UNIVERSITY OF CALIFORNIA,
IRVINE

Belowground Carbon Cycling
in Three Temperate Forests of the Eastern United States

DISSERTATION

submitted in partial satisfaction of the degree requirements for the degree of

DOCTOR OF PHILOSOPHY

in Earth System Science

by

Julia B. Gaudinski

Dissertation Committee:
Professor Susan E. Trumbore, Chair
Professor William S. Reeburgh
Professor Ellen R.M. Druffel
Professor Michael L. Goulden

2001

The dissertation of Julia B. Gaudinski is approved
and is acceptable in quality and form
for publication on microfilm:

Committee Chair

University of California, Irvine
2001

Dedication

For my mom ShirleyAnne Anderson and my friend Susan Harder

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Curriculum Vitae

Julia B. Gaudinski

EDUCATION

Ph.D. Earth System Science, University of California, Irvine, March 2001.
M.S. Earth System Science, University of California, Irvine, December 1997.
B.A. Earth Science, B.A. Environmental Studies, University of California, Santa Cruz, March 1991.

WORK EXPERIENCE

Staff Hydrologist (1991-1994) Golder Associates Inc., Redmond, WA
Oceanographer/Chemist (1993) University of Washington, Seattle WA
Independent Research/Technical Assistant (1989-1991) Wildland Fire Management, Walnut Creek, CA
National Park Service (Summer 1988) Crater Lake National Park, Crater Lake, OR

PEER REVIEWED JOURNAL PUBLICATIONS

Gaudinski JB, Trumbore SE, Erickson EA and Zheng S (2000) Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes, *Biogeochemistry* 51: 33-69.

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Abstract of the Dissertation

Belowground Carbon Cycling
in Three Temperate Forests of the Eastern United States
By
Julia B. Gaudinski
Doctor of Philosophy in Earth System Science
University of California, Irvine, 2001
Professor Susan E. Trumbore, Chair

Rates of carbon (C) cycling in soils are an important component in the equation of forest carbon balance yet at present they are poorly quantified. This research focuses on quantifying rates of soil C cycling at three temperate forests in the eastern United States along a latitudinal gradient from Maine to Tennessee. Measurements of C and radiocarbon (^{14}C) stocks and fluxes are our principal measurement tools.

Total soil C stocks (to 80 cm depth) decrease along the gradient and are 14.6, 8.4 and 4.9 kgC m^{-2} at Howland ME, Harvard Forest MA, and Walker Branch TN, respectively. Much of this trend is due to decreasing C stocks in the organic (O) horizons. Howland and Harvard Forest both have large humified C stocks in the O horizon with long turnover times (15-50 years), while at Walker Branch this humified component is largely absent and turnover times are much shorter (7-15 years). On timescales of human interest, significant C accumulation in these soils will happen only in the O and A horizons, which have large C stocks that cycle on decadal and centennial timescales. The deeper mineral horizons, despite their large stocks, have long turnover times (200-2000

years) and can store C effectively only over millennia. Soils of northern sites such as Howland and Harvard Forest have greater C storage potential than the southern site of Walker Branch. Currently, well-drained soils account for an uptake of 5-50 gC m^{-2} y^{-1} or 1-25% of the measured net ecosystem C uptake at each of the sites.

Measurements of the ^{14}C in respired CO_2 from incubations of soil organic matter combined with C and ^{14}C mass balance allow partitioning of soil respiration into heterotrophic and autotrophic sources. Heterotrophic respiration contributed from 44-84% of total soil respiration for well-drained soils at Howland and Harvard Forest in 1999. The average age of heterotrophic respiration at all three sites is 8-9 years. The amount of total soil respiration from C fixed >1-2 years ago decreases along the latitudinal gradient and is 55, 42 and 33% at the Howland, Harvard Forest, and Walker Branch, sites respectively for 1998.

Chapter 1: Dissertation Summary

Introduction

The concentration of CO_2 in the atmosphere continues to increase at a rate of 3.3 ±0.1 Pg of carbon (C) per year as the result of inputs from fossil fuels (5.5± 0.5 Pg of C per year) and land use change (1.6±1Pg of C per year). Oceanic uptake of CO_2 is 2.0±0.8 Pg of C per year and the remaining 1.8±1.4 Pg of C per year has been attributed to terrestrial uptake--primarily regrowing forests in the northern hemisphere (IPCC 1995).

The role of the terrestrial biosphere as a source or sink of C has taken on increased importance as the global scientific community begins to understand the potential negative impacts of global climate change caused by anthropogenically induced green house gas emissions. Regulation of greenhouse-gas emissions, primarily CO_2, have been debated nationally and internationally. In December 1997, the Kyoto protocol was agreed to by 84 industrialized nations (as of November 7, 2000 only 31 have ratified the agreement). This protocol calls for reduction of total C emissions. However, it allows for these reductions not only by decreased emissions, but also by offsetting emissions with increased net C uptake in terrestrial vegetation, particularly forests, that happen to be within a country's borders. Within the United States, government interest with respect to total C emissions management has focused on 1) quantifying the net flux of C, from natural and managed ecosystems and 2) finding ways to enhance their ability to store as much carbon as possible on long timescales.

Despite an increasingly political climate pushing for quantifiable and large net C sinks within countries, measuring terrestrial C fluxes still has methodological problems. Our mechanistic understanding of the intricate processes controlling C fluxes (both C uptake via photosynthesis and C release via respiration) is still uncertain. While we know that on average the terrestrial biosphere is a C sink, its strength can vary by as much as 3-4 Gt C from year to year (Canadell et al., 2000). Global climatic anomalies such as ENSO or volcanic eruptions like Mt. Pinatubo may perturb or mask the annual global terrestrial sink strength (Canadell et al., 2000) (Trumbore et al., 1996). Yet at the ecosystem scale we still do not understand and cannot accurately measure many factors influencing year-to-year variation in forest-C balance. Likely, increased atmospheric CO_2 (the CO_2 fertilization effect), enhanced atmospheric N deposition, and climate variability all play a role (Canadell et al., 2000).

Largely unknown in the forest-C balance equation is how much of the net flux (net C storage) is due to live vegetation versus soil C stocks. Temperate forests of the northeastern United States store between 200-525 g C m^{-2} y^{-1}, depending on location (Hollinger et al., 1999, Greco and Baldocchi, 1996, Goulden et al., 1996). These forests currently act as C sinks because they are young ecosystems recovering from disturbance in the last two centuries. However, the partitioning of this net uptake between vegetation and soils is largely unknown. Also unknown is how both the rate of uptake and the partitioning between vegetation and soils may vary in the future as the ecosystem matures and the climate changes.

Another uncertainty is the behavior of soil C stocks. Quantifying soil C to within 10-20% is challenging and requires hundreds of careful labor-intensive measurements

(Fernandez et al., 1993, Huntington et al., 1988). Quantifying soil-cycling rates through these C stocks is even more difficult. This is because soil C is in compounds that cycle on timescales ranging from days to millennia, and respiration-C losses include both autotrophic (metabolic live root) and heterotrophic (decomposition of soil organic matter by microbes and soil fauna) sources. While soil respiration is one of the largest causes of variation in net ecosystem carbon-balance in forests from year to year (Goulden et al., 1996, Savage and Davidson, in Press), we do not understand how much these variations are due to changes in autotrophic versus heterotrophic respiration. Without this knowledge, it is difficult to quantify how changing soil-respiration rates affect decomposition of soil C and thus the size of soil-C stocks.

The research performed as part of this doctoral dissertation addresses the uncertainties in forest C balance discussed above. Its principle tool is the measurement of radiocarbon (^{14}C), the "bomb C" produced by nuclear weapons testing in the late 1950s and early 1960s. The ^{14}C in soil organic matter (SOM) and CO_2 is a useful indicator of soil carbon dynamics, providing an isotopic tracer for C cycling over decades. Its amount in carbon reservoirs, such as SOM, reflects the rate of exchange with the atmosphere. Bomb ^{14}C is particularly powerful because it tags the age of C (since photosynthetic fixation), in both soil-C stocks and soil-C fluxes (soil respiration), to within 1-2 years.

Work was carried out at three temperate forest ecosystems of the eastern United States (Howland, ME, Harvard Forest, MA and Walker Branch, TN), all of which are presently a net sink of atmospheric C (Hollinger et al., 1999, Greco and Baldocchi, 1996, Goulden et al., 1996). The sites span a latitudinal gradient from 45 to 36° N and therefore have climate variations that were expected to cause differences in C-cycling rates across sites. The specific questions addressed in this thesis are:

1. How does the net C sink at these sites partition between soils and vegetation? Has the soil sink varied with time and is it likely to decrease in the future?
2. What is the age distribution of soil C in soil organic matter at each site and how does this vary across a latitudinal gradient from Maine to Tennessee?
3. What relative amounts of total soil respiration come from A) root respiration and carbon with cycles less than a year and B) decomposition of carbon with cycles greater than a year? Can measurements of ^{14}C in soil organic matter and CO_2 be used to constrain these two respiration sources? Can ^{14}C measurements be used to determine autotrophic vs. heterotrophic sources?
4. How do fine root inputs and fine root dynamics affect the average ^{14}C age of heterotrophic respiration and the response time of soil C to changes in fine-root input?
5. How does the age of total soil respiration, and thus partitioning from the two soil respiration sources, vary latitudinally over a climate gradient from Maine to Tennessee?
6. How does moisture in the organic horizon affect total soil respiration fluxes, especially with respect to summertime drought?

Chapter Summaries

Chapter 2: Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates, and partitioning of fluxes

This chapter is a reformatted version of a paper published in Biogeochemistry (Gaudinski et al., 2000). The main purpose of this paper is to develop methods for 1) measuring the C and ^{14}C inventory in several fractions of soil organic matter; 2) estimating rates of net C storage in soils, using a knowledge of the distribution of residence times of soil organic matter; 3) developing methods to measure ^{14}C in soil respiration and soil CO_2; 4) estimating CO_2 and $^{14}CO_2$ production with depth based on CO_2 concentration profiles and diffusivity estimates; and 5) combining the information from 1, 3, and 4 and using a C and ^{14}C mass-balance approach to partition soil respiration into two components: Recent-C (C fixed from the atmosphere within one year) and Reservoir-C (C fixed from the atmosphere more than one year ago). The paper deals with only one of the three sites, Harvard Forest, MA, the first site for which data were collected, and where much of the methodology required to deal with heterogeneous temperate forest soils were developed. The major conclusions of this chapter are:

- SOM pools are accumulating C in well-drained Harvard Forest soils as they recover from historic disturbance. However, the rates of accumulation we infer, 10-30 g C m^{-2} yr^{-1}, are only 5-15% of the 200 g C m^{-2} yr^{-1}calculated from the eddy flux tower measurements. More poorly drained soils also occur in the tower footprint and may accumulate more C per square meter, although they are far less widespread.

- Measurements of ^{14}C in soil organic matter predominately reflect organic matter fractions with longer turnover times (TT) that dominate soil carbon inventory. Calculations of TT derived by dividing total C inventory by estimated heterotrophic respiration are not good predictors of the response time of soils because soil organic matter (SOM) is not homogeneous.
- Measurements of $\Delta^{14}C$ in CO_2 are required to correctly model the C that is actually respiring and to fully understand belowground C dynamics.
- Interpretation of ^{14}C data in SOM at Harvard Forest is complicated by fine-root inputs with ^{14}C elevated by ~65‰ relative to the atmosphere, implying that the fine-root C was fixed on average 7±1 years ago.
- We estimate 41% of total soil respiration comes from decomposition of SOM that decomposes on timescales of 1-100+ years**.** Of this, 80% involves direct decomposition of leaf and root litter with TT of 2-10 years, and 20% represents low-density humified C pools and C associated with minerals which have TTs on the order of several decades or greater.
- About two-thirds of total soil respiration is produced within the O and A horizons (top 10-15 cm of the entire soil profile). These organic rich horizons are comprised of 1) small pools of live roots and recent leaf and root litter that have residence times in the plant + soil system of ~1-10 years and 2) relatively large pools of humified root and leaf litter which reside in the plant + soil system for 40-100+ years.

- Radiocarbon measurements of total belowground respiration measure the average time C spends in the plant + soil system from original photosynthetic fixation until respiration by autotrophs or heterotrophs. We estimate this time to be 4±1 years for total soil respiration and 8±1 years for heterotrophic respiration in well-drained soils at Harvard Forest, MA.

Chapter 3: Characterization of Soil Organic Matter

This chapter presents data on total C and ^{14}C measurements of SOM stocks at Howland, ME, Harvard Forest, MA and Walker Branch, TN. These data are used to understand and predict the decadal to centennial scale dynamics of soil organic matter stocks. The methods used are those reported in Chapter 2. The major findings of this chapter are:

- The components of soil C can be split into three components with characteristically different turnover times: 1) low-density ($\rho < 2.0$ g/cc) detrital material (recognizable leaves and roots) with turnover times ranging from one to ten years, 2) low-density humified material with much longer turnover times ranging from tens to hundreds of years, and 3) high-density ($\rho > 2.0$ g/cc) mineral associated SOM with turnover times ranging from hundreds to thousands of years.
- Carbon inventories decrease from Maine to Tennessee from 14.6 to 4.9 kg C m^{-2}. Much of this trend is due to decreasing C stocks in the O horizons of the soil profiles where there is a large change in both turnover time and the type of SOM present. Both Howland and Harvard Forest have large humified C stocks in the O horizons with long turnover times (15-50 years). At Walker Branch this humified

component is largely absent in the O horizon where total stocks are small, primarily detrital, and turnover times are much shorter (7-15 years).

- The mineral horizons show no clear trend in SOM turnover time across sites for either the low- or the high-density components. The absence of such a trend for the low-density material may in large part be due to the processing of the low-density samples being inconsistent across sites. The presence of fine roots can artificially decrease measured turnover times if roots are included in the humified portion and therefore obscure any trends due to climate. Size separation (sieving with an 80 μ sieve) is an effective way to differentiate samples. However, fine roots may still complicate interpretation, particularly for the >80μ size fraction. We found that a combination of sieving and hand picking best isolates the most humified portion of low-density SOM. A lack of a latitudinal trend in the high-density (mineral associated) SOM may be due to differences in soil age and mineralogy between the two northern sites (which are quite similar) and the southern site, which is much older with very different mineralogy.
- When using ^{14}C to understand SOM dynamics on short timescales (1-10 years) it is important to consider time lags between photosynthesis and respiration of SOM (the time C spends in living plant tissue prior to senescence and addition to SOM pools). Failure to do so will accurately estimate how long the measured carbon spent in the plant + soil system, but will overestimate decomposition rates within the soil system alone. The overestimate will roughly equal the time spent as live plant tissue prior to addition to SOM. To correct for this time lag, measurements of ^{14}C in the different components of litter added to the system are required.

Unfortunately, because the rate of decrease of atmospheric $\Delta^{14}CO_2$ declines with time, a correction has errors of ± 1 to 2 years in the 1990s and will likely increase with time.

- Relatively small C pools with fast turnover times, such as detrital leaf and fine-root litter, dominate decomposition fluxes. These pools are most sensitive to time lags between photosynthetic fixation and input to SOM. Their ^{14}C signature is therefore not an appropriate measurement for determining decomposition fluxes.
- On human timescales, significant C accumulation will occur only in the O and A horizon of these temperate forest soils. These horizons are the only ones with significant C stocks that cycle on decadal and centennial timescales. Soils of more northern sites, such as Howland and Harvard Forest, with more C stored in the O and A horizons, have a greater C storage potential than more southern sites like Walker Branch. At present, all well-drained soils in the eastern temperate forests studied account for an uptake of 5-50 g C m^{-2} y^{-1} or 1-25% of the measured net-C uptake at each of the sites. Extrapolating globally, temperate forest soils may account for 0.6-6% of the total terrestrial-C uptake.

Chapter 4: Heterogeneity of Fine-Root Dynamics Measured by Radiocarbon

This chapter is a reformatted version of a paper in review for the journal *Oecologia* (Gaudinski et al., in review). It explores the use of $\Delta^{14}C$ measurements on fine roots as a new tool for learning more about their age and dynamics. This work builds on initial findings from Harvard Forest (discussed in Chapter 2) that showed fine roots to be significantly enriched in ^{14}C compared to the current atmospheric $\Delta^{14}C$ of CO_2. These results were unexpected because most literature values for fine-root turnover are 1-2 years or less. The major findings of this chapter are:

- Fine roots grow from recently fixed photosynthate rather than C stored in the plant for several years.
- Although absolute ages depend on the model of root growth used, our $\Delta^{14}C$ data clearly indicate that a large percentage of fine-root stocks in forests live for many years.
- Roots age from months to decades or more.
- The commonly used definition of fine roots as those with < 2 mm diameter is problematic because it lumps together populations of roots that cycle carbon at significantly different rates.
- Improved understanding of ecosystem carbon balance will require combined measurement approaches that further explore the ecology of fine roots.

Chapter 5: Soil respiration fluxes: Age, Variability, and Partitioning

This chapter builds on work presented in Chapters 2 and 3. Chapter 2 presents a method for partitioning soil respiration into two components using the $\Delta^{14}C$ signature of soil respiration and ^{14}C-derived turnover times of soil organic matter fractions at Harvard Forest. Chapter 3 discusses ^{14}C-derived SOM turnover times and dynamics at Howland, Harvard Forest and Walker Branch. Here, decomposition dynamics based on $^{14}CO_2$ measurements at all three sites is explored. Treatment of soil respiration is expanded to introduce a second, new, method of partitioning based on measuring $^{14}CO_2$ evolved during soil incubations. We compare the two methods using data from the Howland and Harvard Forest sites (Walker Branch is compromised due to an unexpected ^{14}C release in 1999). Additionally, this chapter assesses the impact of inter-annual variability of climate on decomposition dynamics and respiration partitioning at the same site in years with varying climate. The major findings of this chapter are:

- At all three sites decomposition fluxes from decadal cycling SOM are an important component of total soil respiration and soil gas (to a depth of 80 cm) within the soil profile.
- Fine-root decomposition plays a very important role in decomposition fluxes, particularly at depth (below ~ 15 cm) where it is the dominant source of heterotrophic respiration.
- The amount of C fixed from the atmosphere >1-2 years ago contributing to soil respiration decreases from Maine to Tennessee. On average, C fixed >1-2 years ago makes up 50%, 41% and 33 % of soil respiration at Howland, Harvard Forest and Walker Branch.
- The average age of heterotrophic respiration is 8±2 years at both Harvard Forest and Walker Branch..
- Fluxes of CO_2 and $^{14}CO_2$ from soils are affected by interannual variability in climate.
- Variation in decomposition flux from decadal cycling SOM has a significant impact on net ecosystem productivity. Respiration partitioning using incubations is the best way to quantify this variability from year to year.

Chapter 6: Moisture Manipulations

Chapter 6 presents the results of moisture manipulations on well-drained soils at Harvard Forest during 1998 and 1999. The purpose of the manipulations was to determine the importance of moisture in the O and A horizons to both total CO_2 and $^{14}CO_2$ fluxes. Included are the results of a new technique (DC half bridges) to monitor moisture content in the O horizons. This work finds:

- Using DC half bridges to estimate continuous moisture content of the O horizon in 1999 shows promising results. Voltage readings track rain events very well in the uppermost (0-1 cm) of the O horizon (litter), and show less or no response to rain events deeper within the O horizon, as one would expect. Conversion of voltage readings to an actual moisture measurement via a calibration curve can likely be improved by insulation of the half bridge leads.
- Drying of the organic horizon by rainfall exclusion created a dramatic decrease in soil respiration fluxes but not in their ^{14}C signature. The $\Delta^{14}CO_2$ decrease suggests a decrease in decomposition in the mineral horizons, implying that decomposition within the organic horizon shifted to deeper, more isotopically enriched sources within the O horizon. In order to determine the changes in decomposition sources vertically within the soil profile, depth measurements of CO_2 and $^{14}CO_2$ are required. Estimates of CO_2 production with depth are needed to complete the C and ^{14}C mass balance and to test the hypothesis of changing production with depth.

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Chapter 2: Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes

Abstract

Temperate forests of North America are thought to be significant sinks of atmospheric CO_2. We developed a below-ground carbon (C) budget for well-drained soils in Harvard Forest Massachusetts, an ecosystem that is storing C. Measurements of carbon and radiocarbon (^{14}C) inventory were used to determine the turnover time and maximum rate of CO_2 production from heterotrophic respiration of three fractions of soil organic matter (SOM): recognizable litter fragments (L), humified low density material (H), and high density or mineral-associated organic matter (M). Turnover times in all fractions increased with soil depth and were 2-5 years for recognizable leaf litter, 5-10 years for root litter, 40-100+ years for low density humified material and >100 years for carbon associated with minerals. These turnover times represent the time carbon resides in the plant + soil system, and may underestimate actual decomposition rates if carbon resides for several years in living root, plant or woody material.

Soil respiration was partitioned into two components using ^{14}C: recent photosynthate which is metabolized by roots and microorganisms within a year of initial fixation (Recent-C), and C that is respired during microbial decomposition of SOM that

resides in the soil for several years or longer (Reservoir-C). For the whole soil, we calculate that decomposition of Reservoir-C contributes approximately 41% of the total annual soil respiration. Of this 41%, recognizable leaf or root detritus accounts for 80% of the flux, and 20% is from the more humified fractions that dominate the soil carbon stocks. Measurements of CO_2 and $^{14}CO_2$ in the soil atmosphere and in total soil respiration were combined with surface CO_2 fluxes and a soil gas diffusion model to determine the flux and isotopic signature of C produced as a function of soil depth. 63% of soil respiration takes place in the top 15 cm of the soil (O+A+Ap horizons). The average residence time of Reservoir-C in the plant+soil system is 8±1 years and the average age of carbon in total soil respiration (Recent-C + Reservoir-C) is 4±1 years.

The O and A horizons have accumulated 4.4 kgC m^{-2} above the plow layer since abandonment by settlers in the late-1800's. C pools contributing the most to soil respiration have short enough turnover times that they are likely in steady state. However, most C is stored as humified organic matter within both the O and A horizons and has turnover times from 40 to 100+ years respectively. These reservoirs continue to accumulate carbon at a combined rate of 10-30 gC m^{-2} yr^{-1}. This rate of accumulation is only 5-15% of the total ecosystem C sink measured in this stand using eddy covariance methods.

Introduction

Well drained temperate forest soils in the northeastern United States have accumulated carbon (C) over the past century as forest has regrown over former fields and pastures. The rate at which mid-latitude forest vegetation and forest soils are still accumulating C and can act to ameliorate future anthropogenic inputs of CO_2 to the atmosphere is still uncertain. The capacity for ecosystems to store CO_2 depends both on their productivity and the residence time of C (Thompson et al. 1996). Hence, the average time between fixation of C by photosynthesis and its return to the atmosphere by respiration or decomposition is an important parameter for determining the timing and magnitude of C storage or release in response to disturbances like climate or land use change (Fung et al. 1997).

Eddy flux tower measurements made since 1990 in a temperate deciduous forest in central Massachusetts (Harvard Forest) show consistent net ecosystem uptake of C averaging nearly 200 gC m^{-2} yr^{-1} (Wofsy et al. 1993; Goulden et al. 1996). Interannual variability in the rate of net C storage has been linked to climate (Goulden et al., 1996). The Harvard Forest is growing on land used for agriculture or pasture in the 19th century and was damaged by a hurricane in 1938. Net carbon storage in a forest recovering from these disturbances is not surprising. However, the partitioning of C storage among vegetation and soils at this site is unknown, as is the potential for C storage rates to change in the future as recovery from disturbance progresses.

The goal of this work is to quantify the below ground carbon cycle in well drained soils that dominate the footprint of the eddy flux tower at the Harvard Forest. We use radiocarbon (^{14}C) measurements in soil organic matter (SOM) and CO_2 to quantify the residence time of C in the plant+soil system and to determine the contribution of well-drained soils to the net sink measured by Wofsy et al. 1993 and Goulden et al. 1996. We also partition total soil respiration into two components using ^{14}C: (1) root respiration and microbial metabolism of recent photosynthate within a year of initial fixation (Recent-C), and (2) CO_2 derived from microbial decomposition of SOM that resides in the soil longer than a year (Reservoir-C).

Radiocarbon measurements of SOM and CO_2 are an extremely useful tool to determine the dynamics of soil carbon. ^{14}C produced by atmospheric weapons testing in the early 1960s (i.e. ‘bomb C’) is used as an isotopic tracer for C cycling on decadal time-scales. Carbon reservoirs such as SOM that exchange with the atmosphere reflect the rate of exchange through the amount of 'bomb' ^{14}C incorporated (**Figure 1**). ^{14}C in atmospheric CO_2 is currently decreasing at a rate of about 8‰ per year in the Northern Hemisphere (Levin and Kromer 1997) because of uptake by the ocean and dilution by burning of ^{14}C-free fossil fuels. The ^{14}C content of a homogeneous C reservoir in any given year since 1963 may be predicted from the turnover time and the known record of atmospheric $^{14}CO_2$. Utilization of bomb-produced ^{14}C as a continuous isotopic label has advantages over other isotopic methods because it can be used in undisturbed ecosystems and can resolve dynamics that operate on annual to decadal time scales.

Soil organic matter is made up of C fractions that cycle on a continuum of time scales ranging from days to millennia. Because of this complexity, ^{14}C measurements of bulk SOM at a single point in time do not yield useful information about the rate of SOM cycling (Trumbore, in press). At the Harvard Forest, we separated SOM into distinct pools with different characteristic turnover times (see **Figure 2**): recognizable leaf (L_L) and recognizable fine (<2 mm) root litter (L_R), organic matter that has been transformed by microbial action or humified, but is not stabilized by interactions with mineral surfaces (H), and organic matter that is associated with soil minerals and thus is separable by density (M). These four pools collectively comprise Reservoir-C as defined for this paper and represent detrital C that remains in the soil for one year or more. Carbon pools in SOM that cycle on timescales of less than one year are included in our definition of Recent-C.

Carbon dynamics derived from measurements of ^{14}C in SOM fractions alone tend to underestimate the flux of CO_2 from soils. Heterotrophic respiration is dominated by decomposition of C with short turnover times and small reservoirs that are difficult to measure. The majority of easily measurable SOM stocks represent slowly cycling material with relatively long turnover times. Measurements of ^{14}C in CO_2 can be used to determine the relative contributions of the recalcitrant C, which dominates SOM stocks, and the more rapidly cycling C, which dominates heterotrophic and autotrophic respiration. To derive a below-ground C budget that includes soil respiration, we combined measurements of CO_2 and $^{14}CO_2$ surface fluxes and soil atmosphere profiles with a model of soil gas diffusion to determine the rate and ^{14}C signature of CO_2 production in soil by horizon. This, combined with the predicted production of CO_2 and $^{14}CO_2$ derived from the L_L, L_R, H and M fractions of SOM, allowed us to partition soil respiration into Recent-C and Reservoir-C.

Site Description

The Harvard Forest is a mixed deciduous forest located near the town of Petersham in central Massachusetts. The study area is located on the Prospect Hill Tract (42.54°N, 72.18°W). The terrain is moderately hilly (average elevation 340 m) and currently about 95% forested (Wofsy et al. 1993). The soils are developed on glacial till deposits which are predominantly granitic. Drainage varies from well-drained uplands, which make up most of the area in the flux tower footprint, to very poorly drained swamps. The data reported here are for well drained soils with very low clay content and mapped as Canton Series (coarse-loamy over sandy or sandy skeletal, mixed mesic Typic Dystrochrepts). We sampled soils, soil respiration and soil gas profiles within 100 meters of the eddy flux tower where a multi-year record of soil respiration measured by flux chambers is maintained (Davidson et al. 1998). The sites are within a mixed deciduous stand, dominated by red oak (*Quercus rubra*) and red maple (*Acer rubrum*) with some hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*). The area comprising our study site was cleared in the mid-1800s, plowed and used primarily for pasture. The pasture was abandoned between 1860 and 1880 (Foster 1992). The regrowing forest was largely leveled by a hurricane in 1938 but has been growing undisturbed since that time.

Methods

Field

We sampled soils using the quantitative pit methodology as discussed by Huntington et al. 1989 and Hamburg 1984. This method involves sampling a large volume of soil to allow calculation of horizon-specific bulk densities. Two 0.5 X 0.5 m quantitative pits were dug in 1996 to a depth of about 80 cm. Pit locations were selected to be similar to those where Davidson et al. 1998 are monitoring soil respiration and soil CO_2 concentrations and are within 20 meters of their soil respiration collars. In each pit excavation proceeded downward to the base of each pedogenic horizon which, was differentiated by color and textural changes. In order to minimize sampling errors due to repeated grid placement and removal, the top of each pedogenic horizon was calculated by taking a weighted mean of 25 measurements from within the 0.5 X 0.5 m grid. This system weights the center nine measurements 4X, the sides of the grid (not including the corners) 2X and the corners 1X. Additional samples which integrated each soil horizon were collected for radiocarbon and total C and N analyses from one of the pit faces. Samples of the forest floor (0.15 X 0.15 m squares), core samples of A horizons and grab samples of Ap and B horizons were collected in order to analyze the abundance and ^{14}C of roots. During the summer of 1997, a third, shallower (0.17m X 0.37 m) pit was dug to obtain more data for the O and A horizons. Samples were taken in approximately 2 cm vertical increments to the base of the Ap horizon.

Collars sampled were the same as those used by Davidson et al. (1998) to monitor soil respiration fluxes. Closed dynamic chambers were used for sampling isotopes in soil respiration, as shown in **Figure 3**. First, atmospheric CO_2 initially inside the chamber cover was removed by circulating air at flow rates of ~.5 L min^{-1} from the chamber headspace through a column filled with soda lime. Scrubbing continued until the equivalent of two to three chamber volumes had been passed over the soda lime. Then the air flow was switched and flowed through a molecular sieve trap (mesh size13X). Molecular sieve 13X traps CO_2 quantitatively at room temperatures and then releases it when baked at 475 °C (Bauer et al. 1992). CO_2 was trapped from circulating chamber air until the amount required for isotopic (^{13}C and ^{14}C) measurements (~2 mg of C) was collected. Trapping times varied from about 10 minutes to an hour, depending on the soil CO_2 emission rate. To achieve 100% yields of CO_2 from the molecular sieve traps we have found that it is important to put a desiccant in-line (Drierite) in order to minimize the amount of water getting to the molecular sieve

To measure CO_2 and its ^{14}C signature in the soil atmosphere we collected soil gas samples from stainless steel tubes (3 mm OD) inserted horizontally into soil pit walls (the soils pits were subsequently backfilled). The air within the tubing was first purged by extracting a 15 ml syringe sample through a fitting with a septum. Two more 5 ml samples were then withdrawn from each tube, the syringes were closed with a stopcock, and the CO_2 concentrations of the syringe samples were analyzed the same day in a LiCor infrared gas analyzer as described by Davidson and Trumbore (1995). For the ^{14}C analysis, we filled evacuated stainless steel cans (0.5 - 2.0 L volume) by attaching them to the buried stainless steel tubes. A flow restrictor was used to fill the cans slowly during a 4 hour period so as to minimize disturbance of the concentration gradient. The soil gas tubes were installed along with TDR and temperature probes in one pit in 1995 (not dug quantitatively for bulk density) and in a second pit dug in 1996 (dug quantitatively as discussed above). All pits were located within a few meters of each other. The concentrations of CO_2, water content, and temperature were measured weekly during the summer, once every two weeks during the autumn and spring, and once per month during the winter.

Aboveground litter inputs were collected in six 0.41 by 0.41 m baskets. Each basket was screened at the base and nailed into the ground. Samples were collected, dried and weighed, once in the spring and then on a biweekly basis from late September through early November 1996.

Laboratory

Prior to C and ^{14}C analyses, soil samples were separated into different SOM fractions as defined for this paper (L_L, L_R, H and M) according to procedures outlined in **Figure 2**. For mineral samples, material that was less than 2.1 g/cc was primarily humified material (H). Fine roots (L_R) were a significant component of low density organic matter only in the A horizon samples. To test for the importance of L_R in determining bulk low density ^{14}C values, after density separation, one A horizon sample was sieved to 80µ and then hand picked to separate H from L_R components for ^{14}C analysis. The Ap, Bw1 and Bw2 horizons had such a small proportion of fine root material this additional processing was not performed. Once a soil C fraction was isolated, it was split and half the sample was archived while the other half was ground or finely chopped and analyzed for carbon and nitrogen content in a Fisons 5200 Elemental Analyzer. Grinding was done with an air cyclone sampler for the Oi horizon. Oe +Oa samples and root samples were chopped finely with scissors and mineral samples were ground by hand with a mortar and pestle.

In order to quantify fine root biomass, samples were taken by coring or from subsamples dug from our quantitative pits. Samples were frozen immediately after collection, then stored and processed at the Woods Hole Research Center. Oe +Oa horizons were thawed, a sub-sample removed (approximately 8 cm^3) and quantitatively picked for fine roots (<2mm in diameter). Mineral soils were thawed, sieved through a 5.6 mm sieve and the fine roots that did not pass through the sieve were weighed. In order to pick live versus dead fine roots, a sub-sample of the sieved soil was used (approximately 8 cm^3). Graphite targets of all SOM fractions and soil gas (CO_2) were prepared at UCI using sealed tube zinc reduction methods (Vogel et al. 1992). The ^{14}C analyses of these targets were made by accelerator mass spectrometry (AMS) at the Center for AMS, Lawrence Livermore Laboratory, Livermore, California (Southon et al. 1992). Radiocarbon data are expressed as $\Delta^{14}C$, the per mil deviation from the $^{14}C/^{12}C$ ratio of oxalic acid standard in 1950, with sample $^{14}C/^{12}C$ ratio corrected to a $\delta^{13}C$ value of –25‰ to account for any mass dependent isotopic fractionation effects (Stuiver and Polach 1977). The precision for radiocarbon analyses prepared using the zinc reduction technique in our laboratory is ± 7‰, for values close to modern (0‰).

We measured ^{13}C in a subset of our SOM samples to determine the proper ^{13}C correction for calculating $\Delta^{14}C$ values. Low density samples had $\delta^{13}C$ values which ranged between -24.78 and -27.57‰. Low density H fractions averaged 0.38‰ higher in ^{13}C than the M fractions (density >2.1 gC m^{-3}). Because the overall variation in $\delta^{13}C$ was greater than the difference between fractions, we used the same correction (-26‰) for all

SOM. The maximum error introduced to our ^{14}C determination by this assumption (5.1‰) is less than the analytical uncertainty of 7‰.

Measurements of ^{13}C for surface CO_2 flux samples were used to correct for mass dependent fractionation as well as to correct for incomplete stripping of atmospheric CO_2 in the chamber system during CO_2 trapping. The δ^{13}C value for CO_2 in air ($\delta^{13}C_{\text{atmosphere}}$) is ~ -8.5‰, whereas the δ^{13}C of soil respiration should be close to that of SOM ($\delta^{13}C_{\text{soil}}$ = -26‰). The fraction of air (X) in our sample is then:

$$X = \frac{\delta^{13}C_{measured} - \delta^{13}C_{soil}}{\delta^{13}C_{atmosphere} - \delta^{13}C_{soil}} \qquad \textit{Equation 1}$$

and we calculate the $\Delta^{14}C$ of the soil respiration:

$$\Delta^{14}C_{soil} = \frac{\Delta^{14}C_{measured} - X \times \Delta^{14}C_{atmosphere}}{(1 - X)} \qquad \textit{Equation 2}$$

The value of $\delta^{13}C_{atmosphere}$ at the level of the respiration collars (~5-10 cm) can become as light as ~ –11‰ due to atmospheric inversion which traps plant respired CO_2 and any fossil fuel derived CO_2 (particularly in winter) near the surface. Therefore, during each sampling event we trap one air sample and analyze this for δ^{13}C. The resulting δ^{13}C is then used for $\delta^{13}C_{atmosphere}$ in calculation of equations 1 and 2 for that suite of samples. Values of X ranged between 0.09 and 0.61. The highest values of X are associated with the samples taken in May, 1996, when no attempt was made to strip the initial chamber of atmospheric CO_2 (values in May were .61, .49, .40 and .34). For the July, September and December sampling events when 2-3 chamber volumes were stripped prior to sampling, values of X were all below 0.31 with an average of 0.17.

Modeling

Our methods for data analysis involve four modeling components: 1) determination of CO_2 production by horizon, 2) estimation of $\Delta^{14}C$ of CO_2 produced within each horizon, 3) calculation of the amount of CO_2 derived from decomposition of Reservoir-C sources and 4) partitioning of soil respiration into Recent- versus Reservoir-C sources based on a C and ^{14}C mass balance approach. Each modeling component is discussed in turn below.

1) CO_2 Production Within Each Horizon

The production of CO_2 within each horizon was calculated by combining estimates of diffusivity with measured CO_2 concentration gradients. Effective diffusivity was estimated for each soil horizon using the model of Millington and Quirk 1961, modified for the presence of rocks and for temperature:

$$\frac{D_S}{D_o} = a^{2x}\left(\frac{a}{\varepsilon}\right)^2 \times \frac{(100 - \%RF)}{100} \times \left(\frac{T}{273}\right)^{1.75} \qquad \text{Equation 3}$$

where D_s is the diffusion coefficient in soil, D_o is the diffusion coefficient of CO_2 in air (0.139 $cm^2\ s^{-1}$ at 273 °K at standard pressure), a is the total air-filled porosity, ε is the total porosity, %RF is the percent rock fraction, and T is the soil temperature (°K).

As described by Collin and Rasmuson 1988 and by Davidson and Trumbore 1995, the exponential term, *2x*, is usually close to 4/3, and can be approximated by the polynomial:

$$x = 0.477a^3 - 0.596a^2 + 0.437a + 0.564 \qquad \text{Equation 4}$$

The first term in the Millington and Quirk 1961 equation estimates diffusivity in the wet porous soil medium. The second term, which we have added here, adjusts for rock content of these glacial soils, assuming that diffusion of gases through rocks is negligible. The third term, adjusts for the effect of temperature on gaseous diffusion (Hendry et al., 1993). Total porosity is estimated as:

$$\varepsilon = 1 - \left(\frac{\mathrm{BD}}{\mathrm{PD}}\right) \qquad \text{Equation 5}$$

where BD is bulk density of the <2 mm soil fraction measured in our quantitatively sampled soil pits, and PD is a weighted average of particle density, assuming that organic matter has a PD of 1.4 g cm^{-3} and soil minerals have a PD of 2.65 g cm^{-3}. Air filled porosity (*a*) was calculated as the difference between total porosity and volumetric water content measured by time domain reflectometry (TDR) probes, as described by Davidson et al. (1998).

The soil CO_2 concentration profile was fitted to an exponential function (**Figure 4**):

$$[\mathrm{CO}_2]_z = \mathrm{CO}_{2\infty}(1 - e^{-\beta z}) + 0.04 \qquad \text{Equation 6}$$

where $[\mathrm{CO}_2]_z$ is the concentration of CO_2 at depth *z* in percent, $\mathrm{CO}_{2\infty}$ is the fitted asymptotic CO_2 concentration at infinite depth, *z* is soil depth in cm, β is a fitted parameter, and 0.04 is an adjustment for the approximate concentration of CO_2 at the soil surface (i.e., about 400 $\mu\mathrm{L}\ \mathrm{CO}_2\ \mathrm{L}^{-1}$ air). The first derivative of this equation is used to estimate the diffusion gradient as a function of depth:

$$\frac{\mathrm{dCO}_2}{\mathrm{dz}} = \mathrm{CO}_{2\infty} \times \beta \times e^{-\beta z} \qquad \text{Equation 7}$$

Applying Fick's first law and combining equations, the flux of CO_2 at a given depth (F_z) can be calculated from the product of the diffusion gradient and the effective diffusivity:

$$\begin{aligned} F_z &= \frac{\mathrm{dCO}_2}{\mathrm{dz}} \times D_s \times \frac{52700}{T} = \mathrm{CO}_{2\infty} \times \beta \times e^{-\beta z} \times a^{2x}\left(\frac{a}{\varepsilon}\right)^2 \\ &\times \frac{(100 - \%\mathrm{RF})}{100} \times \left(\frac{T}{273}\right)^{1.75} \times D_o \times \left(\frac{52700}{T}\right) \end{aligned} \qquad \text{Equation 8}$$

where F_z has units of gC $\mathrm{m}^{-2}\ \mathrm{hr}^{-1}$, and where 52700/T is the factor needed to convert to these units.

Using this equation, the flux at the top of each mineral soil horizon (see **Figure 4**) was calculated for each sampling date in each of the two instrumented soil pits. Our approach to calculating diffusivity differs from many others (e.g., de Jong and Schappert, 1972; Johnson et al. 1994; Mattson 1995), in which the flux was calculated from an assumed linear diffusion gradient between two points where CO_2 concentrations were measured. The exponential fit used here for characterizing the CO_2 profiles (**Figure 4**), while imperfect, appears more appropriate.

Finally, estimation of the production of CO_2 within each genetic horizon (P_h) was calculated from the difference between the flux at the top and bottom of a given soil horizon such that:

$$P_h = F_{h\text{-out}} - F_{h\text{-in}} \qquad \text{Equation 9}$$

where $F_{h\text{-out}}$ and $F_{h\text{-In}}$ correspond to the appropriate F_z (**Figure 4**). Production within the O horizon was estimated by the difference between the mean of the six surface chamber flux measurements and the calculated flux at the top of the A horizon. This approach avoids the difficult problem of estimating diffusivity in the O horizons, where small differences in measured bulk density and water content (both of which are difficult to measure well) would have a large effect on our estimate, and where diffusion may not always be the dominant mechanism of gas transport.

2) $\Delta^{14}C$ of CO_2 Produced Within Each Horizon

The total CO_2 and $^{14}CO_2$ flux leaving a soil horizon results from a mixture of the CO_2 that is diffusing through that horizon and that which is produced within the horizon. Therefore, based on horizon specific estimates of CO_2 production (P_h) and measurements of the ^{14}C in CO_2 coming into ($\Delta F_{h\text{-in}}$) and going out ($\Delta F_{h\text{-out}}$) of a subset of the soil horizons (in this notation, Δ refers to ^{14}C of F in ‰ units, and not "change in F"), we can use a simple mixing equation to calculate the ^{14}C of CO_2 produced within that horizon

(ΔP_h) from both Recent- and Reservoir-C sources. The equations used to calculate ΔP_h (in ‰ units) from CO_2 production rates and fluxes (in gC m^{-2} yr^{-1}) are Equation 9 and:

$$(F_{h\text{-}in} + P_h) \times \Delta F_{h\text{-}out} = F_{h\text{-}in} \times \Delta F_{h\text{-}in} + P_h \times \Delta P_h \qquad \text{Equation 10}$$

In this approach chamber measurements of ^{14}C in CO_2 from the surface efflux serve as $\Delta F_{h\text{-}out}$ for the O horizon and are used to calculate ΔP_h for the entire O horizon. We lumped O, A and Ap horizons (representing the top ~15 cm) because of the large variability in the $^{14}CO_2$ data available for constraining the O/A and A/Ap transitions.

3) Decomposition of Reservoir-C

We calculate decomposition of Reservoir-C fluxes by first calculating turnover times for each SOM component using its ^{14}C signature and then calculating a decomposition flux based on that turnover time.

