)$$

where J is the diffusive flux density of the gas (mg m^{-2} s^{-1}), c is the concentration for the gas in the soil air (mg m^{-3}), z is the distance (m), and D is the diffusion coefficient (m^{-2} s^{-1}) (Ballard 1998).

Three factors that regulate the exchange of CO_2 and O_2 within the soil matrix are: 1) soil macroporosity; 2) soil water content; and 3) gas exchange by respiring organisms (Brady and Weil 2002). The exchange of these gases occurs under non-steady state conditions. This creates an ever-changing environment in the soil pores that are affected by seasonal variations of moisture and temperature extremes. Biological activity of soil organisms and plant roots, most requiring 0.1 L/L of O_2 in the soil air, compared to 0.2 L/L in the atmosphere, are extremely sensitive to these changes. If the severity of the change to the soil is too drastic (aerobic to anaerobic conditions after a heavy precipitation) inactivity may result (Brady 1974).

1.3. Soil organisms & the rhizosphere

Microorganisms are the most abundant organisms in the soil and it is estimated that about 80% of the total soil metabolism is due to the microflora. On a global basis, microbial production of CO_2 roughly equals terrestrial net primary productivity (NPP) (Davidson and Trumbore 1995). Soil organisms are classified as either autotrophic or heterotrophic based on where they obtain the C needed to build cell components. Heterotrophic soil organisms obtain C from the breakdown of organic materials previously produced by other organisms, and are much more abundant in soil than autotrophs. Heterotrophic organisms include: soil

fauna, all fungi, actinomycetes, and most bacteria (Brady and Weil 2002). Heterotrophs consume organic carbon and assimilate part of it into cellular material; the remainder (> 40%), is lost as heat and CO_2 (Coleman and Crossley 2003). Autotrophs obtain C from CO_2 gas or carbonate minerals. Photoautotrophs use solar energy to obtain energy while chemoautotrophs use energy released by the oxidation of inorganic elements such as nitrogen, sulphur, and iron from organic material. Autotrophs are not as abundant as heterotrophs but are much less restricted in spatial distribution. Autotrophic organisms include algae and certain bacteria like cyanobacteria (Fisher and Binkley 2000).

Microbial populations are greatest within the top few centimeters of forest soils (where oxygen and organic matter are more abundant). Microbial abundance is primarily determined by the amount and quality of substrate available but other factors such as moisture, temperature, pH, predation, and competition are also important. Each group of organisms has an optimal temperature and moisture range, but most grow best at 25-35°C in soil at 50-75% of water-holding capacity (Pritchett and Fisher 1987).

The rhizosphere consists of soil influenced mostly by roots, and extends about 2 mm from the root surface (Brady and Weil 2002). Populations of microbes can be 19-32 times larger in the rhizosphere than in root-free soil (Kuzyakov 2002a) because of the substantial amounts of C released as rhizodeposits (Brady and Weil, 2002). Between 30 and 60% of net fixed C is transferred to the roots in annual plants and between 40-90% of this C is lost as rhizodeposition or respiration (Lynch and Whipps 1990). Lynch and Whipps (1990) reported Douglas-fir transferring 73% of its net fixed C to the roots, and 40-47% of that C being lost as rhizodeposits and/or respiration. Overall, their estimate of rhizodeposits was 5.8-7.5 Mg C ha^{-1} yr^{-1}.

Five groups of substances are released as rhizodeposits: 1) exudates (water-soluble low-molecular-weight substances like sugars, proteins, and amino acids);
2) secretions (high-molecular-weight substances); 3) lysates (contents of sloughed cells and dead roots); 4) gases such as CO_2, ethylene, hydrogen cyanide; and 5) mucilage of plant and microbial origin (Grayston et al. 1996). As a result of these substances, photosynthetically-fixed C through root metabolism and organisms consuming rhizodeposits increases CO_2 concentrations in the rhizosphere.

1.4. Partitioning heterotrophic and rhizospheric respiration

Total soil respiration (R_s) arises from: 1) heterotrophic respiration (R_h) - organisms decomposing soil organic matter from aboveground litter/debris, and 2) rhizospheric

respiration (R_r) - living roots with their associated mycorrhizal fungi and microbial populations (Ekblad and Högberg 2001):

$$R_s = R_h + R_r. \qquad (2)$$

Current estimates of the proportional contribution of R_r to R_s range from 10-90% (Hanson et al. 2000). In temperate coniferous forests R_r contributions to R_s can be as high as 65% (Bhupinderpal-Singh et al. 2003, Ewel et al. 1987b, Raich and Tufekcioglu 2000) or as low as 30% (Buchmann 2000), with the median around 50% (Ewel et al.1987a, Maier and Kress 2000, Andrews 1999). R_s from these forests soil ranges from 19.2 Mg ha^{-1} yr^{-1} (Drewitt et al. 2002) to 4.38 Mg ha^{-1} yr^{-1} (Longdoz et al. 2000).

Partitioning soil respiration into rhizospheric and heterotrophic components is very difficult since each is controlled by unique belowground processes that are interrelated. However, techniques that have been used to partition these components can be separated into three categories. The first is physically removing each component (i.e. soil, roots, and litter) and quantifying their fluxes individually before integrating them (Hanson et al. 2000, Maier and Kress 2000, Uchida et al. 1998, Widén and Majdi 2001). The second is only excluding roots using trenches, or physically removing them so R_h can be quantified separately (Boone et al. 1998, Ewel et al. 1987b, Fierer et al. 2003, Hanson et al. 2000, Högberg et al. 2001, Lee et al. 2003, Li et al. 2004). The third category is isotopic analysis using stable or radioactive isotopes, including utilizing differences in photosynthetic fractionation between C_4 and C_3 (Andrews et al. 1999, Bhupinderpal-Singh et al. 2003, Ehleringer et al. 2000, Ekblad and Högberg 2001, Hanson et al. 2000, Kuzyakov 2002b, Kuzyakov and Cheng 2001, Rochette et al. 1999). Isotopic techniques are considered the most accurate because they are the least intrusive to the soil matrix, but if done carefully, root exclusion techniques yield comparable results (Hanson et al. 2000, Rochette et al. 1999). In this study the second category was employed such that roots and hyphae were excluded using a mesh barrier. Mesh barriers have been used to provide root and/or mycorrhiza-free soil compartments depending on mesh size (Johnson et al. 2001).

The objectives of this study were to measure R_s and partition rhizospheric and heterotrophic contributions for 15 months in a mature coastal Douglas-fir (*Pseudotsuga menziesii* (Mirbel) France) forest on Vancouver Island, Canada. R_h was measured in cylinders from which roots, hyphae, and associated rhizosphere organisms were excluded by a 0.5-micron mesh. Also measured were potential sources of error associated with this technique such as increased respiration resulting from severed roots, cylinder installation, and lateral diffusion.

2. Materials and Methods

2.1. Site description

All measurements were taken near the flux tower at the coastal British Columbia Fluxnet Canada research site. The site is in the driest part of the Coastal Western Hemlock (CWHxm2) biogeoclimatic zone near Campbell River, on the east side of Vancouver Island, British Columbia, Canada (49°51'N, 125°19'W) (Figure 4). The site is 320 m above sea level and has a slope of 5-25% with a northeast aspect (Thandi and Trofymow 2002). The mean annual temperature and precipitation for 2001-2004 were 8.6°C and 1451.5 mm respectively, with most precipitation falling in the winter months (Environment Canada 2002). The site series is 05 (Green and Klinka 1994). The stand naturally regenerated after a forest fire in 1949 and is dominated by Douglas-fir but western redcedar (*Thuja plicata* Donn ex D. Don) represent 17% and western hemlock (*Tsuga heterophylla* (raf.) Sarg.) represents 3% of the trees respectively. Average tree height is 33 m, average tree

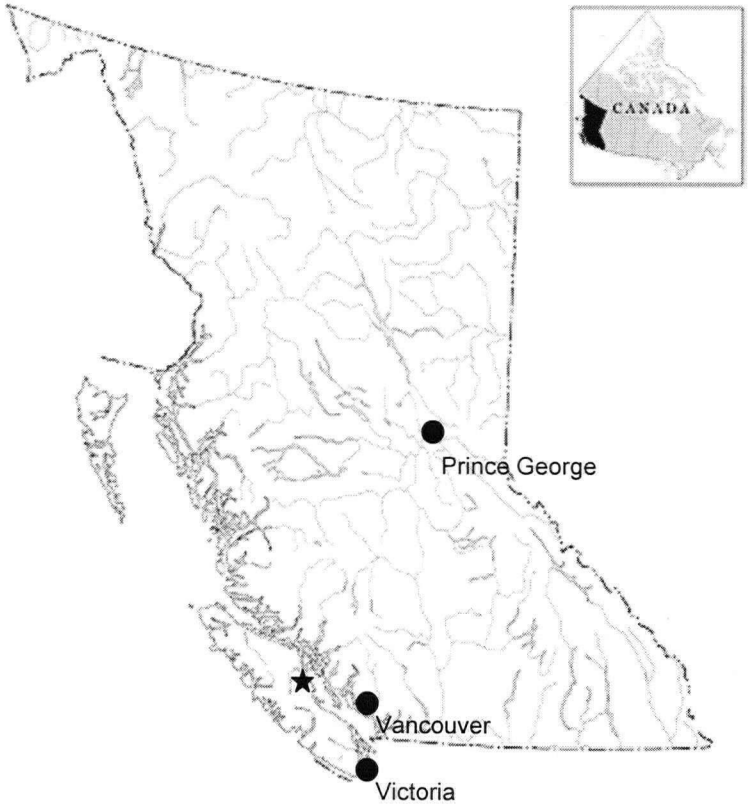

Figure 4. Map of British Columbia, star indicates study site on Vancouver Island (Natural Resources Canada 2002).

diameter at 1.3 m is 29 cm, and stand density is 1105 stems ha^{-1} (Drewitt et al. 2002). The sparse understory consists of mosses, ferns, and herbs such as Oregon grape (*Berberis*

nervosa Pursh), salal (*Gaultheria shallon* Pursh) and vanilla-leaf deer foot (*Achlys triphylla* (Smith) DC) (Thandi and Trofymow 2002). The soil series is Quimper (Jungen 1985) and is classified as a humo-ferric podzol (Canadian Agricultural Services Coordinating Committee 1998) with dense compacted till at 1 m depth, a forest floor 1-10 cm thick, and a pH of 5.4. Below the forest floor is gravelly loamy sand that changes to gravelly sand at 40 cm, with abundant coarse fragments throughout the profile (Drewitt et al. 2002). Belowground carbon to 1 m depth was estimated to be 15.9 kg C m^{-2}, of which 1.3 kg C m^{-2} was roots and 3 kg C m^{-2} was forest floor; aboveground carbon was estimated to be 19 kg C m^{-2} (Jassal et al. 2004). Bedrock geology is the Comox formation, composed of Benson conglomerate overlain by Comox sandstone, shale, and coal (Muller and Jeletzky 1970).