3.1) SOM Turnover Times from ^{14}C

We used two approaches to determine turnover times for SOM fractions from radiocarbon measurements. For organic matter in the Oi and mineral horizons (Ap and B), we used a time-dependent, steady state model as presented in Trumbore et al. (1995):

$$C_{(t)} \times R_{som(t)} = I \times R_{atm(t)} + C_{(t-1)} \times R_{som(t-1)} - k \times C_{(t-1)} \times R_{som(t-1)} - \lambda \times C_{(t-1)} \times R_{som(t-1)}$$

Eq. 11

Collecting terms:

$$R_{som(t)} = \frac{I \times R_{atm(t)} + \left(C_{(t-1)} \times R_{som(t-1)} \times (1 - k - \lambda)\right)}{C_{(t)}} \qquad \text{Equation 12}$$

where:

C = Stock of carbon for the given C pool in gC m^{-2} I = Inputs of C above and below ground in gC m^{-2} yr^{-1}

k = Decomposition rate of SOM in yr^{-1}

$$R = \left(\frac{\Delta^{14}C}{1000}\right) - 1$$

R_{atm} = The ratio of ^{14}C in the atmosphere normalized to a standard.

R_{som} = The ratio of ^{14}C in the given SOM pool: L, H or M, normalized to a standard.

λ = radioactive decay constant for ^{14}C = 1/8267 years.

t = time (year) for which calculation is being performed

I and k are adjusted to match both observed C inventory and ^{14}C content for the fraction in 1996. Note that the R_{som} at any time t, depends not only on the $R_{atm(t)}$ but on both C inventory and R_{atm} of previous years.

For the Oe+Oa and A horizons that have accumulated above the plow layer since abandonment between 1860 and 1880, we used a non-steady state model that matches both the total amount of C and ^{14}C in 1996. We assumed zero initial C in 1880. Assuming constant I and k, the amount of carbon initially added in each year j (since 1880) that remains and can be measured in 1996 (C_j) will be:

$$C_j = I \times e^{-k(1996-j)} \qquad \text{Equation 13}$$

The ^{14}C signature of C_j will be $R_{atm(j)}$. Therefore the total amount of carbon and radiocarbon measured in 1996 is shown by equations 14 and 15 respectively:

$$C_{1996} = \sum_{j=1880}^{j=1996} C_j \qquad \text{Equation 14}$$

$$R_{som(1996)} = \frac{\sum_{j=1880}^{j=1996} R_{atm(j)} \times C_j}{\sum_{j=1880}^{j=1996} C_j} \qquad \text{Equation 15}$$

Again, I and k were adjusted until they matched observations of C and ^{14}C for each fraction in Oe+Oa and A horizons. The rate of accumulation of carbon for a given fraction in 1996 is the difference in C inventory calculated for 1995 and 1996.

Both steady state and non-steady state accumulation models assume (1) all carbon within a given SOM fraction (L_L, L_R, H, or M) is homogenous with respect to decomposition; (2) the time lag between photosynthetic fixation and addition of fixed C to SOM is one year or less (i.e. the Δ^{14}C of C added to each SOM fraction each year is equal to $R_{atm(j)}$) and (3) radiocarbon does not fractionate during respiration. We have already corrected for mass-dependent fractionation effects when calculating Δ^{14}C values. Any time lag that does exist between photosynthetic fixation and addition of fixed C to SOM (contrary to assumption 2) will cause an overestimation of turnover time (TT) equal to this lag (Thompson and Randerson, 1999). Assumption 2 holds for the majority of aboveground litter inputs (deciduous leaves) which are fixed and fall to the ground within one year. Effects of this assumption with respect to other SOM inputs will be discussed later in the text. **Figure 5** shows the Δ^{14}C of a SOM fraction as a function of turnover times in 1996 for both the steady-state and non-steady state models. Significant differences between approaches appear only for fractions with turnover times greater than about 25 years. This is because the assumption of zero initial carbon in 1880 in the accumulation model limits the amount of pre-bomb ^{14}C in the SOM that is available to dilute the post-bomb carbon that has accumulated since 1963.

3.2) Calculating SOM decomposition fluxes

Decomposition fluxes for the L_L, H and M components of SOM are determined as the inventory in each fraction divided by the turnover time derived from ^{14}C. Since the turnover times for fine roots are too uncertain (as will be discussed in the results section), we treat the flux from L_R as an unknown and solve for it in the C and ^{14}C mass balance section.

The turnover times derived from ^{14}C data may represent the time scales for C loss via several mechanisms, including (1) decomposition loss of CO_2 to the atmosphere; (2) C transfer to another SOM fraction (for example litter to humified material i.e., L_L or L_R to H or M); or (3) loss by leaching. Data for dissolved organic carbon (DOC) transport from similar stands in Harvard Forest are available from Currie et al. 1996, and show leaching losses to be minor compared to the other fluxes, except in the O horizon where DOC loss is approximately 20 gC m^{-2} yr^{-1}. This loss is only a few percent of the total annual CO_2 flux, hence we have excluded it from consideration here. Consequently, we assume all loss to be from decomposition or transfer from one C fraction to another.

We model the litter components L_L and L_R as having two fates: decomposition to CO_2 or transfer to the H or M fractions. For the H and M fractions we assume that their source of C is transfer from L_L and L_R fractions and that their most important loss process is decomposition to CO_2. The flux of CO_2 derived from decomposition of leaf litter (F_{LL}) is the inventory of leaf C divided by its turnover time, corrected for the fraction of L_L that is transferred to the H+M pools. Since we cannot independently partition the flux of L_L into either CO_2 or a transfer flux, we bracket our estimates by assuming two extreme cases in which all of the H+M inputs come from either (1) L_L or (2) L_R.

Partitioning of Soil Respiration Sources

The total amount of radiocarbon in soil respiration equals the amount of CO_2 derived from Recent-C sources (root respiration and C metabolized within one year of original fixation; R), plus that derived from Reservoir-C (decomposition of L_L, L_R, H and M fractions that reside in the soil for longer than one year). If the $\Delta^{14}C$ signatures of these components differ significantly, we may use a mass balance approach to determine the relative contribution of each to total soil respiration. We use an isotopic mass balance based on estimates of CO_2 production, the $\Delta^{14}C$ in CO_2 and ^{14}C-derived estimates of decomposition fluxes from the SOM fractions. For the whole soil profile, equations of mass balance for C and ^{14}C are:

$$P = F_R + F_{LL} + F_{LR} + F_H + F_M \qquad \text{Equation 16}$$

and

$$P \times \Delta P = F_R \times \Delta R_{atm(1996)} + F_{LL} \times \Delta L_L + F_{LR} \times \Delta L_R + F_H \times \Delta H + F_M \times \Delta M$$

Eq. 17

In equations 16 and 17, P is the total annual soil respiration flux and F_R is the flux of CO_2 derived from Recent-C. F_{LL}, F_{LR}, F_H and F_M are fluxes of CO_2 derived from their respective Reservoir-C sources. The Δ values required for the ^{14}C mass balance are either measured (for ΔL_L, L_R, ΔH and ΔM), assumed to equal $\Delta R_{atm\ (1996)}$ (for Recent-C), or calculated from CO_2 and $^{14}CO_2$ fluxes (ΔP). For the soil profile as a whole, P and ΔP are the measured surface flux and its $\Delta^{14}CO_2$ signature respectively.

We then solved equations 16 and 17 for the remaining unknowns, F_R and F_{LR}. Since C stocks and rates of C turnover vary vertically within the soil profile, the relative proportions of CO_2 from F_R versus the SOM fractions will vary with soil depth and horizon. Equations 16 and 17 may also be written and solved for each individual soil horizon. However, because of difficulties in characterization of the O/A horizon transition, and uncertainties in the production of roots as a function of depth, we have combined the O+A+Ap horizons and performed the ^{14}C mass balance on only three layers: the O+A+Ap (uppermost 15cm of soil), B and C horizons.

Results

Carbon Inventory

Average carbon stocks are shown in **Table 1** by pedogenic horizon. Carbon stocks decrease rapidly with depth at all sites, from 450 gC Kg^{-1} dry soil in the O horizons to less than 10 gC Kg^{-1} dry soil for the Bw2 horizon. We report carbon inventories only to the bottom of the Bw2 horizon because the presence of large boulders limited our ability to measure bulk densities below this depth. The total C stock averages 8.8 kgC m^{-2}, with the majority of C (80%) in the upper 15 cm, which make up the organic and A + Ap horizons. Measured litterfall inputs to the O horizon were 150 gC m^{-2} yr^{-1} in 1996.

The fraction of soil volume taken up by rocks is spatially variable. In two of the three pits the O and A horizons were much less rocky (0-2% rocks) than the B horizons (10-35% rocks). However one of our three pits had no less than 15% rocks in all horizons down to 60 cm. Spatial heterogeneity in soil C stocks has been studied in rocky forest soils similar to those found at Harvard Forest. Fernandez et al. 1993 show that between 73 and 455 samples are required to quantify C stocks to within 10% depending on soil depth. Huntington et al. 1988 were able to quantify C stocks to within 20% only after digging 60 .74 X .74 m pits. Therefore in this study instead of quantifying variability within a site we focus on the C dynamics for specific profiles and assume C dynamics will be the same even if the inventory of a given SOM fraction varies spatially for sites with similar drainage.

The four rightmost columns of **Table 1** show the inventory of the isolated soil C fractions L_L or L_R, H and M. Carbon in low density fractions decreases rapidly with soil depth, from 100% in O horizons to <1% in B horizons. Low density carbon (L_L + L_R + H) makes up 54% of the total soil carbon stock, but is 87% of the carbon in O + A horizons.

Quantitative picking of roots showed they make up 7-19% (n = 5) and 1-4% (n = 5) of the dry mass in the Oe +Oa and A horizons, respectively. Assuming roots are 50% C by weight, the fraction of carbon in live and dead roots make up ~14% of the total C stocks in the Oe +Oa horizon, decreasing to ~0.2 % in the Bw2 horizon. Our estimate of total fine root mass of 360 gC m^{-2} (live + dead) is lower than that of McClaugherty et al. 1982, who found 525 gC m^{-2} (live + dead) in well-drained mixed hardwood soils at a neighboring study area within the Harvard Forest. Fahey and Hughes 1994, found ~320 and 350 gC m^{-2} (live+dead) in June and October respectively in a mature northern hardwood forest. Our values also decrease more rapidly with depth than those of McClaugherty et al. 1982 who found 70, 55, and 15 g C m^{-2} for 15-30, 30-45 and > 45 cm respectively for live + dead fine roots. In addition, our ratio of live:dead fine roots (data not shown) at all depths are significantly greater than those reported by McClaugherty et al. 1982, suggesting either differences in procedures for distinguishing live from dead roots or that we sampled during a seasonal maximum in live root abundance. Technically, it is the dead roots, not the live roots, that are decomposing and contributing to CO_2 fluxes. Therefore, live roots should not be considered part of the SOM. However, because we were not able to reliably distinguish live from dead with confidence, we report them together as L_R.

CO_2 production estimates

Total soil respiration as determined from chamber measurements in 1996 was 840 gC m^{-2} yr^{-1} (Davidson and Savage, unpublished data)). Production rates for CO_2 (**Figure 4**) by soil horizon were 190, 340, 235 and 75 gC m^{-2} yr^{-1} for the O, A+Ap, B and C horizons respectively. The estimates of CO_2 production within each soil horizon include uncertainties associated with the diffusion model, the exponential fit of the CO_2 concentration profiles, and, in particular, measures of rock content. We used the average rock content of two quantitatively sampled soil pits dug in 1996. One had almost no rocks in the O and A horizons while the other had 20-30% coarse fragments. Repeating the calculations assuming either no rocks or the higher estimate of rock content, changed CO_2 production rates for the A horizons by roughly 50 gC m^{-2} yr^{-1}.

Radiocarbon in SOM fractions

The average radiocarbon content and the range of values measured in the isolated SOM fractions are plotted by horizon in **Figure 6**. Δ^{14}C values for the low density SOM (L_L or H) fractions increase from the Oi horizon (L_L) where values are 132 ± 8‰ to a maximum in the Oe +Oa horizon (H) of 200 ± 19‰. Humified material in the A horizon is 121‰, and its ^{14}C signature decreases rapidly in the Ap and B horizons. Within all mineral horizons, the low density carbon, which is primarily humus (H), has consistently higher Δ^{14}C values than mineral-associated (M) carbon, with the largest difference (55‰) in the Ap horizon. Large negative Δ^{14}C values in both H and M fractions in the Bw1 and Bw2 horizons indicate the majority of soil carbon at these depths has not exchanged with the atmosphere since 1950 and has, in fact, remained in the soil long enough for significant radioactive decay to occur (half life = 5730 years).

The Δ^{14}C content of live and dead fine roots by horizon are also shown in **Figure 6**. All roots have Δ^{14}C values between 134 and 238‰, significantly higher than the atmosphere or live deciduous leaves sampled during 1996 (97±7‰). Live roots on average have lower Δ^{14}C values than dead roots, and Δ^{14}C values for both increase with soil depth. The Δ^{14}C values we measure for live fine roots are surprisingly high, as fine roots in this size class (< 2 mm diameter) are thought to have annual or faster turnover based on studies that calculate turnover from the ratio of fine root biomass to production (see review by Vogt et al. 1986) and on direct measurements from rhizotrons, minirhizotrons or root screens (Burke and Dudley 1994, Hendrick and Pregitzer 1992, Hendrick and Pregitzer 1993 and Fahey and Hughes 1994). There are three possible interpretations to explain our data. First, the bulk of the fine root mass may live for significantly longer than one year. Second, carbon in roots may be allocated from elsewhere in the plant, i.e., the roots may live for only a short time, but the carbon from which its tissues are constructed was fixed some time ago and was translocated from storage reservoirs when the root grew. Third, roots may take up SOM (Simard et al. 1997) either directly or via mycorrhizal associations, and incorporate it into their tissues. It is possible our root picking procedure may have mistaken dead roots for live ones, which could potentially be the cause of the elevated ^{14}C in live roots. To address this, we sampled one obviously living fine root in 1997. The main stem (1mm in diameter) had Δ^{14}C of 134‰ while a smaller growth off that stem had Δ^{14}C of 116‰. While these values are lower than the 1996 root numbers they are still significantly higher than the atmosphere in 1997 (92±7‰), confirming that at least this one live root contained relatively “old” carbon. This one root may not be representative of all species and growth forms, which were averaged during the 1996 quantitative root picking.

The 1997 root data show that different parts of the same root have C that differs in age by 2 years. Thus if longer turnover is the explanation for elevated ^{14}C, fine roots even 1 mm in diameter and less may not be acting as a single pool with one TT. The data would then imply that the tips (a small part of the mass) may turn over significantly faster than the rest of the root (the bulk of the mass). In a manner analogous to SOM stocks, the most recalcitrant root biomass pool is the largest fraction of the total root biomass pool and is the portion most easily separated from a soil sample for analyses.

Presently, we do not know which of the three above hypotheses for explaining high Δ^{14}C values in root biomass is correct, and additional research is being conducted to address this important issue. We can however, proceed with our mass balance approach without calculating any turnover times for fine roots based on their Δ^{14}C values. We instead solve for F_{LR} as one of the unknowns. However, even without an understanding of the mechanism, our Δ^{14}C data show that live fine roots, upon their death, are adding carbon to SOM that averaged roughly 165‰ in 1996 and that must have been fixed on average 7±1 years previously.

Figure 7 shows the distribution of C and ^{14}C among the different low density components in O and A horizons. In the O horizon (**Figure 7a**), deciduous leaf parts had Δ^{14}C values that increased with depth, from 113‰ in the Oi to 132‰ in the Oe +Oa, where leaves became difficult to recognize. Radiocarbon in fine roots, which represent 14% of O horizon C (**Table 1**), ranged from 153‰ (live roots) to 188‰ (dead roots). The remaining, undifferentiable, material (H) had a Δ^{14}C value of 201±19‰ (n =2). Visual inspection shows H, which contained 63% of C in the O horizon sample, consisted of extremely fine root fragments (< 0.5 mm), and dark, humified material that could not be identified.

Figure 7b shows the distribution of C and Δ^{14}C for the A horizon low density fraction, which was sieved to 80μ and hand picked to remove roots. The measured components range in value from 48‰ to 266‰. The >80μ material makes up 82% of this low density sample and has a Δ^{14}C of 130‰. Roots (live + dead) are 7% of the carbon with a weighted average Δ^{14}C of 256‰ (n=2). The <80μ fraction had the lowest measured ^{14}C value (48‰). The inventory-weighted average Δ^{14}C for all four components was 132‰. To calculate a flux for the H component alone, we take a stock weighted ^{14}C for the two components greater and less than 80μ (**Figure 7b**) which equals 121‰ (.82*130‰ + .09*48‰)/0.91.

Radiocarbon in the 1996 atmosphere at Harvard Forest

Partitioning of soil respiration using isotopic mass balance requires that we know the $\Delta^{14}C$ of CO_2 for the atmosphere in 1996 (variable $\Delta R_{atm(1996)}$ in Equation 17). For 1996, this value was obtained from two measurements of air within the Prospect Hill Tract on July 11, 1996, and one measurement of a live deciduous leaf collected on the same date. The three values are 98±7, 96±6 and 97±7‰, averaging 97 ±1 ‰. We assume the C lost within a year of being fixed by photosynthesis, including root respiration and decomposition of labile SOM, will have this value in 1996. We support this asssumption with two lines of evidence. First, Horwath et al. 1994 performed a whole tree labeling study on two year old, three meter tall tulip poplar trees. They found that respiration of labeled C from the roots occurred within 12 hours of labeling, the peak activity in respiration was measured after two days and within two weeks the activity of root respiration was less than 5% of the maximum value. Second, three fruiting bodies of the genus *Boletus*, a mycorrhizal fungal symbiont, collected in 1996 at Harvard Forest had $\Delta^{14}C$ of 97, 99 and 98‰. The fact that their $\Delta^{14}C$ signature is the same as the 1996 atmosphere, indicates they are living off of Recent-C substrates, namely root exudates, and not the relatively ^{14}C enriched Reservoir-C of the O horizon in which they are rooted. Since root exudates are Recent-C it follows that maintenance metabolism by trees in this ecosystem must also be respiring Recent-C.

Radiocarbon in soil CO_2

Figure 8A&B shows CO_2 fluxes and measured $\Delta^{14}C$ in CO_2 of the surface flux for four sampling periods in 1996. The CO_2 fluxes shown in **Figure 8A** range between 40 and 200 mgC m^{-2} hr^{-1}. The largest values measured were in the early summer and the lowest in the winter (see Davidson et al., 1998 for more complete seasonal CO_2 flux data). All flux measurements were made within 1-2 days of ^{14}C sampling, except for the late September sampling event when fluxes were measured 8 days previously. Measured $\Delta^{14}C$ in CO_2 values for 1996 in **Figure 8B** range from 103-176‰ and are all higher than the atmospheric $\Delta^{14}CO_2$ for 1996 (97±1‰). Hence, decomposition of organic matter in the L_L, L_R and H fractions, primarily in the O and A horizons, and which have $\Delta^{14}C$ values greater than 100‰, must contribute significantly to the total soil CO_2 flux. In 1996, the highest $\Delta^{14}C$ values in soil respiration were observed in the spring and summer with values of 138 and 149‰ respectively. The lowest values were in fall and winter where $\Delta^{14}C$ drops to 111 to 121‰ respectively. The data from **Figure 8A&B** were used to calculate an annual flux weighted mean $\Delta^{14}C$ in soil respiration for 1996 of 128±9‰ (n = 11).

The concentration-weighted annual average $\Delta^{14}C$ in CO_2 for soil air (by depth) is shown in **Figure 6** and **Table 2**. $\Delta^{14}C$ values range from 128 to 136‰, all significantly greater than the 1996 atmosphere (97±1‰). Temporal variability in measured $\Delta^{14}C$ values are greatest at 10 cm (the A horizon) where the values used for averaging ranged from 113 to 161‰. At all other depths the annual variation was 20‰ or less. The fact that the $\Delta^{14}C$ in CO_2 is greater than either atmospheric CO_2 or H and M carbon in the mineral

Ap and B horizons shows decomposition fluxes must be dominated by root litter (F_{LR}) which has much higher $\Delta^{14}C$ values.

Fluxes and Turnover time of C in SOM fractions

Table 2 shows the turnover times for SOM fractions as derived from their radiocarbon content and the functions shown in **Figure 5**. Modern $\Delta^{14}C$ values (>100‰) have two possible turnover times for each $\Delta^{14}C$ value. For example, the $\Delta^{14}C$ of H in the Oe +Oa horizon is 201‰ which corresponds to turnover times of either 9 or 40 years (**Figure 5**, non-steady state model). Based on the requirements for total CO_2 and $^{14}CO_2$ production in each horizon, we chose the longer turnover time for the H fraction in this and other horizons. We did not calculate turnover times for root litter (L_R) because of the potential for a significant lag time to affect the $\Delta^{14}C$ values measured in 1996. The time lag would also affect the TT for undifferentiable (H) material that is derived from both leaf litter and fine roots. In each case, failure to correct for any lag will cause overestimation of turnover times by as much as the inferred ^{14}C-derived lifetime of live roots (7±1years). Failure to account for time lags if roots are the principal source for more recalcitrant organic matter would result in turnover times for H and M fractions that are ~7 years too long.

The flux of CO_2 derived from decomposition of L_L, H and M fractions is calculated in **Table 2** from the C inventory and turnover time. Again, no flux is calculated for fine root decomposition (F_{LR}); instead we use the CO_2 and $^{14}CO_2$ mass balance to calculate this below.

Partitioning of soil respiration

Equations 16 and 17 contain three unknowns: F_{LL}, F_{LR} and F_R. We therefore introduce an additional constraint so that we may solve for all three fluxes. As we have defined them, L_L and L_R pools represent the detrital root and leaf material that take longer than one year to decompose and are identifiable in SOM. From the inventory of detrital leaf litter (L_L; 380 gC m^{-2}) measured in the soil, and its turnover time (4 years; **Table 2**), we calculate the annual flux of C into the L_L pool as 95 gC m^{-2} yr^{-1}. The fate of leaf detritus is either to decompose directly to CO_2 (this is the flux F_{LL}) or to be incorporated into soil humus and mineral pools (H+M). We do not know this partitioning; however, based on C and ^{14}C inventory and our non-steady state model, we assume the the annual rate of input to the H+M pools equals the decomposition flux from these pools(~70 gC m^{-2} yr^{-1}, see **Table 2**). We then consider the two extreme cases, where all humus and mineral C is derived from leaf detritus, or all of it is derived from root detritus. F_{LL} is thus constrained to be between 25 and 95 gC m^{-2} yr^{-1}. In **Table 3**, we use these minimum and maximum values for F_{LL} and solve for the two remaining fluxes, F_{LR} and F_R. **Table 3** also shows cases for using the minimum and maximum values for observed $\Delta^{14}C$ of detrital leaf (113 and 132‰) and root (180 and 214‰) pools. The ranges and means of this approach are shown in **Figure 9**.

Our results from partitioning soil respiration for the entire soil profile using CO_2 and $^{14}CO_2$ mass balance are summarized in **Table 3** and **Figure 9**. Approximately 41% (34%-51%*)* of CO_2 produced annually is derived from decomposition of low density SOM with TT greater than one year (L_L, $L_{R,}$ H and M, i.e.Reservoir-C). The decomposition of H and M fractions with turnover times >40 years contributes only 8%

of the total annual respiration flux, with the remaining 33% (26%-43%) from root and leaf litter decomposition (with plant+soil residence times of 2 to 10 years). The fluxes into and out of the H+M pools are constrained by their ^{14}C-derived TT and reservoir size (**Table 2**) and represents an average over decadal time scales. The average flux of 70 gC m^{-2} yr^{-1} shown in **Figure 9** implies the H+M pool to be in steady state. The uncertainty of 40-70 gC m^{-2} yr^{-1} is an estimate based on accumulation rates discussed in the following section.

Note that the flux of C into and out of the L_L pool is less than the total annual measured leaf litterfall (150 gC m^{-2} yr^{-1}; **Figure 9**). We infer that 55 gC m-2 yr-1 (1/3rd) of the freshly deposited litter is decomposed in < 1year (and hence is not detected from leaf detritus collected the following summer). Similarly, comparing the range of fluxes of C out of the L_R pool (170- 270 gC m^{-2} yr^{-1}, which is equal to F_{LR} + the flux of root C transformed to humus) with annual root production estimates by McClaugherty et al. 1982 of 270 gC m^{-2} yr^{-1} indicates that 0-100 gC m^{-2} yr^{-1} of root litter is decomposed in less than one year.

Depth-dependence

Figure 4 and **Table 4** show that 310 gC m^{-2} yr^{-1} or 37% of the total annual soil respiration is produced below 15 cm within the B and C horizons. Comparison of isotopic data for the SOM fractions in these horizons in **Figure 6** and **Table 2** clearly demonstrates that the two main sources must be root decomposition and Recent-C, because the decomposition of H+M reservoirs accounts for <2 gC m^{-2} yr^{-1} (with $F_{LL} = 0$). Application of C and ^{14}C mass balance to the B and C horizons shows that 39% and 37%

respectively, of the respiration comes from Reservoir-C (**Table 4**) and that essentially all of this flux is decomposition of roots with high $\Delta^{14}C$ values relative to the atmosphere. In the upper 15 cm of the soil profile (O+A+Ap) we estimate that 44% is Reservoir-C, with 32% from the decay of leaves and roots with TT of 2-10 years, and 12% from H and M fractions with TT >40 years. More frequent measurements of ^{14}C in total soil respiration and within the vertical profile will allow for more detailed calculation of depth dependence of the make-up of soil respiration. Our measurement of root biomass in the B horizon (**Table 1**) is insufficient to support the approximately 90 gC m^{-2} yr^{-1} of decomposition required by the mass balance approach, if fine root mass is homogenous with respect to turnover.

Discussion

Rate of Carbon Accumulation in SOM

The O and A horizons have accumulated 4.4 kgC m^{-2} above the plow layer (Ap horizon) since the late-1800s. This is roughly half the carbon in the soil profile. Carbon pools with turnover times that are less than several decades (leaf and root litter), which make up 15% of the soil carbon in these horizons, must have achieved steady state with vegetation inputs by 1996. Most of the C in the O and A horizons, however, is in the form of altered, humified (H) material not associated with minerals. The rate of turnover of these fractions is slow enough (40 to 100+ years) that the annual C inputs (I in Eqs. 11-13) required to support the inventory and ^{14}C observed in 1996 are small (20-50 gC m^{-2}

yr^{-1} in the Oe + Oa and 10-30 gC m^{-2} yr^{-1} in the A horizon. The rate of C accumulation in 1996 estimated using our accumulation model is 2-7 gC m^{-2} yr^{1} for the Oe +Oa and 8-23 gC m^{-2} yr^{-1} for the A horizon. The ranges reported bracket the values obtained for different model runs representing mean, low and high values (i.e. ± 1 standard deviation) of both C stocks (**Table 1**) and their ^{14}C values (**Table 2**). Also included in the range are runs done using the specific C inventories and $\Delta^{14}C$ values for each of the two pits (data not shown). Variability in rock content between the two pits affected the overall C stock calculated for each pit and thus the pit with the most rocks had the smallest rates of C accumulation.

While these rates are large compared to storage rates in soils over longer timescales (e.g. Schlesinger, 1990; Harden et al., 1992), they are less than the annual net C uptake measured for this ecosystem of ~200 gC m^{-2} yr^{-1} (Goulden et al. 1996). Overall C accumulation rates by the well drained soils which dominate the area within the tower footprint account for 5-15% of this net ecosystem uptake. The predominant wind directions at the tower site are southwesterly and northwesterly. A small area of poorly drained soils close to the tower to the southwest and a swamp 500m from the tower to the northwest could be larger sinks per unit area than are the well drained soils.

We have assumed the leaf and root litter pools, which have TTs <10 years, are at steady state. However, if net primary productivity has been increasing as a result of CO_2 or N fertilization, then leaf and root litter pools may be sequestering C. As discussed earlier, annual inputs to L_L and L_R pools are 150 and 270 gC m^{-2} yr^{-1} (see **Figure 9**). Assuming a 1% per year increase in NPP between 1991 and 1996 and correcting for the inputs respired during the same year then the L_L and L_R pools could also be storing a combined ~20 g C m^{-2} yr^{-1} ((270 –15) +(150-55)) gC m^{-2} yr^{-1} *.01 yr^{-1} *5 yr) through this period. Combined with the accumulation in the humic fractions of the O and A horizons this could account for as much as 25% of the net ecosystem uptake.

Partitioning of Soil Respiration

We estimate from our radiocarbon studies that 59% of the soil respiration was derived from C that resided in the plant+soil system for less than one year. Using trenched plots to exclude roots, Bowden et al. (1993) estimate that root respiration (plus decomposition of roots killed during trenching) was 33% of the total soil respiration at a nearby study site at the Harvard Forest. Using litterfall exclusion and addition manipulations, these authors estimate that 11% of the total soil respiration was from above-ground litterfall less than one year old. Hence, Bowden et al. (1993) estimated a total of 44% of the respiration was derived from C with a residence time in the *soil* system of less than one year. Both radiocarbon measurements and root and litter manipulations have uncertainties, and the best interpretation is probably that these two very different approaches yield estimates that about 50% ± 10% of the soil respiration is derived from C that is less than one year old. Bowden et al. (1993) also estimate that 30% of soil respiration was from root litter that had resided in the soil more than one year, which is consistent with our radiocarbon data that show somewhat surprisingly long mean residence times for live and dead roots.

Time Lags in the Soil C Reservoir – potential for interannual variability

The measured $\Delta^{14}C$ of total soil respiration is 128±9‰ for 1996 which corresponds to a mean residence time for C in the plant+soil system of 4±1 years. This represents the time an average C atom spends in the plant+soil system since original photosynthetic fixation and includes both root respiration and all decomposition sources. We also calculate the average value for $\Delta^{14}C$ of heterotrophic respiration is 167‰ which corresponds to an average age of 8±1 years. Thus a significant time lag exists between initial C fixation and ultimate respiration by heterotrophs. Therefore, variations in C storage or loss in any one year must partially reflect the net ecosystem uptake of previous years. (Schimel et al. 1997, Fung et al. 1997).

The age of C respired from soil can be used to predict the ^{13}C isotope disequilibrium for Harvard Forest. The ^{13}C isotope disequilibrium is the difference between the ^{13}C signature of atmospheric CO_2 being fixed by plants and the ^{13}C respired from soils. A difference is expected because the ^{13}C in the atmosphere has been decreasing with time due to the addition of ^{13}C-depleted fossil fuels to the atmosphere (e.g. Ciais et al. 1995, Fung et al. 1997). Using the $\delta^{13}C$ trend of –0.02‰ per year (Fung et al. 1997), and an average age of 8±1 years for heterotrophic respiration, we estimate the ^{13}C isotope disequilibrium at the Harvard Forest to be -0.16±.02‰. This is less than that predicted using the CASA model for temperate deciduous forests (Thompson and Randerson, 1999, Fung et al. 1997), largely due to the influence of woody debris in the CASA model. Woody debris is relatively small at the Harvard Forest floor, because of clearing of downed wood following the 1938 hurricane. However, Johnson and Todd (1998) note that woody debris does not seem to be an important source of humified SOM in a deciduous forest at Oak Ridge, TN. Further work should place more emphasis on measuring radiocarbon in CO_2 respired from decomposing logs to asses the importance of this component to total soil respiration.

Heterogeneity issues

Comparison of the bulk SOM $\Delta^{14}C$ with the $\Delta^{14}C$ in CO_2 at depth (**Figure 6**) clearly demonstrates that the $\Delta^{14}C$ signature of the SOM alone is not enough to estimate C dynamics. Even with density separations into low and high density pools, $\Delta^{14}C$ of SOM is usually biased toward recalcitrant C stocks. This is particularly true in the mineral horizons where the vast majority of C stocks are hundreds of years old and have large negative $\Delta^{14}C$ values. The small pools of fast cycling SOM (fine roots) with significant amounts of ‘bomb C’ are effectively diluted beyond isotopic recognition. Our technique of respiration partitioning, which accounts for decomposition via $^{14}CO_2$ measurements, is particularly robust in the mineral horizons where the respiration sources are so isotopically different and have less spatial and temporal heterogeneity.

Methods of estimating bulk soil turnover rates by taking soil C stock divided by CO_2 flux also do not account for soil profile heterogeneity. Particularly in temperate forest soils with significant O and A horizon carbon stocks, this approach will yield poor estimates of the response time of soils to climate change scenarios. **Figure 10** shows differences in soil C increase in response to a 10% increase in C inputs for a one-pool model with a turnover time of 25 years versus a multi-pool model representing the well drained soil at Harvard Forest. The one pool model overestimates the amount of C sequestered both in the short and long term. After 100 years, the one-pool model over predicts C storage by almost 600 gC m^{-2}.

Similarly, bulk SOM radiocarbon measurements may also cause an overestimation of decadal scale SOM response. For example, had we not partitioned the low-density carbon in the A horizon into different components (fine roots, undifferentiable material >80μ and < 80μ), the bulk ^{14}C value would have been 132‰ with a TT of 66 years. Instead, **Figure 7B** shows the sample to be composed of components with ^{14}C-derived TTs ranging from ~8 to >100 years. Analogous to taking an average TT for the whole soil, the response of SOM would be overestimated if the $\Delta^{14}C$ signatures of the low-density C sample components were represented using the bulk radiocarbon value (see **Figure 10**).

The turnover times we derive from modeling the ^{14}C content of SOM fractions are averages over several years to decades. Actual decomposition rates in any given year may deviate from these averages. For example soil respiration measured in Harvard Forest well-drained soils in 1997 (a dry year relative to 1996) was 660 gC m^{-2} yr^{-1} (Davidson and Savage, unpublished data), compared to 840 gC m^{-2} yr^{-1} for 1996. Monitoring of soil respiration isotopic composition should shed light on whether the reduction in soil respiration in future years is caused by changes in decomposition, changes in root respiration, or both. The power of coupling this approach to measuring soil profiles of CO_2 and $^{14}CO_2$ will allow determination of where in the soil profile changes occur in response to climate.

Conclusions

- SOM pools are accumulating C in well-drained Harvard Forest soils as they recover from historic disturbance. However, the rates of accumulation we infer, 10-30 gC m^{-2} yr^{-1}, are only 5-15% of the 200 gC m^{-2} yr^{-1}observed by the eddy flux tower. More poorly drained soils also in the tower footprint may be accumulating larger amounts of C per square meter area, although they are far more limited in areal extent.
- Measurements of ^{14}C in soil organic matter emphasize organic matter fractions with longer turnover times (TT) which dominate soil carbon inventory. Calculations of TT derived by dividing total C inventory by estimated heterotrophic respiration are not good predictors of the response time of soils because soil organic matter (SOM) is not homogeneous.
- Measurements of $\Delta^{14}C$ in CO_2 are required to correctly model the C that is actually respiring and to fully understand below ground C dynamics.
- Interpretation of ^{14}C data in SOM at Harvard Forest are complicated by fine root inputs with ^{14}C elevated by ~65‰ relative to the atmosphere, implying that the fine root C was fixed on average 7±1 years ago. We do not currently understand the mechanism behind this lag in radiocarbon input.
- We estimate 41% of total soil respiration comes from decomposition of SOM that decomposes on timescales of 1-100+ years**.** Of this, 80% involves direct decomposition of leaf and root litter with TT of 2-10 years and 20% represents

low density humified C pools and C associated with minerals (H and M respectively) which have TTs on the order of several decades or greater.

- About two-thirds of total soil respiration is produced within the O and A horizons. These organic rich horizons are comprised of 1) small pools of live roots and recent leaf and root litter that have residence times in the plant+soil system of ~1-10 years and 2) relatively large pools of humified root and leaf litter which reside in the plant+soil system for 40-100+ years.
- Radiocarbon measurements of total below ground respiration measure the average time C spends in the plant+soil system from original photosynthetic fixation until respiration by autotrophs or heterotrophs. We estimate this time to be 4±1 years for total soil respiration and 8±1 years for heterotrophic respiration in well-drained soils at Harvard Forest, MA.

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Table 1. Carbon stocks by soil horizon.

					--------------Low Density SOM--------------			--High Density SOM-
	Bulk Density[1,2]	Soil Carbon[3]	Bottom Depth[4]	Total C Stock[5,6]	Leaf Litter L_L[7, 8]	Fine Root Detritus L_R[7, 8]	Humified H[8, 9]	Mineral Associated M[8]
Horizon	(g cm^{-3})	(g C Kg^{-1} soil	(cm)	(g C m^{-2})	(g C m^{-2})	(g C m^{-2})	(g C m^{-2})	(g C m^{-2})
Oi	0.06 (.01)	450 (20)	2 (1)	380 (110)	380 (110)	0	--	NA
Oea	0.1 (.02)	470 (10)	6 (1)	1640 (750)	--	230 (40)	1410 (750)	NA
A	0.35 (.03)	270 (30)	10 (2)	2400 (820)	--	60 (25)	1780 (630)	560 (200)
Ap	0.54 (.13)	60 (1)	16 (2)	2620 (660)	--	70	790 (200)	1760 (450)
Bw1	0.85 (.07)	20 (1)	32 (4)	1245 (190)	--	4	40 (10)	1200 (180)
Bw2	0.93 (.04)	6 (1)	59 (3)	510 (110)	--	1 (1)	5 (1)	500 (110)
Total				8800 (1310)	380 (110)	360 (70)	4030 (1000)	4020 (540)

[1] Gravel free bulk density (i.e. less than 2mm).

[2] For Oi, Oe +Oa and A horizons n = 3, standard error in parenthesis; n = 2 for all other horizons; range in parenthesis.

[3] For all horizons n = 2; range in parenthesis.

[4] For Oi, Oe + Oa and A and Ap horizons n = 3, standard error in parenthesis; n = 2 for all other horizons; range in parenthesis.

[5] Includes live root mass below the Oi horizon; total error in parenthesis.

[6] C stock calculated using a z value (not shown) that accounts for waviness of horizon boundary and rocks.

[7] On a dry weight basis; error term includes extrapolation from subsample to whole soil where subsample n = 3 to 5, otherwise n = 1 and no error is shown.

[8] Low density means $\rho < 2.1$ g/cc, high density $\rho > 2.1$ g/cc.

[9] Calculated by subtracting total roots from the total low density SOM.

Table 2. Calculation of high and low density decomposition fluxes with associated $\Delta^{14}CO_2$ and measured profile $\Delta^{14}CO_2$.

Horizon	Stock (g C m^{-2})	Δ^{14}C of SOM[1] (‰)	Turnover Time[2] (years)	CO_2 Flux (g C m^{-2}-yr^{-1})	Flux Horizon Total (g C m^{-2}-yr^{-1})	Δ^{14}C of SOM Horizon Total (‰)	Measured Profile $^{14}CO_2$[3] (‰)
Oi (L_L)	380	132 (8)	4	25-95[4]	60-130	151-172	136
Oe+Oa (L	230	188[5]	NA	NA			
Oe+Oa (	1410	201 (19)[6]	40	35			
A (L_R)	60	216[5]	NA	NA	<22	111	130
A (H)	1780	121[7]	73 to >100[8]	<18			
A (M)	560	68 (26)	130 to>200[8]	< 4			
Ap (H)	790	24.5 (28)	220	4	8	*-3*	--
Ap (M)	1760	-31(20)	480	4			
Bw1 (H)	40	-97 (18)	990	0.04	< 2	-118	131
Bw1 (M)	1200	-119 (17)	1200	1			
Bw2 (H)	5	-129 (40)	1300	0.004	< 1	-171	128
Bw2 (M)	500	-172 (4)	1760	0.3			

NA = Not applicable, see text for details.

-- = no data

[1] Values are the average for two pits with range in parenthesis.

[2] A non-steady state model is used for the Oe+Oa and A horizons and a steady state model used for Oi, Ap and deeper horizons.

[3] Represents an annual concentration weighted average of the measured Δ^{14}C in CO_2 at the boundary with the horizon below.

[4] Represents a range based on assuming all loss is as CO_2 or that 100% of inputs to the H+M fractions are from leaf litter.

[5] Represents the Δ^{14}C samples picked for dead roots (n = 1).

[6] Represents the humified organic material after quantitative root picking for the Oe + Oa (n = 2).

[7] Represents a weighted Δ^{14}C value for the two humified (H) components shown in Figure 7 (B), also see text for discussion.

[8] Range reflects that the Δ^{14}C values may include pre-disturbance C. The minimum represents the steady state case.

Table 3. Parameters used and results of respiration partitioning for the whole soil profile based on eight scenarios.

Case	Parameters	Leaf Litter F_{LL}[1] ($gC\ m^{-2}\ yr^{-1}$)	Leaf Litter ΔL_L[2] (‰)	**Fine Root Litter F_{LR} ($gC\ m^{-2}\ yr^{-1}$)**	Fine Root Litter ΔL_R[3] (‰)	**Recent-C F_R ($gC\ m^{-2}\ yr^{-1}$)**	**Reservoir-C $F_{LL} + F_{LR} + F_{H+M}$ ($gC\ m^{-2}\ yr^{-1}$)**	**Recent-C Fraction**	**Reservoir-C Fraction**
Case 1	min L_L, min ΔL_L, min ΔL_R	25	113	**277**	180	**470**	**370**	**0.56**	**0.44**
Case 2	min L_L, min ΔL_L, max ΔL_R	25	113	**197**	214	**550**	**290**	**0.66**	**0.34**
Case 3	min L_L, max ΔL_L, min ΔL_R	25	132	**272**	180	**475**	**365**	**0.57**	**0.43**
Case 4	min L_L, max ΔL_L, max ΔL_R	25	132	**193**	214	**554**	**286**	**0.66**	**0.34**
Case 5	max L_L, min ΔL_L, min ΔL_R	95	113	**264**	180	**413**	**427**	**0.49**	**0.51**
Case 6	max L_L, min ΔL_L, max ΔL_R	95	113	**187**	214	**490**	**350**	**0.58**	**0.42**
Case 7	max L_L, max ΔL_L, min ΔL_R	95	132	**242**	180	**435**	**405**	**0.52**	**0.48**
Case 8	max L_L, max ΔL_L, max ΔL_R	95	132	**172**	214	**505**	**335**	**0.60**	**0.40**
Average		60		**219**		**493**	**347**	**0.59**	**0.41**
Minimum				**172**		**413**	**286**	**0.49**	**0.34**
Maximum				**277**		**554**	**427**	**0.66**	**0.51**

For all scenarios, $\Delta^{14}C$ of the atmosphere (ΔR) = 97‰ , the $\Delta^{14}C$ of total soil respiration (ΔP) = 128‰, the flux of H+M is 70 $gC\ m^{-2}\ yr^{-1}$ with a $\Delta^{14}C$ of 135‰. We combine the fluxes and their associated ^{14}C values of the H and M pools because their combined fluxes are relatively low (less than 10% of the annual total). Non-bold face values are parameters used in equations 16 and 17, while bold faced values are the resulting calculations.

[1] Range reflects the two cases where either none or all of the inputs to H+M fractions are derived from leaf litter.

[2] Range is for the lowest and highest measured values of recognizeable leaf parts.

[3] Range reflects a mass weighted ^{14}C average of all dead roots (180‰) and the highest measured dead root value (214‰).

Table 4. Summary of respiration partitioning results.

Horizon	Total Respiration (g C m-2)	Fraction Total Respiration	Fraction produced that is Reservoir-C	Min	Max
Whole Soil	840	1.00	0.41	0.34	0.51
O+A+Ap	530	0.63	0.44	0.35	0.54
B	235	0.28	0.39	0.32	0.45
C	75	0.09	0.37	0.31	0.43

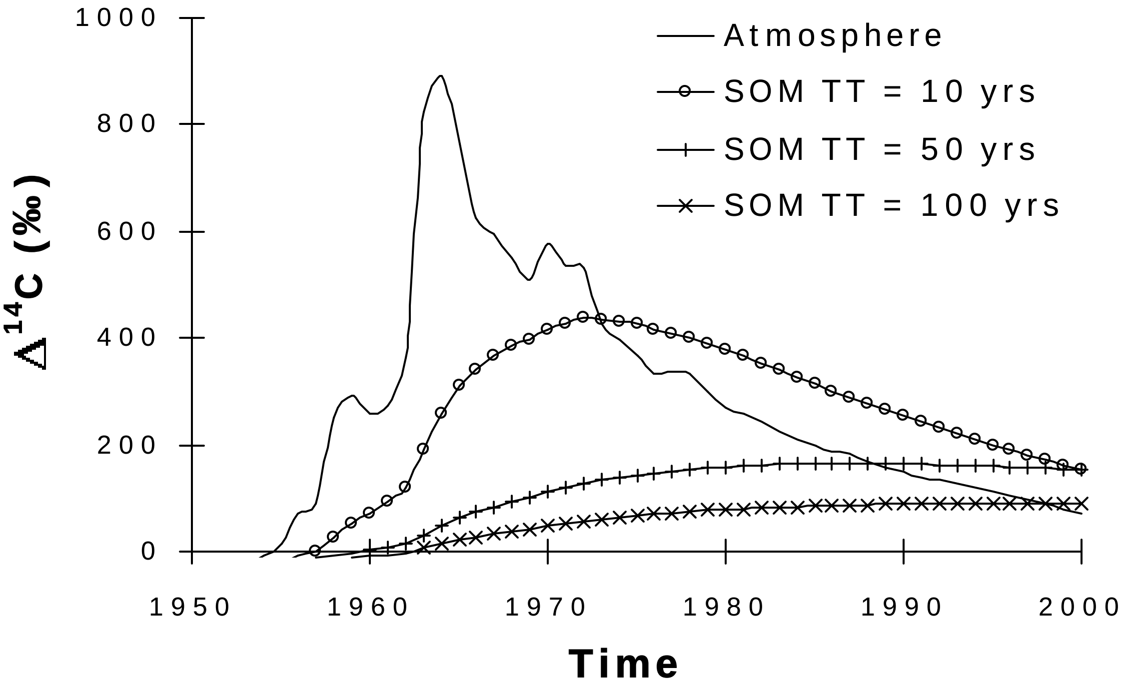


Figure 1. The time record of ^{14}C in the atmosphere (Northern Hemisphere) based on grapes grown in Russia (Burchuladze et al. 1989) for 1950-1977 and direct atmospheric measurements for 1977-1996 (Levin and Kromer, 1997). We express radiocarbon data here as $\Delta^{14}C$, the difference in parts per thousand (per mil or ‰) between the $^{14}C/^{12}C$ ratio in the sample compared to that of a universal standard (oxalic acid I, decay-corrected to 1950). All samples are corrected for mass-dependent isotopic fractionation to 25‰ in $\delta^{13}C$. Expressed in this way, $\Delta^{14}C$ values greater than zero contain bomb-produced radiocarbon, and those with $\Delta^{14}C$ less than zero indicate that carbon in the reservoir has, on average, been isolated from exchange with atmospheric $^{14}CO_2$ for at least the past several hundred years. The ^{14}C content of a homogeneous, steady state C reservoir with turnover times of 10, 50 or 100 years is compared with that of the atmosphere through time.

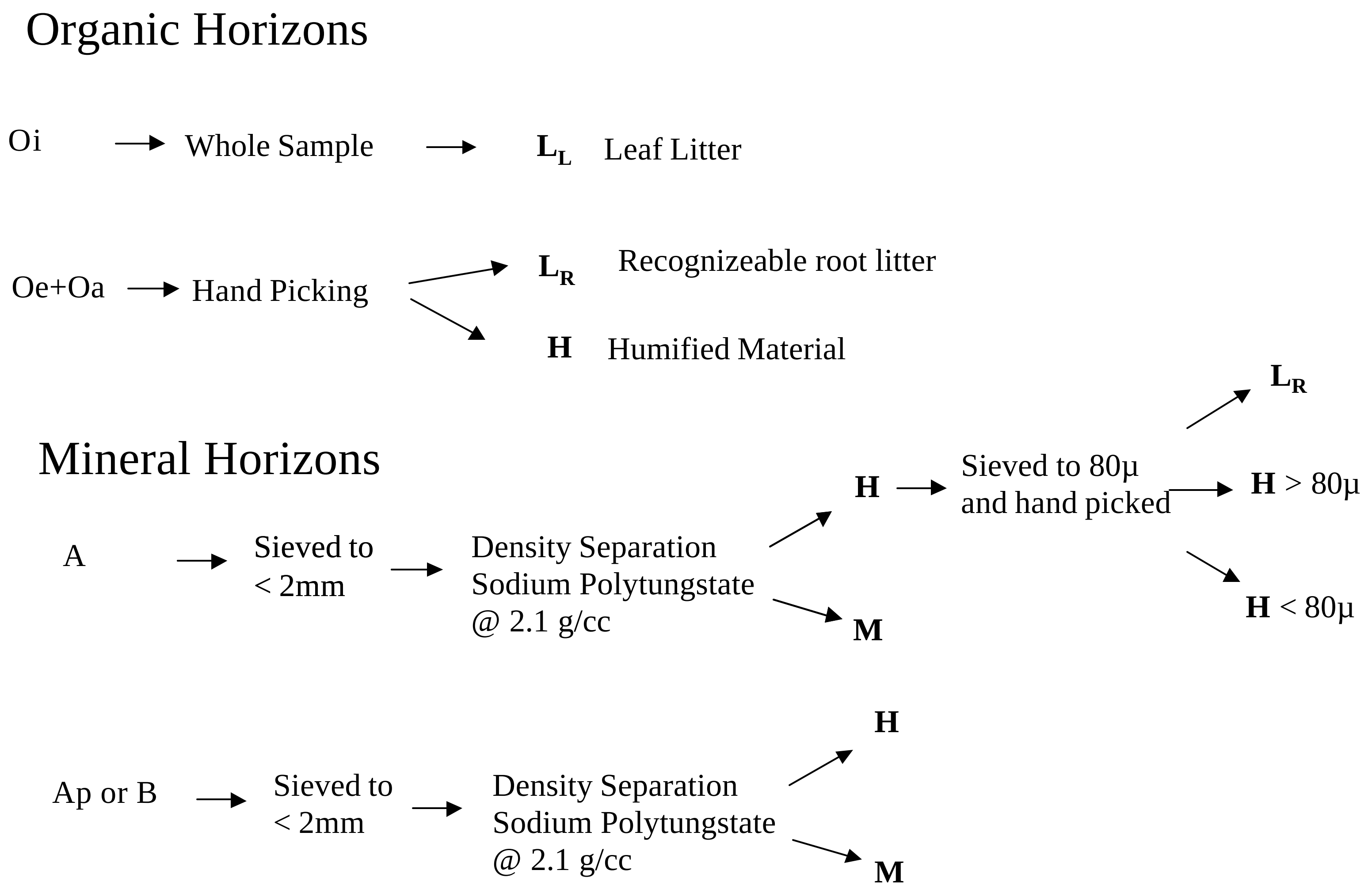


Figure 2. Schematic representation of soil sample processing into the homogeneous soil organic matter pools as defined in this paper; L_L or L_R (recognizable leaf or root *litter* respectively), H (undifferentiable SOM which is considered to be microbially altered or *humified*), and M (organic matter associated with *mineral* surfaces). All L_L, L_R and H components are low density (i.e. <2.1 g/cc) while the M components are considered high density (i.e. >2.1 g/cc).

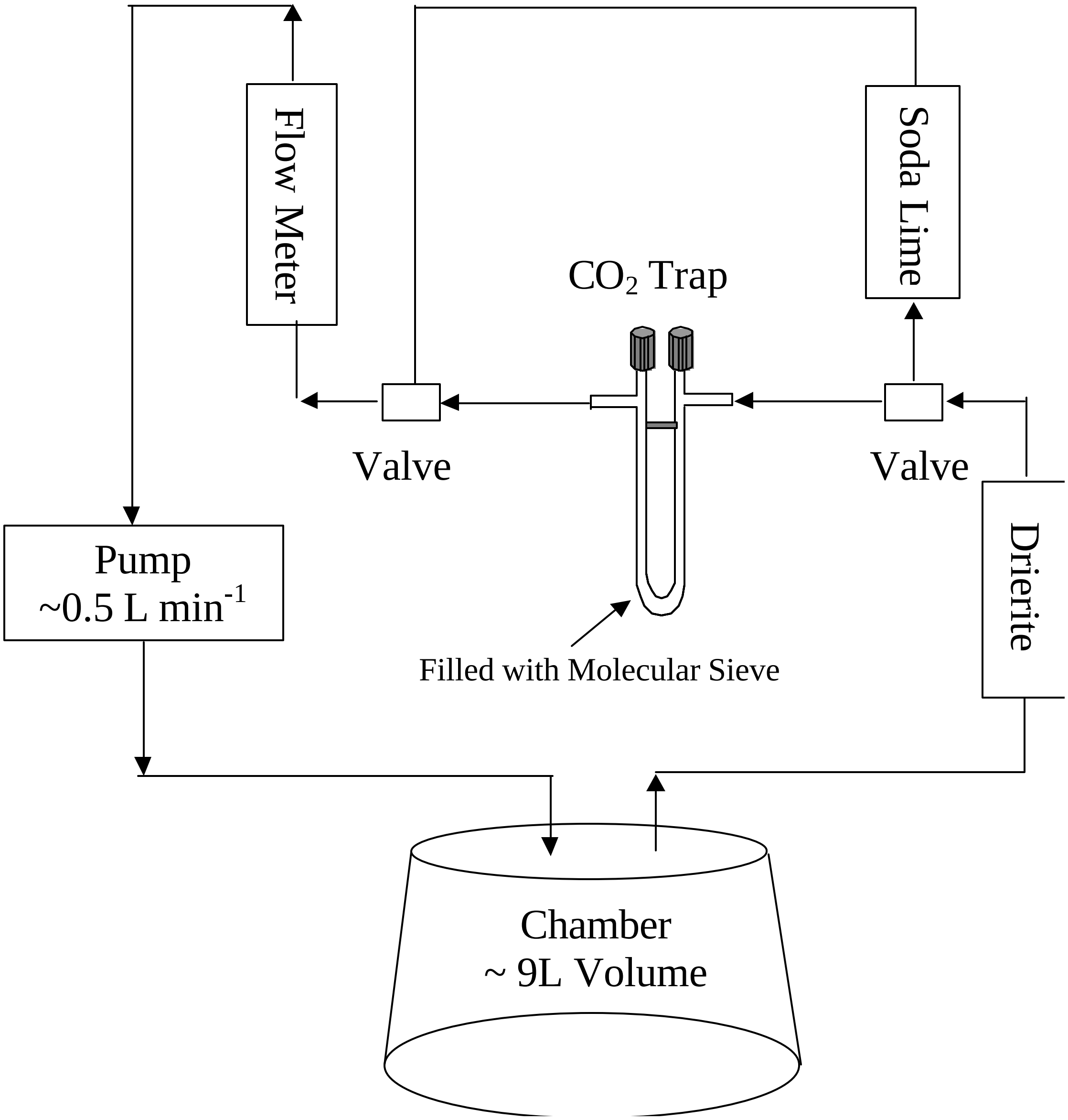
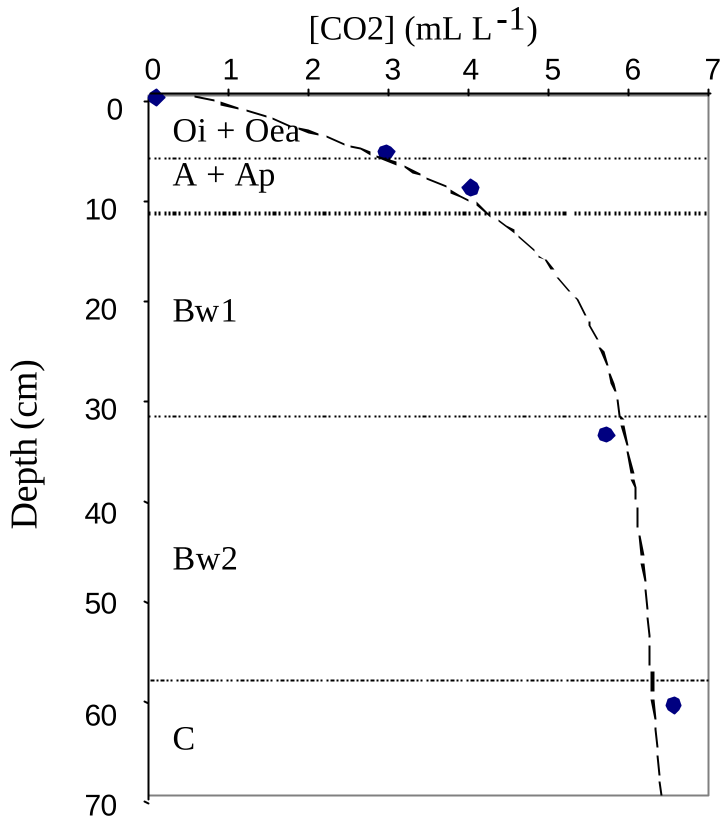


Figure 3. Sampling scheme for trapping CO_2 on molecular sieve (mesh size 13X) using a closed dynamic chamber system. Molecular sieve 13X traps CO_2 quantitatively at room temperatures and then releases it when baked at 475 °C (Bauer et al. 1992). The evolved CO_2 is purified cryogenically.

CO_2 Flux and Production Estimates



CO_2 Flux as a Function of Depth		Total Soil Hori
$F_{0cm} = dC/dZ * D_A$	= 0.162	$P_O = F_{0cm} - F_6$
$F_{6cm} = dC/dZ * D_A$	= 0.142	$P_{A + Ap} = F_6$
$F_{12cm} = dC/dZ * D_{Bw1}$	= 0.064	$P_{Bw1} = F_{12cm}$
$F_{32cm} = dC/dZ * D_{Bw2}$	= 0.029	$P_{Bw2} = F32_{cm}$
$F_{58cm} = dC/dZ * D_C$	= 0.011	$P_C = F58_{cm}$

Figure 4. Calculation of CO_2 flux estimates by depth (F_z, where z indicates the profile depth) and CO_2 production estimates by soil horizon (P_h, where h indicates the specific soil horizon) in gC m^{-2} hr^{-1}. The values shown here are from measurements made on August 25, 1997. Interpolations among similar measurements made throughout the year were summed to obtain annual estimates. These estimates are for well drained soils within the footprint of the eddy flux tower at Harvard Forest.

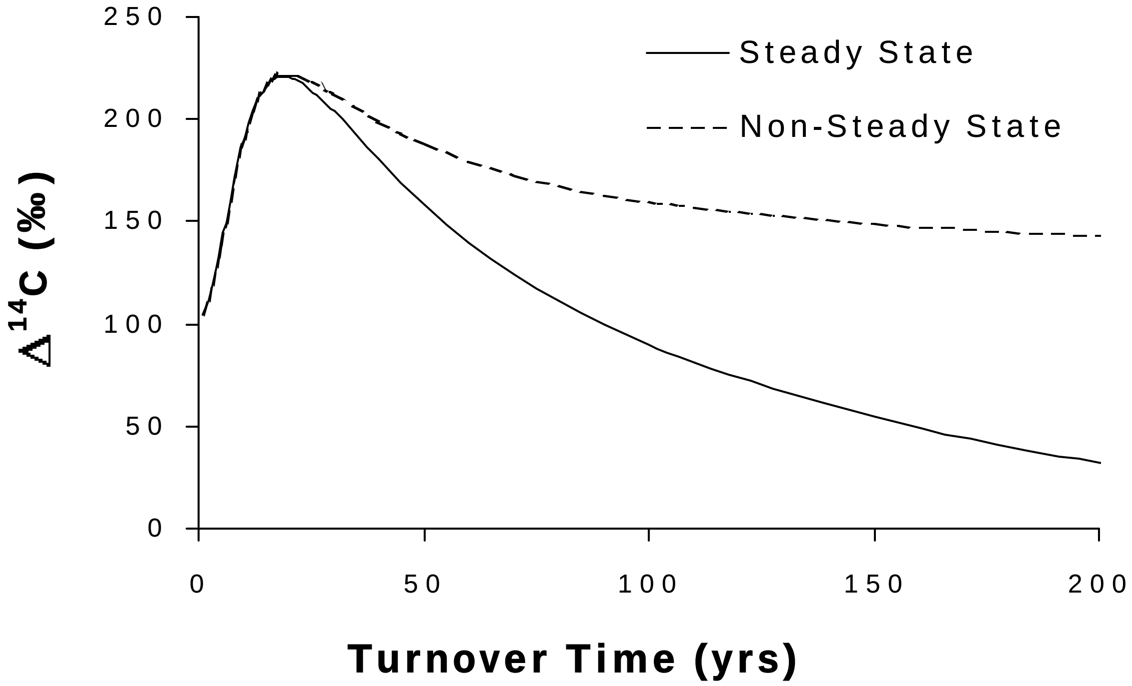


Figure 5. The predicted $\Delta^{14}C$ value in 1996 for homogeneous C reservoirs as a function of different turnover times. The curves represent results for our steady state and non-steady state (accumulation) model.

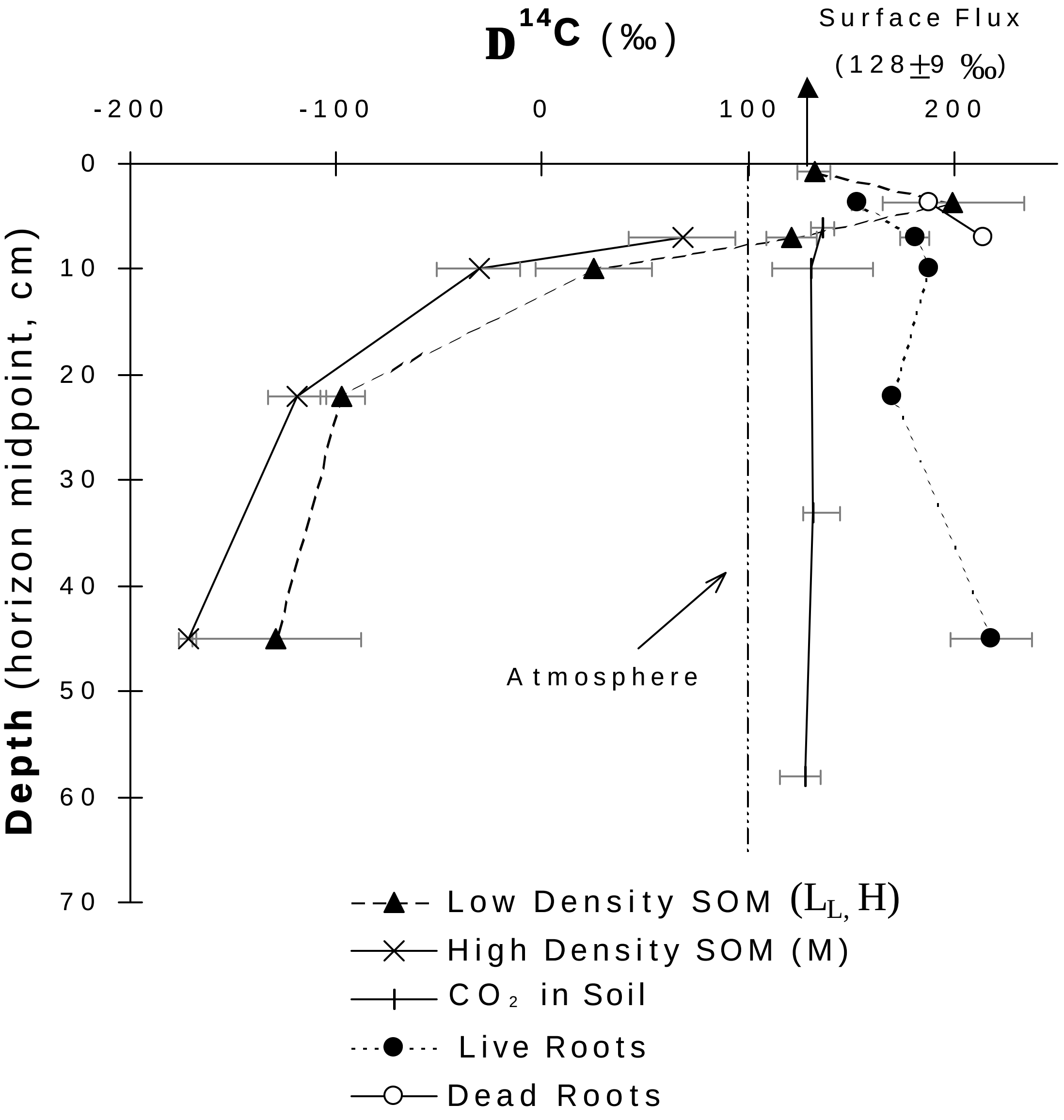


Figure 6. Δ^{14}C of below ground soil organic matter fractions and CO_2 by depth. All values except the Δ^{14}C of CO_2 are plotted at the midpoint of the soil horizon. For the soil organic matter fractions L_L, H and M, the error bars represent the range (n=2) or the standard error of the mean (n=3). For live and dead roots, the error bars where present, represent the error of the mean (n=3) otherwise n=1. For the soil CO_2 profiles values are an annual concentration weighted mean (n=3 or 4) with error bars showing the entire range of values measured. The surface flux represents a flux weighted annual average from four sampling events. The Δ^{14}C for the atmosphere for 1996 (97±1‰) is also shown.

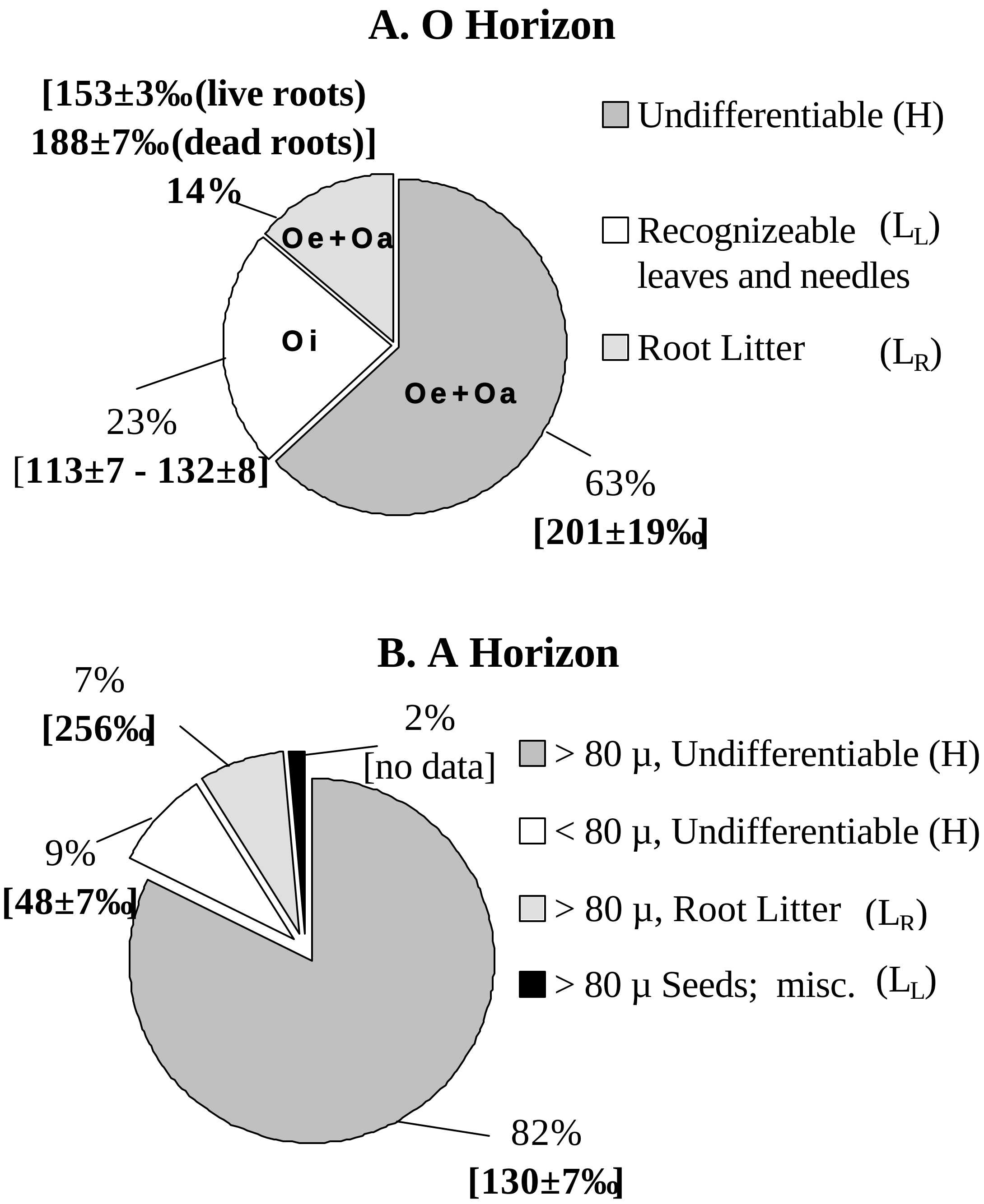


Figure 7. Heterogeneity of the O (top, Figure 7A) and A (bottom, Figure 7B) horizons. An error of 7‰ indicates analytical error, as n=1. Errors other than 7‰ indicate either a range (n = 2) or standard error of the mean (n = 3).Values for the O horizon (Figure 7A) represent a composite of several samples and are representative of an average O horizon. Values for the A horizon in Figure 7B represent the results of quantitative sieving and picking one sample as outlined in Figure 2. The roots in the A horizon represent a stock weighted mean of two samples representing roots of two morphological types with values of 231±7‰ and 266±7‰.

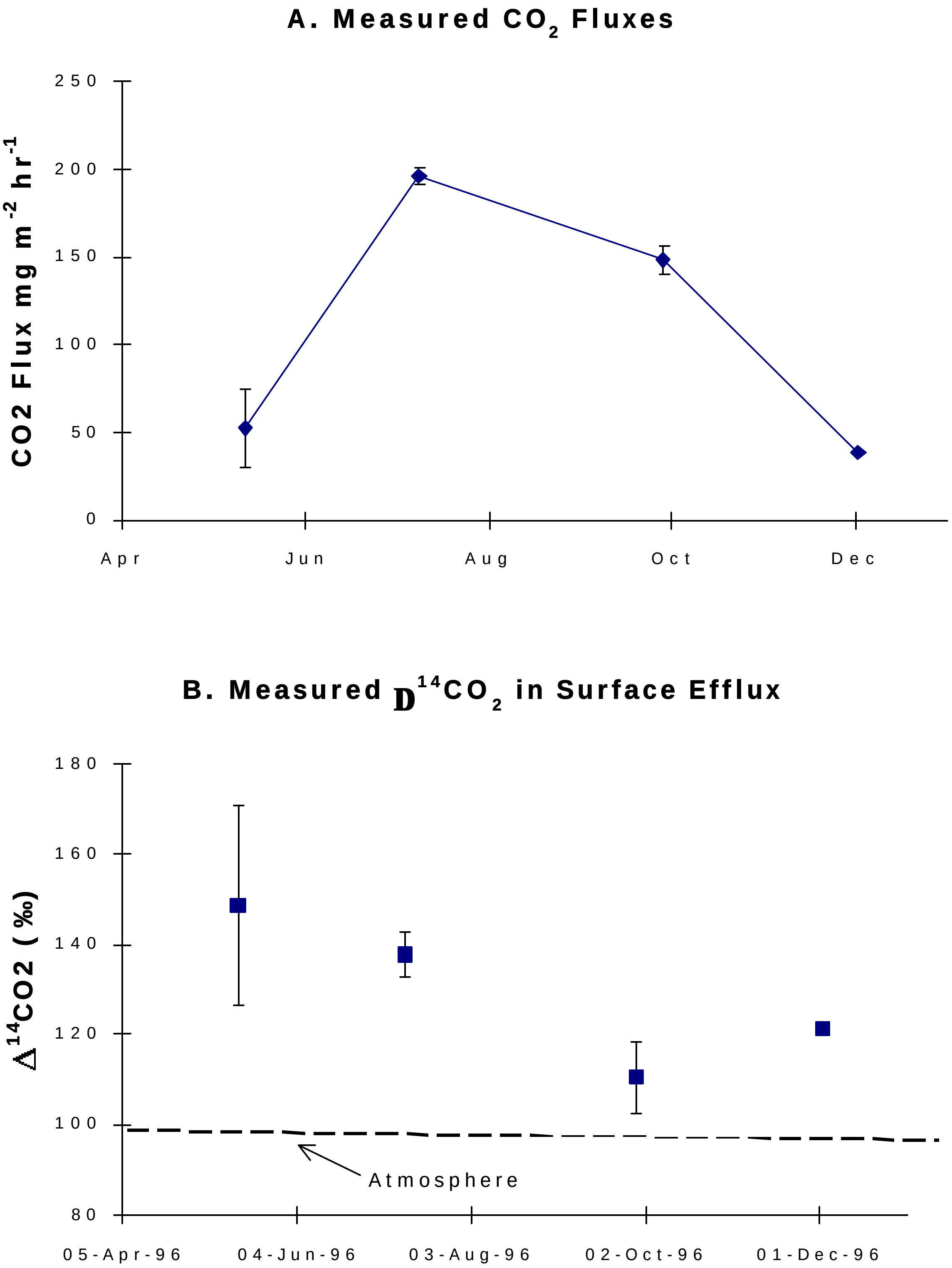


Figure 8. CO_2 fluxes for 1996 (top, Figure 8A). Error bars represent standard error (n = 6). $\Delta^{14}CO_2$ of soil CO_2 efflux (bottom, Figure 8B) Error bars where present represent standard error (n = 3) except in December 1996 where n = 1.

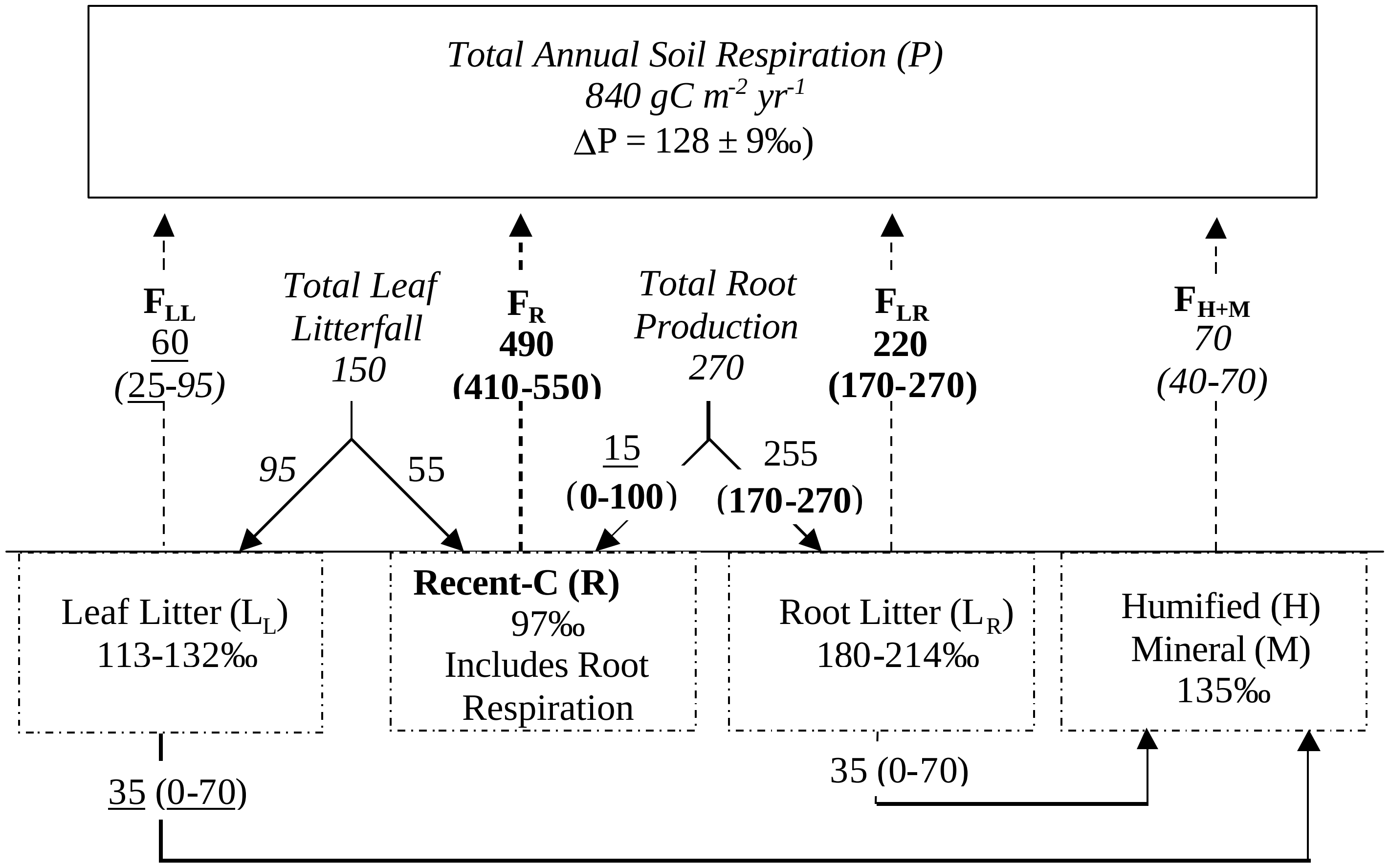


Figure 9. Results of isotopic mass balance approach to partitioning soil respiration into Recent- versus Reservoir-C sources. Solid arrows represent fluxes of organic C, while dashed arrows represent fluxes of CO_2. All units are in gC m^{-2} yr^{-1} with the average (and range). Production of litter (leaf and root) is assumed to have the isotopic composition of the atmosphere (97‰) in 1996. Bold numbers represent direct results from isotope mass balance model. Italicized numbers are independent measurements or calculated values used to constrain the model (see text for details) and underlined numbers are the resultant fluxes and transfers due to the model results and its constraints.

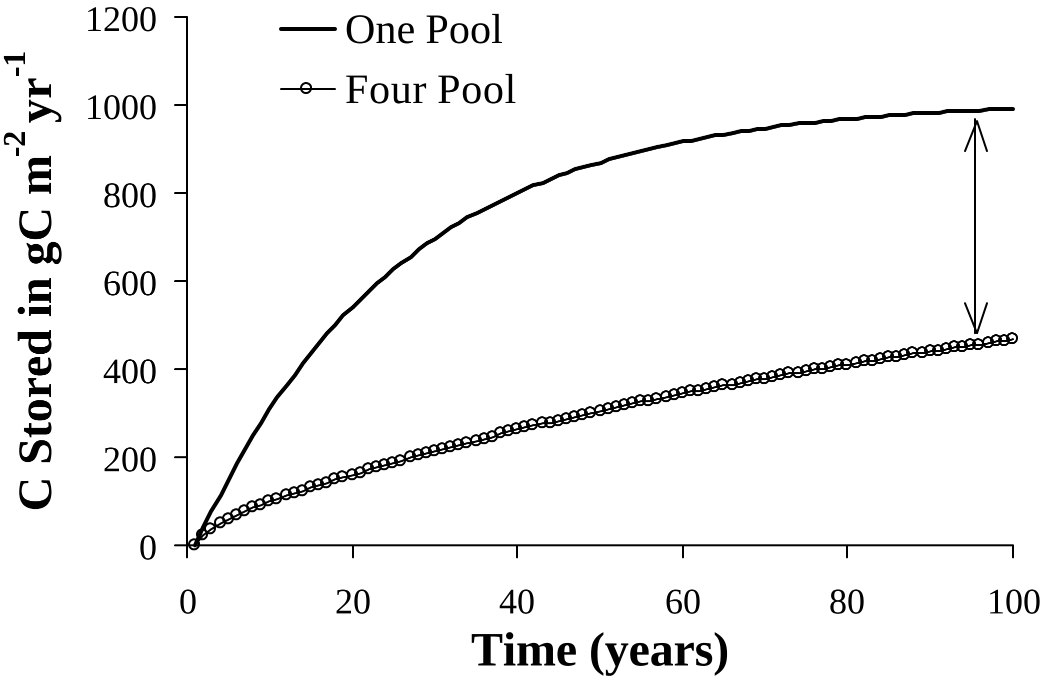


Figure 10. Increase in C storage associated with a 10% increase in NPP for two non-steady state models based on a one pool or four pool representation of soil organic matter stocks. In the one pool case the TT is 25 years and is equivalent to the total soil carbon stocks (8800 gCm^{-2}) divided by the total soil respiration (840 gCm^{-2} yr^{-1}) multiplied by the amount of decomposition from Reservoir-C (41%). In the four pool case stocks and TTs are modeled after those for the Harvard Forest well drained soils with TTs of 1, 4, 80 and 500 years. Both systems are not at steady state; the increases are relative to a non-steady state run for each case.

Chapter 3: Characterization of Soil Organic Matter

Introduction

Forest ecosystems cover 31% of the earth's ice-free land area (Hart, 1985) and contain roughly 50% of all soil C stocks (Dixon et al., 1994). Although mid-latitude temperate forests comprise only 25% of the worlds total forests and 13% of soil C, they represent globally significant C sinks because: 1) they are generally young ecosystems recovering from large-scale deforestation as a result of agricultural expansion (Lal et al., 1998), 2) they are the only forest ecosystems that is increasing in global area rather than decreasing (Dixon et al., 1994), and 3) they are responsible for a C sink of 0.5 ± 0.5 Pg of C per year (IPCC, 1996).

The net carbon balance of forests is the small difference between very large fluxes of carbon uptake (via photosynthesis) and carbon loss (via respiration). If carbon uptake exceeds C loss, the forest is a net sink of atmospheric C. The mechanisms of C uptake by the forest canopy and C loss by decomposition comprise many complex processes. Small shifts in the sizes of these processes, in both vegetation and soils, can affect the overall forest C balance significantly.

Currently, regrowing temperate forest ecosystems of the northeastern United States store between 200-525 g C m^{-2} y^{-1}, depending on location (Hollinger et al., 1999, Greco and Baldocchi, 1996, Goulden et al., 1996). However, the partitioning of this net uptake between forest vegetation and forest soils is largely unknown and is an important parameter in assessing ecosystem response to future climate change scenarios.

In temperate forests, for soils to 1 m depth, there is roughly 1.7 times more C in soil than in vegetation (Dixon et al., 1994). The greatest controlling factor in this multiple is the residence time of C between input into the soil system and subsequent decomposition. Thus the sizes of soil carbon stocks are in general tied to rates of soil C cycling. However, other important factors also influence the ability of soils to store or release C. For example, a soil that has been storing carbon for millennia may become a source to the atmosphere given a sustained change in climate or nutrient status. Overall, the sum of all the component processes determines future soil C balance.

To evaluate potential responses of the soil system to future climate change scenarios, we must first understand the general character of soil organic matter (SOM) stocks. We need to know how SOM carbon is partitioned among detrital material, humified compounds, and/or associated with minerals. Moreover, we need to know the timescales with which different portions of SOM stocks respond to changing climate or nutrient status.

Several techniques have been used to determine the dynamics of SOM. These include direct observations of C inventory and fluxes, manipulation studies involving decomposition of SOM after removing roots or overlying soil horizons, litter decomposition experiments, ^{14}C labeling of substrates, and soil chronosequence studies (Trumbore, 2000). In this study we combine traditional measurements of soil C inventories and fluxes with measurements of their radiocarbon (^{14}C) inventories and fluxes. Adding ^{14}C measurements is a powerful improvement. It allows separation of

SOM into components contributing variable amounts to decomposition fluxes instead of treating SOM as one homogeneous reservoir. It also has an advantage over manipulation studies because the measured rates are for an intact, undisturbed ecosystem. While ^{14}C labeling and chronosequence studies are limited to investigations of very fast (months to a year) or very slow (millennial scale) cycling C pools respectively, using natural abundance ^{14}C allows investigation of C cycling on annual, decadal, and millennial timescales.

This chapter focuses on total C and ^{14}C measurements of SOM stocks as a tool to understand and predict the general characteristics of SOM stocks and their dynamics. Chapter 5 includes measurement of C and ^{14}C fluxes to further investigate SOM dynamics. We use three temperate forest sites located along a latitudinal gradient from Maine to Tennessee (**Figure 1**).

Site Descriptions

Site characteristics, average annual soil CO_2 emissions, and net ecosystem productivity (NEP) for the three sites we studied are shown in **Table 1**. The northern-most site, Howland Forest (Howland), is a spruce-fir forest located near the town of Howland in east-central Maine. It is within the International Paper Company's Experimental Forest. The forest was selectively logged around 1900 (Hollinger et al., 1999). The central site, Harvard Forest, is a mixed deciduous forest located near the town of Petersham in central Massachusetts. At Harvard Forest, the area of our study site was cleared in the mid-1800s, plowed and used primarily for pasture. The pasture was abandoned between 1860 and 1880 (Foster et al., 1992). The regrowing forest was largely leveled by a hurricane in 1938 but has been growing undisturbed since then. The soils at both Howland and Harvard Forest are developed on glacial tills that are predominantly granitic. Drainage varies from well-drained uplands to very poorly drained swamps. The data reported here are for well-drained soils with very low clay content. The southern-most site (referred to here as Walker Branch) is mixed deciduous forest located on the Walker Branch Watershed on the Oak Ridge Reservation near Oak Ridge National Laboratory in eastern Tennessee. The site was selectively logged and used for hog or cattle grazing prior to government aquisition in 1942. The trees are variable in age but the stand age is 80-120 years (Dale et al., 1990). The soils at this site are developed on dolomitic bedrock. However, little evidence remains of their carbonate parent material (Hanson et al., 1998). The soils are well-drained and the predominant clay type is kaolinite (Johnson and Van Hook, 1989).

Methods

Field and Laboratory

Samples for carbon and ^{14}C inventories were taken from two soil pits dug using the quantitative pit methodology of (Huntington et al., 1989), and Hamburg, 1984, at the Harvard Forest and Walker Branch sites (**Table 2**). This method involves sampling a large volume of soil to allow calculation of horizon-specific bulk densities. Two 0.5 m x 0.5 m quantitative pits were dug at both the Harvard Forest and Walker Branch sites. Excavations proceeded downward to the base of each pedogenic horizon, differentiated by color and textural changes. To minimize sampling errors due to repeated grid placement and removal, the top of each pedogenic horizon was calculated by taking a weighted mean of 25 measurements from within the 0.5 m x 0.5 m grid. This system weights the center 9 measurements 4X, the sides of the grid (not including the corners) 2X, and the corners 1X. At the Howland site, pits were not dug quantitatively. Instead, data on bulk density comes from (Fernandez et al., 1993), and Fernandez (personal communication). For all pits, samples which integrated each soil horizon were collected for radiocarbon and total C and N analyses from one of the pit faces. Carbon inventories are reported to a depth of about 80 cm for all sites.