2.2. Total, heterotrophic, and rhizospheric respiration measurements

Total soil respiration (R_s) was measured within an opaque polyvinyl chloride (PVC) cylinder 10 cm in diameter and 7 cm long (Figure 5), installed 2 cm into the soil. Heterotrophic respiration (R_h) was measured within a PVC cylinder 10 cm in diameter and 55 cm long, installed to a depth of 50 cm. Windows, 4 cm wide and 7 cm long, were cut out on either side and a 0.5-micron nylon mesh (Plastok, United Kingdom) was glued using Plumber's Goop™ (Eclectic Products Inc., Oregon) to the inside of this cylinder.

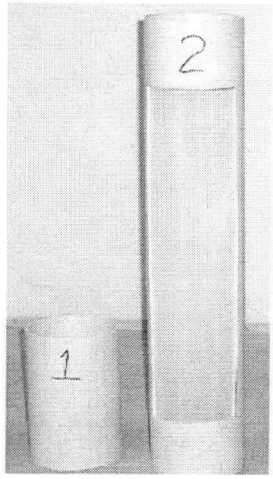

Figure 5. Cylinders used to estimate total soil respiration (R_s) and heterotrophic respiration (R_h). Cylinder 1, used to quantify R_s; Cylinder 2, used to quantify R_h.

Ten pairs of cylinders were randomly placed at ten locations within a 7-ha area near the main flux tower. Cylinder pairs were installed adjacent to one another at the same time. Soil respiration measurements began in May 2004, 2 weeks after the cylinders were

installed, and continued every two weeks until October 2004, then monthly until March 2005, and then every two weeks from April through July 2005.

A slide hammer and soil core was made following the design of Ruark (1985) (Figure 6). The slide hammer was made from 43-40 stressed-relief heat-treated metal and weighed 18 kg. The soil core was 12 cm in diameter and 60 cm long and made of stainless steel. It had a removable end piece that was tapered (10.5 cm in diameter) to ease insertion and to hold the soil inside when being removed. About 150 hits with the slide hammer were needed to reach 50 cm depth. The slide hammer was then removed and a metal rod was placed through drilled holes on either side of the soil core. Using the rod as a handle, the core was then lifted out of the ground. The fresh hole was carefully cleaned to remove any material that fell in and a cylinder was inserted into the hole. The bottom of the soil corer, with the end piece removed, was placed on top of the cylinder and the soil contained within the soil corer was allowed to fall into the cylinder with no physical contact from the field crew or the atmosphere.

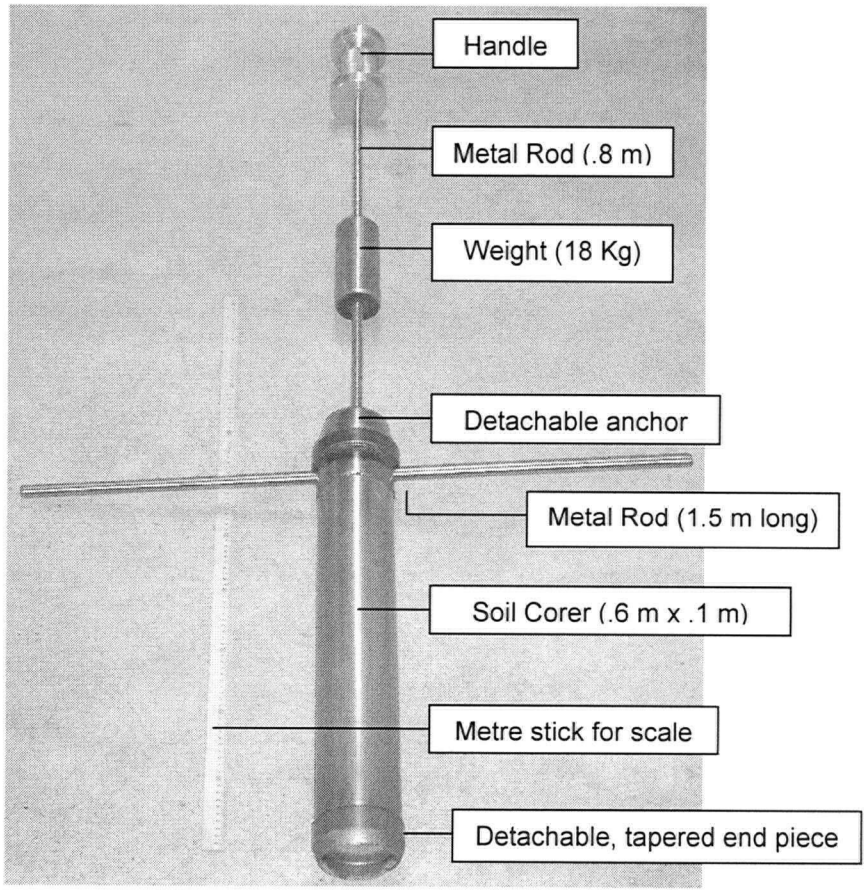

Figure 6. Soil Sampler (slide hammer with soil corer attached).

R_s from each cylinder was measured on 17 occasions between May 26, 2004 and July 18, 2005. The increase in CO_2 concentration over a 2-minute period was measured with a homemade closed chamber system and an infrared gas analyzer (IRGA) (Model LI-820; LI-COR Inc., Lincoln, NE) (Humphreys et al. 2006). The headspace of the chamber was made with opaque PVC pipe, 10 cm diameter, fitted with a PVC pipe cap as a top (volume 1426 cm^3, surface area 75 cm^2). Air temperature and relative humidity inside the chamber headspace was measured with a sensor (model HMP35CF, Campbell Scientific Inc. (CSI), Logan, UT, USA). A diaphragm pump (model TD-4X2N, Brailsford Co., Rye, NY) cycled air through the chamber at 2 L min^{-1} and pulled air through the IRGA at 0.8 L min^{-1}. The 4-mm metal/plastic composite tubing (Type 1300, Synflex, Mantua, OH, USA) that returned air to the inside of the chamber, was perforated and wound around the center of the chamber to cause mixing. A vent maintaining equal pressure between the chamber and the environment was made with 10 cm of 4-mm tubing set into the top of the pipe cap and pinched slightly at the top. A foam gasket 0.25 cm wide and 0.25 cm high, located 2.5 cm from the bottom of the chamber provided an adequate seal between the cylinder and the chamber. Data were recorded and stored at 1-second intervals with a data logger and storage module (models 21X and SM 192, CSI) (Humphreys 2004). Before each new measurement the chamber headspace was returned close to ambient concentrations of CO_2 (390-405 ppm).

CO_2 efflux was calculated as (μm CO_2 m^{-2} s^{-1}):

$$R_s = \frac{V_e P \Delta S_c}{[RTA\,(1+ s_v)]} \qquad (3)$$

where R_s is the total respiration, V_e is the effective volume (m^3) that was determined for each cylinder, $P/[RT(1+s_v)]$ is the density of dry air (mol dry air m^{-3}) calculated using the universal gas constant (R= 8.31 J mol^{-1} K^{-1}), T is the mean chamber air temperature (K), and $P/(1+s_v)$ is the partial pressure of dry air (Pa) where s_v is the mean water vapor-mixing ratio (mol H_2O mol^{-1} dry air) within the chamber. ΔS_c is the increase in CO_2 mole-mixing ratio (mol CO_2 mol^{-1} dry air) during the 2-minute measurement, and A is the soil surface area within the chamber (m^2). CO_2 concentration was converted from mole fraction (χ_c, mol CO_2 mol^{-1} moist air) to mole-mixing ratio using the water-vapour mole fraction, $S_c=\chi_c/(1-\chi_v)$, where χ_v is the water-vapour mole fraction, prior to determining ΔS_c (Humphreys 2004).

2.3. Root decomposition inside meshed cylinders

Soil coring associated with the installation of meshed cylinders, severed roots that remained inside the cylinders. Decomposition of these roots would release CO_2 and cause an overestimate of R_h. R_s from decaying severed roots was estimated by comparing respiration rates from a cylinder that contained severed roots with a cylinder from which the roots had been removed (Figure 7). Ten cylinders of each type were installed at the ten locations used for the main experiment.

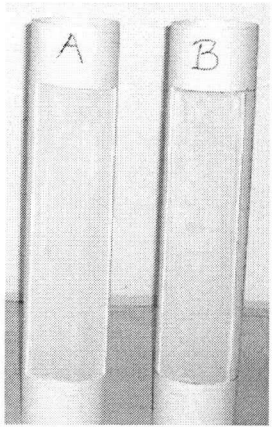

Figure 7. Cylinders used to estimate respiration from decaying roots. Cylinder A contains soil with severed roots; Cylinder B contains soil from which severed roots were removed.