Quantification of fine root biomass was done only at the Harvard Forest site, as described in Chapter 2. At Howland, data on coarse (> 0.5 mm) root biomass from Fernandez et al., 1993, are used. At Walker Branch data from Joslin and Wolfe, 1999, for roots < 2 mm are used.

Soil samples were separated into different fractions using a combination of hand sorting and density separations. Density separations are performed using a sodium polytungstate solution at $\rho = 2.1$ g/cc. Material that floats is defined as low density, while material that sinks is defined as high density and assumed to be associated with minerals. These methods, along with descriptions of how the samples were prepared for radiocarbon analysis, are described in detail in Chapter 2. Analytical error in the ^{14}C measurement of a graphite target prepared via zinc reduction is ± 6‰. At Howland and Walker Branch, we obtained soils that were dug by previous investigators and archived. These samples were similarly processed and also analyzed for radiocarbon content (**Table 2**).

Radiocarbon Techniques

Radiocarbon is produced naturally in the upper atmosphere when high-energy cosmic rays collide with atomic nuclei to produce neutrons. The neutrons then collide with nitrogen to form ^{14}C via the following reaction:

$$^{14}_{7}N + ^{1}_{0}n \rightarrow ^{14}_{6}C + ^{1}_{1}H$$

^{14}C is a radioactive isotope which decays back to ^{14}N via beta-decay (electron emission with a maximum energy of 0.155 Mev) with a half life of 5,730 years. Once produced, the ^{14}C quickly oxidizes to form $^{14}CO_2$ and follows the same physical and chemical pathways as $^{13}CO_2$ and $^{12}CO_2$. The estimated natural production rate of ^{14}C over the earth's surface is 2.50 ± 0.50 atoms of ^{14}C cm^{-2} sec^{-1}, and the steady state natural $^{14}C/^{12}C$ ratio is $1.2 \pm 0.2 \times 10^{-12}$ (Linick, 1975). This $^{14}C/^{12}C$ ratio is referred to as ‘Modern’ and by definition refers to the atmosphere of 1950. Decay counting of ‘Modern’ atmospheric carbon yields 13.6 ± 0.1 disintegrations per minute per gram of C (Linick, 1975).

Radiocarbon is also produced by aboveground thermonuclear explosions (bomb ^{14}C) that release neutrons into the atmosphere. Atmospheric weapons testing in the late 1950s and early 1960s increased atmospheric ^{14}C by 10^{29} atoms (160 kg ^{14}C), or twice modern values (Linick, 1975, Hesshaimer et al., 1994). Over 70% of this ^{14}C came from massive Soviet and American tests during 1961-1962 that injected ^{14}C into the stratosphere as well as the troposphere (Linick, 1975). The Limited Test Ban Treaty of 1963 largely stopped aboveground testing (Reidar and Lovseth, 1983). However, due to slow stratosphere-troposphere exchange, and slow mixing across the equator, peak tropospheric $^{14}CO_2$ values occurred in 1963 in the northern hemisphere and in 1965 in the southern hemisphere (Linick, 1975).

The $^{14}CO_2$ concentration has been decreasing since its peak values in the early-mid 1960s (**Figure 2**-top). The decrease was rapid at first due to dilution by the oceans and terrestrial biosphere, which were then depleted in $^{14}CO_2$ relative to the atmosphere because they were in equilibrium with 'Modern' pre-bomb atmospheric $^{14}CO_2$ concentrations. The rate of decline has slowed as bomb ^{14}C approaches equilibrium with the surface ocean and terrestrial reservoirs, though increased fossil fuel use also contributes to the continued decline. Since the early 1980s, the decline has decreased exponentially from -13 ‰ yr^{-1} in 1982 to -4‰ yr^{-1} in 1998 (Levin and Hesshaimer, 2000). Currently, the terrestrial biosphere is likely a net source of $^{14}CO_2$ to the atmosphere in both mid and low latitudes where mean carbon turnover times span decades (Levin and Hesshaimer, 2000, Gaudinski et al., 2000).

As discussed in Chapter 2, radiocarbon measurements of SOM and CO_2 are a useful for determining the dynamics of soil carbon. Carbon reservoirs such as SOM that exchange with the atmosphere reflect the rate of exchange through the amount of bomb ^{14}C incorporated (Chapter 2, Figure 1). A critical aspect is an accurate record of atmospheric ^{14}C of CO_2 over time at the sites being studied. Several records of direct atmospheric $^{14}CO_2$ measurements exist from the late 1950s and early 1960s for both hemispheres (Levin and Hesshaimer, 2000) at sites that represent both clean tropospheric background as well as more polluted continental regions (Levin and Kromer, 1997, Burchuladze et al., 1989). Polluted continental sites tend to have $\Delta^{14}C$ values that are a few per mil lower relative to clean background sites due to the influence of fossil fuel emissions in continental regions (**Figure 2**). The history of atmospheric ^{14}C in CO_2 at any given site may differ somewhat from global records because local fossil fuel contamination may also be exacerbated periodically by stagnant air conditions and in unusual circumstances, such as local anthropogenic sources of $^{14}CO_2$.

At all three sites, the $\Delta^{14}C$ record of atmospheric CO_2 (Northern Hemisphere), based on grapes grown in Russia for 1950-1977 (Burchuladze et al., 1989), and direct atmospheric measurements for 1977-1996, which represent summer means (May – August) taken at Schauinsland Black Forest, Germany, at an elevation of 1205 m asl (Levin and Kromer, 1997), are used as the base for the input to our ^{14}C SOM models. Both the Russian and Schauinsland sites are representative of a similarly polluted continental setting relative to the eastern United States. After 1996, we assume a continued decrease of 4 ± 2‰ per year (Levin and Hesshaimer, 2000), which yields values of 100.3‰, 96.3‰, and 92.3‰ for 1997, 1998, and 1999 respectively. The 1997 and 1998 values are consistent with preliminary growing season means for Schauinsland for 1997 and 1998 (Ingeborg Levin, personal communication).

To test how well our sites agree with the Schauinsland atmospheric trend, we compare them with local atmospheric measurements made by trapping atmospheric CO_2 onto molecular sieve, as described in Chapter 2, at a height of approximately 10 cm off the ground surface (**Figure 3**). The data agree quite well with the Schauinsland-derived trend, with the exception of Walker Branch, which is discussed in more detail below. However, close examination of the ^{13}C values, which range from –7.38‰ to –12.60‰, with an average of –9.39‰ and a standard deviation of 1.21‰, show that the samples have some re-respired CO_2 from soils and plants or fossil fuel contamination (see Appendix 1 for complete ^{14}C and ^{13}C data). Therefore these samples, originally taken only to correct for leaks while sampling soil respiration with chambers, are not representative of the free troposphere as seen by the majority of the forest canopy. Thus we have chosen to use the Schauinsland trend instead of these local data. The data shown in **Figure 3**, however, do give some confidence that the Schauinsland data are appropriate.

The history of atmospheric $\Delta^{14}C$ of CO_2 for the Walker Branch site is more complicated. Several hazardous waste incinerators in the nearby area apparently have released ^{14}C to the local atmosphere beginning in 1995, with a release of unprecedented magnitude in 1999. The evidence for this history is shown by a time series of ^{14}C in cellulose from annual tree rings of a white oak tree on the Walker Branch site (Figure 4). The large 1999 release was discovered by measurements of $^{14}CO_2$ in soil respiration and soil gas as part of this work (see Figure 5). The release(s) appear to have occurred between June 12 and August 22, 1999, although the exact timing, duration, and incinerator(s) responsible are still unknown. According to **Figure 4** (bottom), the enrichment from 1995-1998 appears to be less than 20%, thus data collected from this site through the 1998 growing season will be presented here. At this site, the $\Delta^{14}C$ data from tree ring cellulose (**Figure 4**) is used as a proxy for the local atmospheric ^{14}C beginning in 1990 (instead of the Schauinsland data set).

We have also measured the ^{14}C of deciduous leaves at all three sites as a potential surrogate for the current year's atmospheric ^{14}C signature because they integrate over the growing season (**Figure 6**). However, we do not use these data as local proxies for the atmosphere because data from (McNeely, 1994) show that the ^{14}C signature of maple leaves from Canadian forests lag atmospheric $\Delta^{14}CO_2$ measurements by one to two years. Thus deciduous leaves likely draw from a reserve starch pool and do not necessarily represent CO_2 fixed in that growing season. This is confirmed by data for leaves at Walker Branch that had $\Delta^{14}C$ values between 117‰ and 198‰ throughout all of 1999, despite a midsummer ^{14}C release (see **Figure 4** and **Figure 5**). $\Delta^{14}C$ values of leaves that grew between April and June 2000 were significantly higher, 184‰ to 322 ‰, implying utilization of stored non-structural carbohydrate from the 1999 season. Another reason not to use the leaf values as proxies for atmospheric $^{14}CO_2$ is that most of the leaves we sampled came from the understory and are also likely made with some re-respired CO_2. Comparison of upperstory and understory leaf $^{14}CO_2$ is difficult, because the species of trees in the two canopy positions tend to be different. ^{14}C leaf data taken in the area around the Walker Branch watershed in 2000 shows clear differences in the amount of stored starch used by maple versus oak trees, with the oaks tending to have more of the enriched ^{14}C label, implying that they used more stored starch photosynthesized in 1999. Despite these uncertainties in interpretation of the leaf ^{14}C data, leaves from Walker Branch do appear to be higher than the Schauinsland atmosphere and are more in line with the tree ring cellulose data (**Figure 6**).

Results

Carbon Inputs

Measured leaf litter inputs to the O (organic) horizon increase from north to south, and average 147 ± 28, 184 ± 21, and 227 ± 13 gC m^{-2} for Howland, Harvard Forest, and Walker Branch, respectively, for the periods shown in **Table 3**, largely derived from literature values. The available data on fine root production and root stocks are also shown in **Table 3**. Unfortunately, cross-site comparison is complicated because the size classes measured are not equivalent for roots.

Soil Carbon and Radiocarbon Inventories

Carbon

Soil carbon inventories decrease from Howland to Walker Branch. Total soil C stocks (as an average of all pits dug at each site) decrease from north to south, and are 14.6, 8.4, and 4.9 kg C m^{-2} at the Howland, Harvard Forest, and Walker Branch sites, respectively (**Table 4**, **Figure 7**). At all sites, carbon stocks decrease rapidly with depth from 445-470 gC kg^{-1} dry soil in the O horizons to less than 5 gC Kg^{-1} dry soil for the B horizons (**Table 4** and **Table 5**). At all three sites, a large portion of the carbon (45‰, 80‰, and 60% for Howland, Harvard Forest, and Walker Branch respectively) is in the upper 15 cm, which makes up the organic and upper mineral horizons of the soil profile. The amount of C in the organic (O) horizons varies by an order of magnitude from north to south, with 4.0 kgC m^{-2} (25% of the total C stock) at Howland decreasing to 0.4 kgC m^{-2} (9% of the total C stock) at Walker Branch (**Figure 7**). In Howland particularly, the

O horizon varies considerably in thickness due to hummocky topography, causing large variation in total C stocks.

Most of the SOM in soil profiles at all three sites is low density ($\rho < 2.1$ g/cc) and not mineral associated (high density; $\rho > 2.1$ g/cc). SOM was separated into isolated soil C fractions: recognizable leaf (L_L) and recognizable fine (< 2 mm) root litter (L_R); organic matter transformed by microbial action or humified, but not stabilized by interactions with mineral surfaces (H); and organic matter associated with soil minerals and thus separable by density (M). Specific methods for separating these fractions are discussed in Chapter 2. Low density SOM ($L_L + L_R$ + H) makes up 64%, 80%, and 64% of the total C at Howland, Harvard Forest, and Walker Branch, respectively (**Table 4** and **Table 5**). Humified organic material (H) at Howland, Harvard Forest, and Walker Branch makes up 51%, 88%, and 90% of the total low density C respectively (**Table 4** and **Table 5**)

All three sites contain soils with a significant and spatially variable fraction of coarse fragments (gravel + rocks + coarse organics) throughout the soil profile. At Howland, coarse fragments make up 31% of the total soil volume (Fernandez et al., 1993). At Harvard Forest, in two of the three pits, the O and A horizons had less coarse fragments (0-2%) than the B horizons (10-35%) (see Appendix 2). However, one of the three pits had no less than 15% coarse fragments in all horizons down to 60 cm. At Walker Branch, coarse fragments in the mineral horizons were 10-23% in one pit and 36-46% in another (Appendix 2). As discussed in Chapter 2, accurate quantification of the spatial heterogeneity of rocky soils requires the sampling of large numbers of soil pits (Fernandez et al., 1993, Huntington et al., 1988). Therefore, in this study, instead of quantifying variability within a site, we focus on the C dynamics for specific profiles and assume C dynamics will be the same, even if the inventory of a given SOM fraction varies spatially for sites with similar drainage.

Radiocarbon

The greatest amount of bomb ^{14}C is in the uppermost portion of the soil profile. The $\Delta^{14}C$ of atmospheric CO_2 has decreased from its 1964 peak of 900‰ to between ~ 92-104‰ during the time period of this study (1996-1999). Therefore, SOM measured during this study with $\Delta^{14}C > 92‰$ reflects a dominance of ^{14}C derived from bomb C, while SOM with $\Delta^{14}C < 0‰$ consists primarily of C fixed from the atmosphere before 1960. SOM values between 0-92‰ represent a mixture of pre- and post-bomb C. The distribution of radiocarbon with depth in the temperate forest soils studied here shows that SOM in low and high density fractions is dominated by bomb carbon inputs ($\Delta^{14}C >$ 92‰) in the upper ~ 0-10 cm of the soil profile (measured from the top of the organic horizon), a mixture of pre- and post-bomb C inputs from ~ 10-20 cm, and dominated by pre-bomb C ($\Delta^{14}C < 0$ ‰) below ~ 20 cm (**Figure 8**). The amount of pre-bomb C at depths below 10-20 cm is variable across sites.

Depth Dependence of SOM Fractions

Carbon

Carbon in low density ($\rho < 2.1$ g/cc) fractions generally decrease with soil depth, from 100% in O horizons (by definition) to 93-99% in the uppermost mineral horizon to 20-30% in the B horizons (see **Table 5**; Harvard Forest and Walker Branch pits). An important exception occurs in the Bs horizon of the Spodosol at Howland. The Bs horizon is formed when dissolved organic matter leached from overlying O and E horizons becomes sorbed to minerals at the different pH conditions found in the B horizon. Thus, low density carbon is 57% in the first mineral (E) horizon (**Table 5**; Howland-1996 pit) but increases to 60% and 71% respectively in the Bh and Bhs horizons below.

Radiocarbon

All three sites have overall decreases in $\Delta^{14}C$ with depth in both low and high density fractions below the O horizon (**Figure 9**). **Figure 9** and **Table 6** show the radiocarbon profiles of low density (L_L or H) and high density SOM (M), and fine roots (L_R)**.** In **Figure 9**, the uppermost value in the profile represents the Oi horizon, which is bulk leaf litter that is still recognizable to the species level. The value directly below represents the humified component of the Oe + Oa horizon after roots and recognizable leaf parts have been removed (unless otherwise indicated). The values in the mineral soil represent bulk low and high density SOM samples.

The $\Delta^{14}C$ of low density components within the O horizon at Harvard Forest and Walker Branch are lowest in the Oi layers and increase in the deeper Oe + Oa layers, while Howland shows the opposite trend. In **Figure 9**, all three sites show overall decrease in $\Delta^{14}C$ with depth in the mineral horizons in both low and high density fractions.

An important exception again occurs in the Bs horizon of the Spodosol at Howland, where ^{14}C in bulk SOM is higher than $\Delta^{14}C$ values in horizons immediately above and below. The decrease in $\Delta^{14}C$ of high density fractions with depth is steepest (and very similar) in the Harvard and Howland sites, but much more shallow at the Walker Branch TDE site. Changes in low density fractions with depth are not as consistent as the high density fractions among or between sites. We suspect that heterogeneity in the low density fraction is largely responsible (See Discussion, below).

Fine Roots

In contrast to the $\Delta^{14}C$ of SOM, which decreases with depth and reaches negative values within 10-20 cm, fine root $\Delta^{14}C$ values remain elevated with respect to both high and low density SOM components (**Figure 9**). Fine root $\Delta^{14}C$ values at Howland are 112-182‰, and at Harvard Forest 152-218‰. At both sites, the highest fine root $\Delta^{14}C$ values tend to be at the greatest depths (**Figure 9**). Fine roots, which ideally should be removed from the low density SOM sample, will therefore cause the bulk low density SOM $\Delta^{14}C$ signature to be higher than it would be if the roots were removed completely. The larger the percentage of fine root C in a sample, the more noticeable the effect will be. For example, a sample containing humified low density C with a $\Delta^{14}C$ of –80‰ and fine root C with a ^{14}C signature of 175‰ will have a bulk of -16‰, and 48‰ if fine roots make up 10%, 25%, or 50% of the total low density C respectively. Thus the actual measured $\Delta\ ^{14}C$ signature of the humified SOM located at depth is very sensitive to the amount of fine roots present in the sample.

At Walker Branch, data are not available for the ^{14}C signature of fine roots at depth, although it is likely that roots here follow the same elevated trend as those at Howland and Harvard Forest. Inspection of low density Walker Branch samples did indeed show the presence of fine roots in the low density fraction at all depths for both pits. Thus, inadequate separation of fine roots from the low density samples, especially at the TDE site, is the likely explanation for the continued presence of bomb C with depth at that site.

Heterogeneity of Low Density Fraction

The steady state and non-steady state models that will be used to estimate turnover times of SOM fractions from their $\Delta^{14}C$ values (Chapter 2, equations 11-15) assume that all carbon within a sample is homogeneous with respect to turnover; i.e., although the sample may represent SOM input fixed from the atmosphere over a 10-year period, the entire C sample analyzed is cycling at the same rate. Separation of SOM into truly homogenous pools is unlikely, given the complexity of the medium. However, hand picking for density, size, and/or chemical fractionation do separate SOM into components that have clearly different $\Delta^{14}C$ signatures, and hence C dynamics. (Trumbore and Zheng, 1996) have shown that a series of chemical fractionation processes (involving acid/base hydrolysis) will produce older and older carbon. However, this study is most concerned with SOM that is contributing to soil respiration and decadal cycling C pools, therefore chemical fractionation techniques have not been applied here.

In an effort to isolate components with different characteristic turnover times (homogenous C pools), we sieved the low density portion of mineral samples with an 80 μ sieve at all sites (**Table 7**). At Harvard Forest and Walker Branch, we additionally removed roots by hand (**Table 7**). In all cases, the < 80 μ material has lower ^{14}C values relative to the > 80 μ fraction. The resulting differences in steady state turnover times range from 10 years for the < 80 μ fraction to 320 years for the > 80μ fraction. Calculation of mass-weighted $\Delta^{14}C$ values for the low density fractions are dominated by the > 80µ material that makes up most of the mass (**Table 7**, Composite $\Delta^{14}C$). Much of the material in the > 80µ fraction is fine root material. In the A horizons at Walker Branch (TDE) and Harvard Forest, roots make up 16‰ and 7% of the total sample mass and have ^{14}C signatures elevated by 80‰ and 130‰ relative to the > 80 µ fraction at each site respectively. Removing roots decreases the composite $\Delta^{14}C$ by 18‰ for Walker branch and 10‰ for Harvard Forest.

Age of Litter Inputs

A key uncertainty in using ^{14}C to interpret dynamics, particularly on short timescales (1-10 years), is the $\Delta^{14}C$ value assigned to plant detritus inputs to the SOM pool. $\Delta^{14}C$ values may not reflect the $\Delta^{14}C$ of atmospheric CO_2 of the year they are input into SOM for one of two reasons: 1) plant tissues may spend several years as live biomass prior to death and input to SOM stocks, and 2) plant tissues may have originally been constructed from starch pools stored in the plants for several years. The steady state and non-steady state models discussed in Chapter 2 assume that plant tissues live for only one year, and that their carbon has the $\Delta^{14}C$ signature of that year. If either of these assumptions is untrue, lags between atmospheric fixation and input into SOM are introduced, and the ^{14}C-derived turnover time will be overestimated by an amount roughly equal to these lags (i.e., the lifetime as live biomass, the age of the C reservoir, or the sum of both).

In an effort to quantify the effects of lagged ^{14}C inputs to the soil system, we measured the ^{14}C of the inputs to the soil system at Howland (from archived 1992 litter) to see how they compare to the ^{14}C of atmospheric CO_2. In 1992 at Howland Forest, aboveground litter was collected (by Ivan Fernandez and co-workers) and sorted quantitatively into four categories: 1) coniferous litter; 2) deciduous litter; 3) fine woody debris (sticks and twigs); and 4) miscellaneous (unsortable remains). The ^{14}C values and associated turnover times (which in this case correspond to the lag time between fixation from the atmosphere and input to SOM) for 1992 are shown in **Table 8**. Inspection of these data, which range from 132‰ to 287‰, relative to the 1992 atmosphere (134 ± 4‰), clearly show a significant lagtime between photosynthetic fixation and input of C to the soil as litter for all components except deciduous leaves. Coniferous litter, fine woody debris, and "miscellaneous litter" have lags times of 3, 15, and 5 years respectively. Fine roots also represent a lagged input of ^{14}C to the soil system (see Chapter 4).

Quantification of time lags will be very important in interpreting Δ^{14}C values in terms of a turnover time for a given SOM fraction in the next section.

Archived Soils

Radiocarbon values for archived soils dug in the early 1970s (Walker Branch) and late 1980s (Howland) are elevated relative to those dug in the late 1990s (all three sites) for low and high density SOM fractions (**Table 9**). This trend is exactly as we would expect based on the known record of the Δ^{14}C of atmospheric CO_2 (see Chapter 2, **Figure 1**). Similar to the modern soils, the < 80μ fractions also have less ^{14}C enrichment than the > 80μ fraction.

Discussion

Radiocarbon Derived Dynamics

Soil organic matter stocks reflect a complex milieu of inputs from leaf litter, root litter, and woody debris that have turnover times ranging from days to millennia. Carbon reservoirs, such as SOM that exchange with the atmosphere, reflect the rate of exchange through the amount of bomb ^{14}C incorporated (Chapter 2, Figure 1). The ^{14}C signature of decomposing SOM will range from the current atmospheric value (~ 92‰ in 1999) to

-92‰, and < 0 ‰ for SOM cycling on decadal, centennial, and millennial timescales respectively. SOM with Δ^{14}C between 0-92 ‰ in 1999 may also be a mix of decadal- and millennial-cycling material.

The three sites studied here have different amounts of decadal- versus longer-cycling C stocks (**Figure 8**) that reflect the overall C cycling rates at each site. The amount of decadal cycling low density C present in the top 10 cm of the soil profile at Howland (O and E horizons) and Harvard Forest (O + A + Ap horizons) is 4500 and 4000 g C m^{-2} respectively. In contrast, Walker Branch contains an order of magnitude less decadal cycling low density C in the top 10 cm (O + A horizons; 440 g C m^{-2}). Because litter inputs increase from Howland to Walker Branch, the presence of larger stocks of low density C and ^{14}C in the uppermost horizons at the two northern sites indicate clearly that they cycle C more slowly than the Walker Branch site. At Howland and Harvard Forest, decadal cycling SOM is present to ~ 10cm depth, while at Walker Branch it is present to only 5 cm depth before centennialcycling SOM becomes dominant. Between 10-20 cm, both low and high density C and ^{14}C stocks decrease, with millennial cycling becoming dominant by 20 cm at both northern sites. The ^{14}C content of low and high density SOM at Walker Branch indicates centennial scale cycling from 5 to 38 cm. However, it is likely that fine roots in the low density samples have artificially elevated the ^{14}C signature at depth.

Turnover Times of SOM Fractions

To quantify SOM dynamics more accurately than is shown in **Figure 8**, the $\Delta^{14}C$ of isolated SOM fractions with similar cycling rates must be used with a model that uses the record of ^{14}C in atmospheric CO_2 to estimate turnover times of SOM fractions (see Chapter 2 for details of the model(s)). The ^{14}C-derived turnover time of a bulk sample is not a good predictor of cycling rates if the bulk sample contains components that cycle at different rates (i.e., less than 10 years and 10-100+ years). Failure to adequately separate SOM typically causes an under prediction of the rate of SOM response to changes in inputs or loss. This is because the ^{14}C of a bulk measurement will be dominated by the SOM fraction with the largest inventory, which is generally the most recalcitrant portion of the SOM. Faster cycling components decompose rapidly when formed and make up a small portion of the total SOM. Thus their ^{14}C signature is "lost" in the measurement.

The effect of lagged ^{14}C inputs (from either plant tissues that spend several years as live biomass prior to death and input to SOM stocks or plant tissues originally constructed from stored starch pools) on the measured $\Delta^{14}C$ signature of SOM must also be accounted for. Several litter components have lifetimes as live tissue prior to being input to the soil system. Coniferous needles tend to live on the tree for 1-3 years and up to 13-20 years in boreal forests (Trumbore and Harden, 1997) prior to falling to the soil surface. In contrast, deciduous leaf litter stays on the tree only one growing season. Fine woody debris at Howland lives on average 5 years (**Table 8**), and coarse woody debris can live for many tens to hundreds of years, depending on species, forest health, and forest management. Roots can live in the soil system for 1-40+ years, depending on size class and functional type. In fact, as discussed in Chapter 2 and Chapter 4, it appears that the bulk of fine root stocks < 2 mm in diameter live an average of 5-10 years. The effect of lagged root inputs is most significant where decomposing roots contribute the most to soil carbon stocks (i.e., the Oe + Oa and A horizons). Below the A horizon, root inputs decrease, SOM cycles much more slowly, and the effect of ^{14}C lags from root inputs on estimates is minimal if the soil fractions have been adequately homogenized and fine roots removed. We expect the effects of lagged leaf litter inputs to be greatest at Howland (where 52% and 16% of aboveground litter inputs were from coniferous and deciduous species respectively) and decrease along the latitudinal gradient from Howland to Walker Branch as the ratio of coniferous trees to deciduous trees decreases. However, the effect of lags due to fine roots will be more consistent across sites (see Chapter 4).

The significance of these potential lags to the ^{14}C modeling and turnover time estimates depends on the timescales of the particular SOM pool. For SOM decomposing on 1-30 year time scales, these lags are significant because they are similar to the turnover time inferred from ^{14}C. These lags are much less significant for humified SOM decomposing on 50-100+ year time scales (**Figure 10**).

The turnover times and SOM flux numbers presented in this section are based on the ^{14}C values of fractions shown in **Figure 9** and **Table 6**, using the steady state and non-steady state (Harvard Forest only) modeling methods discussed in Chapter 2. The non-steady state model is used only for the Oe + Oa and A horizons at Harvard Forest because this is the only site with a relict plow layer (Ap horizon) and a known time of agricultural abandonment. Thus we can parameterize a non-steady state model which uses the amount of C accumulated since agricultural abandonment and its ^{14}C signature.

Also utilized are comparisons of pits dug during this work with $\Delta^{14}C$ signatures for archived soils for both the Howland and Walker Branch sites (**Table 9**). Combining $\Delta^{14}C$ data for modern and archived soils allow for more accurate quantification of SOM cycling rates than using data from only a single time point (Trumbore, 1993). Archived soils are particularly important in the organic horizons, where $\Delta^{14}C$ values are typically above 100‰ and have two potential turnover time solutions (Chapter 2, Figure 5) that usually differ by a factor of ten or more. By having ^{14}C samples from two time points post-1963 (preferably one in the mid 1970s), a unique turnover time can be chosen (**Figure 11**).

Organic Horizons

Oi Horizon - Without ^{14}C Lags

The turnover times for C in the uppermost Oi horizon are 12, 4, and 5 years at Howland, Harvard Forest, and Walker Branch respectively (based on averaging the ^{14}C-derived turnover times for two pits at each site; **Table 6**) if lagged ^{14}C inputs to the system are not accounted for. **Table 6** shows for all three sites two sets of ^{14}C-derived turnover times for the Oi horizon (short and long). At all three sites, the shorter turnover times are chosen based on either flux considerations, or archived soils data if available. For example, the shorter turnover time is selected at Harvard Forest based on steady state flux considerations. Dividing inventory by turnover time yields fluxes of 95 or 5 gC m^{-2}

y^{-1} for a stock of 375 gC m^{-2} and turnover times of 4 vs. 64 years respectively. The larger flux is chosen as a more reasonable annual estimate of litter decomposition fluxes (although problems with these flux estimations will be discussed below). At Walker Branch, the 1998 pit also has two possible turnover times for Oi of 5 or 68 years (**Table 6**). The same argument based on fluxes can be made, but we also archived soils from 1972 (for pit P5). **Figure 11** shows how helpful archived soils can be in determining which turnover time is most appropriate. Addition of the $\Delta^{14}C$ signature for the Oi in the 1972 archived soils indicates that the 5 year turnover time curve and not the 68 year curve fits the ^{14}C data for both points in time. Thus it is clear that the shorter turnover times are the correct choices.

Oi Horizon - With ^{14}C Lags

At Howland, we have estimated a 5 year lag between photosynthetic fixation and input of organic matter to the soil system based on measurements of aboveground litter input rates and their ^{14}C values (**Table 8**). Correcting for this lag in ^{14}C input at Howland, we estimate the turnover time of SOM in the Oi horizon to be 7 years (instead of 12 years). At Harvard Forest and Walker Branch, we are unable to correct for the effect of lagged ^{14}C inputs because we do not have quantitative C and ^{14}C measurements of aboveground litter inputs. Thus the estimated 4 and 5 year turnover times for Harvard Forest and Walker Branch respectively, based on bulk measurements of the Oi horizon, are upper bounds and should not be used to estimate decomposition fluxes based on Oi stock divided by turnover time. Even the lag corrected 7 year turnover time for Howland is likely to be inappropriate for calculating decomposition fluxes for the Oi as a whole because the correction averages over the varying lifetimes of all the inputs.

The inappropriateness of ^{14}C measurements of Oi material for estimating short timescale dynamics or CO_2 fluxes of leaf litter is reiterated by analysis of literature derived values for leaf decomposition. Leaf litter decomposition studies in temperate forests have reported decomposition rates of 1.2 to 2.5 years for deciduous and coniferous species based on constant mass loss over time (Aber et al., 1990, Dwyer and Merriam, 1984, Knutson, 1997) and 2.9 to 5.6 years if a two phase model of mass loss (which assumes decomposition slows dramatically after the first year) is used (Berg et al., 1996). Our turnover times for Howland (7 years lag corrected) Harvard Forest (4 years) and Walker Branch (5 years) agree fairly well with the longer 2.9- to 5.6year estimates. However, the Oi is defined as litter that is fresh or fairly undecomposed (and the species is easily identifiable) and therefore is not likely to include litter that has been on the surface for several years and undergone a large degree of decomposition (such litter would be sampled as Oe and/or Oa). Thus the constant mass loss estimates from the literature are likely more appropriate to estimate turnover times (and decomposition fluxes) for the Oi relative to two phase litter decomposition models and ^{14}C measurements of the Oi horizon material.

Oe + Oa Horizon - Without ^{14}C Lags

The turnover times for the humified portion of the Oe + Oa horizons (**Table 6**) are fairly similar between the Howland and Harvard Forest sites (15-50 and 40 years respectively), given the large degree of heterogeneity in those horizons but decrease significantly at Walker Branch (7-15 years). Interpretation of the archived soils data from the Howland 1988 pit with the 1997 pit is a bit more difficult than for the Walker branch Oi example discussed above. In both the 1997 and 1988 data at Howland, there are two choices for each ^{14}C value (**Table 9**). However, by fitting one curve to both sets of data, the best fit for the < 80 micron fraction is clearly the longer turnover time (33 years) and for the > 80 micron fraction (which contains fine roots) it is 10-15 years (**Figure 11**). Clearly, assuming a steady state, a humified component (< 80μ) in the Oe + Oa horizon at Howland is turning over at 30+ years. If the Oe and Oa horizons are accumulating C, which is likely, the turnover of this humified component is even longer. A key point in inspection of the Oe + Oa data for the 1988 and 1997 pits is that both archived data and size fractionation were needed to clearly see that a portion of the SOM is turning over on 30+ year timescales in these very heterogeneous horizons.

At Harvard Forest, the turnover time of 40 years in the Oe + Oa represents the average non-steady state turnover time for pits NWN 1 (28 years) and NWN 2 (50 years). See **Table 6**. For comparison, the steady-state turnover times for the NWN 1 and NWN 2 pits are 20 and 38 years respectively.

At Walker Branch, the ^{14}C-derived turnover time using the 1998 P5 pit data alone, is 7 or 55 years. For the 1972 P5 pit it is 13 years (**Table 9**). Combining the 1972 and 1998 data clearly shows that the appropriate turnover times for the Oe + Oa horizons at Walker Branch are 7-15 years, and not the longer 55 year turnover time (**Figure 11**). The Δ^{14}C for the bulk Oe + Oa at the TDE site is 136‰ (**Table 6**), which corresponds to a turnover time of 6 years (using the shorter of the two values) and thus is in very good agreement with data from the P5 site. Although the data for the Oe + Oa horizons in **Table 6**, **Table 9**, and **Figure 11** for the P5 site are for the bulk Oe + Oa, picking of O horizon material from the TDE site yielded ^{14}C values that only ranged between 130‰ and 136‰ in 1998 for all components in the sample. Thus the O horizon material at

Walker Branch shows less variation with respect to its ^{14}C signature and SOM dynamics, both within a site and across sites.

In the Oe + Oa horizons, turnover times of the humified fraction show a clear difference in variability of turnover with a trend toward decreasing turnover between the two northern sites, Howland and Harvard Forest, and the southernmost Walker Branch site (**Figure 12**). Thus the northern sites have Oe + Oa horizons containing significant humified C stocks with C cycling rates on 30-50+ year time scales, while the Walker Branch Oe + Oa horizons have much smaller humified C stocks and store carbon for a maximum of 7-15 years. Lagged inputs of ^{14}C to the Oe + Oa horizon means that these turnover times are overestimations equal to the lifetime of the material as live tissue.

The O horizons (Oi + Oe + Oa) in temperate forests are heterogeneous in nature and contain organic matter that decays both quickly (months) and very slowly (decades). Separation of O horizon components by size and hand picking to remove roots is important in order to recognize and estimate these components and their variable cycling rates. How extensively and carefully a sample is separated will significantly affect the ^{14}C of the measured components. In addition, prior to input to SOM, leaves, roots, and woody inputs may have had lifetimes as live tissue of 1-3, 1-10, and 10+ years respectively. The ^{14}C added to SOM will lag behind the contemporary ^{14}C of atmospheric CO_2 by the length of this lifetime as live tissue. Thus the difficulty of separating O horizons into components with homogenous cycling rates, and the potential for lagged ^{14}C inputs to SOM, make ^{14}C-derived turnover times of O horizon components inappropriate for estimating short timescale (< 10 years) decomposition fluxes (based on stock divided by turnover time).

Mineral Horizons

Turnover times for low density mineral horizons range from 70-100 years in the A horizons, 135 to 245 in the Ap/E horizons, and 550 to 2000 years in the B2 horizons (**Table 6** and **Figure 12**). Values for a given site represent the average of a similar horizon for the two pits. No trend towards increasing turnover times as a function of latitude is apparent. As previously discussed, low density Δ^{14}C values, and hence the ^{14}C-derived turnover times, are sensitive to the amount of fine roots in the sample. Because the less than 80µ size fraction sieving was not isolated on all low density samples in mineral horizons, the composite Δ^{14}C and mass weighted turnover time values (from **Table 7**) are shown in **Figure 12** for the samples at Howland (NC) and Walker Branch (P5) (where sieving was done) in order to compare consistent sample types across all three sites. The idea that fine roots significantly affect the low density ^{14}C values and turnover times is qualitatively supported by the 1972 and 1998 low density data at the Walker Branch P5 site in **Table 9**. The calculated turnover times based on Δ^{14}C values in 1972 are all less than those based on Δ^{14}C values in 1998 by 100 to 1300 years. If fine roots have ^{14}C lags on the order of 5-10+ years, their ^{14}C signature in 1972 and 1998 will be on the order of 500 ± 100‰ and 150 ± 50‰ respectively. Thus, for the same amount of total C input, the 1972 roots would cause a much larger ^{14}C input to the sample and cause greater elevation of the ^{14}C signature of a bulk low density sample, resulting in a faster turnover time. Because of the effect of ^{14}C input from fine roots and low density samples from mineral horizons, like those from the O horizon, are also affected by how they have been processed (i.e., sieved, or not sieved; hand picked for roots, or not).

High density carbon turnover times range from 150-175 years in the A horizons, 210-285 years in the Ap/E horizons, and 1000-1600 years in the B horizons. There is no significant difference in turnover between the two northern sites, which have similar age and parent material. However, Walker Branch does have turnover times on the order of 500 years less in the B horizons. Visual inspection of high density samples shows no fine roots present. So it is likely that the differences seen in the high density samples across sites are real and related to differences in mineralogy and site history (Torn et al., 1997, Trumbore, 2000).

Coarse Woody Debris

One aspect of the litter system that is not dealt with at any of our three sites is coarse woody debris, such as branches and logs. Decomposition of coarse woody debris will add SOM whose $\Delta^{14}C$ is lagged significantly (5-100 years) relative to the current atmosphere. With respect to the three sites studied here, dead wood inventories decrease from north to south. Preliminary estimates of dead wood biomass from a survey done by Eric Davidson and co-workers at Howland are 12 Mg C/ha (wood > 5 cm diameter). At Harvard Forest, preliminary estimates, from a survey still being completed by Steve Wofsy and co-workers, are 2 MgC/ha (wood > 7.5 cm diameter). At Walker Branch, estimates of dead wood biomass are 2.3 Mg C/ha for chestnut oak stands (wood > 2.5 cm diameter (Johnson and Van Hook, 1989). These surveys have large uncertainties, and were done with different methods. Therefore, they are not strictly comparable. However, they do support the qualitative conclusion (easily observable by walking around the sites) that stocks of coarse woody debris decrease from north to south. The impact of dead wood inputs to SOM and decomposition fluxes may represent as much as 20% of the total soil flux at Howland (Sue Trumbore and Eric Davidson, unpublished data). The contribution at our other sites is unknown, but is likely greater because stocks are less (implying a higher decomposition flux). Estimates should be made in future studies to determine any latitudinal gradients in dead wood inputs to soil respiration, because this is a component of soil respiration that is poorly parameterized in ecosystem models.

Flux Calculations

As discussed above, ^{14}C-derived estimates of turnover time are not reliable for estimating decomposition fluxes for SOM cycling at rates faster than ten years. Therefore we estimate SOM decomposition fluxes (from both low and high density components combined) based on dividing stocks by ^{14}C-derived turnover times for the humified low density and mineral associated SOM of the Oe + Oa and mineral horizons only (where turnover times are decadal or greater; **Table 6** and **Figure 13**). Fluxes range from 30-50 gC m^{-2} y^{-1} in the Oe +Oa horizons, 20-30 gC m^{-2} y^{-1} in the A horizons, 2-12 gC m^{-2} y^{-1} in the Ap/E horizons, and are less than 2 gC m^{-2} y^{-1} in the lowermost B horizons. The total calculated fluxes are 70, 62, and 99 gC m^{-2} y^{-1} for Howland, Harvard Forest, and Walker Branch respectively. Of these fluxes, 66%, 46%, and 53% come from the Oe + Oa horizon; 14%, 53%, and 45% come from the A + E horizons; and 20%, 1%, and 2% come from the B horizons at Howland, Harvard Forest, and Walker Branch respectively.

C Accumulation Potential at All Sites

Soils

In temperate forests, the potential for C accumulation in soils on human timescales lies predominantly within low density humified organic components that have decadal and centennial cycling rates. Detrital C, such as leaf litter in the Oi horizon, will be a poor C sink because it cycles quickly (1-10 years), has small C stocks, and reaches steady state within years to decades. The Oe + Oa and A horizons, however, have sufficient C stocks and decadal turnover times and therefore the potential to store significant amounts of carbon on human timescales. The deeper mineral horizons, despite their large stocks, have long turnover times (200-2000 years) and can store C effectively only over millennia.

The most likely scenario driving C sequestration in the coming century will be increases in forest NPP (due to CO_2 or N fertilization) that will be larger than any decreases in overall turnover times (i.e., increased decomposition rate due to increases in mean annual temperature or precipitation changes). Assuming no change in SOM decomposition rates, C storage within a 50-100 year period will be largely in the Oe + Oa horizons (with turnover times from 7-50+ years). Largest C accumulation rates will occur at Howland and Harvard Forest, which have larger Oe + Oa horizon stocks with significantly longer turnover times relative to Walker Branch (**Figure 8** and **Figure 12** Top). On longer time scales, the A horizons will contribute the most to C storage.

The well-drained Oe + Oa and A horizons at Harvard Forest have accumulated a total of 4.4 kgC m^{-2} above a relict plow layer since the late 1800s. This is roughly half the carbon in the soil profile. If the accumulation rate were constant, these soils would be currently accumulating about 37 gC m^{-2} y^{-1}. The turnover time of much of the accumulated material is < 10 years. Hence, some of the SOM fractions have achieved steady state, and we estimate the current rate of accumulation is 10-30 gC m^{-2} y^{-1}. This rate (in the absence of an NPP increase) is likely to decrease further in the future. The other two sites do not have a plow layer, and therefore we must assume they are at steady state over historical time.

If there is a 10% increase in NPP at all sites, we predict C storage over the next century of 650, 380, and 245 gC m^{-2} at Howland, Harvard Forest, and Walker Branch respectively (**Figure 14** Top). Estimates are made using our model with four SOM pools (see **Table 10** for the steady state SOM stocks, inputs, and turnover times used to initialize the model). The additional C accumulation expected at Harvard Forest as it continues to recover from past disturbance will add another 10% to the increase shown in **Figure 14**. The rate of C accumulation is actually greatest in the first year at Harvard Forest and Walker Branch. However, this quickly decreases with time (**Figure 14** bottom). The e-folding time for each site is 59, 65, and 40 years for Howland, Harvard Forest, and Walker Branch respectively (taken as years to achieve 1/e of the rate of change after the first year, because the first year is such a large "step"). It is clear from **Figure 14** that C storage potential decreases from north to south, is greatest at Howland, and least at Walker Branch.

Soils Versus Forest Biomass

The three temperate forests studied here are currently storing 210, 200, and 525 gC m^{-2} y^{-1} for the Howland, Harvard Forest, and Walker Branch sites respectively, according to eddy flux measurements (**Table 1**). Partitioning of this storage between soils and live biomass is largely unknown and has been a goal of this work. At Harvard Forest, well-drained soils are responsible for storing 10-30 gC m^{-2} y^{-1}, or 5-15% of this net flux (Chapter 2). Scaling from the modeling scenario shown in **Figure 14**, well-drained soils at Howland are sequestering between 15-50 gC m^{-2} y^{-1} (25% of the net flux) and 5-20 gC

m^{-2} y^{-1} (1-5% of the net flux) at Walker Branch. Thus the well-drained soils at these sites are not responsible for the majority of the measured net uptake. It is likely that most of the flux is going into live biomass (wood) as the forests continue to mature. An alternative sink for the two northern sites may also be uptake by poorly drained soils and swamps, because both Howland and Harvard Forest have such areas within the footprint of the on-site eddy flux towers. However, at the Walker Branch site such large gradients in soil drainage are not present, therefore uptake by live woody biomass is the most plausible explanation for the measured sink.

Terrestrial ecosystems are estimated to be responsible for an annual C uptake of 1.8 ± 1.6 GtC y^{-1}, and temperate forests for 0.5 ± 0.5 GtC y^{-1}. Applying the total range of estimated soil C sinks at these three sites (5-50 gC m^{-2} y^{-1}) to the land area of temperate forests in the continental United States (241 Mha; (Dixon et al., 1994) yields a C sink of 0.01-0.1 Gt C y^{-1}, or 2-20% of the total ascribed to temperate forests globally and 0.6-6% of the total terrestrial C uptake.

Conclusions

The components of soil C can be split into three components with characteristically different turnover times: 1) low density ($\rho < 2.0$ g/cc) detrital material (recognizable leaves and roots) with turnover times ranging from one to ten years, 2) low density humified material with much longer turnover times ranging from tens to hundreds of years, and 3) high density ($\rho > 2.0$ g/cc) mineral associated SOM with turnover times ranging from hundreds to thousands of years.

Carbon inventories decrease from Maine to Tennessee by a factor of three. Much of this trend is due to decreasing C stocks in the O horizons of the soil profiles where there is a large change in both turnover time and the type of SOM present. Both Howland and Harvard Forest have large humified C stocks in the O horizons with long turnover times (15-50 years). At Walker Branch, this humified component is largely absent in the O horizon, where total stocks are small, primarily detrital, and turnover times are much shorter (7-15 years).

In the mineral horizons there is not a clear trend in SOM turnover time across sites for either the low or the high density components. The absence of such a trend for the low density material may in large part be due to the processing of the low density samples being not consistent across sites. The presence of fine roots can increase the $\Delta^{14}C$ value of the low density fraction, leading to a decrease in estimated turnover times relative to the actual value for the humified portion. Size separation (sieving with an 80 μ sieve) is an effective way to differentiate samples. However, the presence of fine roots is still problematic, particularly for the > 80μ size fraction. We have found that a combination of sieving and hand picking is the best way to isolate the most humified portion of a sample. The lack of a latitudinal trend in the high density (mineral associated) SOM may be due to differences in soil age and mineralogy between the two northern sites, which are quite similar, and the southern site, which is much older with very different mineralogy.

When using ^{14}C to understand SOM dynamics on short timescales (1-10 years), it is important to consider time lags between photosynthesis and respiration of SOM (i.e., the amount of time C spends in living plant tissue prior to senescence and addition to

SOM pools). Failure to do so will yield an accurate estimation of the amount of time the measured carbon spent in the plant + soil system, but will cause an overestimation of decomposition rates within the soil system alone. The overestimate will be roughly equal to the amount of time spent as live plant tissue prior to addition to SOM. To correct for this time lag, measurements of ^{14}C in the litter components input to the system are required.

Relatively small C pools with fast turnover times, such as detrital leaf and fine root litter, dominate decomposition fluxes. These are also the pools that are most sensitive to time lags between photosynthetic fixation and input to SOM. Therefore, their ^{14}C signature is unsuitable for accurately determining decomposition fluxes (based on stock divided by a ^{14}C-derived turnover time) and their overall contribution to soil respiration on annual timescales. ^{14}C measurements for SOM are best for determining longer-term decadal and millennial cycling material. However, this, too, can easily be confounded by insufficient sample fractionation.

On human timescales, significant C accumulation in these temperate forest soils will happen only in the O and A horizon, which have significant C stocks that cycle on decadal and centennial timescales. As such, soils of more northern sites, such as Howland and Harvard Forest, have a greater C storage potential than more southern sites, like Walker Branch. Currently well-drained soils in all of the eastern temperate forests studied here account for an uptake of 5-50 gC m^{-2} y^{-1} or 1-25% of the measured net ecosystem C uptake at each of the sites. Extrapolating globally, temperate forest soils may account for 0.6-6% of the total attributed to terrestrial C uptake.

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Table 1. Site characteristics.

Location	Dominant Species	Soil Type	Latitude	MAT (°C)	MAP (mm)	Stand age (Years)	NEP (gC m^{-2} y^{-1})
Howland, ME	Red Spruce, Eastern Hemlock	Typic Haplorthods	45°N	5.5	1000	100	210[1]
Harvard Forest, MA	Red Oak, Red Maple	Typic Distrochrepts	42°N	8.5	1050	50-70	200[2]
Walker Branch, TN	White Oak, Red Maple	Typic Paleudults	36°N	14.1	1360	80-120	525[3]

[1] Hollinger et al. 1999

[2] Goulden et al. 1996

[3] Greco and Baldocchi 1996

Table 2. Soil pits excavated at each site.

Site	# Pits	Pit Names (year dug)	Dug Quantitatively	Archived Soil
Howland, ME	2	Tower (1996), NC (1997)	No	Yes (1988 NC site)
Harvard Forest, MA	3	NWN 1 (1996), NWN 2 (1996), NWN 3 (1997)	Yes	No
Walker Branch, TN	2	P5 (1998), TDE (1998)	Yes	Yes (1972 P5 site)

Note: The NWN 3 pit was only dug to the base of the A horizon.

Table 3. Litter inputs to all three sites.

Above ground litter inputs (g C m^{-2} yr^{-1})[1]

Site	**1996**	**1997**	**1998**	**1999**	**Source**
HOW		122 (45)	142 (43)	177 (24)	E. Davidson's group (pers. comm.)
HF	157	185	208	185	E. Davidson's group (pers. comm.)
WB	242 (45)	234 (44)	214 (45)	218 (36)	P. Hanson (pers. comm.)

Fine root inputs and stocks

Site	**Inputs** (g C m^{-2} yr^{-1})	**Stocks[2]** (g C m^{-2})	**Size**	**Year Measured**	**Source**
Howland, ME	NA	846 (34)	> 5 mm	1987/88	Fernandez et al. 1993
Harvard Forest, MA	270	525 (60)	< 3 mm	1978/79	McClaugherty et al. 1982
Walker Branch, TN	NA	260 (25)	< 2 mm	1993	Joslin and Wolf 1999

Values in parentheses represent one standard deviation

[1] Assumes litter is 47% carbon.

[2] Live + dead fine roots

Table 4. Average carbon inventory at all three sites.

						--------------Low Density SOM--------------			--High Density SOM--
Site	**Horizon**	**Bulk Density[1] (g cm^{-3})**	**Soil Carbon (g C Kg^{-1} soil)**	**Bottom Depth (cm)**	**Total C Stock[2,3] (g C m^{-2})**	**Leaf Litter LL[4,5] (g C m^{-2})**	**Fine Root Detritus LR[4,5,6] (g C m^{-2})**	**Humified H[5,7] (g C m^{-2})**	**Mineral Associated M[5] (g C m^{-2})**
Howland	Oi + Oe + Oa	0.12	444	6	4026	NA	NA	NA	NA
Howland	E	1.03	31	11	457	--	55	263	139
Howland	5 cm below E	0.65	59	16	2121	--	46	1419	657
Howland	5-40 cm	0.89	15	40	4113	--	233	2046	1834
Howland	40 cm to C	1.39	5	69	3896	--	129	934	2833
Total					**14614**	**4026**	**463**	**4662**	**5463**
Harvard Forest	Oi	--	446	2	375	375		--	
Harvard Forest	Oe + Oa	--	469	6	1801	--	230	1571	
Harvard Forest	A	0.34	272	10	1810	--	60.0	1737	13
Harvard Forest	Ap	0.54	60	14	2748	--	70.0	2114.0	564.0
Harvard Forest	Bw1	0.86	19	32	1122	--	4.0	334.5	783.0
Harvard Forest	Bw2	0.93	6	59	517	--	1.0	149.0	367.0
Total					**8372**	**375**	**365**	**5905**	**1727**
Walker Branch	Oi		456	2.3	195[8]	195			
Walker Branch	Oe + Oa		378	4.0	240[8]	--		240	
Walker Branch	A	0.48	127	7.5	1960	--	109	1793	58
Walker Branch	E	1.01	7	37.0	1878	--	22	667	1189
Walker Branch	B1/Bt1	1.16	3	55.5	660	--	0	166	495
Total					**4933**	**195**	**131**	**2866**	**1742**

NA = Not availible

1 Gravel free bulk density (i.e. less than 2mm).

2 Includes live root mass below the Oi horizon.

3 Oi and Oe horizons calculated on a per area basis and BD is not used for these horizons except those at Howland, Maine.

4 On a dry weight basis.

5 Low density means $\rho < 2.1$ g/cc, high density $\rho > 2.1$ g/cc.

6 Fine root data are from individual pits for Oak Ridge (sorting techniques are not reliable); from McClaugherty et al. 1982 for Harvard Forest; and from Fernandez et al. 1993 For the Howland Tower site and Ivan Fernadez personal communication for the Howland, NC site (these data are specific to this pit originally dug in 1998).

7 Calculated by subtracting total roots from the total low density SOM.

8 Data from TDE site only, from Paul Hanson personal communication for 15 samples taken February 8, 1999.

Note: For Howland, data shown represents an average for two pits.

Table 5 (page 1 of 3). Carbon inventory for all pits.

						--------------Low Density SOM--------------			**--High Density SOM--**
Site Pit	**Horizon**	**Bulk Density[1] (g cm^{-3})**	**Soil Carbon (g C Kg^{-1} soil)**	**Bottom Depth (cm)**	**Total C Stock[2,3] (g C m^{-2})**	**Leaf Litter LL[4,5] (g C m^{-2})**	**Fine Root Litter LR[4,5,6] (g C m^{-2})**	**Humified H[5,7] (g C m^{-2})**	**Mineral Associated M[5] (g C m^{-2})**
Howland, ME									
Tower	Oi	0.14[8]	493	1	**897**	897	--	--	--
	Oe	0.14[8]	478	4	**2075**		230	1845	--
	Oa	0.14[8]	443	9	**2897**		230	2667	--
	E	1.03[8]	5	17	452		92	167	193
	Bhs	0.65[8]	69	19	922		23	532	367
	Bh	0.65[8]	61	23	1616		23	1130	463
	Bs1	0.89[8]	15	31	1341		184	467	691
	Bs2	1.39[8]	13	40	1722		46	574	1102
	BC	1.39[8]	2	73	4792		unknown	934	3858
Total					**16713**				
Howland, ME									
NC	Oi + Oe+Oa	.12[8]	**425**	4.2	**2183**	2142	41.4	--	--
	E	.52[8]	57	5.7	**463**		18.4	360	85
	5 cm below E	.67[8]	53.9	10.3	**1705**		45.08	1176	484
	5-40 cm	.98[8]	16.8	40.3	**5163**		236	3052	1876
	40 cm to C	1.36[8]	8.5	65.1	**3000**		129	unknown	unknown
Total					**12514**				

1 Gravel free bulk density (i.e. less than 2mm).
2 Includes live root mass below the Oi horizon.
3 Oi and Oe horizons calculated on a per area basis and BD is not calculated for all pits except those at Howland, Maine.
4 On a dry weight basis.
5 Low density means r < 2.1 g/cc, high density r > 2.1 g/cc.
6 Fine root data are from individual pits for Oak Ridge (sorting techniques are not reliable); from McClaugherty et al. 1982 for Harvard Forest; and from Fernandez et al. 1993 For the Howland Tower site and Ivan Fernadez personal communication for the Howland, NC site (these data are specific to this pit originally dug in 1998).
7 Calculated by subtracting total roots from the total low density SOM.
8 Gravel free bulk density (i.e.< 2mm) from Fernandez et al. 1993.
9 Gravel free bulk density (i.e. < 2mm) from Ivan Fernadez personal communication (these data are specific to this pit originally dug in 1998).

Table 5 (continued, page 2 of 3). Carbon inventory for all pits.

						-------------Low Density SOM-------------			--High Density SOM--
Site Pit	Horizon	Bulk Density^1 (g cm^{-3})	Soil Carbon (g C Kg^{-1} soil)	Bottom Depth (cm)	Total C Stock^{2,3} (g C m^{-2})	Leaf Litter LL^{4,5} (g C m^{-2})	Fine Root Litter LR^{4,5,6} (g C m^{-2})	Humified H^{5,7} (g C m^{-2})	Mineral Associated M^5 (g C m^{-2})
Harvard Forest, MA									
NWN 1	Oi	--	465	2	360	360	--	--	--
	Oe + Oa	--	463	6	1546		230	1316	--
	A	0.41	245	8	1367		60	1295	12
	Ap	0.67	61	14	3607		70	2961	576
	Bw1	0.79	20	30	1135		4	315	816
	Bw2	0.89	7	60	628		1	170	457
Total					**8643**				
Harvard Forest, MA									
NWN 2	Oi	--	426	1	450	450	--	--	--
	Oe + Oa	--	474	6	1140		230	910	--
	A	0.32	298	8	2252		60	2178	14
	Ap	0.41	59	14	1889		70	1267	552
	Bw1	0.92	19	34	1108		4	354	750
	Bw2	0.97	5	57	406		1	128	277
Total					**7245**				
Harvard Forest, MA									
NWN 3	Oi	--	446	3	314		--	314	
	Oe + Oa	--	469	6	2718		230	2488	
	A	0.30	272	14	3242		unknown	unknown	unknown
Total					**6274**				

1 Gravel free bulk density (i.e. less than 2mm).
2 Includes live root mass below the Oi horizon.
3 Oi and Oe horizons calculated on a per area basis and BD is not calculated for all pits except those at Howland, Maine.
4 On a dry weight basis.
5 Low density means r < 2.1 g/cc, high density r > 2.1 g/cc.
6 Fine root data are from individual pits for Oak Ridge (sorting techniques are not reliable); from McClaugherty et al. 1982 for Harvard Forest; and from Fernandez et al. 1993 For the Howland Tower site and Ivan Fernadez personal communication for the Howland, NC site (these data are specific to this pit originally dug in 1998).
7 Calculated by subtracting total roots from the total low density SOM.
8 Gravel free bulk density (i.e.< 2mm) from Fernandez et al. 1993.
9 Gravel free bulk density (i.e. < 2mm) from Ivan Fernadez personal communication (these data are specific to this pit originally dug in 1998).

Table 5 (continued, page 3 of 3). Carbon inventory for all

						--------------Low Density SOM--------------			**--High Density SOM--**
Site Pit	**Horizon**	**Bulk Density^1 (g cm^{-3})**	**Soil Carbon (g C Kg^{-1} soil)**	**Bottom Depth (cm)**	**Total C Stock^{2,3} (g C m^{-2})**	**Leaf Litter LL^{4,5} (g C m^{-2})**	**Fine Root Litter LR^{4,5,6} (g C m^{-2})**	**Humified H^{5,7} (g C m^{-2})**	**Mineral Associated M^5 (g C m^{-2})**
Walker Branch, TN	Oi	--	456	3	191	191			
P5	Oe + Oa	--	378	5	406			406	--
	A	0.52	203	7	3303		210	3023	70
	E	1.01	7	24	1249		1	452	796
	B1/EB	1.13	2	41	433		0	91	342
	Bt	0.92	2	63	319		0	63	256
Total					**5902**				
Walker Branch, TN	Oi	--	456	2	358	358			
TDE	Oe + Oa	--	378	3	269			269	--
	A	0.44	50	8	616		7	563	46
	E	1.01	7.0	50	2508		43	883	1582
	Bt	1.18	3.0	70	887		unknown	240	647
Total					**4638**				

1 Gravel free bulk density (i.e. less than 2mm).

2 Includes live root mass below the Oi horizon.

3 Oi and Oe horizons calculated on a per area basis and BD is not calculated for all pits except those at Howland, Maine.

4 On a dry weight basis.

5 Low density means r < 2.1 g/cc, high density r > 2.1 g/cc.

6 Fine root data are from individual pits for Oak Ridge (sorting techniques are not reliable); from McClaugherty et al. 1982 for Harvard Forest; and from Fernandez et al. 1993 For the Howland Tower site and Ivan Fernadez personal communication for the Howland, NC site (these data are specific to this pit originally dug in 1998).

7 Calculated by subtracting total roots from the total low density SOM.

8 Gravel free bulk density (i.e.< 2mm) from Fernandez et al. 1993.

9 Gravel free bulk density (i.e. < 2mm) from Ivan Fernadez personal communication (these data are specific to this pit originally dug in 1998).

Horizon	Stock (g C m^{-2})	Δ^{14}C of SOM (‰)	TT short (yrs)	TT long	CO$_2$ Flux (g C m^{-2}-yr^{-1})	CO$_2$ Flux Horizon Total (g C m^{-2}-yr^{-1})	Δ^{14}C of SOM Horizon Total (‰)
Howland Tower 1996							
Oi (L_L)	897	183	9 **(4)**	40 (36)	NA	NA	NA
Oe+ Oa (L_R)	--	128-192	NA		NA		
Oe (H)	2075	107[7]	85 **(80)**[7]	85	26		
Oa (H)	2667	51[7]	158 **(153)**[7]	158	17		
E (LR)	--	121-134	NA		NA	2.4	70
E (H)	167	94	96		1.7		
E (M)	193	7	285		0.7		
Bhs (H)	532	20	235		2.3	3.2	10
Bhs (M)	367	-14	380		1.0		
Bh (H)	1130	-35	510		2.2	2.9	-41
Bh (M)	463	-61	690		0.7		
Bs1 + Bs2 (H)	1041	-21	425		2.4	3.9	-59
Bs1 + Bs2 (M)	1793	-121	1225		1.5		
BC (H)	934	-79	840		1.1	3.5	-135
BC (M)	3858	-161	1630		2.4		
Howland NC 1997							
Oi (L_L)	321	207	15 **(10)**	40 (36)	NA	NA	NA
Oe+ Oa (L_R)	41	128-192	NA		NA		
Oe + Oa (H)	1820	193[3]	8 (3)	**33-50**	36.0		
E (LR)	18	197	NA		NA	NA	NA
E (H)	360	39	172		2.1		
E (M)[1]	85	7	285		0.3		
Bhs + Bh (H)	1176	51.2	160		7.4	8	41
Bhs + Bh (M)[1]	484	-37	535		0.9		
Bs1 + Bs2 (H)	3052	-21	180		17.0	18	-29
Bs1 + Bs2 (M)[1]	1876	-121	1225		1.5		
BC (H)		-79	260				
BC (M)[1]		-161	1630				

[1] Data are from the 1996 tower pit.

Table 6 (page 1 of 3). Δ^{14}C values, turnover times and corresponding fluxes. Fluxes calculated by dividing inventory by the steady state ^{14}C derived turnover time (unless otherwise noted). Where there is more than one possible turnover time shown, bold values indicate the one used to calculate the flux. See text for explanation of multiple values.

Table 6 (continued, page 2 of 3). Δ^{14}C values, turnover times and corresponding fluxes. Fluxes calculated by dividing inventory by the steady state ^{14}C derived turnover time (unless otherwise noted). Where there is more than one possible turnover time shown, bold values indicate the one used to calculate the flux. See text for explanation of multiple values.

Horizon	**Stock** (g C m^{-2})	**Δ^{14}C of SOM** (‰)	**TT short** (yrs)	**TT long**	**CO$_2$ Flux** (g C m^{-2}-yr^{-1})	**CO$_2$ Flux Horizon Total** (g C m^{-2}-yr^{-1})	**Δ^{14}C of SOM Horizon Total** (‰)
Harvard Forest NWN 1							
Oi (LL)	360	140	**5**	57	NA	NA	NA
Oea (LR)	230	188[2]	NA				
Oea (H)	1086	220[3]	20	**28**[4]	4		
A (LR)	60	216[2]	NA		NA	1	1209
A (H)	1235	121[5]	73	**100**[4]	1		
A (M)	12	42	166	**200**[4]	0		
Ap (H)	2891	52	156		19	20	47
Ap (M)	576	-11	396		1.5		
Bw1 (H)	311	-86	896		0.3	1	-98
Bw1 (M)	816	-105	1284		0.6		
Bw2 (H)	169	-169	1724		0.1	0.3	-168
Bw2 (M)	457	-168	2105		0.2		
Harvard Forest NWN 2							
Oi (LL)	450	124	**3**	70	NA	NA	NA
Oea (LR)	230	188[2]	NA				
Oea (H)	910	182[3]	8	38 **(50)**[4]	18		
A (LR)	60	216[2]	NA			29	1211
A (H)	2118	121[5]	73	**100**[4]	29		
A (M)	14	94	130	**200**[4]	0.1		
Ap (H)	1197	-3	330		3.6	4	-11
Ap (M)	552	-51	710		0.8		
Bw1 (H)	350	-108	1096		0.3	1	-122
Bw1 (M)	750	-133	1628		0.5		
Bw2 (H)	127	-91	2230		0.1	0.4	-163
Bw2 (M)	277	-176	910		0.3		

Table 6 (continued, page 3 of 3). Δ^{14}C values, turnover times and corresponding fluxes. Fluxes calculated by dividing inventory by the steady state ^{14}C derived turnover time (unless otherwise noted). Where there is more than one possible turnover time shown, bold values indicate the one used to calculate the flux. See text for explanation of multiple values.

Horizon	**Stock** (g C m^{-2})	**Δ ^{14}C of SOM** (‰)	**TT short** (yrs)	**TT long**	**CO$_2$ Flux** (g C m^{-2}-yr^{-1})	**CO$_2$ Flux Horizon Total** (g C m^{-2}-yr^{-1})	**Δ ^{14}C of SOM Horizon Total** (‰)
Walker Branch P5							
Oi (L$_L$)	191	127	**5**	67	NA	NA	NA
Oe+ Oa (L$_R$)	?		NA		NA		
Oe + Oa (H)	406	144[8]	**7-13**	55	58		
A (LR)	210		NA		NA	16	39
A (H)	3023	40	**195**		15.5		
A (M)	70	22	230		0.3		
E (H)	452	21	235		1.9	8	49
E (M)	796	59	142		5.6		
B1 (H)	91	31	210		0.4	1	-1
B1 (M)	342	-25	625		0.5		
Bt1 (H)	63	-139	1400		0.0	0.4	-87
Bt1 (M)	256	-80	830		0.3		
Walker Branch TDE							
Oi (L$_L$)	358	130	**5**	68	NA	NA	NA
Oe+ Oa (L$_R$)	?		NA		NA		
Oe + Oa (H)	269	136[8]	**6**	60	45		
A (LR)	7		NA		NA	6	960
A (H)	563	99[6]	91		6.2		
A (M)	46	37	189		0.2		
E (H)	883	107	83		10.6	14	84
E (M)	1582	19	435		3.6		
Bt (H)	240	113	80		3.0	3	81
Bt (M)	647	-156	1580		0.4		

NA = Not applicable, see text for details. [1] Data are from the 1996 tower pit.

[2] Represents the ^{14}C samples picked for dead roots (n = 1). [3] Represents the humified organic material after size sieving (Howland) or quantitative root picking for the Oe + Oa (Harvard Forest).

[4] Value calculated using a non-steady state model.[4] Value calculated using a non-steady state model. [5] Represents a weighted ^{14}C value for the two humified (H) components shown in Chapter 2, Figure 7 (B), also see text for discussion.

[6] Represents the ^{14}C value of a composite sample after fine roots have been picked out.[7] Represents the bulk ^{14}C value, this

Table 7. Heterogeneity of low density fractions for mineral horizons.

Horizon	Year Sampled	< 80 μ $\Delta^{14}C$ (‰)	Fraction < 80 μ	> 80 μ $\Delta^{14}C$ (‰)	Fraction > 80 μ	Roots $\Delta^{14}C$ (‰)	Fraction Roots	composite $\Delta^{14}C$ (‰)	< 80 μ TT	> 80 μ TT	composite TT
Howland, ME											
NC site											
E	1997	17.1	0.19	44.2	0.81			38.9	250	172	187
Bhs + Bh	1997	54.3	0.07	51.0	0.93			51.2	150	160	159
Bs	1997	-39.0	0.12	30.0	0.88			21.8	530	210	248
Walker Branch, TN											
P5 site											
A	1998	-0.5	0.11	44.9	0.88			39.9	340	175	193
A1	1972	73.3	0.58	194.5	0.40			122.8	83	32	62
TDE site											
A1	1998	35.6	0.27	130.5	0.53	207.0	0.16	117(99)[1]	192	6 or 65 (90)[1]	124 (138)[1]
E1	1998	55.2	0.42	143.2	0.58			106.2	150	7 or 57	63
E2	1998	48.6	0.15	88.8	0.85			82.8	163	100	109
Harvard Forest											
NWN #1											
A	1996	48	0.09	130	0.82	256	0.07	132 (122)[1]	165	4 or 65 (72)[1]	88 (94)[1]

TT = Turnover Time

Composite TT is calculated using a mass (fractional) weighting of the ^{14}C-derived turnover time for each component.

[1] Values in parenthesis represent the weighted ^{14}C concentration or turnover time without the root component

Table 8. Radiocarbon values of 1992 aboveground litter inputs and estimated time lags. Analytical error for the $\Delta^{14}C$ measurement is 6± ‰.

Litter Type	**Measured $\Delta^{14}C$ (‰)**	**Lag years**	**Fraction of mass**
Conifer	147	3	0.52
Deciduous	132	1	0.16
Wood[1]	287	15[3]	0.23
Miscellaneous	177	5	0.10
Total[2]	**179**	**5**	1.0

[1] Sticks and twigs

[2] $\Delta^{14}C$ and lag time values (in bold) are mass weighted based on the mass fraction and $\Delta^{14}C$ of each component.

[3] Assumes an explicit lag of 5 years for the atmospheric record of ^{14}C in CO_2 (see Figure 11), plus a turnover time of ten years.

Table 9. Radiocarbon values and turnover times for archived and modern soil pits.

Site	**Low Density**				**High Density**			
Horizon	**$\Delta^{14}C$ (‰)**	**$\Delta^{14}C$ (‰)**	**TT (years)**	**TT (years)**	**$\Delta^{14}C$ (‰)**	**$\Delta^{14}C$ (‰)**	**TT (years)**	**TT (years)**
Howland, NC	**1997**	**1988**	**1997**	**1988**				
Oi	207	--	15	--				
Oi-Oa	**163** (194,161)	**284** (218, 284)	**10-15 or 47** (12 or 33, 10-15 or 47)	**10-15** (10-15 or 47)*				
E	**40** (17,44)	**76** (70, 77)	**172** (250, 172)	**112** (120, 109)				
Bhs + Bh	**51** (54,51)	**88** (63,103)	**160** (150,160)	**98** (130, 85)				
Bs	**22** (-39, 30)	**36** (-50, 59)	**235** (530,210)	**180** (590, 135)				
Bc		**10** (-65.3, 21)		**260** (710, 222)				
Walker Branch, P5	**1998**	**1972**	**1998**	**1972**	**1998**	**1972**	**1998**	**1972**
Oi	126.6	549.7	5 or 68	5				
Oe +Oa	144.4	372.8	7 or 55	13				
A	**40** (-1, 45)	**124** (73, 195)	**180** (250,170)	**50** (83,32)	22.4	56.4	230	100
A2(E) upper	21	137.7	235	47	59	107	142	59
A2 (E) lower	30.6		210		-25.4		625	
B1	-139.4	157.3	1400	40	-79.5	-38.2	830	460
B21t	na	na			-89.6	-67.4	930	680

Bold values are a mass weighted composit of the <80 and >80 micron fraction. Values in parentheses are the <80 micron fraction and the > 80 micron fraction respectively.

* Using both the 1997 and 1988 data, and fitting a curve similar to Chapter 1, Figure 1, the best fit turnover times are 33 years for the < 80 micron fraction and 10-15 years for the > 80 micron and composit fractions.

Table 10. Steady state values used to initialize a 4-pool C model for each of the three study sites.

Site	**---------------Howland--------------**			**------------Harvard Forest--------**			**---------Walker Branch---------**		
	Stock gC m^{-2}	TT yr	Input gC m^{-2} yr^{-1}	Stock gC m^{-2}	TT yr	Input gC m^{-2} yr^{-1}	Stock gC m^{-2}	TT yr	Input gC m^{-2} yr^{-1}
Pool 1	75	1	75	150	1	150	200	1	200
Pool 2	4000	40	100	1800	40	45	300	11	27
Pool 3	2600	150	17	1800	100	18	2000	75	27
Pool 4	7950	500	16	4620	500	9	2500	5000	5
Total	14625		208	8370		222	5000		259

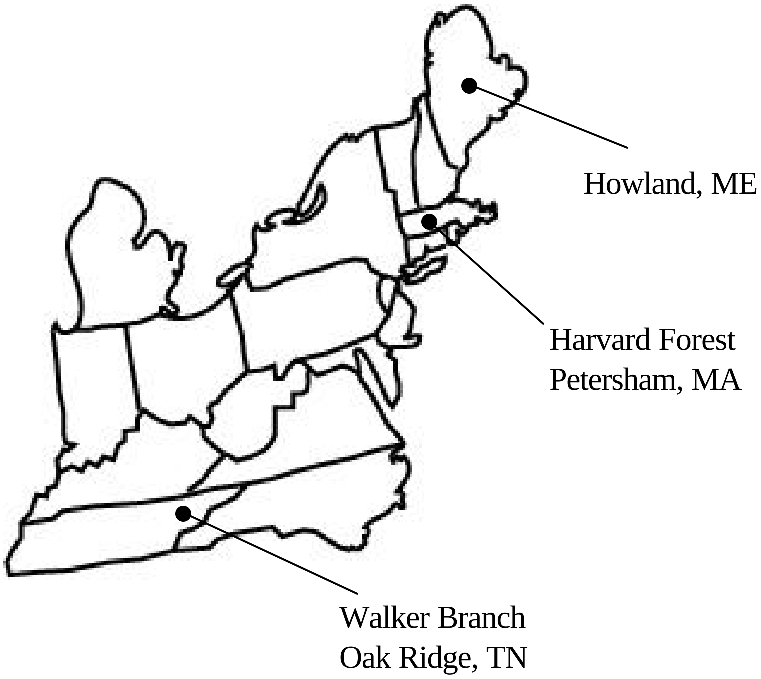


Figure 1. Site map

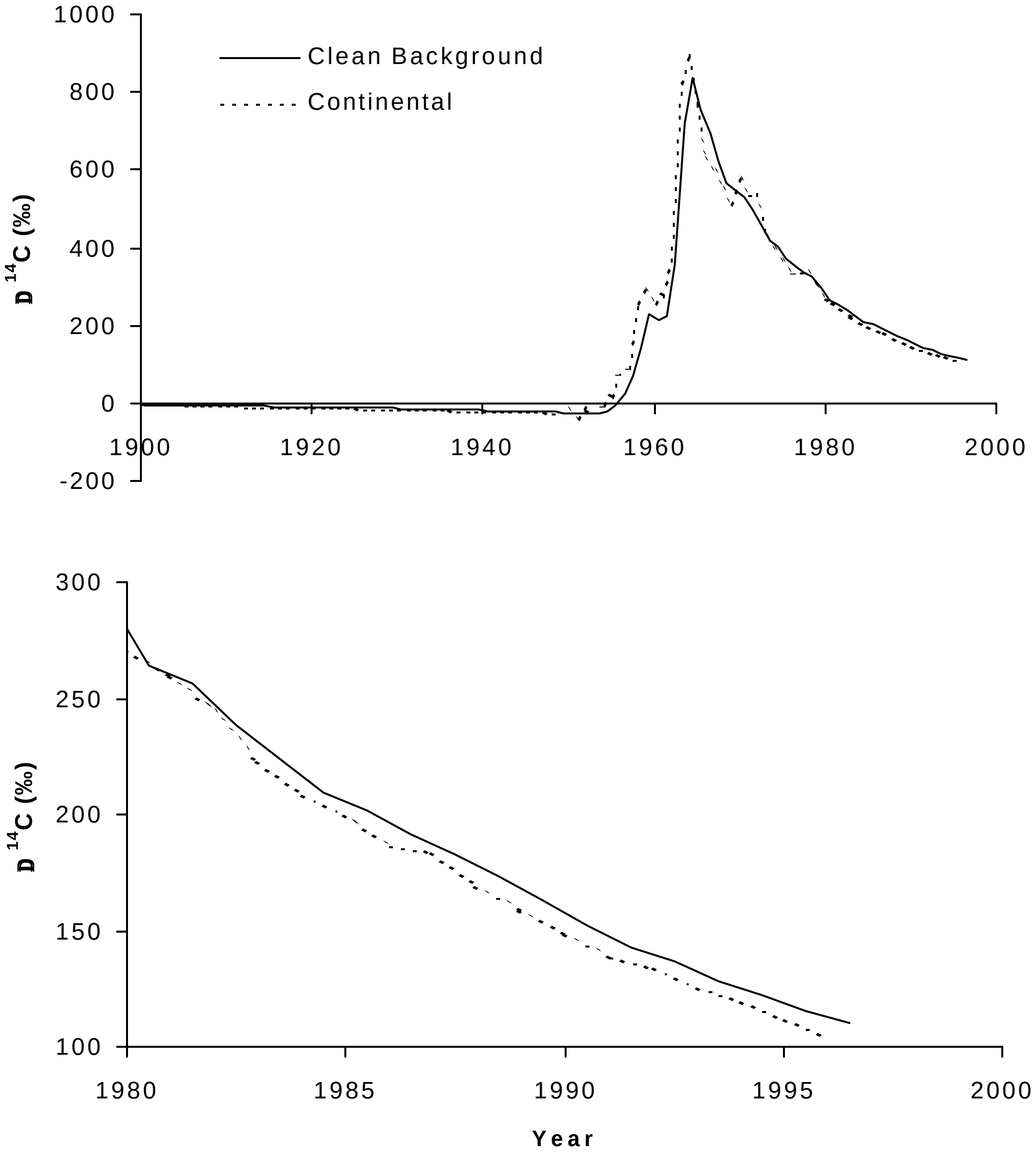


Figure 2. The time record of ^{14}C in atmospheric CO_2 (top) and (bottom) the same record expanded for the period 1980-1997. The clean background data are a compliation of sources representing clean air sites from Ingeborg Levin (personal communication). The continental curve represents a compilation of data based on grapes grown in Russia for 1950-1977 (Burchuladze et al., 1989), and direct atmospheric measurements for 1977-1996 which represent summer means (May – August) taken at Schauinsland, Black Forest, Germany at an elevation of 1205 m asl (Levin and Kromer 1997).

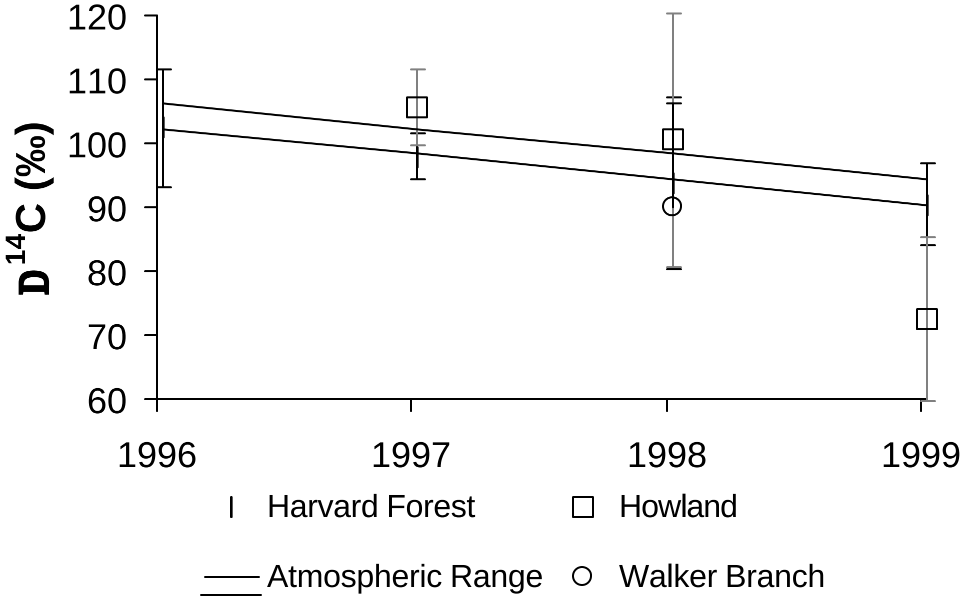


Figure 3. Local measures of ^{14}C in atmospheric CO$_2$. Only samples for which there are δ^{13}C values are used. Error bars represent one standard deviation (n = 3 to 6) for all samples except Howland in 1997 where n = 1 and the error shown represents the analytical error (6 ‰). The two solid lines encompass the range of ^{14}C in atmospheric CO$_2$.

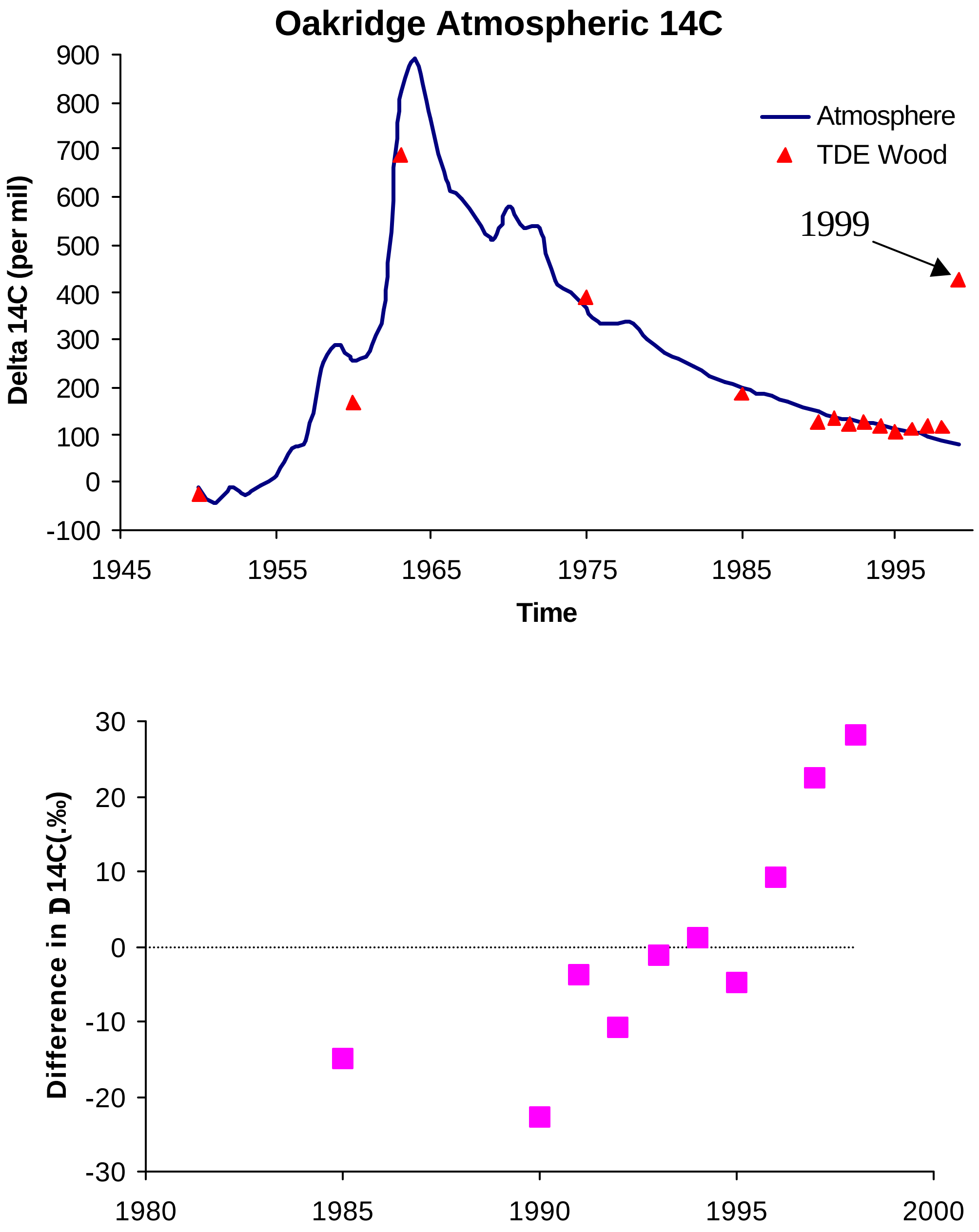
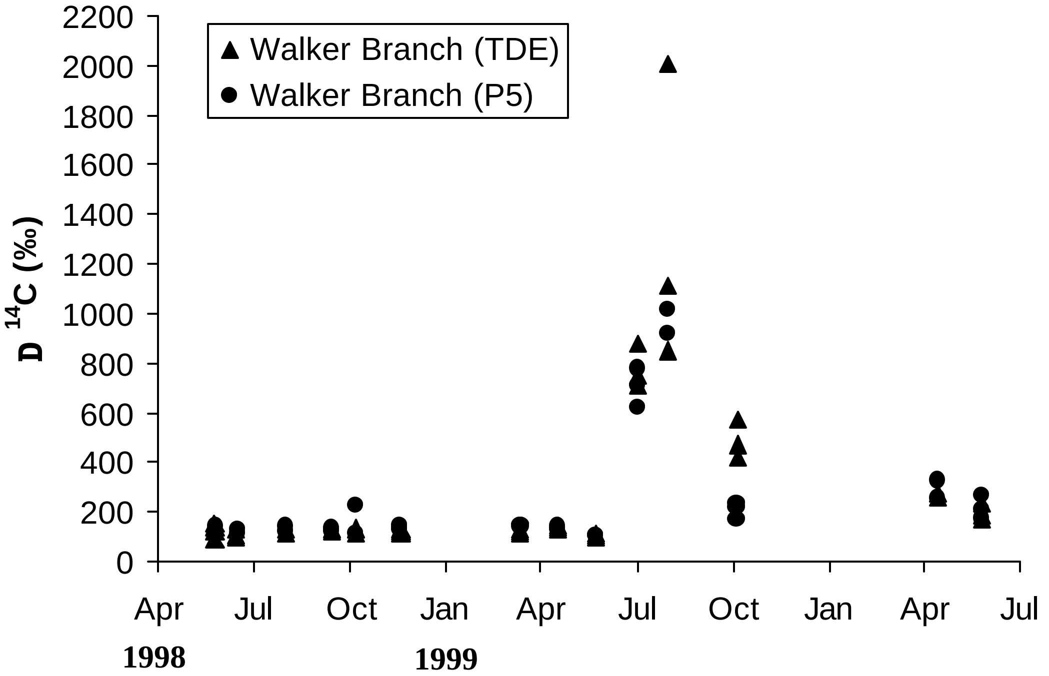


Figure 4. (Top) Time series of ^{14}C in tree alpha cellulose sampled from annual tree rings of a white oak on the Walker Branch TDE site in October 1999. Samples underwent a solvent extraction followed by an acid-base-acid rinse. (Bottom) The same data as above for 1990-1998, except plotted as the relative difference between the alpha cellulose and the atmospheric trend from Schauinsland, Gerrmany).