To remove the severed roots from the soil in Cylinder B, the soil was removed from the core and carefully placed on a tarp, in a manner that maintained the soil profile. Beginning with the top of the soil profile the soil was gently hand-sorted and all visible roots were removed and placed in clear plastic Ziplock© bags. The soil was then placed into Cylinder B that was already installed in the hole, with care being taken to maintain the soil profile. A second soil core was removed from beside Cylinder B and Cylinder A was inserted. The soil from this core was processed in exactly the same manner except that the roots were not removed before inserting it into Cylinder A. R_s was measured on eleven occasions between May 26, 2004 and November 28, 2004, as described for the main experiment.

Three of the ten Cylinder Bs were not sampled because the soil replaced into them did not reach the surface, which might have allowed CO_2 to diffuse in from the sides. Thus, Cylinders A and B were compared at only seven locations.

The roots removed from the soil were washed free of soil and pebbles and air-dried for 24 hours. The roots were then partitioned into fine (< 2 mm) and coarse (> 2 mm) size classes, dried for 48 hours at 70°C, weighed, and placed into labeled envelopes for storage.

At the end of the 15-month experiment roots remaining inside Cylinder 2 were removed and processed in the same manner. Root mass and carbon loss was calculated by subtracting dry root weights of Cylinder B from dry root weights of Cylinder 2. Values were converted to twelve months for yearly estimates.

2.4. Disturbance of cylinder installation

Disruption of the soil matrix associated with installation of meshed cylinders could stimulate R_s and cause an overestimate of R_h. R_s from cylinder installation was estimated by comparing respiration rates from a not-installed cylinder with an installed 50-cm long mesh-less cylinder, Cylinder 3 (Figure 8). The difference in respiration rates between the two cylinders should serve as an estimate of the increase in respiration associated with cylinder installation, since both cylinders incorporate R_r and R_h. This value was subtracted from the estimated average of R_h at each measurement to remove the installation effect. Ten Cylinder 3s were installed within 50 cm of a Cylinder 1 at the ten locations used for the main experiment. R_s from these cylinders was measured on 17 occasions between May 26, 2004 and November 28, 2004 as described for the main experiment. Six of the ten Cylinder 3 were not sampled because the soil replaced into them did not reach the surface, which might have allowed CO_2 to diffuse in from the sides. Thus, Cylinders 3 and 1 were compared at only four locations.

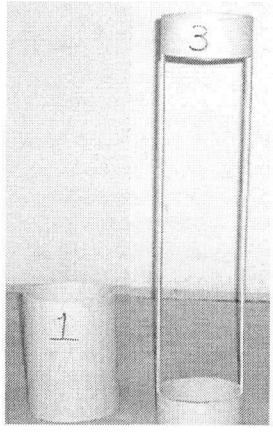

Figure 8. Cylinders used to estimate respiration from cylinder installation. Cylinder 1 is not-installed; Cylinder 3 is installed 50 cm into the soil.

Bulk density was measured from three meshed cylinders removed after the completion of the experiment. The volume of soil within each cylinder (V_c) was calculated

after marking the surface of the soil within the cylinders, removing the soil, and filling the cylinder up to the mark with marbles of a known size. The dry weight of soil (W_d) within each cylinder was measured after removing the soil from each cylinder, drying it at 70°C for 48 hours, and weighing it. Bulk density (ρ_b) was calculated using the formula (kg m^{-3}):

$$\rho_b = W_d / V_c. \qquad (4)$$

Removing soil from these cylinders was difficult so measurements were not divided into depth profiles. Thus, bulk density values represent mineral soil from 0-50 cm.

2.5. Lateral diffusion of CO_2 through the meshed cylinders

Slight changes in total or partial pressure in the soil matrix can create mass flow or diffusion of CO_2 from areas of high concentration to areas of low concentration. Installing the cylinders may have created pressure differences that would alter R_s, hence our estimate of R_h. To account for lateral diffusion of CO_2 in the meshed cylinders, respiration rates in a meshed cylinder (C) was compared with that in a solid cylinder (D), in which lateral diffusion of CO_2 was prevented (Figure 9). The solid cylinder was the same dimension as the meshed cylinder, but no windows were cut out and the bottom was capped. Three cylinder pairs were installed at three random locations near the Fluxnet tower. R_s from these cylinders was measured on four occasions between July 23, 2004 and September 9, 2004; when the first major rain event occurred and it became apparent that there was inadequate drainage in the capped, solid cylinders.

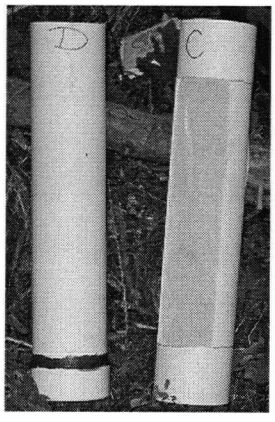

Figure 9. Cylinders used to estimate lateral diffusion of CO_2. Cylinder C is a meshed cylinder; cylinder D is a solid PVC cylinder that has the bottom capped.

2.6. Soil temperature and soil moisture

Soil moisture and temperature were measured concurrently with soil respiration. Volumetric water content of the soil was measured at 12-cm depth using a portable Hydosense™ soil moisture probe (CSI). Soil temperature was measured at a 2-cm depth with a copper-constantan thermocouple that directly attached to the data logger inside the portable IRGA system. There were no measurements during the winter (January-February, 2005) because the ground was frozen.

There was concern that the mesh might impede drainage, causing R_h to be underestimated. To assess this concern, gravimetric water content was measured at the end of the experiment in soils removed from meshed cylinders and not-meshed cylinders at two locations. Five grams of soil from each cylinder was removed from the 0-10 cm depth and 10-20 cm depth and weighed to obtain a wet weight (W_w). After 48 hours in the oven at 70°C the samples were re-weighed to obtain a dry weight (W_d). Water content (% by weight) (W_c) was calculated using the formula:

$$W_c = ((W_w - W_d) / W_d) \times 100. \qquad (5)$$

2.7. Sampling and statistical analysis

At each visit I changed the order in which locations were sampled to facilitate temporal variability throughout the sampling period, although sampling occurred at the same time of day. Respiration data from February, March, and end-of-April 2005 were removed from the data set because a leak was detected in the tubing that connected the pump to the IRGA. Respiration values were removed if they were larger or smaller than a known outlier value. This value was determined for each cylinder, calculated as the mean +/- 3 standard deviations. The number of values removed were: Cylinder 1 (2), Cylinder 2 (6), and Cylinder 3 (1). Respiration values were also removed if there was not a steady increase in CO_2 concentration during the 2-minute sampling period (r^2 = <.90). Cylinder 1 had 2, Cylinder 2 had 4, and Cylinder 3 had 1 respiration value removed for this reason.

To test for differences among treatments, locations, and time an analysis of variance of a split-plot experiment in a randomized complete block design was used, with treatment as the whole-plot factor, and time as the subplot factor. Treatment was considered a fixed effect but location and time were considered random effects. If there was a significant interaction effect between treatment and location this value was then used as an error term to determine if there was a significance difference in treatment despite the spatial variability of the site. An alpha value of 0.05 was used for all analysis. Statistical analysis was

performed using Statistical Analysis Software version 8.2 (SAS Institute Inc. 1999, Cary, NC).

T-test for two independent groups was used to compare mean total and heterotrophic respiration rates, and mean water content between cylinder types. If variances were not equal, the Welch ANOVA F-test was used to determine significance. Multiple regression analyses was used to test the relationship between soil temperature, soil moisture, and soil respiration with JMP® Start Statistics version 4 (SAS Institute Inc., 2001, Cary, NC). Non-linear regression was used to further test the relationship between soil temperature and soil respiration according to equation five, using SigmaPlot® version 9 (SPSS Inc., 2001, Chicago, IL):

$$y = \beta_0 e^{\beta_1 T} \qquad (5)$$

where y is the C flux, β_0 and β_1 are fitted constants and T is the temperature. Seasonal Q_{10} values, defined as the factor by which soil respiration increases for an increase of 10°C in temperature (Widén and Majdi 2001), were calculated according to equation six:

$$Q_{10} = e^{10\beta_1} \qquad (6)$$

3. Results

3.1. Total soil respiration

The average total soil respiration (R_s) was 12 Mg C ha^{-1} yr^{-1} (3.3 g C m^{-2} d^{-1}). Respiration rates for the first summer (May – August, 2004) ranged from 2.98 to 4.05 µmol CO_2 m^{-2} s^{-1}. Throughout the cooler months (October – April), respiration rates ranged from 0.71 to 3.58 µmol CO_2 m^{-2} s^{-1}. Respiration rates during the second summer (May – July, 2005) were higher, ranging from 5.42 to 6.57 µmol CO_2 m^{-2} s^{-1} (Figure 10).

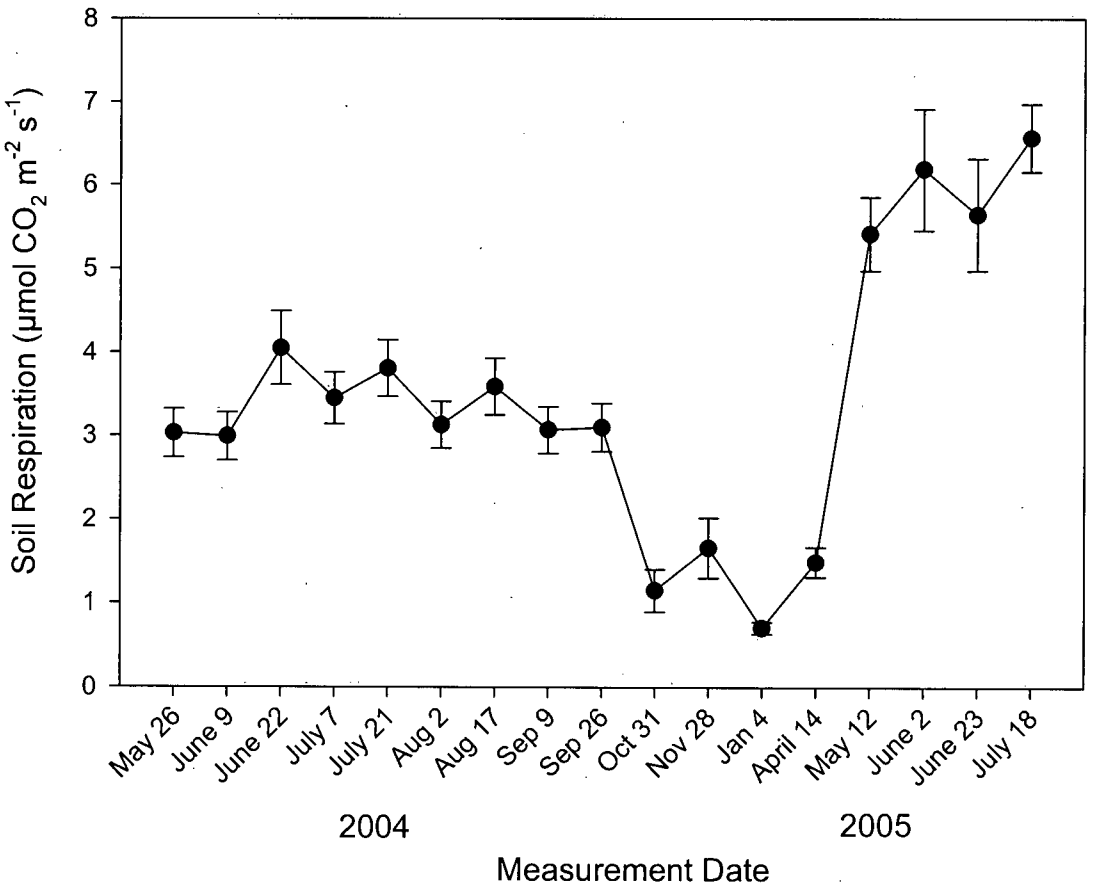

Figure 10. Total soil respiration rate. Error bars indicate +/- one standard error of the mean (n=10).

3.2. Root decomposition inside the meshed cylinders

Root biomass in the upper 50 cm of soil (including the forest floor) was 1837 g C m^{-2}. Coarse and fine roots contributed 62% and 38%, respectively of the total root biomass. Severed roots lost about 70% of their mass during the 15 months that they were in the meshed cylinders. This is equivalent to 684 g C m^{-2} yr^{-1}(assuming biomass is 50% C and

decomposition is constant throughout the year) (Table 2). Despite the apparent decay of severed roots, there was no significant difference (p=0.1527) in soil respiration rates from cylinders with severed roots present and those with severed roots removed (Figure 11).

Table 2. Root mass in the upper 50 cm of soil, and loss of mass and carbon from severed roots after 15-months inside the meshed cylinders.

Root Size	Root Biomass (g)		Mass Loss	Carbon Loss	
	Before	After	(g m^{-2} yr^{-1})	(g C m^{-2} yr^{-1})	(%)
Coarse (>2 mm)	4.08	1.33	745.76	372.88	67
Fine (<2 mm)	3.06	0.76	623.73	311.87	75
Total	7.14	2.09	1369.49	684.75	

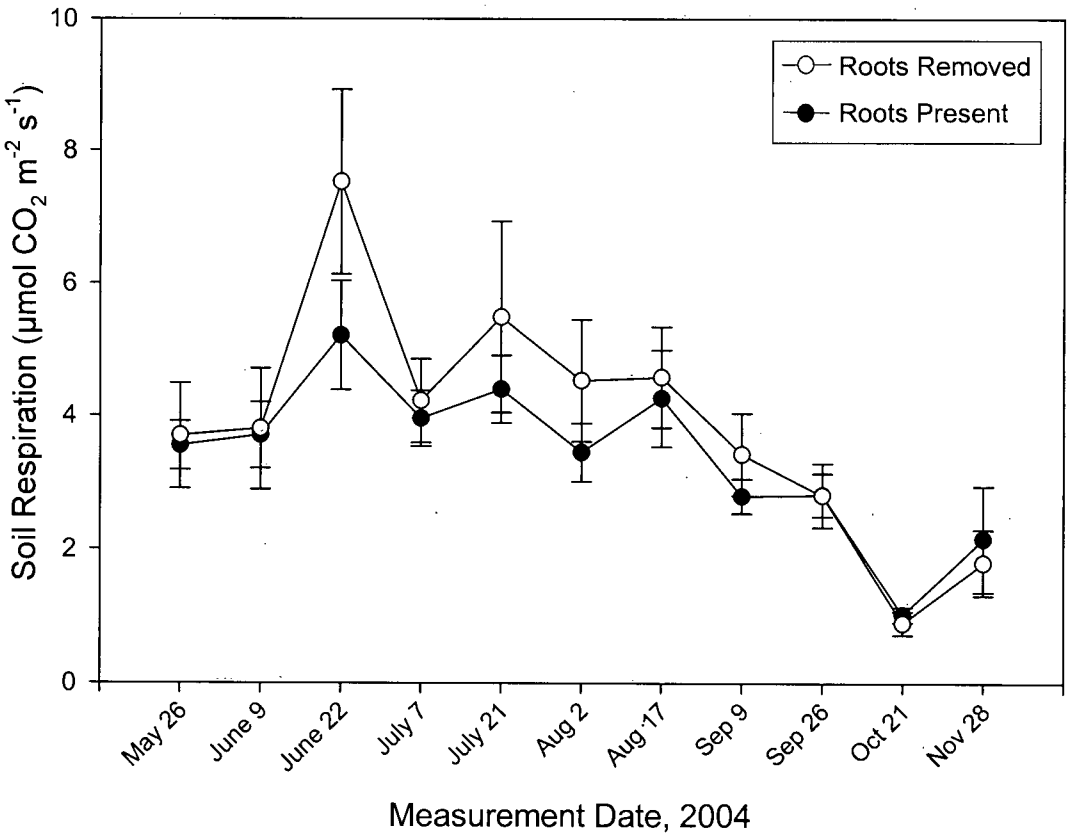

Figure 11. Soil respiration rates in meshed cylinders containing soil with and without severed roots. Error bars indicate +/- one standard error of the mean (n=7).

3.3. Disturbance of cylinder installation

Installed cylinders had consistently higher mean respiration rates than not-installed cylinders, although the differences were not significant (p=0.097) (Figure 12). The difference in respiration rates between installed and not-installed cylinders at each measurement time was subtracted from the corresponding R_h value to correct for the stimulation of respiration caused by cylinder installation. All R_h values reported have been corrected.

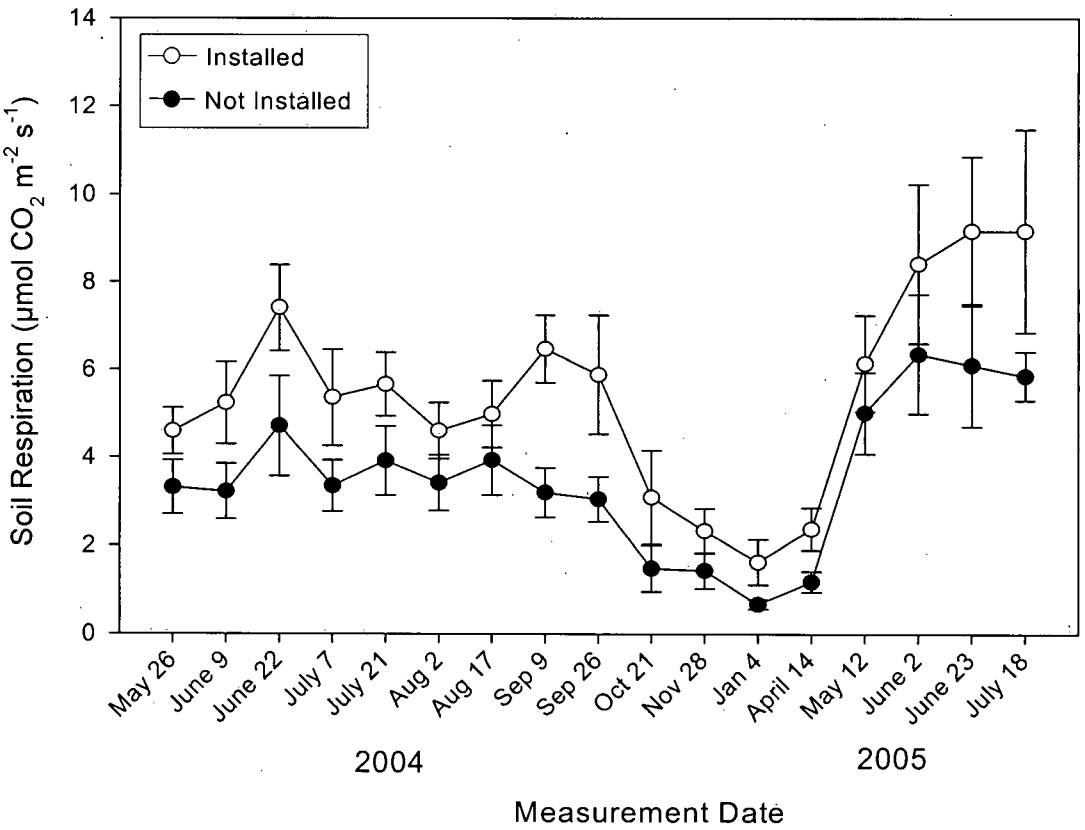

Figure 12. Soil respiration rates in installed and not-installed cylinders. Error bars indicate +/- one standard error of the mean (n=4).

3.4. Lateral diffusion of CO_2 in the meshed cylinders

There was no significant difference in respiration rates between the solid cylinders and the meshed cylinders (p=0.562), indicating that lateral diffusion of CO_2 through the meshed cylinders was negligible (Figure13).