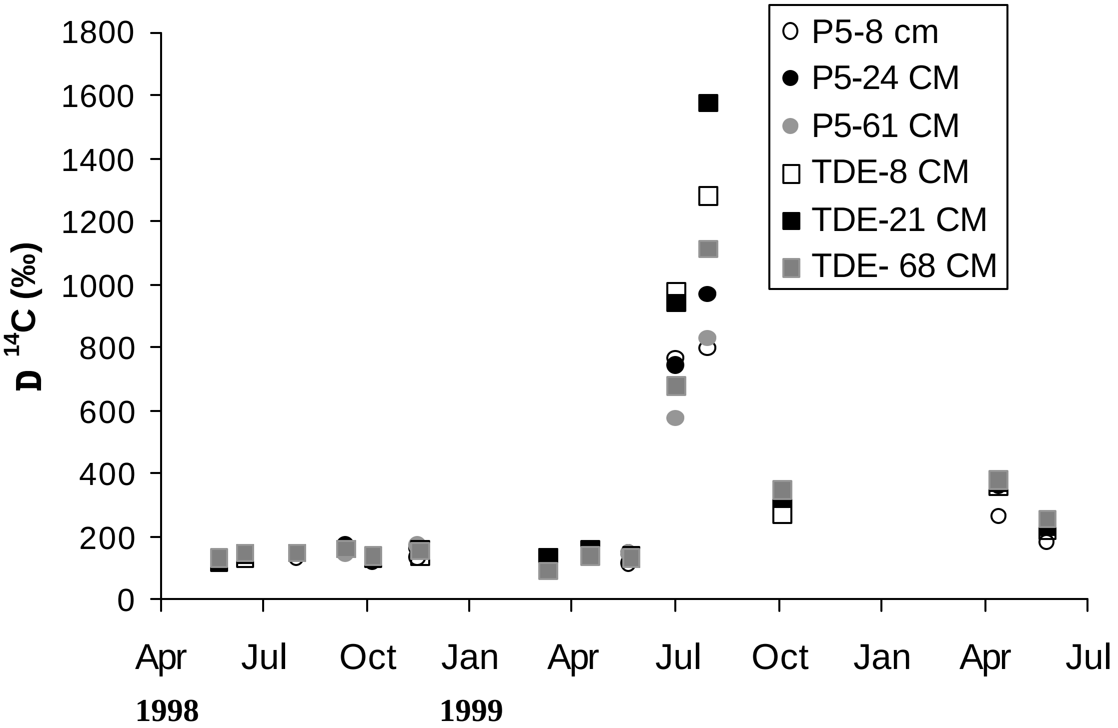


Figure 5. Radiocarbon in CO_2 of total soil respiration (top) and soil gas (bottom) for two sites on the Walker Branch watershed from June 1998 through June 1999.

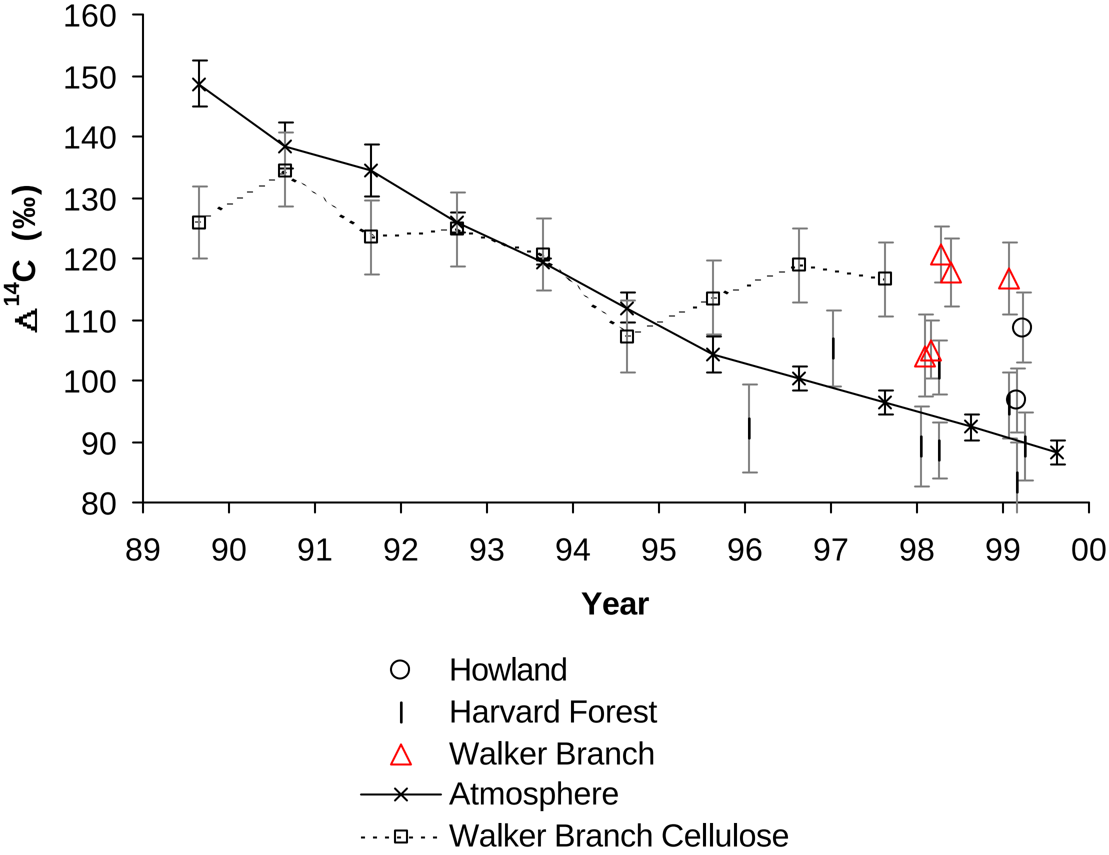


Figure 6. Global tropospheric ^{14}C of CO_2 compared to deciduous leaves at all three sites and tree-ring cellulose from Walker Branch. Error bars represent analytical error on all leaf and cellulose measurements (as n = 1). The $\Delta^{14}C$ of atmospheric CO_2 comes from Levin and Kromer, 1997, and Levin and Hesshaimer, 2000

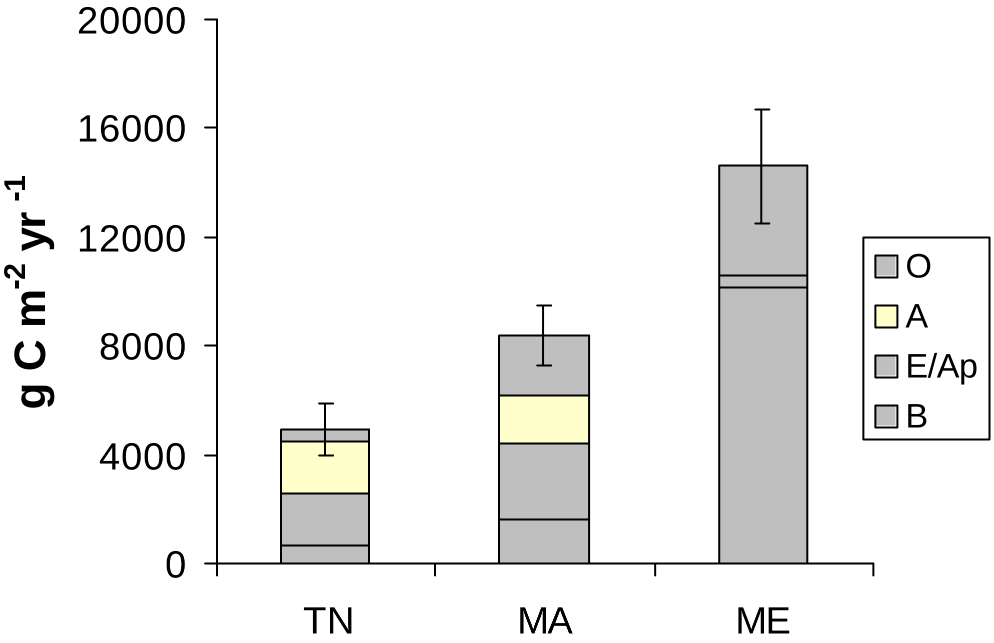


Figure 7. Carbon stocks at all three sites (values represent an average of all pits dug at each site). Error bars represent the range or standard deviation for the entire profile.

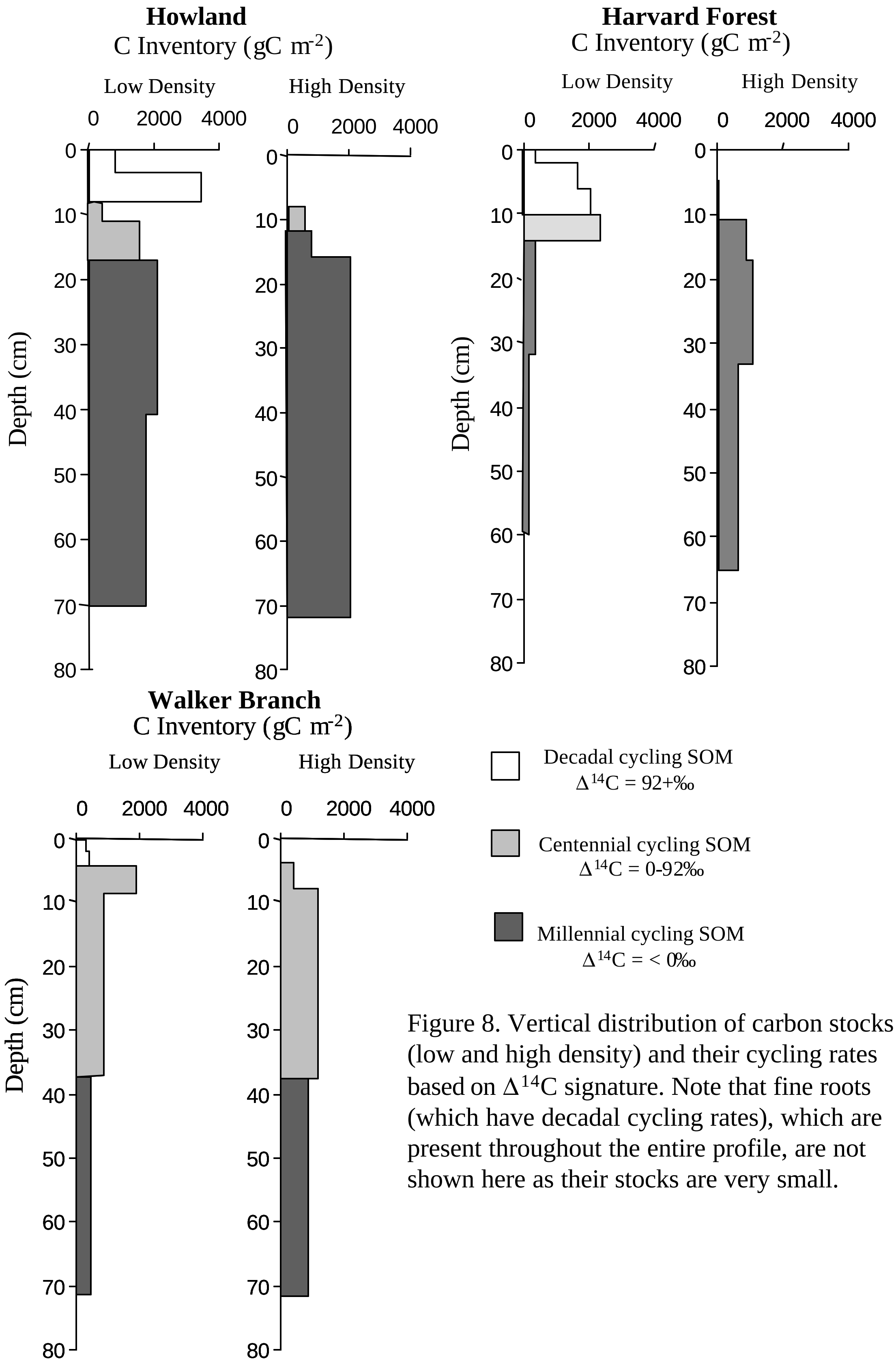


Figure 8. Vertical distribution of carbon stocks (low and high density) and their cycling rates based on $\Delta^{14}C$ signature. Note that fine roots (which have decadal cycling rates), which are present throughout the entire profile, are not shown here as their stocks are very small.

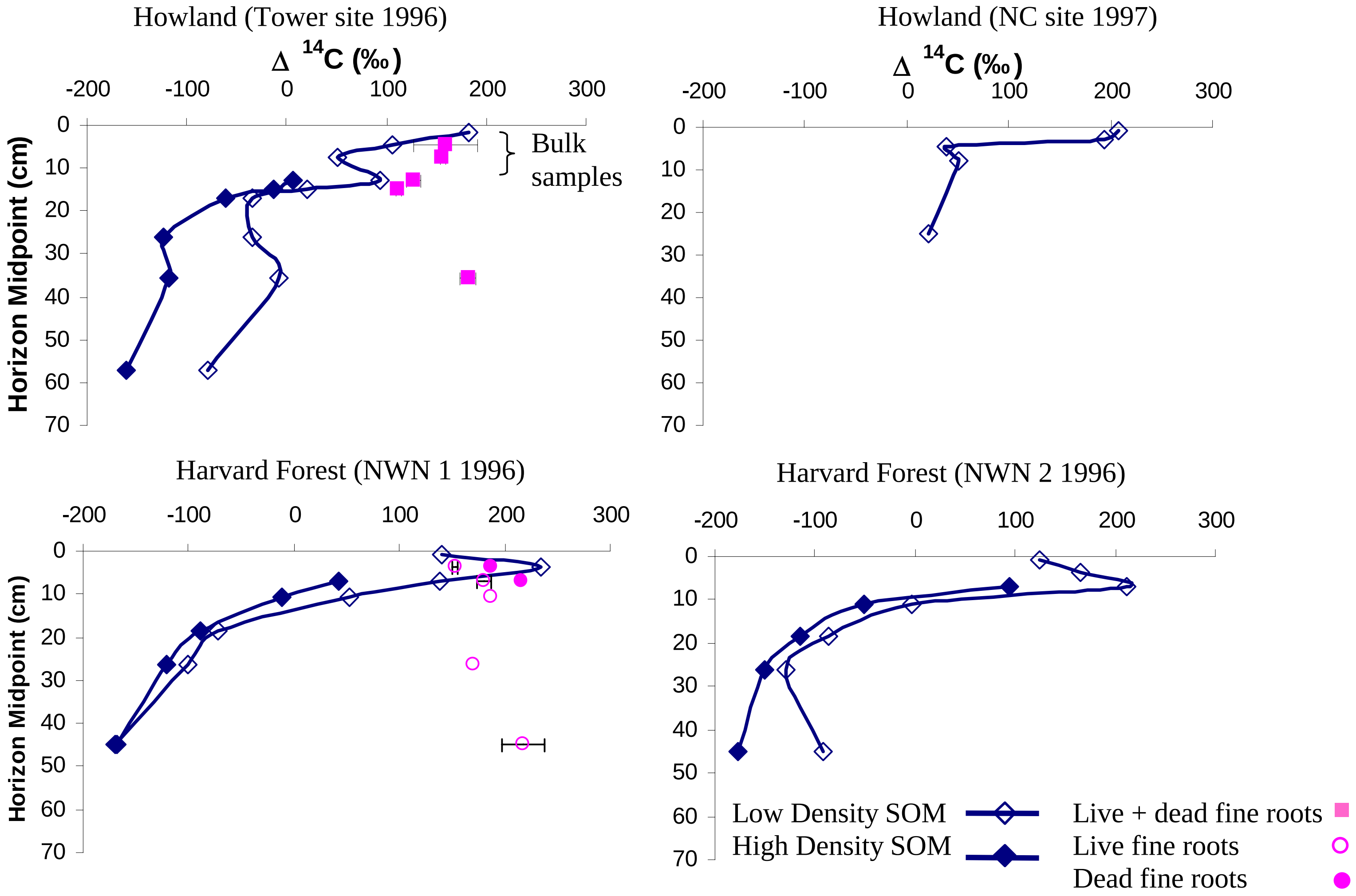


Figure 9. (page 1 of 2). Radiocarbon profiles of low density (open symbols) and high density (closed symbols) SOM at all sites for all pits.

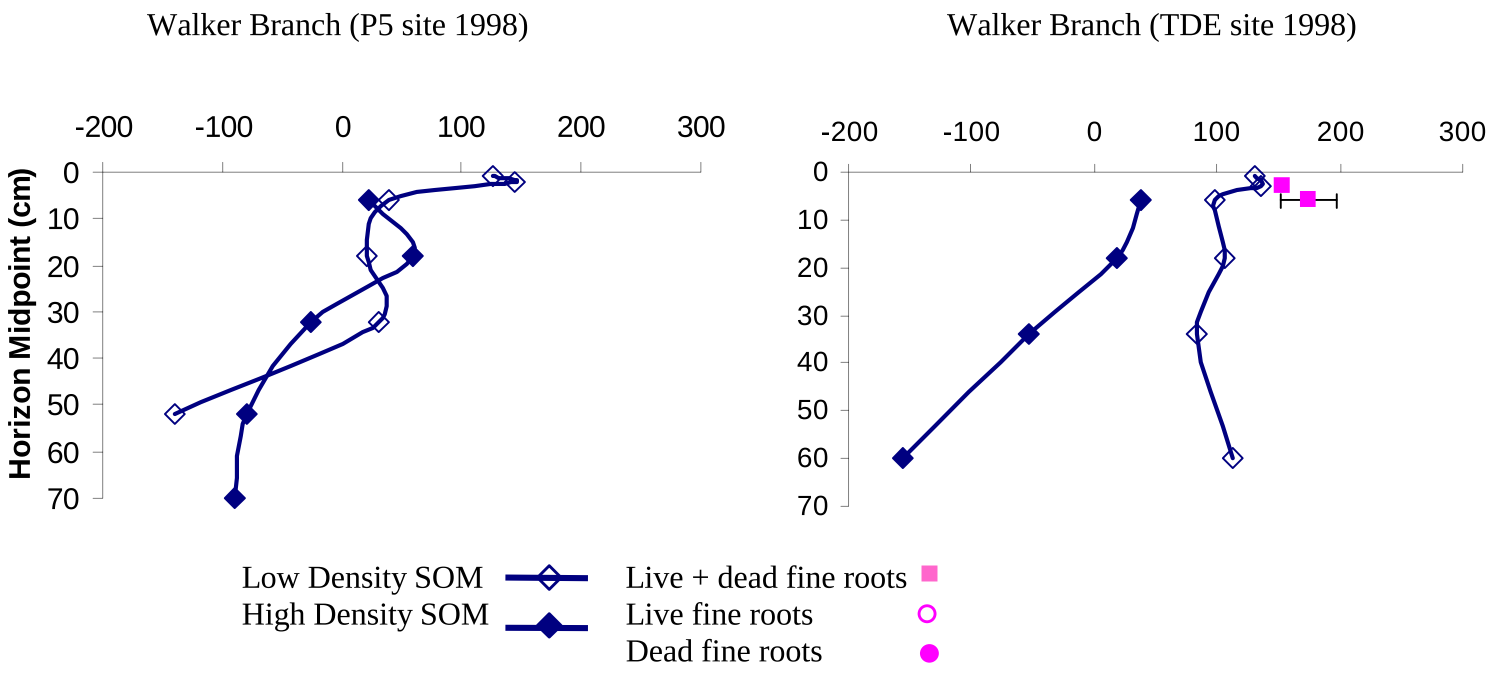


Figure 9 (continued, page 2 of 2). Radiocarbon profiles of low density (open symbols) and high density (closed symbols) SOM at all sits for all pits.

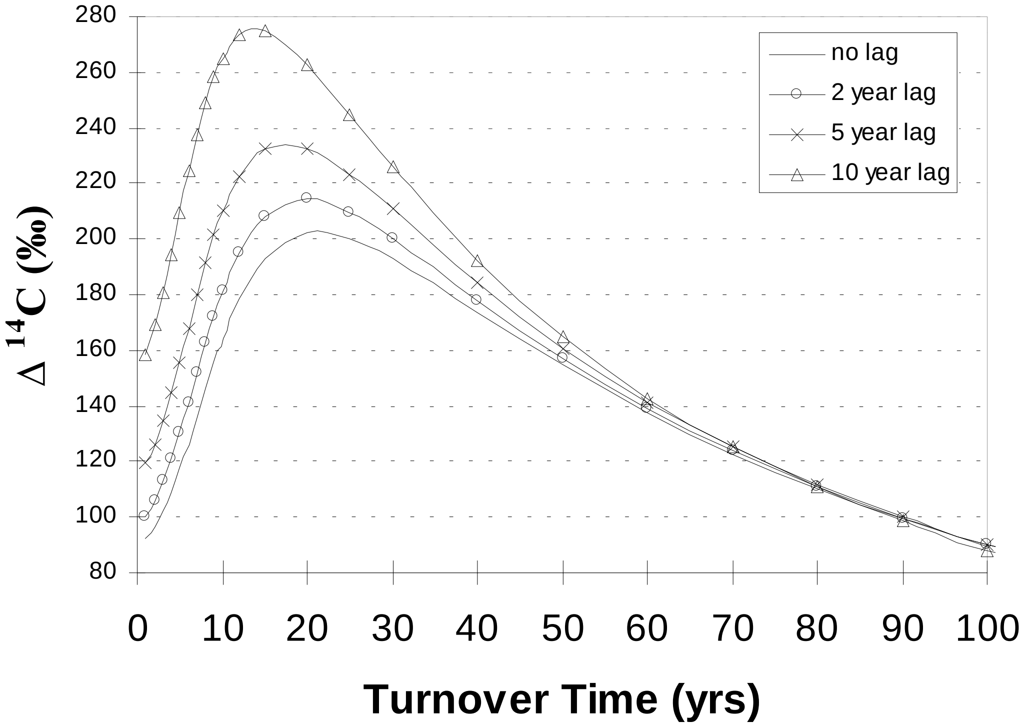


Figure 10. Effect of lagged ^{14}C inputs on calculated turnover times for 1999. The lagged curves are generated by our steady-state model by having the Δ^{14}C of atmospheric CO_2 inputs be n years behind the actual value (where n = the lag time).

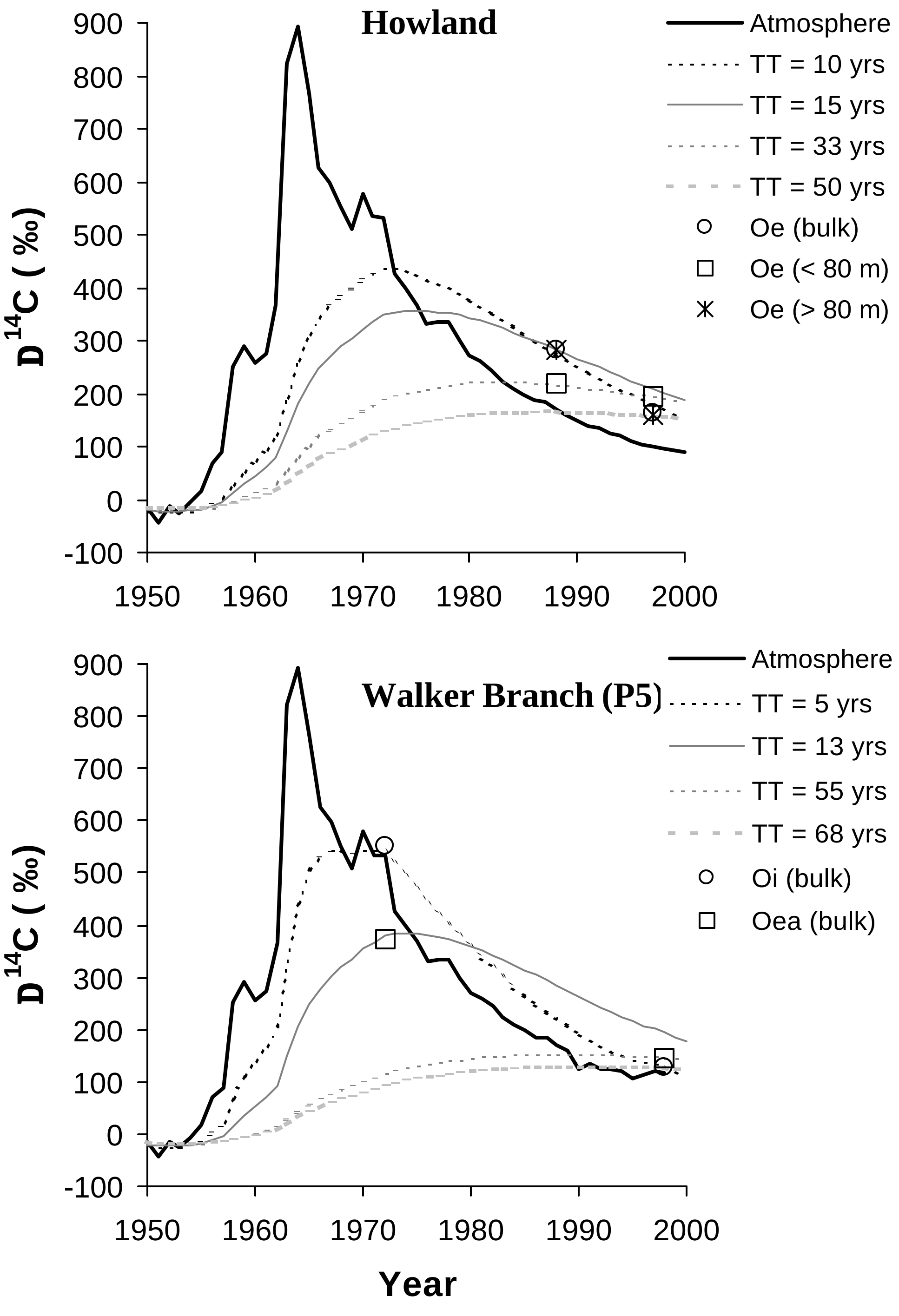


Figure 11. Δ^{14}C values for atmospheric CO_2 and organic horizon components for archived and modern soils and modeled (steady state) turnover time curves. The Walker Branch input data differs from that shown for Howland forest in that the input data for the ^{14}C of atmospheric CO_2 is derived from tree ring cellulose starting in 1990 (in order to account for the unusual atmospheric ^{14}C history at this site, see text for details).

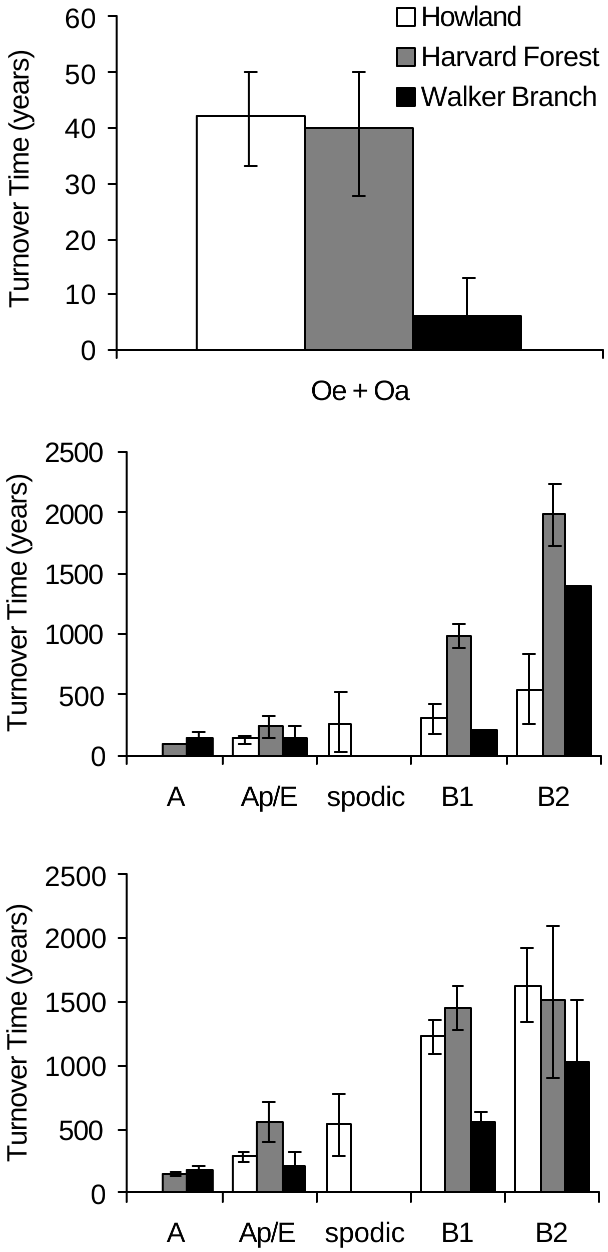


Figure 12. Average turnover times by soil horizon. Oe + Oa horizon (top), low-density mineral fractions (middle), and high-density mineral fractions (bottom). (Top) Error bars include all possible values measured for fractionated samples. (Middle and Bottom) Error bars when shown equal a range if n = 2 or standard error if n = 3, otherwise n = 1. The high-density Walker Branch samples include data from the 1972 archive pit.

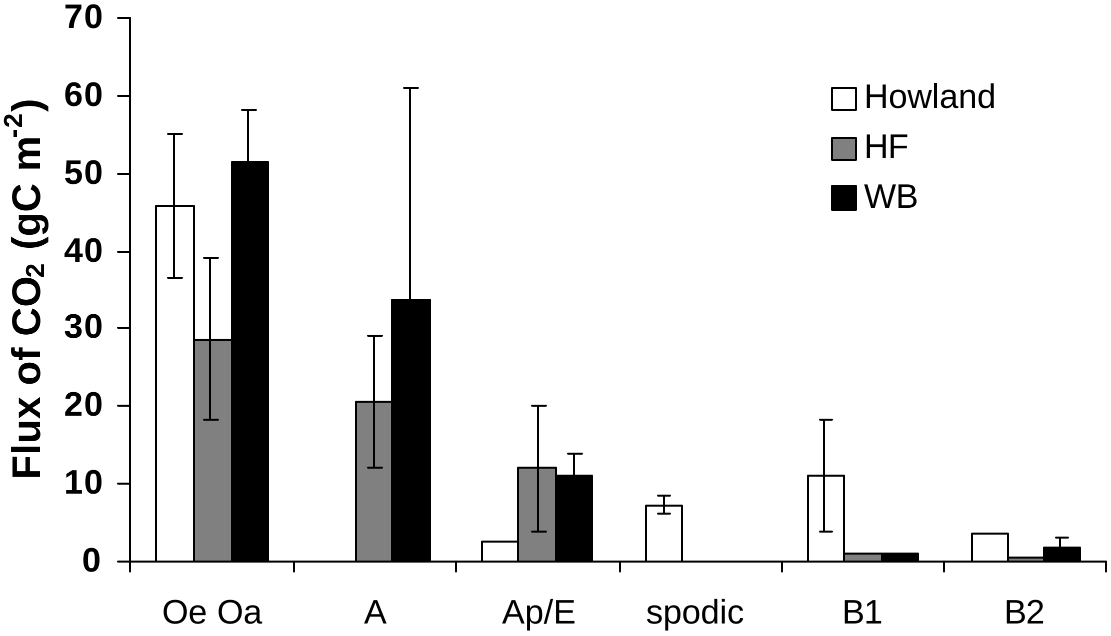


Figure 13. Average decomposition fluxes by horizon (for low-density and high-density SOM combined) at all three sites. Values shown are the average between respective horizons for two pits at each site. Error bars where present represent the range as n = 2 otherwise n = 1.

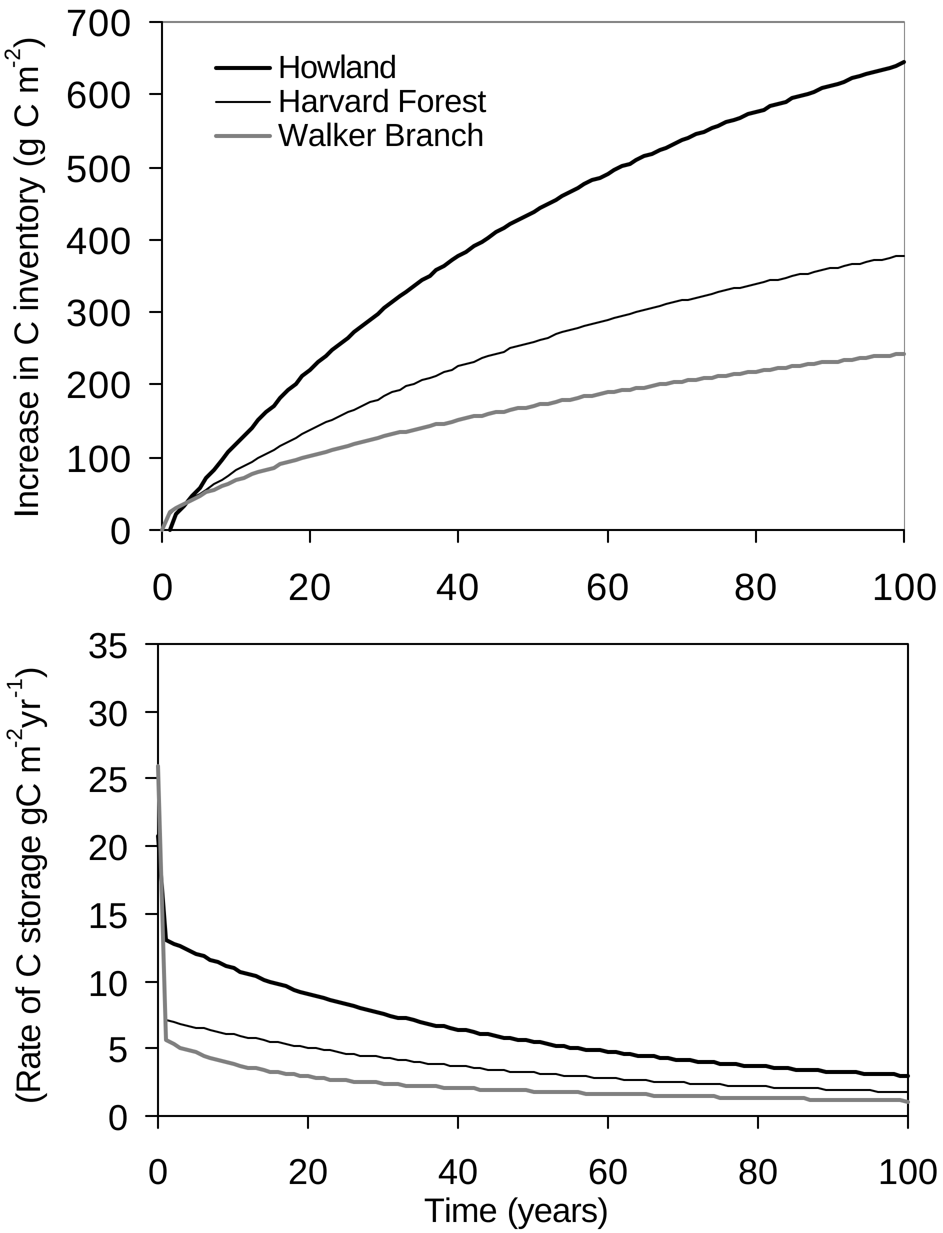


Figure 14. (Top) Carbon storage as a result of a 10% increase in NPP using a four-pool (steady state) model with C stocks and turnover times characteristic for the fast pool, Oe + Oa, A/E and B horizons at each site; see Table 10 for steady state stock, turnover times, and inputs for each SOM pool. (Bottom) The rate of carbon storage at each site through time, following a 10% increase in NPP.

Chapter 4: Variability of Fine Root Dynamics Measured by Radiocarbon

Abstract

Using a new approach involving one-time measurements of radiocarbon (^{14}C) in fine root tissues we have measured the actual age of C in fine root stocks. We find that the bulk of fine roots in deciduous and coniferous forests of the eastern United States live for 6-11 years before they die. Significant variation of C residence time exists in different parts of the same root as a function of branching order and within fine root stocks as a function of depth within the soil. The smallest fine roots tend to be the youngest, while the larger fine roots tend to be the oldest. Our results differ sharply from previous estimates of fine root age made using mass balance approaches and root-viewing cameras, which generally report fine root ages of a few months to one or two years. Each method, including this new radiocarbon method, has biases that tend to overemphasize one end of the range of sizes and ages. Our results indicate that the classic definition of fine roots, as those with diameters of < 2 mm, should be subdivided into more size classes. Recognizing this Variability in fine roots is necessary to obtain better estimates of root longevity, turnover and belowground C inputs.

Introduction

One of the biggest uncertainties in predicting ecosystem carbon balance and the role of terrestrial ecosystems in the global carbon cycle is our inability to track the allocation and subsequent longevity of recently fixed carbon into various plant tissue components. Methods for estimating allocation to aboveground biomass and net primary productivity (NPP) are well developed (Schlesinger, 1997). However, our ability to estimate allocation and longevity below-ground is still poor (Gower et al., 1996, Vogt et al., 1996). Fine roots (< 2 mm diameter) make up ~2.5% of total terrestrial plant biomass and have been estimated to receive one third of global NPP (or 20 gigatons of C per year) assuming they grow and die within a year (Jackson et al., 1997). The robustness of such an estimate depends greatly on the assumption of fine root turnover, a measure of longevity and lifespan, that ecologists have long struggled to estimate in natural ecosystems.

Traditional methods of quantifying root turnover typically divide the standing stock of root mass by the estimated annual production or loss rate (Vogt et al., 1996). Direct methods for estimating production and loss rates are labor intensive, time consuming, and involve multi-year observations. These include sequential coring, in-growth root cores, root screens, minirhizotrons or rhizotrons, and litter bags (Fahey and Hughes, 1994, Vogt et al., 1998). Sequential coring techniques have high uncertainty due to spatial and temporal variability in root distributions (Fogel, 1990, McClaugherty and Aber, 1982), whereas other methods have significant disturbance effects (Joslin and Wolfe, 1999, Vogt et al., 1998). In an effort to minimize time consuming direct methods, indirect methods such as the N budget (Aber et al., 1985, Nadelhoffer et al., 1985), or carbon flux approaches (Raich and Nadelhoffer, 1989) have been developed. These indirect approaches require data on the N or C inputs and fluxes and assume that only N or C drives fine root dynamics. In general, studies of fine root turnover yield turnover times of two years or less (Hendrick and Pregitzer, 1993a, Nadelhoffer et al., 1985, Aerts et al., 1992, Hendrick and Pregitzer, 1993b, Burke and Raynal, 1994), though some studies report turnover of several years (Joslin and Henderson, 1987, Ostertag, in review, Milchunas and Lauenroth, 1992).

Species, nutrient status, and presence or lack of mychorrhizal associationclearly affect lifespan. But methodology also appears to influence lifespan estimates. In hardwood forests of the northeastern USA, estimates of turnover times for roots in the upper parts of soil profiles are on the order of months, using root screen and minirhizotron techniques (Hendrick and Pregitzer, 1993a, Fahey and Hughes, 1994, Johnson et al., 2000, Hendrick and Pregitzer, 1992, Eissenstat and Yanai, 1997), typically less than two years for sequential coring and in-growth root cores (Vogt et al., 1986, Fahey and Hughes, 1994, Powell and Day, 1991), and <1-3 years for nutrient budget techniques (Aber et al., 1985, Nadelhoffer et al., 1985). Despite a lack of agreement between field methods, turnover times for fine roots incorporated into ecosystem models reflect a general consensus that the majority of fine roots grow and die within roughly one year (Hoffmann, 1995, Rasse et al., 1999).

Here we use a new method based on radiocarbon (^{14}C) that allows estimates of the ages of fine roots directly. This approach takes advantage of the spike in atmospheric $^{14}CO_2$ from thermonuclear weapons testing in the early 1960’s (**Figure 1**), which can be used as a tracer for the timing of photosynthetic uptake and C cycling rates in an ecosystem. After the nuclear test ban treaty in 1963, ^{14}C in atmospheric CO_2 decreased rapidly due to exchange with the ocean and terrestrial biosphere. Since 1982, atmospheric $\Delta^{14}CO_2$ has continued decreasing because of uptake by the ocean and increased burning of ^{14}C-free fossil fuel. It follows an exponential curve with a rate of change of –13‰ in 1982 and about –4‰ in 1998 (Levin and Hesshaimer, 2000). Precision in the ^{14}C measurement by accelerator mass spectrometry (AMS) is ± 5 to 6‰ (which includes both machine and laboratory error for unknown samples). Thus we can resolve when organic matter was fixed from the atmosphere within one to two years.

If, as is generally thought, fine roots grow and die within one year, and if they grow from carbon fixed from the atmosphere within the last year, then the ^{14}C content of their tissues should have the same ^{14}C content (corrected for mass-dependant fractionation effects) as the atmospheric CO_2 for that year. However, at a mixed deciduous forest in central Massachusetts, USA, we measured significantly elevated ^{14}C values relative to the atmospheric $\Delta^{14}C$ of CO_2 for both live and dead roots collected in 1996 (**Figure 2**). These data imply that the bulk of fine root stocks (both live and dead) are either: (1) living significantly longer than one year; (2) made from carbon reserves stored in the plant for several years prior to translocation to fine roots; or (3) actively taking up soil organic matter with elevated ^{14}C values from the surrounding soil (potentially from mycorrhizal interactions). In this paper, we test the above hypothesis at three temperate forests in the eastern United States and discuss the implications of our results.

Methods

We selected three temperate forests in the eastern United States located along a latitudinal transect from Maine to South Carolina: a coniferous forest in Howland, Maine (Howland), a mixed hardwood forest in Massachusetts (Harvard Forest), and a loblolly pine plantation planted in 1957 in South Carolina (Calhoun Experimental Forest). Specific site characteristics, including the dominant vegetation type, are given in **Table 1**.

Sample Collection

In spring 1999 at the Howland and Harvard Forest sites, we collected roots known to be less than one year in age by placing screens horizontally at the base of the organic horizons where fine roots are proliferate (following the experimental design of Fahey and Hughes 1994). Roots that grew through the screens were harvested in late August 1999 and were therefore less than one year in age. For comparison we also collected grab samples of the total fine root population by depth from pits dug in late July 1999. Roots from both screens and pits were separated from soil and divided into two size classes (< 0.5 mm, 0.5-1mm). At the Calhoun Experimental Forest roots were collected from 6 cm diameter soil cores taken at 3 depth intervals (organic horizon, 0-15 cm and 15-30 cm) in late July 1998. Live roots were separated from dead and sorted into two size classes (< 2 mm and > 2mm).

All sampleswere either frozen or refrigerated, and then dried in an oven at 60°C for at least 24 hours. From the roots sampled from Harvard Forest in1996 (**Figure 2**) fine roots were quantitatively sorted into live versus dead (Gaudinski et al., 2000) and processed directly into graphite as discussed below. Roots collected after 1996 were first given an acid/alkali/acid procedure to remove labile carbon, that is easily hydrolysable, as well as any sorbed organic compounds. This procedure leaves behind primarily "structural" carbon components. Root samples were soaked in 1N HCl in 20 ml glass vials for 15 minutes, repeatedly soaked in 1N NaOH until the liquid remained clear, and soaked for 15 minutes in 1N HCl. Finally, samples were soaked three times for 15 minutes in deionized water. During all stages of pre-treatment the glass sample vials were placed in a hot water bath (approximately 80°C) and sonicated. The samples were then dried at 60°C and converted to graphite. The ^{13}C values were also measured for each sample to correct ^{14}C data.