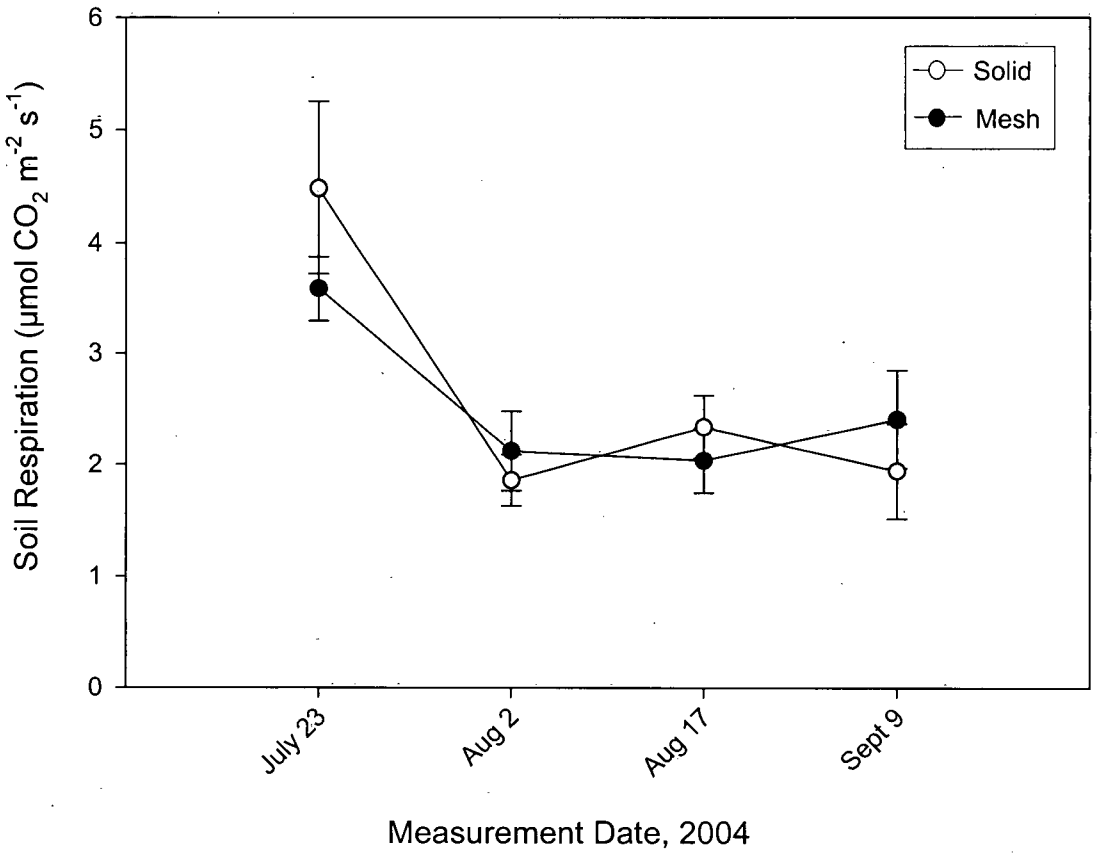

Figure 13. Soil respiration rates in solid and meshed cylinders. Error bars indicate +/- one standard error of the mean (n=3).

3.5. Heterotrophic and rhizospheric respiration

Average heterotrophic respiration rate (R_h), measured in the meshed cylinders was 7.8 Mg C ha^{-1} yr^{-1} (2.1 g C m^{-2} d^{-1}), which is 65% of R_s. The proportion of R_s contributed by R_h ranged from 9% (on October 31, 2005) to 97% (on May 12, 2005). Seasonal patterns of R_h mimicked R_s (Figure 14), especially during the first summer, but R_h was significantly lower than R_s on eight of the 17 occasions.

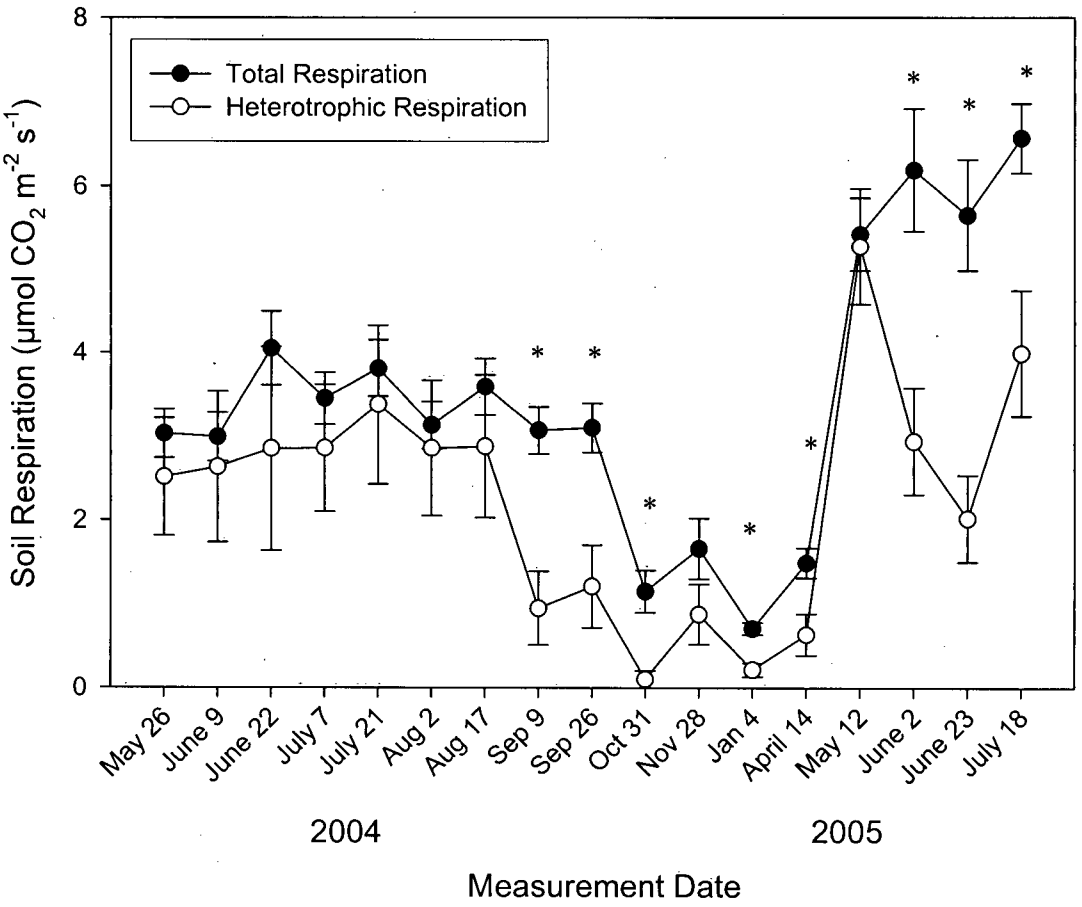

Figure 14. Total and heterotrophic respiration rates. Error bars indicate +/- one standard error of the mean and asterisks above specific observations represent significant differences between means ($p<0.05$, $n=10$).

Calculated rhizospheric respiration (R_r) was 4.2 Mg C ha^{-1} yr^{-1} (1.15 g C m^{-2} d^{-1}; 35% of R_s). The proportion of R_s contributed by R_r ranged from 3% (on May 12, 2005) to 91% (on October 31, 2005). Seasonal trends in R_r were unlike those of R_h (Figure 15) - R_r increased in fall and decreased throughout the winter and spring.

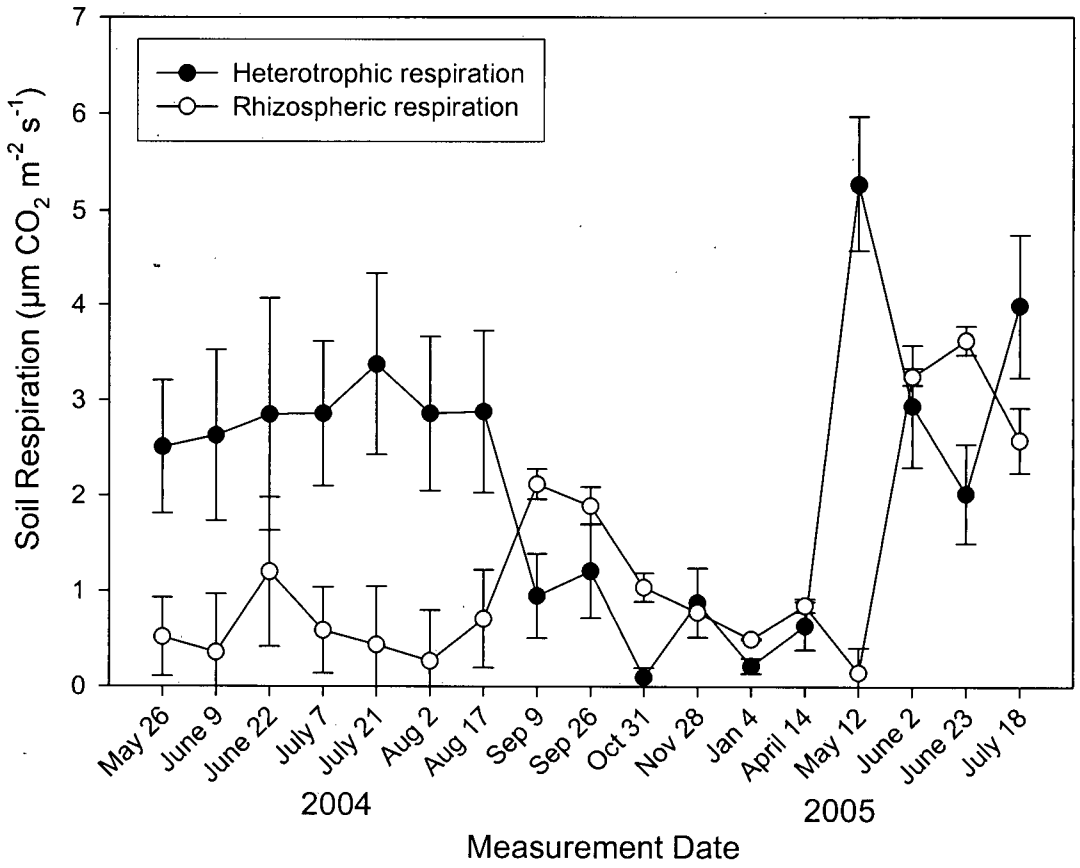

Figure 15. Heterotrophic and rhizospheric soil respiration rates. Error bars indicate +/- one standard error of the mean (n=10).

3.6. Relationships between respiration rates, soil temperature and moisture

Temperature and moisture influences on soil respiration rates are indicated by some of the trends shown in Figure 16. For example, between April 12 and May 14, 2005, respiration increased from 1.49 to 5.42 µmol CO_2 m^{-2} s^{-1} and soil temperature increased by 8°C, while soil moisture decreased by 12%. Multiple regression analysis revealed a weak, positive relationship (r^2=0.21) between R_s and soil temperature ($p<0.0001$). Including the interaction of soil temperature and moisture (p=0.0016) increased the r^2 to 0.27. Relationships between respiration and soil moisture were not significant (p=0.372), but there were some interesting trends. Between October 31, 2004 and April 14, 2005, temperatures remained fairly constant but R_s fluctuated from 0.42 to 4.38 µmol CO_2 m^{-2} s^{-1}, possibly in response to fluctuations (14% to 31%) in soil moisture at the same time. The significant relationship between soil temperature and R_s was best described by a non-linear equation (Figure 17)

equation (Figure 17) which indicated that soil temperature explained some of the variability associated with R_s. However, the higher R_s in 2005 was not associated with higher temperatures (Figure 17).

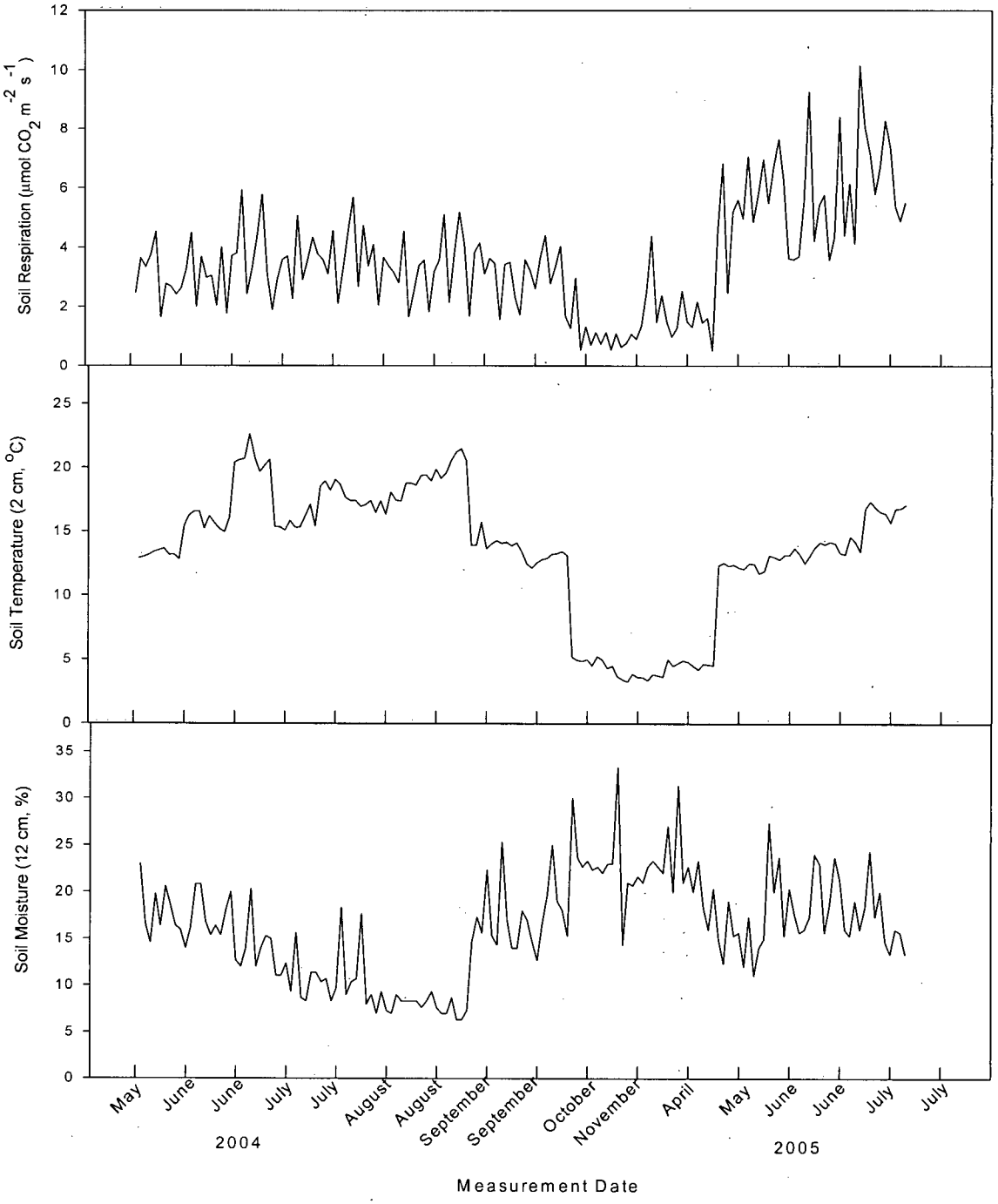

Figure 16. Annual soil moisture (12 cm, %), soil temperature (2 cm, °C), and total soil respiration rates (µmol $CO_2\,m^{-2}\,s^{-1}$) (n=153).

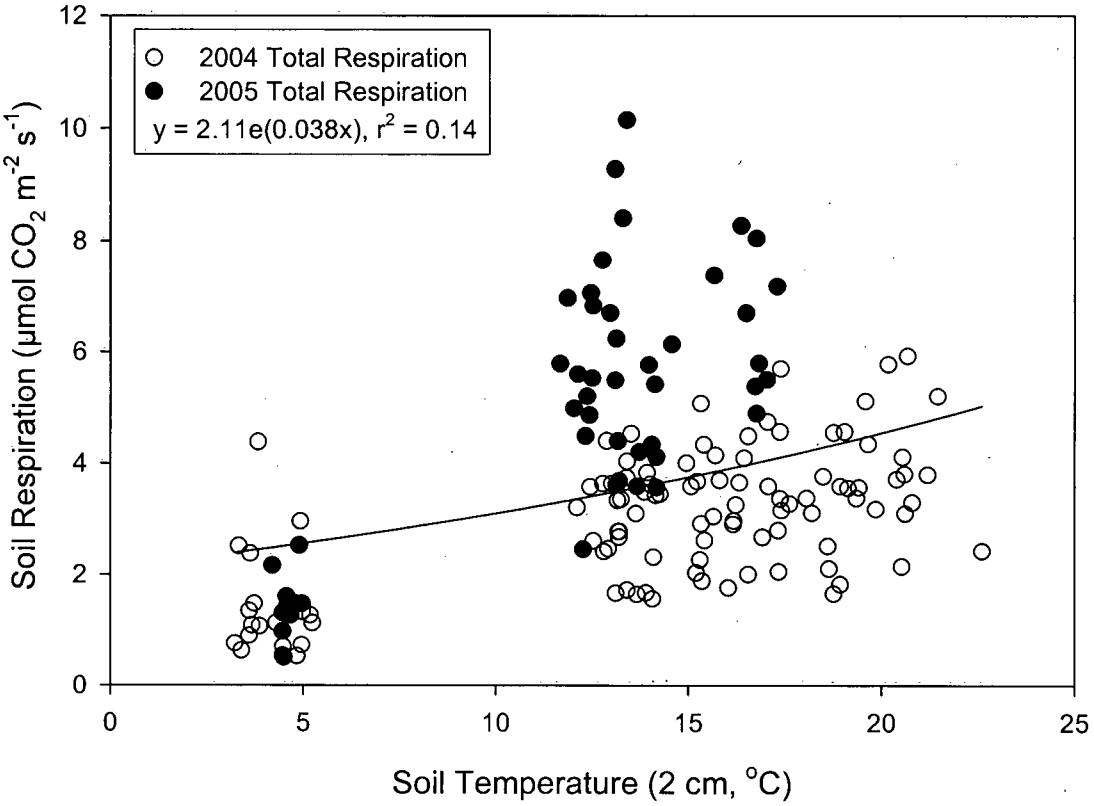

Figure 17. Non-linear relationship between soil temperature (2 cm, °C) and total soil respiration rates (µmol CO_2 m^{-2} s^{-1}).

Non-linear regression analysis was used to investigate individual relationships between soil temperature and soil moisture with R_s, R_h, and R_r rates. When 2005 data were removed and 2004 data were averaged monthly, soil temperature better explained the variation in R_s, as the r^2 value increased from 0.14 to 0.85 (Figures 17 and 18). Significant relationships with soil temperature existed with R_s ($p<0.0001$) and R_h ($p=0.0009$) but not with R_r ($p=0.193$) (Figure 18). The relationship between soil moisture and respiration rates (Figure 19) was poor ($r^2=0$), indicating that soil moisture did not explain much of the variability associated with any of the respiration rates.