We were also able to obtain archived live fine roots (< 0.5 mm and 0.5-3 mm) sampled in a similar mixed hardwood forest at Harvard Forest in 1979 by Charles McClaugherty (McClaugherty and Aber, 1982). The samples were originally sorted by hand into size class and into live and dead categories. The samples were then dried, ground, and stored in glass vials. We show only the live samples here because the ground dead root samples contained significant amounts of soil organic matter. Because the samples were already ground, we performed the acid/alkalai/acid step by placing the them in a polyester, heat sealed "tea bag". The polyester bag has a very tight weave and its fibers did not contaminate the sample.

Atmospheric record of Δ^{14}C in CO_2

We interpret the Δ^{14}C in root tissues in terms of age or turnover, using two time-dependent models that simulate incorporation of bomb ^{14}C into the fine root pool. A necessary input to both models is the history of ^{14}C in atmospheric CO_2 incorporated by plants. We use the atmospheric Δ^{14}C record of atmospheric CO_2 (Northern Hemisphere) based on grapes grown in Russia for 1950-1977 (Burchuladze et al., 1989), and direct atmospheric measurements for 1977-1996 that represent summer means (May – August) taken at Schauinsland Black Forest, Germany, at an elevation of 1205 m asl (Levin and Kromer, 1997). After 1996 we assume a continued decrease of 4 ± 2 ‰ per year (Levin and Hesshaimer, 2000), which yields values of 100.3‰, 96.3‰ and 92.3‰ for 1997, 1998 and 1999 respectively. The 1997 and 1998 values are consistent with preliminary growing season means for Schauinsland for 1997 and 1998 (Ingeborg Levin, personal communication).

We took local atmospheric measurements at roughly 10 cm above the forest floor at both the Howland and Harvard Forest sites in order to correct soil respiration samples for atmospheric contamination. The Δ^{14}C values and their standard errors for CO_2 from air (at 10 cm) at Howland and Harvard Forest are 102 ± 7 ‰ (n = 5) and 90 ± 4‰ (n = 7) respectively in 1998 and 74 ± 5‰ (n = 3) and 89 ± 1‰ (n = 7) respectively in 1999. Measurements made so close to the soil, however, are shown by their δ^{13}C content (which ranged from –8.24 to –12.3 ‰) to be influenced by localized pollution and/or re-respired CO_2 from soils and plants. Thus they do not necessarily represent the ^{14}C of CO_2 taken up by the tree canopy. We therefore use the Schauinsland data set with a 4‰ per year decrease since 1996, rather than our own measurements at Harvard Forest or Howland, to set the Δ^{14}C of CO_2 fixed by plants between 1997 and 1999 at all three of our sites.

Radiocarbon (^{14}C) Analysis

We converted all root samples to graphite via sealed-tube zinc reduction (Vogel, 1992) and measured the ^{14}C content on an accelerator mass spectrometer (AMS) at the

Center for AMS atLawrence Livermore National Laboratory. We express radiocarbon data as $\Delta^{14}C$, the difference in parts per thousand (per mil or ‰) between the $^{14}C/^{12}C$ ratio in the sample compared to that of a universal standard (oxalic acid I, decay-corrected to 1950). All samples are corrected for mass-dependent isotopic fractionation to -25‰ in $\delta^{13}C$. This accounts for plant-based photosynthetic discrimination of atmospheric $^{14}CO_2$ is accounted for (^{14}C is assumed to fractionate twice as much as ^{13}C) and the reported $\Delta^{14}C$ values reflect the atmospheric $\Delta^{14}C$ of CO_2 from which the C was originally fixed. Precision in the AMS measurement is typically ±6‰ (which includes both machine and laboratory error for unknown samples). The AMS at LLNL measures the ratio of ^{14}C to ^{13}C (not $^{14}C/^{12}C$). Therefore, accurate ^{14}C measurement requires $\delta^{13}C$ measurements of each sample. The $\delta^{13}C$ values for roots from Harvard Forest and Howland in 1999 ranged from –23.09 to -29.65‰, though most were between -26 and -29‰ and were measured at the University of California, Irvine, using an Isotope Ratio Mass Spectrometer (with a precision of ± 0.05‰). The $\delta^{13}C$ values for roots from Calhoun Experimental Forest were assumed to be –25‰.

Modeling Fine Root Age

Based on the measured $\Delta^{14}C$ values, we estimate an average age for fine roots with two different methods. The first method assumes that all structural carbon in the root grew in one year, and added no new C since that time. In this case, the age of the root is determined by comparing the $\Delta^{14}C$ of structural C directly to the record of $\Delta^{14}C$ of CO_2 in the atmosphere. This method is most appropriate when aging a single root as opposed to a composite sample that represents a population of roots. For composite samples a time-dependent, steady-state model (method 2) is better because it integrates the $\Delta^{14}C$ concentration of atmospheric CO_2 over the past **n** years (where **n** equals the average age of the population). This model assumes that variation in radiocarbon values of a population of similar root samples, and hence any variation in ages of that population of roots, is normally distributed around the mean. The basic modeling equation is:

$$C_{(t)} \times R_{som(t)} = I \times R_{atm(t)} + C_{(t-1)} \times R_{som(t-1)} - k \times C_{(t-1)} \times R_{som(t-1)} - l \times C_{(t-1)} \times R_{som(t-1)}$$

Collecting terms:

$$R_{som(t)} = \frac{I \times R_{atm(t)} + \left(C_{(t-1)} \times R_{som(t-1)} \times (1 - k - l)\right)}{C_{(t)}}$$

where:

C = Stock of carbon for the given C pool in $gC\ m^{-2}$

I = Inputs of C above and below ground in $gC\ m^{-2}\ yr^{-1}$

k = Decomposition rate of SOM in yr^{-1}

$$R = \left(\frac{\Delta^{14}C}{1000}\right) - 1$$

R_{atm} = The ratio of ^{14}C in the atmosphere normalized to a standard.

R_{som} = The ratio of ^{14}C in the soil organic matter or root sample normalized to a standard.

λ = radioactive decay constant for ^{14}C = 1/8267 years.

t = time (year) for which calculation is being performed

The two methods for using $\Delta^{14}C$ values to estimate an average age are shown in **Figure 3**. With method 1, a root measured in 1999, with its structural material having a hypothetical $\Delta^{14}C$ of 145‰, has an age of 10 ±1 years because the atmosphere last had a $\Delta^{14}CO_2$ of 145‰ in 1990 (1999-1990 = 10 years including the 1999 growing season).

As stated above, method 1 is most appropriate for estimating the age of an individual fine root, while method 2 is most appropriate for a population of roots. However, as shown in **Figure 3**, the difference between the two models is not significant for samples that are less than 110‰, and only 1-2 years for values between 110 and 185‰ (with method 1 predicting older ages relative to method` 2). For roots with $\Delta^{14}C$ values greater than 185‰, the difference in the two methods becomes quite large and opposite in sign because method 2 dampens the bomb signal, especially for larger average ages. In fact, in 1999, $\Delta^{14}C$ values between 174-200‰ do not have a unique solution when applying method 2, and values higher than 200‰ cannot be explained with method 2 (or have no solution).

Results

Radiocarbon values of fine roots

The $\Delta^{14}C$ values for fine roots from the organic horizon less than one year in age (grown during the 1999 growing season only) at both the Harvard Forest and Howland sites are shown in **Table 2**. The $\Delta^{14}C$ values at Harvard Forest range from 86 to 96‰ with a mean of 90‰ and a standard deviation of ± 4‰ (n = 5). The $\Delta^{14}C$ values at Howland range from 71 to 94‰ with a mean of 85‰ and a standard deviation of ± 9‰ (n = 8).

The $\Delta^{14}C$ values for fine roots harvested from soil pits at all three sites are shown in **Table 3** by depth and size class. The $\Delta^{14}C$ values at the Calhoun Experimental Forest (for 1998), the Harvard Forest and Howland (for 1999) range from 116 to 262‰, 97 to

229‰ and 109 to 192‰ respectively. There is considerable variation in $\Delta^{14}C$ values at all three sites with a trend toward increasing $\Delta^{14}C$ as depth and size class increase, particularly at the Calhoun Experimental Forest and at Harvard Forest. The $\Delta^{14}C$ values for fine roots collected in 1979 at Harvard Forest range from 340 to 366‰ for roots < 0.5 mm in diameter, and 225 to 273 for roots between 0.5-3 mm in diameter.

Fine root $\Delta^{14}C$ values for Harvard Forest and Howland (for 1999) from both **Table 2** and **Table 3** are shown in **Figure 4** in relation to the $\Delta^{14}C$ of atmospheric CO_2 in 1999 (92 ± 2‰). The fine roots that grew only for the 1999 growing season are close to the atmospheric $\Delta^{14}C$ of CO_2 in 1999 (from –19 to + 4‰). In contrast, fine roots from the soil pits have $\Delta^{14}C$ values that are greater than the 1999 atmospheric $\Delta^{14}C$ of CO_2 by +17 to +180‰.

Two individual fine roots collected in 1997 at Harvard Forest and analyzed for the $\Delta^{14}C$ of structural C in the main stem and the secondary growth off that stem are shown in **Figure 5**. Each $\Delta^{14}C$ value shown represents components from one root and not a composite of several roots. The $\Delta^{14}C$ values for the primary growth on the main stem are 134 and 177‰ for **Figure 5A** and **5B** respectively. The secondary growths off the stems are 116‰ in both cases.

Modeling Fine Root Age

The ^{14}C data in **Table 3** and **Figure 2** are also shown in **Figure 6** (for all depth and size classes combined) along with curves showing the modeled ranges in fine root age that fit the data, using method 1 (**Figure 6A**) and method 2 (**Figure 6B**). The $\Delta^{14}C$ values for all fine roots measured at all time points at our three sites are consistent with ages significantly longer than one year using either of our root age models (**Figure 6A** and **6B**). Method 1 (**Figure 6A**) basically slides the atmospheric record back and forth through time, with the curves representing the age of an individual root whose structural carbon has not exchanged with more recently fixed carbon since it originally grew. All data shown are bracketed by model curves that represent individual roots with structural carbon fixed 2 to 20 years ago, except of the 0.5-3 mm live roots sampled in 1979, which are lower than the atmospheric $\Delta^{14}C$ of CO_2 in 1979 by 26 to 75‰ (**Table 3**). The fact that these coarser roots are significantly lower than the atmosphere also implies that these roots were fixed several years previously. They are lower than the atmospheric $\Delta^{14}C$ of CO_2 in 1979 (299‰) only because the bulk of their carbon was fixed from atmospheric CO_2 prior to 1958 (the first time the atmospheric $\Delta^{14}C$ of CO_2 was above 200 per mil). Thus, their age is consistent with the leading edge of a curve representing 22 year old roots (not shown). Using method 2 (**Figure 6B**), which represents a population of roots, the Harvard Forest and Calhoun Experimental Forest data are in many cases above the maximum $\Delta^{14}C$ value that can be calculated by this model in 1999 (20 years; see discussion in methods section). Again, the coarser 0.5-3mm roots from 1979 can only be explained with a curve representing an older average age (24-32 years).

The calculated ages for fine roots sampled in 1998 and 1999 (using method 1) as a function of depth and size class range in age from 3-18 years (**Figure 7**). The error bars indicate the error associated by method 1 plus any additional range in age that would be calculated from method 2 (when applicable). For example, method 1 predicts that a sample with a $\Delta^{14}C$ value of 160‰ has an age of 11±1 years, and method 2 predicts 10±1 years. Thus the age would be shown on **Figure 7** as 11 +1 and –2 years.   In the Calhoun

Experimental Forest live roots < 2 mm range in age from 5-16 years, while roots > 2 mm range in age from 12-18 years. Taking a stock-weighted average, roots < 2mm in diameter are 9 years and roots > 2mm are 15 years in age. At Howland, fine root (< 1 mm, live and dead) ages range from 5-14 years. Taking a stock-weighted average which assumes all roots are in either the <0.5 or .5-1 mm size class, (since we do not know the relative partitioning of root mass into either class) results in average ages of 10 and 11 years for roots <0.5 and 0.5-1 mm respectively. At the Harvard Forest, ages range from 3-15 years, with a stock-weighted average of 6 and 10 years if we assume all roots are in either the <0.5 or 0.5-1 mm size class respectively. The 1999 samples from Harvard Forest and Howland were not sorted into live and dead fractions. However, the 1996 data (**Figure 2**), which were sorted into live and dead categories, show significantly different means for live and dead roots in the organic (O) horizon, with the dead roots having higher $\Delta^{14}C$ values by 48‰ (about six years). The number of samples is too low to determine such a trend for the A and B horizons. The data for the organic horizons imply that dead roots may persist in the soil for several years, which is consistent with published rates for root decomposition on the order of several years at Harvard Forest (McClaugherty et al., 1984). Therefore, the age calculations for the roots collected in 1999, that combine live and dead roots, may overestimate the period that fine roots live by up to several years.

The profiles in **Figure 7** show a tendency for changes in average fine root age with depth in the soil profile. At the Calhoun Experimental Forest, a mono-specific loblolly pine plantation, fine root ages increase with both depth and size class. Roots were not separated by species at Howland or Harvard Forest, but in the well developed

Spodosols at Howland, fine root age is related to soil horizon, with the youngest ages at ~8-10 cm depth where humic materials accumulate beneath an E horizon (a zone of nutrient leaching). In all three locations, where a significant difference exists between size classes, the roots in the smaller size classes are younger. This trend also holds for the archived roots collected at Harvard Forest in 1979 (**Figure 6**). Roots < 0.5 mm range in age from 3-5 years while the roots between 0.5-3mm range in age from 22-32 years depending on the model used.

Discussion

Fine root longevity

We have tested our first two hypotheses (that roots live significantly longer than one year or that they are synthesized from carbon reserves stored in the plant for several years) by comparing the measured $\Delta^{14}C$ of the structural C in roots (live + dead) that are known to have grown through root screens placed in the soil within the past year (and are thus one year or less in age) to the structural C of roots (live and dead) sampled from a soil pit dug near the time of screen harvest (**Tables 2** and **3**; **Figure 4**). All fine roots known to have grown in 1999, and to be less than one year old, all have a strikingly different range of $\Delta^{14}C$ values relative to those dug from the soil pits (**Figure 4**). All roots less than one year in age are within two standard deviations of the atmospheric $\Delta^{14}C$ of CO_2 for 1999 (92 ±2‰), and all but four values are within one standard deviation of this value (**Table 2**). Roots from the soil pits, however, are all elevated by a consistently higher degree (**Table 3**). The contrast in $\Delta^{14}C$ between newly grown fine roots and those sampled from the soil pits (**Tables 2** and **3**, **Figure 4**) argues quite clearly that: 1) Newly grown fine roots are formed with photosynthate fixed within the last one to two years. 2) Fine roots randomly sampled in a pit represent a population whose $\Delta^{14}C$ is significantly elevated relative to both the atmospheric $\Delta^{14}C$ of CO_2 and the $\Delta^{14}C$ of newly grown roots, consistent with average ages of many years.

The third hypothesis (that roots actively take up C via mycorrhizal association from surrounding soil organic matter with elevated $\Delta^{14}C$) is unlikely because their $\Delta^{14}C$ content remains elevated relative to the atmosphere through the entire soil profile. Indeed, the carbon in soil organic matter below 15 cm depth is depleted in ^{14}C (i.e. $\Delta^{14}C < 0‰$) at all three sites (Gaudinski et al., 2000, Richter et al., 1999) yet the roots found there are enriched in bomb ^{14}C (with values from 108-260‰). Additionally, for this hypothesis to be correct, between 20 to >100% of the structural carbon would have to come from soil organic carbon in order to explain the degree of elevated $\Delta^{14}C$ of fine roots relative to the atmosphere for over 99% of the roots we sampled from the soil pits. While it is possible some exchange is taking place, it is unlikely to contribute such large amounts of structural carbon. Therefore, we have concluded that the first hypothesis is the correct one: Live and dead roots with $\Delta^{14}C$ values substantially greater than that of the contemporary atmosphere (i.e. greater than 2 standard deviations) live and persist for several years.

Neither of our models is ideal for calculating fine root age. Method 1 is imperfect because the samples are not individual roots, but rather are composites of several fine roots which likely vary in age. Method 2 is problematic because it does not adequately capture age distributions for a population, especially for those populations that are not normally distributed about the mean, but skewed towards longer residence times. But despite the uncertainties in modeling fine root age to within one to two years, both models clearly show that the radiocarbon content of fine roots collected in both the late 1970's and the late 1990's cannot be explained by rapid turnover and in many cases the lifespan of these fine roots must be on the order of a decade.

Variability in fine root lifespan

Our finding of relatively long fine root ages based on radiocarbon can be reconciled with shorter turnover times estimated with steady-state mass balance methods (dividing stock by production or loss rate) or using minirhizotrons and screen counting techniques if fine roots have a range of lifespans, from months to many years, and each method is biased toward emphasizing one end of the range. It is important to recognize that age only equals turnover time in a homogeneous system whereevery root has the same probability of death. Fine root depth profiles (**Figure 7**), however, clearly indicate that turnover varies within fine root populations. Individual fine roots also show multi-year age differences between root tips and the stem from which they grow. In **Figure 5**, the ages (using method 1) for the primary stem and the secondary growth off that stem are three and five years for the well drained site and four and eleven years for the poorly drained site, respectively. For these two sites, the Δ^{14}C values correspond to age differences of two and seven years between different parts of the same fine root (**Figure 5**). Hence, if a large fraction of the fine root mass has a high radiocarbon content (i.e., a slow turnover time) and a relatively small fraction of the fine root mass has lower radiocarbon content (i.e., a fast turnover time), then the mass-weighted average radiocarbon content will indicate a relatively long turnover time (age) of C in fine roots.

Conversely, a steady-state mass balance based calculation would yield a much shorter estimate of turnover time because of the large flux of C through the most active fraction of the pool that has relatively low biomass and low radiocarbon content.

Variation in turnover may explain some of the inconsistencies between different methodologies for sampling fine roots. Minirhizotrons and screen counting techniques are biased towards roots with fast turnover because they selectively look for changes in root length, or root appearance and disappearance at the root tips. Root tips may well be die earlier than the main stem of the root. Conversely, the use of ^{14}C measurements directly on root tissues is biased toward longer turnover because the largest mass accumulates in the most recalcitrant part of the assemblage. The dynamics of any small, yet fast-cycling, components will consequently be underestimated unless the heterogeneous components can be fractionated into homogenous pools prior to ^{14}C analysis (Trumbore, 2000, Gaudinski et al., 2000). The current ^{14}C data clearly indicate that fine roots are highly heterogeneous with respect to age, and suggest that root tips cycle more rapidly than primary fine root stems, even though both are small enough (< 2 mm) to be lumped into a size-defined class called “fine roots”.

The timescales within which minirhizotron experiments are typically undertaken may also contribute to their fast fine root lifespan estimates. For example, minirhizotron techniques are extremely labor intensive and therefore encourage short deployment (one to two years). As such, they do not typically have the opportunity to observe roots living for many years. One unusually long four year minirhizotron study in ponderosa pine seedlings grown in the foothills of the Sierra Nevada Mountains found that, for the 18 cohorts of roots they followed, all but one had roots which survived through the last sampling date. For the fine root cohort measured at the beginning of the study, 4% of the observed roots were still alive at the end of the study 1350 days later (Johnson et al., 2000). In this study the cohorts of fine roots first observed in year one had higher death rate than those first observed in year two, and those of the second year tended to die faster than those first measured in the third year. This pattern suggests that root dynamics shifted toward longer lifespans as the 1.5 year old seedlings (when the study began) aged and grew.

An untested hypothesis relating to the long ages that are calculated from $\Delta^{14}C$ values that are substantially elevated relative to the $\Delta^{14}C$ of atmospheric CO_2 may also come from a "concentration effect" of ^{14}C in fine roots as they age. The data in **Figure 4** show that when roots first grow, they are made primarily of recently fixed photosynthate. However, roots that last for several years may use translocated carbon (with higher $\Delta^{14}C$ content) from stored reserves within the tree, perhaps in coarse woody roots. This "concentration effect' would then make roots appear older than they actually are. To determine if this is plausible, roots of known ages from long running minirhizotron experiments should be tested for radiocarbon content.

Globally, fine roots have been estimated to comprise 33% of NPP, assuming annual turnover (Jackson et al., 1997), and about 50% of NPP in forest ecosystems (Vogt et al., 1998). Our finding that fine roots vary significantly in age, and can indeed live and persist in the soil environment for a decade or longer, emphasizes the uncertainty in our current understanding of below-ground C allocation. Whether this implies that estimates of a large NPP expenditure to fine roots are inaccurate is uncertain. Possibly, a small percentage of the fine root population (or root exudation) is dynamic enough to account for a large NPP flux. We can put some bounds on belowground NPP for temperate forests by using the approach of Raich and Nadelhoffer (1989) for soils near steady state with respect to carbon storage:

$R_s - P_a - R_r \approx P_b$

R_s = soil respiration for an average temperate forest (665 gC m^{-2} yr^{-1}; (Raich and Schlesinger, 1992)

P_a = above ground detritus production for an average temperate forest (175 gC m^{-2} yr^{-1}; (Raich and Nadelhoffer, 1989))

R_r = root respiration for an average temperate forest (gC m^{-2} yr^{-1}; floating variable)

P_b = below ground detritus production (gC m^{-2} yr^{-1}; unknown) = belowground NPP

Assuming NPP of an average temperate forest is 600 gC m^{-2} yr^{-1} (Raich and Schlesinger, 1992) and R_R is 20% of R_S, then below-ground NPP would be 60% of total NPP. A review of methods for separating root and soil microbial contributions to soil respiration (Hanson et al., 2000) shows that R_r for temperate forest studies, which integrate over an entire year or growing season, is most commonly between 40-60% of R_s (with a mean of 45.8%). Using this range below-ground NPP is then 35-15% (30% using the mean) of total NPP. This range is less than the 50% below-ground NPP often ascribed to temperate forests. We use this approach only to show that, based on measured C fluxes in forest soils, current estimates of below-ground NPP may be somewhat higher than reality. However, in order to satisfy both the need for substantial annual NPP allocation belowground *and* a fine root stock that average in age from 6-11 years, fine roots must have ages ranging from months to a decade or more.

Conclusions

Although absolute ages are somewhat uncertain, our $\Delta^{14}C$ data clearly indicate that a large percentage of fine root stocks in forest ecosystems live for many years. We also find that fine roots vary in age from months to decades or more. The commonly used definition of fine roots as those with < 2 mm diameter is problematic because it lumps together populations of roots that cycle carbon at significantly different rates. Improved understanding of ecosystem carbon balance will require combined measurement approaches that further explore the ecology of fine roots.

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Table 1. Site descriptions

Location	Dominant Species	Soil Type	Latitude	MAT (°C)	MAP (mm)	Stand age (Years)
Howland, ME	Red Spruce, Balsam Fir	Typic Haplorthods	45°N	5.5	1000	100
Harvard Forest, MA	Red Oak, Red Maple	Typic Distrochrepts	42°N	8.5	1050	50-70
Calhoun Experimental Forest, SC	Loblolly Pine	Typic Kanhapludult	35°N	16	1170	41

Table 2. Δ^{14}C of fine roots less than than one year in age sampled in 1999 at Howland and Harvard Forest.

SITE	**D^{14}C (‰)**
Harvard Forest[1]	**< 1 mm in diameter**
Root screen	86 (6)
Root screen	86 (6)
Root screen	87 (5)
Root screen	91 (6)
Root screen	96 (6)
Howland[1]	**< 1 mm in diameter**
Root screen	94 (5)
Root screen	86 (6)
Root screen	94 (6)
Root screen	71(5)
Root screen	74 (5)
Root screen	86 (5)
Root screen	81 (6)
Root screen	94 (6)

Values in parenthesis represent precision of the AMS measurement which is a combined machine plus laboratory error.

[1] Atmospheric Δ^{14}C in 1999 was 92 +/- 2‰
(Levin and Kromer 1997; see text for further details).

Table 3. Δ^{14}C of fine roots sampled from soil pits at all three

SITE	**D^{14}C (‰)**	**D^{14}C (‰)**
Calhoun Experimental Forest-1998[1]		
Depth (cm)	**< 2 mm in diameter**	**> 2 mm in diameter**
O horizon (+2-0)	116 (5)	
0-15	144 (5)	178 (6)
15-30	228 (6)	262 (6)
Harvard Forest-1999[2]		
Depth (cm)	**< 0.5 mm in diameter**	**0.5-1 mm mm in diameter**
O Horizon (+5-0)	97 (6)	132 (6)
0-2	197 (6)	229 (6)
2-6	116 (6)	149 (9)
6-30	188 (7)	168 (7)
Howland-1999[2]		
Depth (cm)	**< 0.5 mm in diameter**	**0.5-1 mm mm in diameter**
O horizon (+10-4)	128 (6)	192 (6)
O horizon (+4-0)	160 (6)	154 (6)
0-7	134 (6)	121 (5)
7-13	109 (6)	115 (6)
13-30	190 (6)	175 (6)
Harvard Forest-1979[3]		
Depth (cm)[2]	**< 0.5 mm in diameter**	**0.5-3 mm in diameter**
0-15	340 (6)	249 (6)
15-30	377 (8)	273 (6)
30-45	366 (7)	225 (6)

Values in parenthesis represent precision of the AMS measurement which is a combined machine plus laboratory error.

[1] Atmospheric Δ^{14}C in 1998 was 96 +/- 2 ‰ (Levin and Kromer 1997, Levin and Hesshaimer, in press; see text for further details).

[2] Atmospheric Δ^{14}C in 1999 was 92 +/- 2‰ (Levin and Kromer 1997, Levin and Hesshaimer, in press; see text for further details).

[3] Atmospheric Δ^{14}C in 1979 was 299 +/- 9 ‰ (Levin and Kromer 1997).

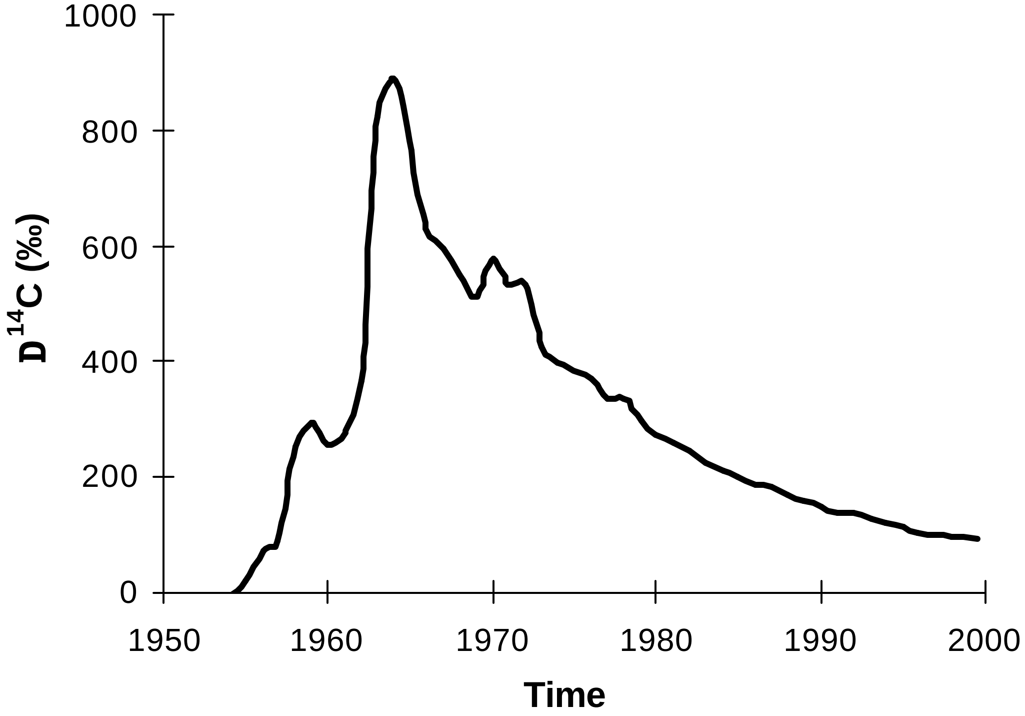

Figure 1. The time record of $\Delta^{14}C$ in atmospheric CO_2 (Northern Hemisphere).

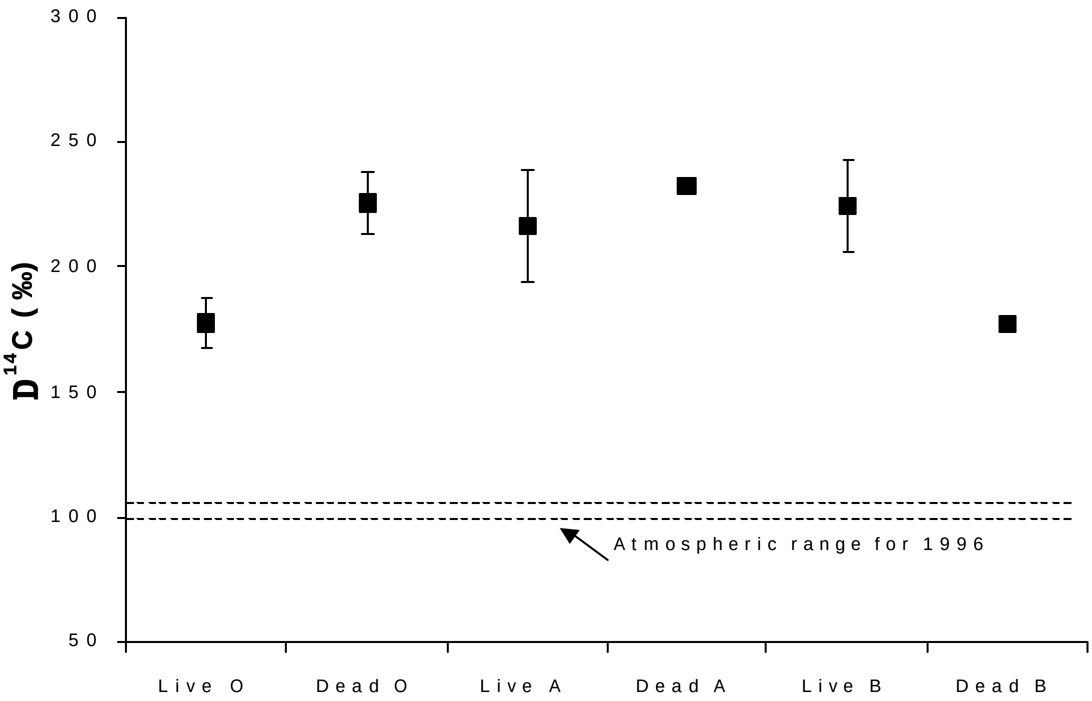

Figure 2. The $\Delta^{14}C$ values by soil horizon for live and dead fine roots collected during 1996 at Harvard Forest. The atmospheric $\Delta^{14}C$ of CO_2 in 1996 was 104.3 ± 3.0‰ (Levin and Kromer, 1997). Error bars represent the standard error where present (n equals 10, 7, 3 and 6 for live O, dead O, live A and live B horizon roots respectively) otherwise n = 1 or 2.

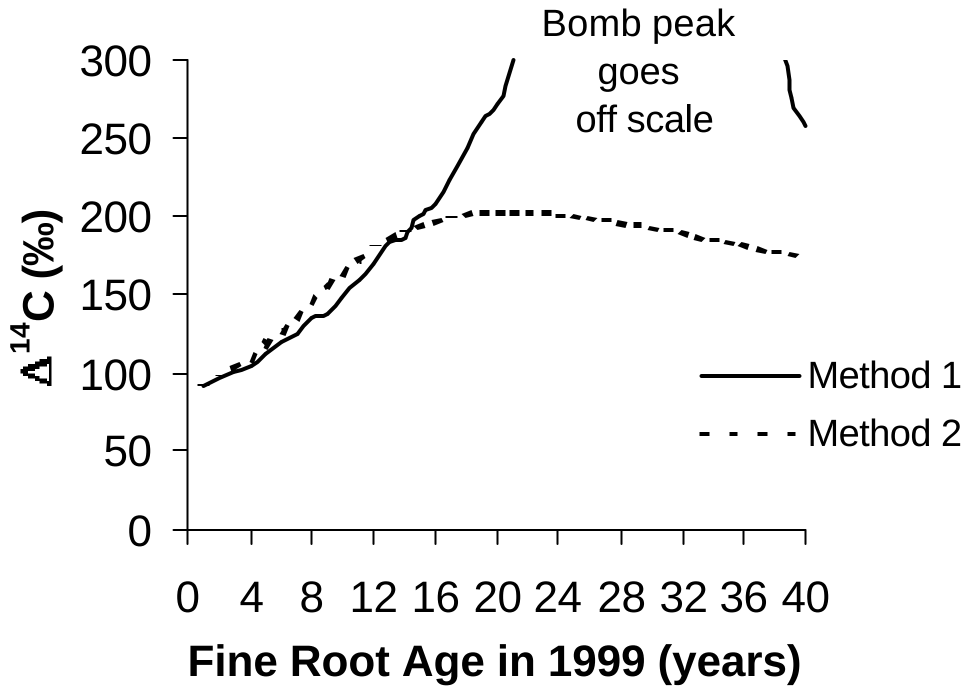

Figure 3. Results from two modeling approaches for calculating fine root age as a function of Δ^{14}C content. Method 1 uses the atmospheric Δ^{14}C of CO_2 as a proxy for calculating fine root age. Method 2 is a steady state time dependant model also based on the atmospheric Δ^{14}C record of CO_2. See text for further details.

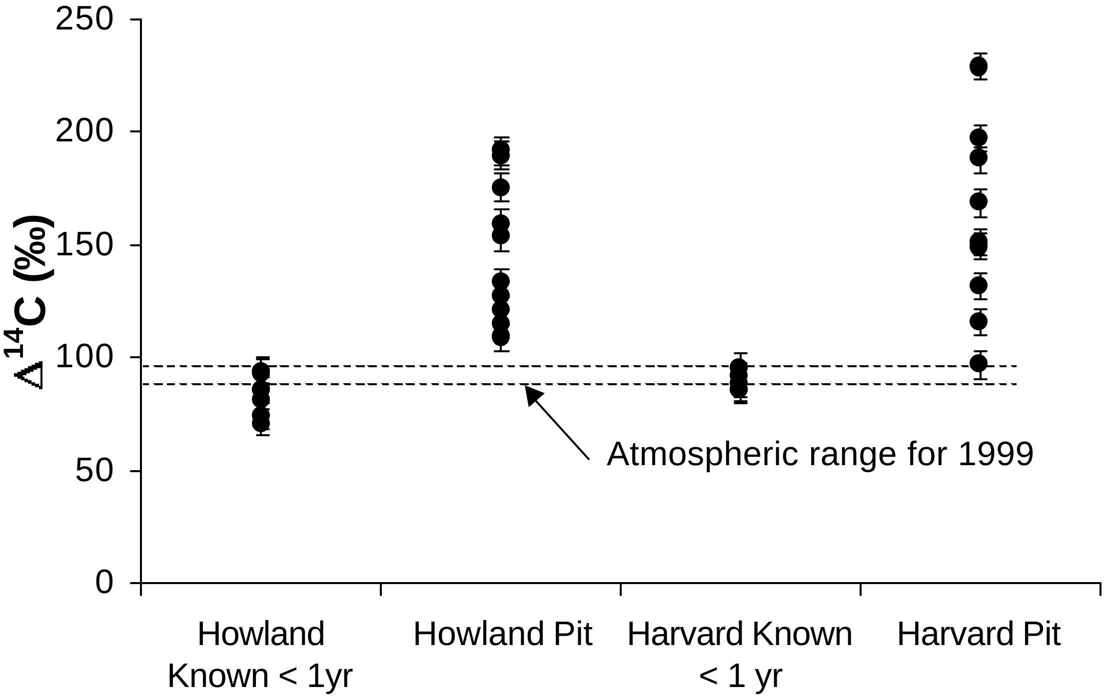

Figure 4. Radiocarbon values for fine roots (< 0.5 mm and 0.5-1mm in diameter) from the Howland and Harvard Forest sites sampled in 1999. Roots "known <1 yr" were sampled from root screens placed in the organic horizon in spring of 1999 and harvested in fall 1999 and are less than one year old. "Pit" samples are roots sampled from soil pits dug in July 1999. The atmospheric range in $\Delta^{14}C$ of CO_2 in 1999 is 92 ± 2‰ (Levin and Kromer, 1997, Levin and Hesshaimer, 2000).

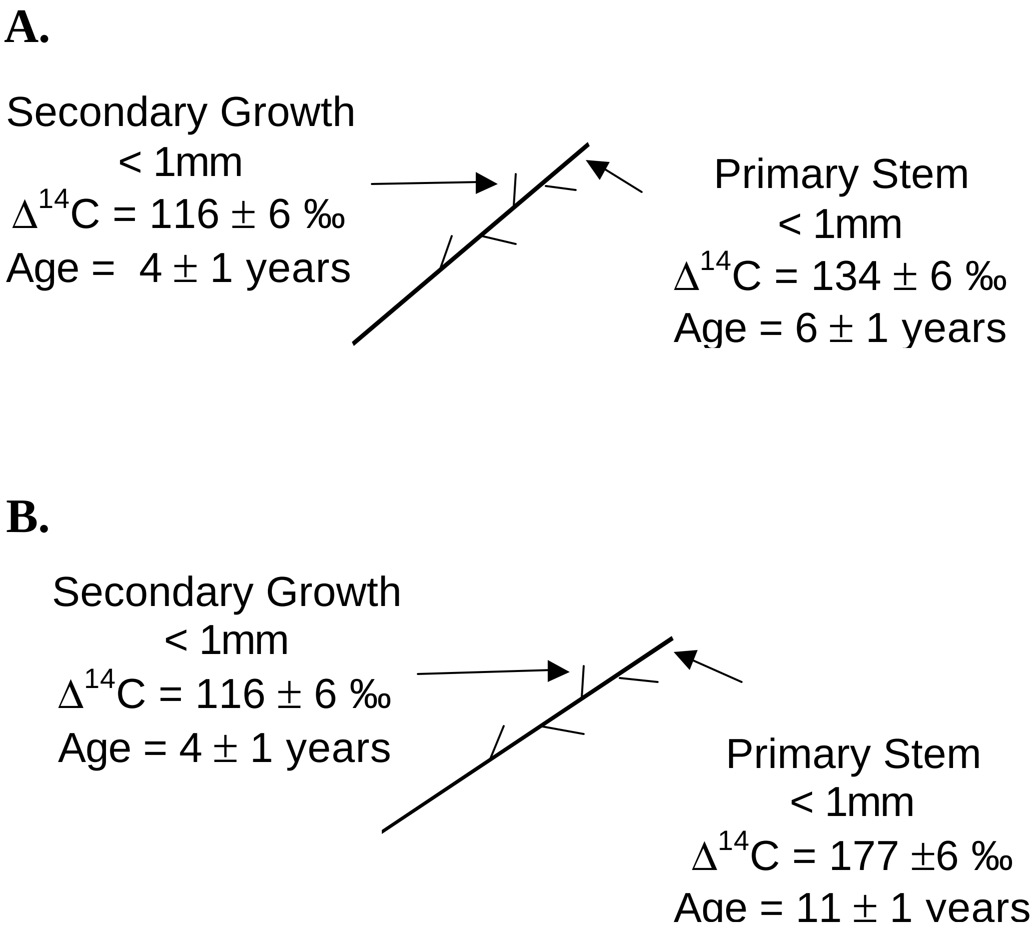

Figure 5. $\Delta^{14}C$ values for individual live fine root components growing in the organic horizon at Harvard Forest in 1997. The ages shown are calculated using method 1 only. The samples are from two different sites (**A** well drained; **B** poorly drained) and each $\Delta^{14}C$ value shown represents components from one root and not a composite. Therefore, they should not be thought of as necessarily representative of site to site differences. The $\Delta^{14}C$ of the atmosphere in 1997 is 100 ±2‰ (Levin and Kromer, 1997, Levin and Hesshaimer, 2000).

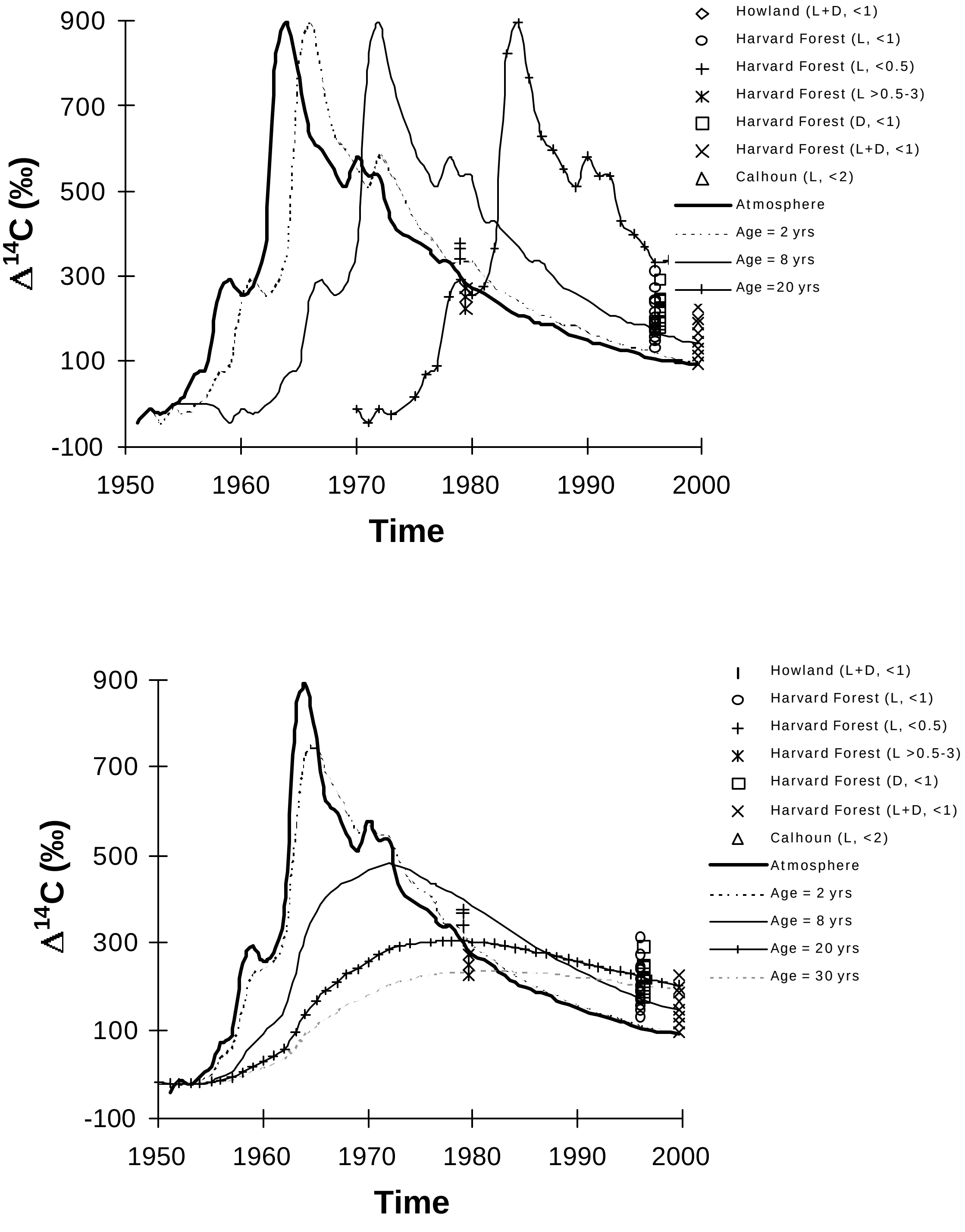

Figure 6. The radiocarbon values of fine roots for all depth intervals measured at Howland, ME (1999), Harvard Forest, MA (1979, 1996 and 1999) and The Calhoun Experimental Forest (1998), SC using method 1 (Figure 6A) and method 2 (Figure 6B). L = live roots; D = dead roots; numbers indicate diameter range of fine roots sampled. Precision with AMS for modern samples is typically ± 6‰ and thus error bars are smaller than the symbols shown.