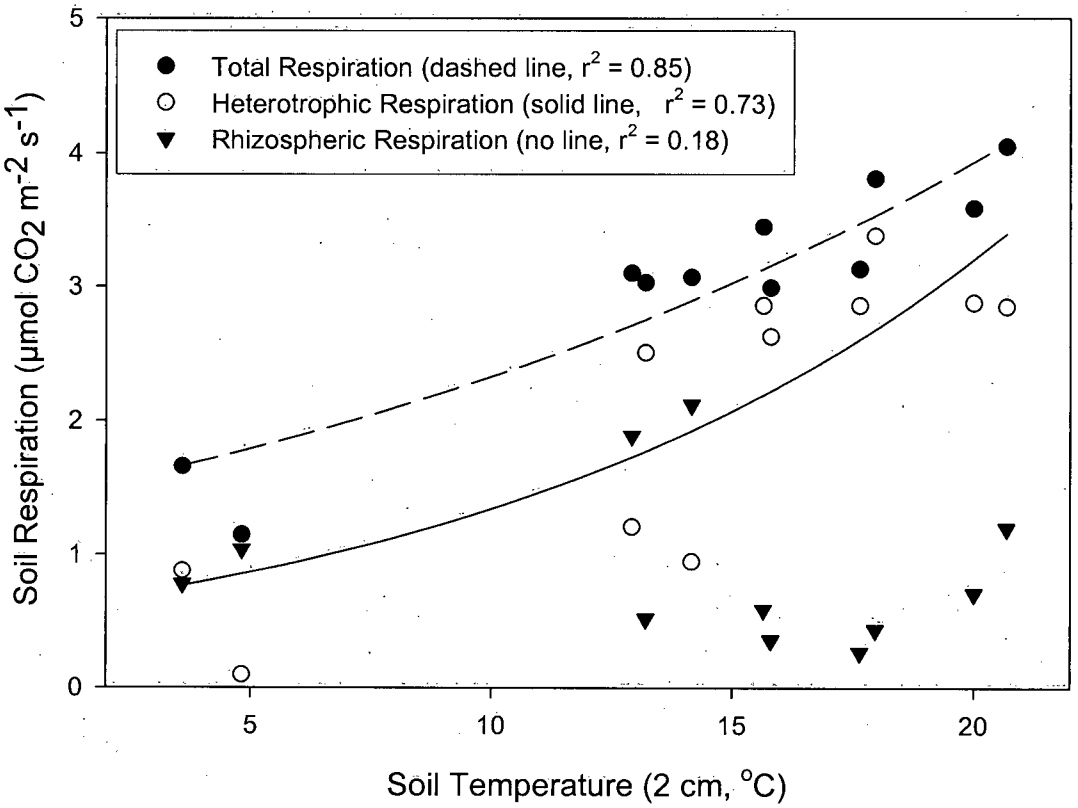

Figure 18. Non-linear relationships between soil temperature (2 cm, °C) and soil respiration (total, heterotrophic, and rhizospheric) rates (µmol CO_2 m^{-2} s^{-1}).

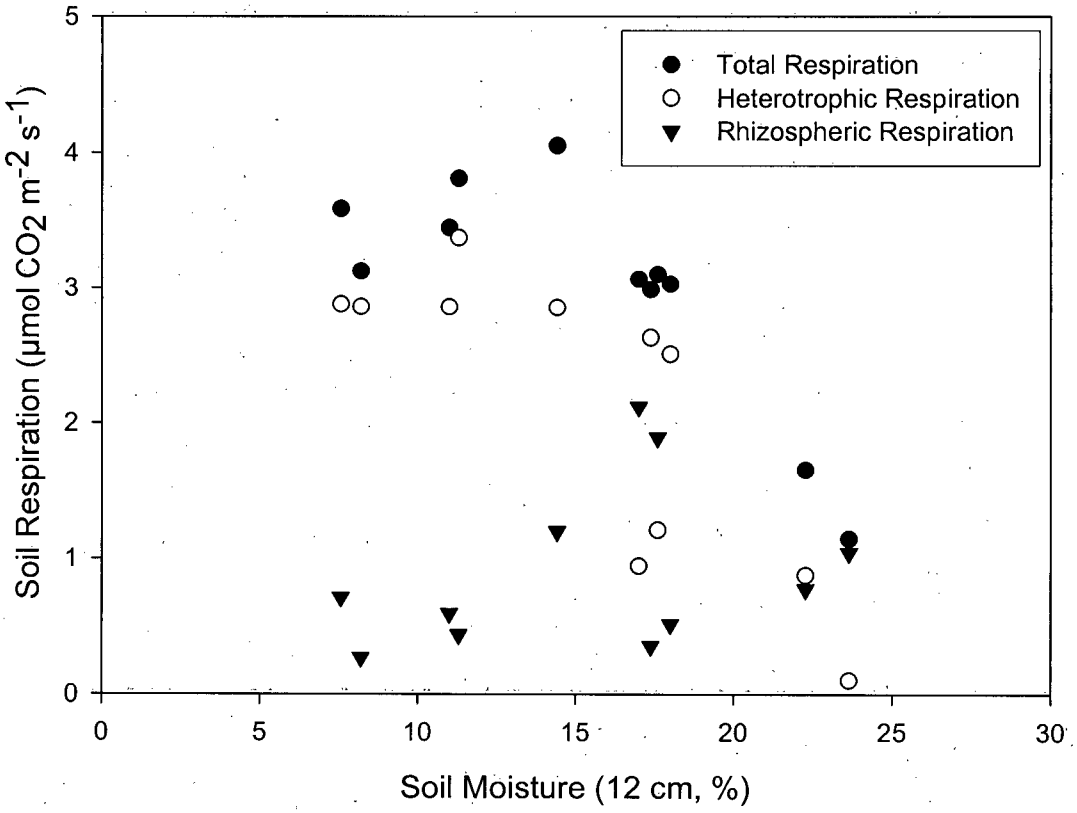

Figure 19. Relationships between soil moisture (12 cm, %) and soil respiration (total, heterotrophic, and rhizospheric) rates (µmol $CO_2\,m^{-2}\,s^{-1}$).

Estimated seasonal Q_{10} values were 1.68 for R_s and 2.23 for R_h. R_r was not determined because the data were too variable (Table 3).

Table 3. Relationships between soil temperature (2 cm, °C) and respiration rates (mean total and mean heterotrophic) (µmol $CO_2\,m^{-2}\,s^{-1}$) in 2004.

Respiration Rate	$y= \beta_o*e(\beta_1*T)$	SE β_o	SE β_1	r^2	Q_{10}	p
Mean total	y=1.38*e(0.052)	0.2	0.0086	0.856	1.68203	<0.0001
Mean Heterotrophic	y=0.6192*e(0.08)	0.2401	0.0222	0.726	2.22554	0.0009

3.7. Spatial variability

There was a significant interaction effect between treatment and location for all tests except for lateral diffusion measurements. To account for this, the interaction effect was treated as an error term and treatment was tested against this value. There was a significant difference in treatment for all tests. Thus, even though the treatments were not always

behaving the same (i.e. meshed cylinders always having the highest soil respiration rates), overall there was a significant difference in respiration rates between them. This "location effect" is an indication of spatial variability within the forest. Location 6 tended to have the highest respiration rates and Location 7 the lowest (Figure 20).

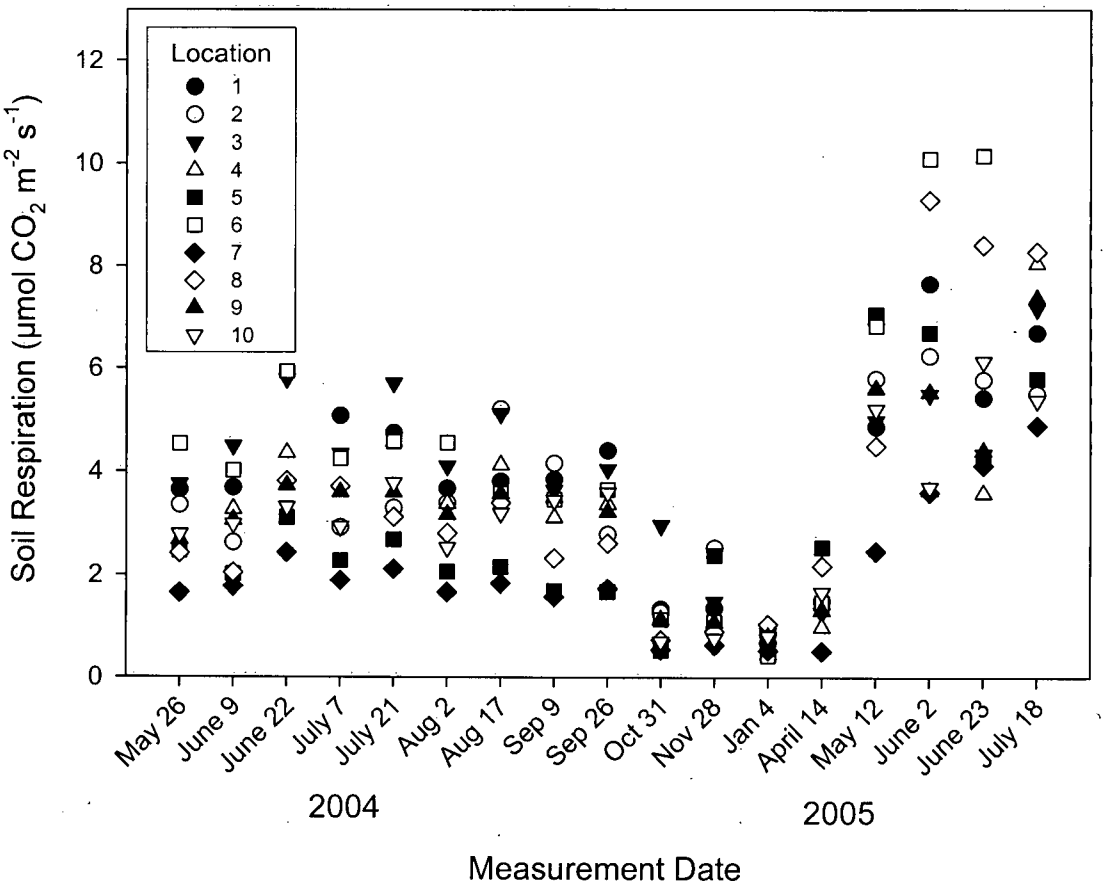

Figure 20. Mean soil respiration rates (µmol CO_2 m^{-2} s^{-1}) at Locations 1 through 10.

4. Discussion

The average total soil respiration (R_s) rate of 12 Mg C ha^{-1} yr^{-1} in this forest is comparable to studies in other temperate coniferous forests that used similar methods (Table 4). The range of R_s values may be related to the use of different chamber methodologies since chambers are associated with many artifacts that can bias measurements (Hutchinson and Livingston 2001). One of the greatest concerns with using a chamber technique is altering natural concentration gradients within the soil profile when the chamber is placed over a cylinder, creating an increased CO_2 concentration inside the chamber headspace. This increase creates a feedback effect that decreases the concentration gradient between soil and air inside the chamber headspace. This decreases the respiration rate to a constant level depending on the duration of the measurement (Rolston 1986). My measurements were only 120 seconds long, so this feedback effect was not likely to have affected my values. The design and placement of a vent within the chamber also minimized this effect and equalized any pressure differences caused by wind and vertical CO_2 gradients (Davidson et al. 2002, Hutchinson and Livingston 2001, Longdoz 2000). The vent was a 10-cm-long, 4-mm-diameter tube pinched slightly at the top and pointed upward with the outlet vertical into the pipe cap. My design differed from that of Hutchinson and Livingston (2001), whom suggested that the vent tube be mounted near the ground surface in the chamber side-wall rather than on the top, and its outlet horizontal and pointed downward. The design of my vent may have allowed greater exposure to winds or vertical pressure than their design, but this error is much smaller than that which occurs from not having a vent (Davidson et al. 2002).

Table 4. Annual total respiration (R_s) rates from other temperate-coniferous studies.

Reference	Rs CO_2-C Mg ha^{-1} yr^{-1}	Temperate Coniferous Forest Type	Location
This study	12.03	Douglas-fir, 55 years old	coastal British Columbia
Drewitt et al. 2002	19.2	Douglas-fir, 55 yeas old	coastal British Columbia
Maier and Kress 2000	14.1	loblolly pine, 11 years old	North Carolina
Ewel et al. 1987b	13	slash pine, 29 years old	Florida
Ewel et al. 1987a	8.2	slash pine, 9 years old	Florida
Longdoz et al. 2000	4.38	Douglas-fir, 35-m-tall trees	Belgian Ardennes
Raich and Schlesinger 1992	6.81	review of coniferous forests	temperate locations
Buchmann 2000	7.1	Norway spruce, 47 years old	northeast Germany
Certini et al. 2003	11.71	silver fir	Florence Italy

R_s may have been slightly overestimated on a few occasions while restoring ambient CO_2 concentrations in the chamber headspace because I occasionally held the chamber well above the soil surface, as discussed by Davidson et al. (2002). On days with little wind or high relative humidity, CO_2 concentrations remained high inside the headspace, so I lifted the chamber to 30-150 cm above the soil surface to increase the mixing of air. Forest floor CO_2 concentrations can be several ppm higher than concentrations at shoulder height (Davidson et al. 2002), so this might have caused soil respiration rates to be overestimated. This may explain the negative respiration values which I occasionally recorded (these were removed from the dataset).

The low R_h rates in the last three measurements may have resulted from prolonged exclusion of roots inside the meshed cylinders. Root exclusion can increase soil moisture content by restricting plant water uptake (Buchmann 2000), which may impede decomposition and respiration rates (Hanson 2000). For example, Epron et al. (1999) found that soil water content was twice as high in a trenched plot than in an untrenched plot in late summer and early autumn. Soil moisture content probably did not cause the low R_h rates measured at the end of the experiment because gravimetric water content at these times did not differ between meshed and not-meshed cylinders. There was no significant difference ($p=0.345$) in soil moisture content between meshed cylinders and not-meshed cylinders; the average moisture content of the upper 20 cm of soils was actually lower (43%) in the meshed cylinders than in the not-meshed cylinders (53%). Thus, excessive moisture in meshed cylinders does not appear to be a concern in this study. Prolonged root exclusion may also limit C substrates for microbial decomposition (Buchmann 2000); this might explain the low R_h and high R_r rates at the end of the experiment.

The high R_r rates during the last three measurements may be the result of the suspected underestimation of R_h at this time, due to prolonged root exclusion, since R_r was calculated as the difference between the two measured rates (R_s and R_h). Alternatively, there could have been a pulse in root growth at this time as there was also an increase in R_r in June of the previous year. The peaks in R_r in June and September reflect pulses of root growth that occur in autumn and spring. In the summer, photosynthates do not reach the roots because of large C requirements of aboveground components. As secondary growth slows in the autumn, assimilates reach the root system and may be respired. Throughout winter the root system accumulates C in starch reserves which are incorporated into growth in the spring (Hansen et al. 1997).

The seasonal R_s Q_{10} of 1.7 was lower than the average values of 2.4 (Raich and Schlesinger 1992), 2.72 (Buchmann 2000) and 3.5 (Boone et al. 1998) for R_s from a range of soils and ecosystems, but temperate coniferous forests tend to have lower Q_{10}s because of the relatively mild winters (Sulzman et al. 2005). The better relationship between temperature and soil respiration rate in 2004 may have resulted from 2004 being dry and warm compared to the cool and wet 2005. The lack of relationship between soil moisture and R_s, R_h, and R_r were unexpected. Perhaps measuring soil moisture content gravimetrically at more soil depths throughout the experiment would have been more accurate than using the Hydosense™ soil moisture probe (CSI).

The small difference in respiration between soil with and without severed roots is in keeping with Högberg et al.'s (2001) finding that most root respiration arises from recent photosynthates, rather than from root turnover. Vogel and Valentine (2005) also found no difference in root respiration between cylinders that were installed one to three weeks earlier with cylinders that were installed nearly 10 months before. The substantial mass loss of severed roots during the 15 months they were inside the meshed cylinders was surprising, because, if these roots had completely decomposed, they would have released 684 g C m^{-2}, which is larger than the difference in C detected in cylinders with and without severed roots. This suggests that soil CO_2 efflux was not the only output pathway of soil C in this forest and that leaching of dissolved organic carbon and/or humification rates should have also been investigated. Lee et al. (2003) assumed that 1/3 of root mass loss was due to humification, and used 2/3 to estimate the C mineralization rate from roots. Epron et al. (1999) assumed the fraction of root C incorporated into soil organic matter to be 22%, which they derived from an earlier study. Further investigations into the process of humus formation and the quantities of dissolved organic carbon in this forest soil are needed.

Installed cylinders had higher respiration rates than not-installed cylinders at each measurement time, indicating that the disturbance caused by cylinder installation lasted throughout the 15-month experiment. This prolonged increase in soil respiration was unexpected, as other root-exclusion studies have indicated that trenching disturbance lasts for only three (Lee et al. 2003), or four (Ewel et al. 1987b) months. The disturbance effect has been attributed to the decomposition of severed roots and stabilization of soil within trenched plots. In this study respiration from severed roots was negligible as there was no difference in respiration between cylinders with and without severed roots. The disturbance effect may have resulted from higher soil bulk density in the installed cylinders than the not-installed cylinders. Conlin and van den Driessche (2000) reported increased respiration

from compacted soil. In this study soil replaced into some of the cylinders did not reach the surface, indicating that it had been compacted during cylinder installation. This could have resulted from vibrations as the core penetrated the soil, or from replacing the soil into the cylinder. My bulk density estimate for the upper 50 cm (1429 kg m^{-3}) was higher than estimates from undisturbed soil at this site (1336 kg m^{-3}, 80 cm depth; Humphreys 2004).

The similar soil respiration rates between the solid and meshed cylinders suggested that lateral diffusion of CO_2 was not influencing soil respiration in the meshed cylinders. This finding was unexpected because Jassal et al. (2004) reported rapid CO_2 diffusion in soil at this site, such that lateral diffusion could be substantial. Diffusivity values ranged from 7 mm^{-2} s^{-1} at the soil surface to less than 2 mm^{-2} s^{-1} at 50 cm. Lateral CO_2 diffusion is often overlooked in root-exclusion studies, assuming instead that lateral gradients are not strong enough to compete with the large vertical CO_2 gradient that exists between the atmosphere and soil (Susfalk et al. 2002). However, lateral diffusion has been blamed for confounding other studies in which the sides of soil pits were exposed to atmospheric air (Davidson and Trumbore 1995), or transplanted soils, with unique isotopic ^{13}C values, were placed adjacent to native soils (Rochette and Flanagan 1997, Susfalk et al. 2002). Silver et al. (2005) expectedly found lower respiration rates in trenched plots than in un-trenched plots in a clay soil but in a sandy soil, there was no significant difference in respiration rates between trenched plots and un-trenched plots. In the sandy soil, which would have a higher diffusivity, lateral diffusion may have contributed to the high respiration in the trenched plots, as the trench was lined with 0.5-mm screen which would allow lateral CO_2 diffusion. In my study, lateral diffusion was estimated from the difference in R_h between meshed cylinders and solid cylinders. This should provide a reliable indication of the magnitude of this flux, but direct measurements of lateral CO_2 diffusion are needed to quantify this flux with certainty.

5. Conclusions

- Total soil respiration in this forest (12 Mg C ha^{-1} yr^{-1}) was in the range of other temperate coniferous forests.
- Heterotrophic respiration contributed 65% of total soil respiration, mostly between May and August.
- Rhizospheric respiration contributed 35% of total soil respiration, and peaked in spring and fall.
- Total and heterotrophic respiration were related to soil temperature but not to soil moisture. Rhizospheric respiration was not closely related to soil temperature or moisture.
- Roots severed during cylinder installation lost 70% of their mass during the 15 months they were inside the meshed cylinders, but additional respiration attributable to decay of severed roots was negligible.
- Increased respiration resulting from cylinder installation persisted for the entire 15-month experiment, possibly as a result of soil compaction.
- Lateral CO_2 diffusion, estimated from the difference in respiration from meshed and solid cylinders, was negligible.

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