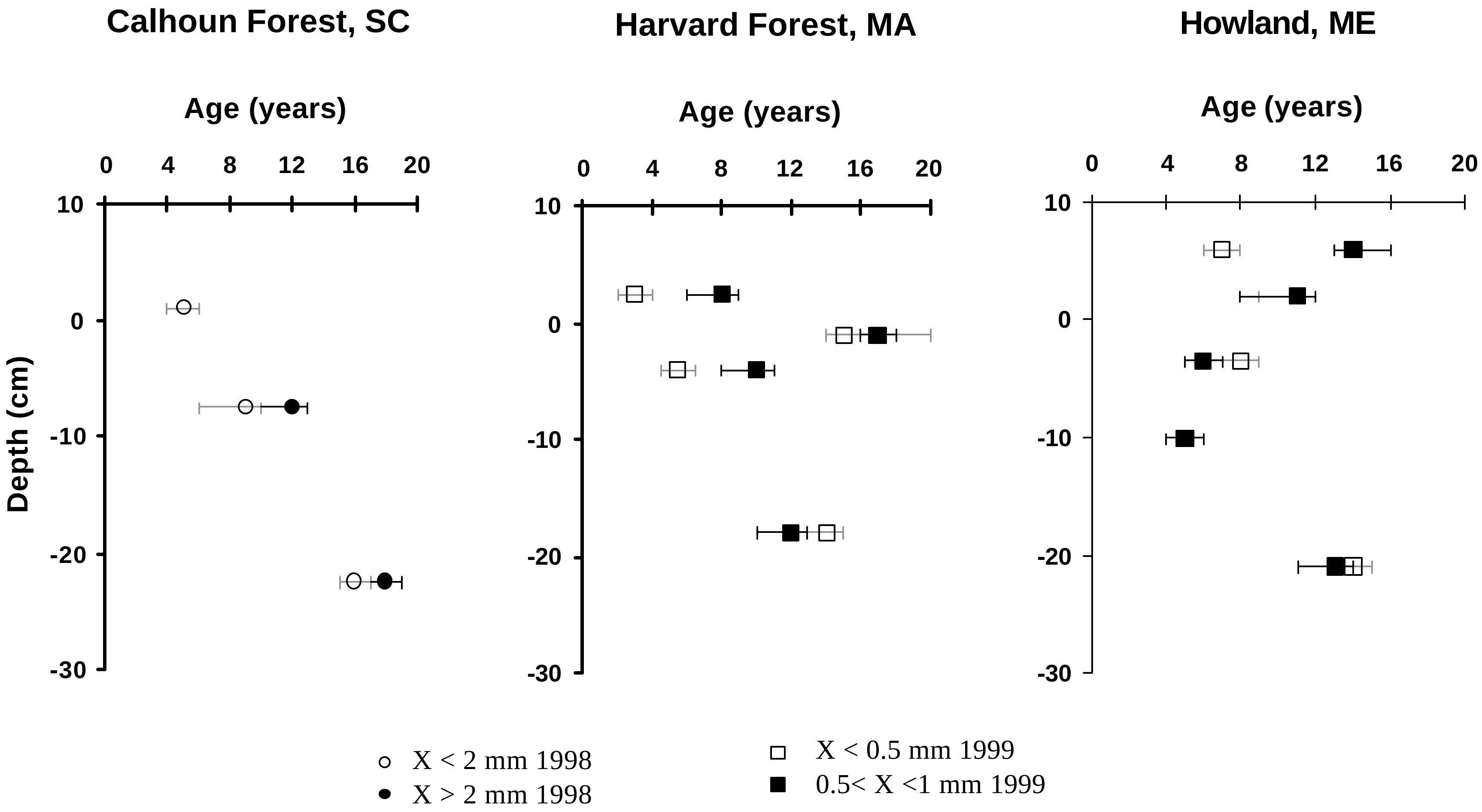

Figure 7. The estimated age of fine roots sampled at Harvard Forest and Howland (1999) and The Calhoun Experimental Forest (1998) using method 1. The error bars indicate the error as calculated by both method 1 plus any additional range in age as calculated by method 2 (when applicable). The depths shown indicate the midpoint of the sampling horizon or depth interval. Depths greater than zero represent the midpoint of the organic (O) horizon.

Chapter 5: Soil respiration fluxes: Age, Variability and Partitioning

Introduction

This chapter builds on work presented in Chapters 2 and 3. Chapter 2 presents a method for partitioning soil respiration into two components using the $\Delta^{14}C$ signature of soil respiration and ^{14}C-derived turnover times of soil organic matter fractions at Harvard Forest. Chapter 3 discusses ^{14}C-derived SOM turnover times and dynamics at Howland, Harvard Forest and Walker Branch. Here, decomposition dynamics based on $^{14}CO_2$ measurements at all three sites is explored. Treatment of soil respiration is expanded to introduce a second, new, method of partitioning based on measuring $^{14}CO_2$ evolved during soil incubations. We compare the two methods using data from the Howland and Harvard Forest sites (Walker Branch is compromised due to an unexpected ^{14}C release in 1999). Additionally, this chapter assesses the impact of inter-annual variability of climate on decomposition dynamics and respiration partitioning at the same site in years with varying climate.

Soil respiration is one of the largest sources of interannual variation in net ecosystem production (NEP) in forests (Goulden et al., 1996, Savage and Davidson, in Press). However, the extent to which variations in NEP are due to changes in autotrophic (metabolic live root) versus heterotrophic (decomposition of soil organic matter by microbes and soil fauna) respiration processes is largely unknown. Potential changes in plant productivity and climate in the coming decades will likely influence both rates of decomposition of soil C stocks and live root respiration, though not necessarily with the same magnitude or direction. Changes in plant productivity will influence the amount and kind of C input to soil organic matter, while changes in soil temperature and moisture will influence microbial activity and decomposition rates. In order to assess the influence of varying rates in soil respiration on ecosystem C balance in both the long and short-term, partitioning of soil respiration into autotrophic vs. heterotrophic sources and ultimately understanding the factors controlling this partitioning is critical.

Several approaches have been used to partition soil respiration fluxes into autotrophic and heterotrophic components (see Hanson et al., 2000 for a review of these techniques). Briefly, these consist of component integration, root exclusion, and isotopic approaches including pulse labeling (^{14}C, ^{13}C) and continuous isotopic labeling (^{13}C Free air CO_2 enrichment (FACE), C3-C4 over-planting and bomb ^{14}C). The isotopic techniques have the advantage over component integration and root exclusion techniques because they provide quantitative results with the least amount of disturbance to the soil system (Hanson et al., 2000). Among the isotopic methods, pulse labeling studies are generally of shortest duration (weeks to months) and measure only C cycling on daily to weekly timescales. They miss the contribution of the slower cycling carbon important in assessing the dynamics of soil carbon stocks. Long-term labeling experiments with fossil fuel CO_2 such as FACE experiments are extremely labor-, equipment- and cost-intensive. C3-C4 over-planting is limited in its application because it requires ecosystems to have undergone a change in vegetation that switches the dominant photosynthetic pathway from C3 to C4 or vice versa. Utilization of bomb produced ^{14}C as a continuous isotopic label has distinct advantages because it does not require the entire system to be disturbed, can resolve dynamics that operate on annual and much longer time scales, can be employed in all ecosystems and does not require extensive field instrumentation.

The utility of bomb ^{14}C in studying the sources of soil respiration derives from the large differences in ^{14}C from autotrophic respiration ($\Delta^{14}C$ = 92‰ in 1999), decomposition of decadal scale ($\Delta^{14}C$ > 92‰ in 1999), and centi-millenial cycling SOM ($\Delta^{14}C < 0$) see (Chapter 3, Figure 9). The ^{14}C of CO_2 in soil respiration content will fluctuate as 1) the partitioning between autotrophic and heterotrophic respiration varies (Dorr and Munnich, 1986, Wang et al., 2000) and 2) SOM sources with differing ages vary in their contributions of decomposition derived CO_2 in response to changes in soil temperature, moisture and nutrient status throughout the profile (Wang et al., 2000).

One disadvantage of using bomb ^{14}C as a tool to partition soil respiration is that the $\Delta^{14}C$ of atmospheric CO_2 which decreased at a rate of ~8‰ per year between 1990-1995 (Levin and Kromer, 1997) has slowed to 4‰ per year between 1996-1999 (Levin and Hesshaimer, 2000). Our analytical uncertainty in ^{14}C measurements is 5-6‰ thus we can resolve the timing of fixation only to within 1-2 years over the duration of this study. Autotrophic respiration, which results from decomposition of Recent-C (C fixed within the past few hours to weeks), will have the ^{14}C signature of atmospheric CO_2. Heterotrophic decomposition of above and belowground litter fixed within the past year will also have the same $\Delta^{14}C$ signature as autotrophic respiration. Hence careful definition of terms of what is actually being partitioned by isotopic mass balance techniques is very important. **Figure 1** shows the belowground forest C cycle, including the definitions of terms used throughout this chapter and their respective ^{14}C isotopic signatures.

Development of methods to partition soil respiration into its component parts and to assess the dynamics of soil carbon stocks via C and ^{14}C measurements of soil respiration is a major goal of this thesis. Chapter 2 presented a method for partitioning soil respiration into two components (Recent-C and Reservoir-C; see **Figure 1**) using the Δ^{14}C signature of soil respiration the ^{14}C-derived turnover times of soil organic matter (SOM) fractions, and mass balance considerations at Harvard Forest. Chapter 3 discussed C and ^{14}C inventories and ^{14}C-derived SOM turnover times at Howland, Harvard Forest and Walker Branch. Here, treatment of soil respiration is expanded to:

- Assess decomposition dynamics based on $^{14}CO_2$ measurements at all sites.
- Introduce a new soil respiration partitioning method based on soil incubations.
- Compare the two respiration partitioning methods at Howland and Harvard Forest (Walker Branch is compromised due to an unexpected ^{14}C release in 1999).
- Explore changes in respiration partitioning at the same site in years with varying climate.

Methods

Total C and ^{14}C inventory

Methods for sampling C and ^{14}C inventory at all sites are discussed in detail in Chapter 1 for Harvard Forest and Chapter 2 for all three sites.

Characterization of CO_2 and $^{14}CO_2$ fluxes

Methods for measuring soil CO_2 and $^{14}CO_2$ in total soil respiration and by depth within the soil profile are discussed in detail in Chapter 2. These same methods were applied to all three sites, with the exception of total soil respiration measurements at Walker Branch. At Walker Branch, soil surface CO_2 fluxes are calculated from a model developed by Paul Hanson. Modeled soil respiration is calculated using empirical relations of soil CO_2 emission to soil temperature, soil water content and litter layer water content. Hourly measures of these variables are then used to estimate CO_2 flux. The model of total soil respiration includes additive functions for litter respiration (function of water content and temperature), mineral soil respiration (function of soil temperature and water potential), and root growth costs. Root maintenance respiration contributions to total soil respiration are assumed to be 50%. The model is run in Ithink or Stella (High Performance Systems, Inc.).

Measured $\delta^{13}C$ data are used to calculate $\Delta^{14}C$ for CO_2 sampled from the soil profiles. Fractionation by diffusion means that CO_2 profile $\delta^{13}C$ values are enriched by up to 4.4 per mil compared to their source material (Cerling et al., 1989). Using this relation, the $\delta^{13}C$ of the soil respiration source is ~-26 per mil, close to the measured δ13C values for labile soil organic matter fractions.

As discussed in Chapter 2, $\Delta^{14}C$ of CO_2 from soil respiration is corrected for any leaks of atmospheric CO_2 ($\delta^{13}C$ of –8.5‰) into the sampling system based on its measured $\delta^{13}C$ signature. The measured $\delta^{13}C$ signature of SOM at these sites is –26‰. Thus soil respiration should also be –26‰ and the degree to which it is heavier reflects mixing with atmospheric CO_2. Unlike soil respiration however, measurements of soil gas profiles are not corrected to a $\delta^{13}C$ of –26‰ because diffusion is known to enrich profile $\delta^{13}C$ of CO_2 by 4.4‰ relative to the source material (Cerling et al., 1989). Thus soil profile $\delta^{13}C$ should be close to –21.6‰. Over 99% of all profile $^{14}CO_2$ measurements made in this study are within 2-3‰ of this value.

Soil temperature and moisture were monitored at all three sites. Methods for monitoring temperature and moisture for Howland and Harvard Forest are described in Chapter 2. At Walker Branch soil temperature was measured at 15 and 35cm depth at the TDE site and logged hourly (Hanson et al., 1998, Hanson et al., submitted). Soil moisture measurements are described in detail in Hanson et al., 1998. Briefly, soil water content (%, v/v) is measured using time domain reflectometry (TDR) probes. At each sampling location two vertical TDR probes (0-35 cm and 0-70 cm) allowed estimation of an integrated volumetric moisture value for the two depth intervals.

Soil Incubations

Incubations of soil organic matter (placing soil in a sealed jar and monitoring CO_2 and $^{14}CO_2$ with time) are a useful tool in deciphering the heterotrophic signal of decomposing SOM because they solve two important problems inherent in any *in-situ* measurement of soil respiration. First, they eliminate the presence of autotrophic respiration from living plant roots. Secondly, they characterize the carbon that is actually decomposing instead of the ^{14}C of the SOM stocks, which are typically dominated by a large mass of more recalcitrant C stocks. The measured isotopic signature of CO_2 derived from heterotrophic decomposition released during the incubation represents a combination of all heterotrophic sources (i.e. Fast-C plus the slower cycling Reservoir-C (see **Figure 1**).

Incubation samples were taken at Howland, Harvard Forest and Walker Branch in mid-July 1999 with a stainless steel bulk density sampling corer 5 cm in diameter and 5 cm long. Two pits were dug at Howland (NC and Tower locations), Harvard Forest (NWN location) and Walker Branch (P5 and TDE locations) and two replicate samples taken for each horizon/depth interval at each pit (thus n = 4 for each site). The corer was hand driven into the soil proceeding downward with focus placed on sampling a particular soil horizon or horizon combination rather than a specific depth interval. Two samples were taken from each horizon at each pit. The depth in the corer was carefully measured and the sample then carefully extruded into a 100 ml glass container (pre-baked at 500 °C), covered with aluminum foil and then capped. Separate soil samples were also collected to determine field moisture at the time of sampling. Samples were taken back to lab, weighed and stored in a refrigerator for 1-2 days and shipped overnight with blue ice to UC Irvine where they were refrigerated at 8°C.

Within two days of arrival at UC Irvine, the 100 ml glass jars were re-weighed, water added to bring them up to gravimetric field moistures similar to those measured in June and July in1996 (as the soils were unusually dry when sampled in July of 1999) and placed inside 1-2 liter mason jars with airtight lids containing stopcocks. Atmospheric CO_2 was removed at the beginning of the incubation by circulating 3 volumes of jar air through a soda lime (80% CaOH, 3%KOH, 2%NaOH) trap. CO_2 concentrations were monitored at one to two day intervals throughout the 12-day incubation period. The temperature range in the room where the incubations took place ranged from 16.2-18.8°C, well within range of the average and maximum summer time temperatures observed in the top ten centimeters (16.3-16.9°C (average) and 19-20.5°C (maximum)) and similar to maximum soil temperatures observed at 33 and 60 cm during the period 1995-1998 (17.1 and 16°C respectively) at Harvard Forest. After 12 days of incubation, total CO_2 concentration and $\delta^{13}C$ of CO_2 was measured for each jar. Based on the rate of evolved CO_2 and the $\delta^{13}C$ of the sample (which will indicate if the jar was leak tight), CO_2 from only one of the two jars from each site/pit/horizon was selected for $^{14}CO_2$ analysis.

To see if the isotopic signal of the evolved C changed over the course of a longer incubation we performed additional incubations of upper and lower O horizons (which have extremely heterogeneous reservoirs of SOM) and sampled for $^{14}CO_2$ after 5 (or 6) days and again after 42 (or 43) days. All CO_2 was scrubbed from the soil jar after the first sampling interval (5-6 days). Thus the ^{14}C of CO_2 sampled on day 42 (43) represents C evolved during the second period (i.e. day 6 or 7 to day 42 or 43). For these incubations two additional samples were taken in the upper and lower O horizon at each pit for a total of 8 extra jars at each site. Selection of which sample would be measured for ^{14}C of CO_2 was based on CO_2 evolution over time and the $\delta^{13}C$ of CO_2 in each jar (as only one sample from each horizon was analyzed for $^{14}CO_2$).

In September of 1997, ten day incubations were also performed on well drained soils in the same study area, using very similar methods by M.Torn. These unpublished data will also be presented for comparison.

Respiration Partitioning

Approaches

Two methods using C and ^{14}C mass balance to estimate respiration partitioning were applied to the collected data. The first uses incubation data to separate respiration into two components, autotrophic and heterotrophic respiration. The second method uses multiple components derived from the turnover time and ^{14}C of SOM fractions to separate Recent-C from heterotrophic components without the use of incubations. The equations used to calculate respiration partitioning for performing both methods are described below.

Method 1: Autotrophic/Heterotrophic

This approach requires the measurement of total soil respiration flux (F_{tot}), its flux weighted ^{14}C signature (Δ_{Tot}) over the time period measured and the ^{14}C signature of heterotrophic respiration (Δ_{Het}), which is determined from incubations. With the two equations listed below, the flux from heterotrophic decomposition (F_{Het}) and from autotrophic decomposition (F_A) can be solved for:

$$\Delta_{Het} * F_{Het} + \Delta_A * F_A = \Delta_{Tot} * F_{tot} \qquad \text{Equation 1}$$

$$F_{Het} + F_A = F_{Tot} \qquad \text{Equation 2}$$

Where Δ_A equals the $\Delta^{14}C$ signature of the CO_2 in the contemporary atmosphere. All fluxes are in gC m^{-2} $time^{-1}$ and all isotopic (Δ) values are in per mil (‰).

Partitioning the fraction of production from each component by depth is achieved by defining F_{Het} and F_A to be a fraction of F_{Tot}. Then for each horizon, Δ_{Het} equals the incubation $^{14}CO_2$ value for that horizon, Δ_{Tot} equals the soil profile $^{14}CO_2$ for that horizon and you can solve for the fraction from F_A.

Method 2: Recent-C/Multiple Heterotrophic (Reservoir-C)

This method of respiration partitioning separates total soil respiration into Recent-C versus Reservoir-C (**Figure 1**). Unlike the first method, autotrophic respiration as a pure end-member is not estimated. The components of Reservoir-C used are leaf litter

(L_L), root litter (L_R) and humified high and low density SOM (H and M respectively). The specific details for this method are described at length in Chapter 2. Briefly, the equations used (with slightly modified symbols to be consistent with this chapter) are:

$$F_{Tot} = F_R + F_{LL} + F_{LR} + F_H + F_M \qquad \text{Equation 3}$$

and

$$F_{Tot} \times \Delta Tot = F_R \times \Delta A_j + F_{LL} \times \Delta L_L + F_{LR} \times \Delta L_R + F_H \times \Delta H + F_M \times \Delta M \quad \text{Eq. 4}$$

F_{Tot} is the total annual soil respiration flux and F_R is the flux of CO_2 derived from Recent-C (autotrophic + Fast-C). F_{LL}, F_{LR}, F_H and F_M are fluxes of CO_2 derived from their respective Reservoir-C sources. The Δ values required for the ^{14}C mass balance are either measured (for ΔL_L, ΔL_R, ΔH and ΔM), assumed to equal ΔA (year j, for Recent-C), or calculated from CO_2 and $^{14}CO_2$ fluxes (ΔTot). For the soil profile as a whole, F_T and ΔT are the measured surface flux and its annual flux weighted $\Delta^{14}CO_2$ signature respectively. Strictly speaking there are two unknowns: F_{LR} and F_R. However, CO_2 fluxes from F_{LL} and the isotopic values of fine roots ΔL_R are not well known and must be parameterized (see discussion below).

Calculation of Annual Average Isotopic Values

An annual average $\Delta^{14}CO_2$ value for soil respiration is calculated by weighting each collar specific $\Delta^{14}CO_2$ value by the CO_2 flux from its respective collar at the time of sampling (or within a few days to a week of the measurement). This "flux weighted" value (Δ_{Tot}) is calculated by the equation below:

$$\Delta^{14}CO_{2\ fluxweighted} = \Delta_{Tot} = \frac{\sum_{n=1}^{n} CO_{2\ flux(n)} * \Delta^{14}CO_{2(n)}}{\sum_{n=1}^{n} CO_{2\ flux(n)}} \qquad \text{Equation 5}$$

The flux weighted average $\Delta^{14}C$ of CO_2 is more representative of the annual $^{14}CO_2$ flux to the atmosphere then a straight arithmetic mean, which does not account for the amount of ^{14}C released at the time of sampling-only its isotopic signature. The same procedure is followed for calculating an average profile $\Delta^{14}C$ of CO_2 value for soil gas at a given depth except the CO_2 concentration at the time of sampling is used for weighting instead (referred to as “concentration weighted’).

In order to compare heterotrophic $\Delta^{14}CO_2$ signatures across sites it is helpful to flux weight each individual incubation sample and calculate a $\Delta^{14}CO_2$ representative of the entire profile (as is reported above). This is done by accounting for the difference in total CO_2 as well as $^{14}CO_2$ production for each incubation sample (which is representative of a soil horizon(s)) and then scaling this by the amount produced by horizon on a per area basis. Flux weighting is performed via the following equation:

$$\Delta^{14}CO_{2\ fluxweighted} = \Delta_{Het} = \frac{\sum_{n=1}^{n} CO_{2\ flux(n)} * BD_{(n)} * D_{(n)} * \Delta^{14}CO_{2incubation(n)}}{\sum_{n=1}^{n} CO_{2\ flux(n)} * BD_{(n)} * D_{(n)}} \qquad \text{Equation 6}$$

where:

$CO_{2\ flux\ (n)}$ = CO_2 produced per gram of dry soil in jar n (mgC g dry soil^{-1})

$\Delta^{14}CO_{2\ incubation\ (n)}$ = $\Delta^{14}CO_2$ produced in jar *n* (‰)

$BD_{(n)}$ = Bulk density of soil horizon in jar *n* (g cm^{-3})

D = Horizon depth (thickness; cm)

n = soil from a given horizon in a given jar

Cross Site Comparisons

Measurements of ^{14}C of CO$_2$ are made in soil respiration and soil gas in different years (when the atmospheric ^{14}C of CO$_2$ is changing). Therefore, in order to compare values of Δ^{14}C of CO$_2$ from different years we calculate the difference between the annual weighted average ^{14}CO$_2$ and the best estimation of local atmospheric ^{14}CO$_2$ for that given year (defined as the $\Delta\Delta^{14}$CO$_2$). This comparison is valid as long as the rate of decrease is constant (as it has been during 1996-1999, with a drop of ~4‰ per year; Levin and Hesshaimer, 2000). Calculation of $\Delta\Delta^{14}$CO$_2$ also allows us to make cross site comparisons of Δ^{14}CO$_2$ values across all three sites in 1998 despite the elevated local ^{14}C history at Walker Branch, which began in 1995 (see Chapter 3). At Walker Branch, the value used for the ^{14}C of atmospheric CO$_2$ in 1998 is 117‰ (from tree ring cellulose, see Chapter 3) compared to 96‰ used for the atmospheric ^{14}C of CO$_2$ at the two northern sites (Levin and Kromer, 1997, Levin and Hesshaimer, 2000).

Results

Characterization of Carbon and Radiocarbon fluxes

CO$_2$ in total soil respiration

Soil respiration rates in temperate deciduous and coniferous forests typically range from 600-700 gC m^{-2} y^{-1} (Raich and Schlesinger, 1992). However significant deviation from these averages can occur from year to year. This can be seen in the measured rates of soil respiration during the 4 years of this study (**Table 1**). Across sites, average annual respiration fluxes are 700, 770 and 820 gC m^{-2} y^{-1} at Howland, Harvard Forest and Walker Branch respectively. Within any one sampling location/site differences between a given year and the multi-year average are between 80-550 gC m^{-2} y^{-1}. Year to year variation in annual respiration amounts is greatest at Harvard Forest. Clearly average net soil respiration flux increases from Howland to Walker Branch, however, the year to year variability in fluxes are such that the differences are not significant to within one standard deviation.

The time series of flux measurements for each site are shown in **Figure 2**. The solid and dashed lines represent data taken by our collaborators; Eric Davidson's group from the Woods Hole Research Center (WHRC) for Howland and Harvard Forest, and modeled values from Paul Hanson from the Oak Ridge National Laboratory (ORNL) for Walker Branch. At Howland and Harvard Forest, data are collected by WHRC weekly throughout the summer months, biweekly in spring and fall, and as weather permits during the winter. Also shown are flux measurements made by myself, Sue Trumbore and other field help from UC Irvine for all three sites. These flux measurements should not necessarily correlate perfectly with the measured fluxes as they were often taken on different days with different moisture and temperature conditions. All sites display a sinusoidal pattern of CO_2 fluxes with maximums in the summer and minimums in the winter, as is characteristic of temperate forests. While Walker Branch tends to have higher annual emissions than the two more northern sites (**Table 1**) this is apparently not due to higher summer time fluxes but because of a relatively long growing season and overall warmer winter temperatures which prevent fluxes from being as low on average in the winter season.

D^{14}C of CO$_2$ in total soil respiration

The Δ^{14}C content of soil respiration and soil gas was monitored at Howland (2 years; 1998-1999), Harvard Forest (4 years; 1996-1999) and Walker Branch (2 years; 1998-1999). However, due to an unexpected large atmospheric release of ^{14}C near Walker Branch during the 1999 growing season, only the data prior to this release will be shown here, i.e. 1998 through early June 1999. The Δ^{14}C values for CO_2 in soil respiration at all three sites are greater than the atmospheric ^{14}C signature of CO_2 (92-104‰ between 1996 and 1999; **Figure 3**). At Howland measured values range from 90-230‰ with most being between 89-160‰. At Harvard Forest the range over a four-year period is 70-200‰ with most measurements between 90-170‰. At Walker branch the range is 100-353‰ but the 353‰ is an outlier and all other points are between 100-160‰. The annual average $^{14}CO_2$ values are compared with the total annual CO_2 fluxes at each site in **Figure 4**. For each year, this figure shows the range of all collected measurements, the arithmetic mean of Δ^{14}C values alone and the average calculated by weighting the Δ^{14}C values according to CO_2 flux at the time they were measured (or within a few days to a week of it).

The range in $\Delta\Delta^{14}CO_2$ for all years at all sites is 12-34‰ (**Table 2**). At Howland, values vary from 30-32‰ (1998) and 25-24‰ (1999) for both the NC and Tower pits respectively with a two year average for both pits of 28±4‰. Harvard Forest has $\Delta\Delta^{14}$C values which vary between 13 and 34 ‰ between 1996-1999 with a four year average of

25±9‰. However, the 1999 values are between 11 and 23‰ lower than the three previous years.

Climate Variability

The average climate for each site is shown in Chapter 3, Table 1. Climate variability is shown only for the one site where we have four years of useable CO_2 and $^{14}CO_2$ data (Harvard Forest). At Harvard Forest, the four years monitored, 1996-1999, happen to have very large differences in the timing and amount of precipitation though not temperature. 1996 was a fairly wet year receiving the largest total precipitation of all four years (**Figure 5**). Similar amounts of rain fell in 1997, 1998 and 1999. However, the timing of precipitation events varied significantly between the three years. In 1997, the magnitude of rainfall was similar across seasons though less fell in the summer months. 1998 was a strong El Nino year with a very wet spring followed by a dry summer that was punctuated by a few heavy late season rains. 1999 had a dry winter and spring followed by a fairly wet summer and fall (**Figure 5**). Temperature patterns across the four year period were not strikingly different though 1996 and 1997 were cooler in all seasons relative to 1998 and 1999 (**Figure 6**). 1998 had the warmest winter followed by a warm spring. 1999 had the warmest average spring and summertime measurements.

Soil Profile CO_2 and D^{14}C of CO_2

Soil CO_2 concentration by depth

Carbon dioxide concentrations increase roughly exponentially with depth as is typical for mineral soils. The average range at each site for Howland, Harvard Forest and Walker Branch to a depth of 60-80 cm are 0.14-0.49%, 0.17-0.48% and 0.15-0.91%

respectively (**Table 3**). There is considerable fluctuation in CO$_2$ concentration about these means throughout the profiles at all sites with values peaking during the growing season. There tend to be lesser fluctuations about the mean at any given depth at Howland and Harvard Forest relative to Walker Branch. One exception to this can sometimes occur at Howland in spring when the snow pack begins to thaw. During spring 1997 at Howland, CO$_2$ was greater than 1.5-2% at all depths for three measurements taken between February 4 and March 4. Concentrations remained at 1.5% or higher at depth until May 6 while normally soil CO$_2$ concentrations at this site are < 1%. The largest concentration measured previously or since this time is ~1% (below 32 cm) 1999. This episode of unusually high concentrations is likely due to a decrease in air filled pore space from melting snow which concentrates CO$_2$ in the remaining air filled pores rather than any anomalously large increase in production.

The average CO$_2$ concentrations for 1996, 1997, 1998 and 1999 are shown by depth in **Figure 7** for Harvard Forest. Annually averaged profile CO$_2$ concentrations do not vary significantly from year to year.

Soil D^{14}C of CO$_2$ by depth

The ranges and average annual concentration weighted ^{14}CO$_2$ values for all depths at Howland, Harvard Forest and Walker Branch are given in **Figure 8**. Ranges for Howland, Harvard Forest and Walker Branch are 97-115‰, 112-121‰ and 127-146‰ for 1998 and 1999 respectively. While the ranges of all measured values are large for all pits at all sites, the concentration weighted averages show consistently lower Δ^{14}CO$_2$ in soil air at Howland relative to Harvard Forest and Harvard Forest relative to Walker

Branch. At Harvard Forest and Walker Branch where there are replicate pits, there is good agreement between concentration weighted $^{14}CO_2$ values and depth trends in $^{14}CO_2$ (**Figure 8**). The concentration weighted average Δ^{14}C of CO_2 for 1996, 1997, 1998 and 1999 are shown by depth in **Figure 9** for Harvard Forest. Unlike CO_2 profiles, which characteristically show an exponential increase in concentration with depth for most soil types, there seems to be no consistent pattern in $^{14}CO_2$ increase or decrease with depth at a given site or across sites.

Factors affecting Δ^{14}C of CO_2 other than decomposition

It is possible $^{14}CO_2$ fluxes may correlate with variables such as the magnitude of CO_2 flux from the collar at the time of sampling, δ^{13}C of soil respiration, or even the specific collar sampled. Looking across all collars at a given area within a site, variability in $^{14}CO_2$ does not appear to be caused by the amount of CO_2 flux from a given collar at the time of sampling (**Figure 10**). There is a slight trend towards heavier δ^{13}C values in the spring relative to the summer and fall (**Figure 11**). The δ^{13}C signature of the surface respiration sample is used to correct the $\Delta^{14}CO_2$ sample for any leaks between the chamber and the atmosphere during sampling. However, a graph of δ^{13}C vs. ^{14}C prior to making any ^{13}C based leak corrections shows no trend between δ^{13}C and $\Delta^{14}CO_2$ (**Figure 12**). There is, however, a correlation between the total CO_2 flux and the measured δ^{13}C of CO_2 (**Figure 13**), indicating (not surprisingly) that under conditions of large CO_2 flux there are fewer problems with leakage of atmospheric CO_2 into the chamber during sampling.

Profile $^{14}CO_2$ values are generally not correlated to CO_2 concentrations (**Figure 14**). One exception to this is for profile measurements close to the surface (~ 6 cm) where some atmospheric air gets into the sample (**Figure 14**; bottom- 6 cm depth). Using $\delta^{13}C$ as a proxy for the amount of atmospheric CO_2 present in the sample (due to leaks or advective mixing between soil gas and the air above the soil surface), **Figure 15** shows that while all depths have a range of ^{13}C values from ~-24 to -18‰ only the upper depths get as heavy as –14 to –16‰ and only for four measurements out of over 170. The higher the concentration of CO_2 in the sample the lighter the $\delta^{13}C$ tends to be (**Figure 15**).

Tracking of $^{14}CO_2$ over time as a function of the specific soil collar sampled shows some consistent spatial variability (**Figure 16**). At Howland, collar 3 and 8 at the Tower site have higher $\Delta^{14}CO_2$ values than collar 5 by 15 and 11‰ respectively. At the NC site, collar 2 is typically less than collars 3 or 5 by ~ 15‰. At Harvard Forest, collar 4 has consistently higher $\Delta^{14}CO_2$ values than collar 6 by 10‰. At Walker Branch no significant differences were found among collars. It is interesting to see that per mil collar differences are greatest at Howland, less at Harvard Forest and not detectable at Walker Branch. This is consistent with the larger degree of spatial heterogeneity in C stocks, and larger reservoirs of SOM cycling on 40-100+ year timescales in the O and A horizons at Howland and Harvard Forest compared to Walker Branch (see Chapter 3).

Tracking of CO_2 flux versus $\Delta\Delta^{14}CO_2$ by collar does show significant correlation in 8 out of 15 collars (as determined by R^2 values > 0.3; **Figure 16**). Correlations are strong for all collars at the Howland Tower site but are weak for all collars at the Howland NC and Harvard Forest sites. The collars for the two sites at Walker Branch show more mixed correlation (**Figure 16**). **Figure 17** shows CO_2 versus $\Delta\Delta^{14}CO_2$ for one collar at Howland (Tower 3) and one at Walker Branch (TDE 1). These are typical in that when a correlation does exist, a larger CO_2 flux is associated with a lower $\Delta\Delta^{14}CO_2$. This is likely due to the fact that large CO_2 fluxes are associated with a large output of autotrophic respiration that has $\Delta\Delta^{14}CO_2$ of 0‰.

Incubations

Two sets of incubations (12-day and 42 to 43-day) were performed on well drained soils sampled from all three sites in July 1999, however, only data from Howland and Harvard Forest will be discussed due to the unexpected ^{14}C release at Walker Branch (which affected the incubation results). The 42 to 43-day incubations were also sampled at 5-6 days from the start date in order to see if the age of CO_2 evolved changed with time. Well drained soils from the same study area in Harvard Forest were also sampled and incubated for ten days in September 1999 by M. Torn and these data are presented for comparison. Sampling information on all incubations is summarized in **Table 4**.

CO_2 evolved from the 12-day incubations performed in 1999 has $\Delta^{14}CO_2$ values that range from 73-154‰ for Howland and 69-154‰ for Harvard Forest. The $\Delta^{14}C$ of evolved CO_2 is variable with depth in the O horizons and decreases with depth in the mineral horizons (**Table 5**). The $\delta^{13}C$ of CO_2 was also sampled at the same time as $^{14}CO_2$ in order to check for leaks. Expected values for $\delta^{13}C$ are between -26 (typical value for SOM) and –28‰ (typical value for roots). Values heavier than -26 to -28‰ indicate some leakage of atmospheric CO_2 (with $\delta^{13}C$ signature of -8.5‰) into the jar. The diffusion fractionation factor of –4.4 ‰ does not come into play in the sealed jars (unless they are leaking). Measured $\delta^{13}C$ values for all samples ranged between -23.70 and -27.61‰, however, out of 21 samples only four were heavier than –26‰. This indicates leakage of atmospheric CO_2 into the samples was not a significant problem. The four jars with samples heavier than –26‰ were all from the deepest mineral horizons sampled and had the lowest CO_2 production per gram of dry soil relative to the other samples.

The $\Delta^{14}CO_2$ values from the individual jars for 12-day 1999 incubations compare well with the individual jar values from the 10-day incubations taken in 1997 (**Table 5** and **Table 6**). Although depth intervals and horizons sampled in 1997 differed from those in 1999, the ^{14}C of the evolved CO_2 is similar in isotopic signature and shows the same trend and magnitude of decreasing $^{14}CO_2$ with depth. The flux weighted profile $\Delta^{14}CO_2$ value for 1997 (142‰) is however larger than for 1999 (126‰). Converting to $\Delta\Delta^{14}CO_2$ to account for the two year difference between sampling dates yields $\Delta\Delta^{14}CO_2$ of 42‰ and 34‰ for 1997 and 1999 respectively, or a difference of 8‰.

CO_2 sampled 5-6 days into the 42-43 day incubations yielded values for ^{14}C of evolved CO_2 of 159‰ (Howland) and 123‰ (Harvard Forest) for the Oi+Oe horizons and 99‰ (Howland) and 159‰ (Harvard Forest) for the Oe+Oa (+A) horizons (**Table 7**). These data are in accord with the 12-day incubation data shown in **Table 5**. Comparison of the isotopic signature from the first 5-6 days to that of the second 37 day period shows no significant difference (i.e. within the analytical error of ± 6‰) in the upper most O horizon (Oi +Oe) at both Howland and Harvard Forest (**Table 7**). However, at both sites there is a 21-27‰ shift in isotopic signature between the CO_2 evolved in the first 5-6 days and the CO_2 evolved in the second period of 37 days for the Oe+Oa (+A) horizon.

Respiration partitioning

Method 1: Autotrophic/Heterotrophic

An estimated 64% of the annual total soil respiration came from heterotrophic respiration at the Howland Tower site, while an average of both the NC and Tower sites showed 84% to be from heterotrophic sources. At Harvard Forest, based on incubations from two different pits heterotrophic respiration comprised 44 or 58% of the total fluxes (with an average of 54%) **Table 8** and **Figure 18**. Site averages were estimated by using an average F_{Tot} and Δ_{Tot} and calculating an average ^{14}C signature from all the replicate results for each measured horizon for both pits, and an average bulk density and thickness for each horizon then using those data to calculate an average Δ_{Het}.

A good estimate of error associated with these results is difficult to make. The outcome is insensitive to the total measured CO_2 fluxes, but sensitive to the values used for the isotopic signature of annual heterotrophic decomposition (Δ_{Het}) and the annual flux weighted isotopic soil respiration value (Δ_{Tot}). Δ_{Het} is particularly sensitive to the values used in equation 6 for flux weighting, and changing bulk density or horizon thickness for one horizon can shift the total profile Δ_{Het} by as much as 5-8 per mil. Changing either Δ_{Het} or Δ_{Tot} by only 1 per mil can change the resultant partitioning by 1-3%. Since the annual variability in the $\Delta^{14}CO_2$ of soil respiration during 1999 was small at both Howland and Harvard Forest we assumed the annual flux weighted ^{14}C of CO_2 for total soil respiration (Δ_{Tot}) to be robust. Thus, the greatest source of error in these analyses comes from the value used for Δ_{Het} and is about 15-20%.

Method 2: Recent-C/Multiple Heterotrophic (Reservoir-C)

This technique, because it does not require incubations, is the only one we can use to compare soil respiration components for multiple years at a given site and across all three sites (for 1998). The specific components and maximum and minimum values used to parameterize method 2 for each site and each year are shown in **Table 9**. At Harvard Forest the total amount of soil respiration coming from Recent-C sources was 63, 50, 58 and 66% for 1996, 1997, 1998 and 1999 respectively (**Figure 19**). At Howland 45 and 57% of soil respiration came from Recent-C sources in 1998 and 1999 respectively. In 1998 the amount of total annual soil respiration coming from Recent-C increases from north to south (**Figure 19**) with an average 45, 58 and 67% at Howland, Harvard Forest and Walker Branch respectively. This same trend however is not seen between Howland and Harvard Forest in 1999 where the total contribution from recent C sources is 56% at Howland and 66% at Harvard Forest. The error associated with these estimations is from 5-25% based on the range of values shown in **Table 9**, however, in most cases it is within 10-15%. Based on this error the only significant difference between sites is between Howland and Walker Branch in 1998 (**Figure 19**).

Discussion

Importance of fine roots

Fine root stocks have ^{14}C signatures that are significantly elevated relative to the atmosphere throughout the entire soil profile at Howland and Harvard Forest (**Figure 20**). While some roots turnover quickly and thus their decomposition will have a $\Delta\Delta^{14}CO_2$ of 0‰ (see Chapter 4) clearly the bulk of fine root stocks have isotopic signatures that will add $\Delta^{14}CO_2$ that is elevated 1-140‰ relative to the atmosphere. The effects of decomposition of these roots can be seen by inspection of the $^{14}CO_2$ of in situ soil gas which is greater than the isotopic signature of autotrophic respiration at all depths in the soil profile (**Figure 20**). Thus in the A and B horizons where both low and high density SOM stocks cycle at centennial and millennial time scales (and have negative $\Delta\Delta^{14}C$ values) fine root decomposition and potentially dissolved organic carbon (DOC) from the O horizon are the likely sources of the elevated ^{14}C inputs.

Comparison of $\Delta^{14}CO_2$ of soil gas with the $\Delta^{14}C$ of the potential decomposition sources (**Figure 20**) indicates that decomposition on short (annual) time scales is a 4-component system in the O and A horizons (autotrophic respiration, fast cycling C, high and low density SOM and root decomposition). Below ~15 cm (typically the B horizons) however, the decomposition flux of low and high density SOM decomposition is minimal (< 5 gC m^{-2} y^{-1}) and the decomposition flux can be represented by only 3 components (autotrophic respiration, Fast-C and fine root decomposition). Failure to account for decomposition of fine roots at depth will lead to an overall underestimate of total CO_2 and $^{14}CO_2$ fluxes.

Respiration Partitioning

Results from both partitioning methods are shown together in (**Figure 21**) for both Howland and Harvard Forest 1999 and Harvard Forest 1997. It is important to remember that both methods are partitioning slightly different components of the total respiration flux. In the non-incubation method (method 2), Recent-C is defined as the sum of both autotrophic respiration and the decomposition of Fast-C (see **Figure 1**). Thus for comparison of method 1 to method 2, the flux of C from Recent-C should be larger than the autotrophic flux alone and this is true in all cases. One way to estimate the amount of C from decomposition of fast C is to subtract the autotrophic component in method 1 from the Recent-C component in method 2. By doing this, 23, 37 and 12% of the total flux at Howland (Tower), Howland (Average) and Harvard Forest in 1999 is from Fast-C and 33% from Harvard Forest in 1997.

Respiration partitioning using method 2 allows for estimation of decomposition fluxes coming from each SOM component (leaf litter, root litter and humified fractions). **Figure 22** shows the average and ranges in contribution of each SOM components and Recent-C to total soil respiration for Howland (1998-1999), Harvard Forest (1996-1999) and Walker Branch (1998). At all sites the largest contributors to soil respiration are Recent-C (43-73%) and fine root litter (5-38%). The leaf litter component is small (6-16%) because it represents only the flux from leaf litter that is greater than 1-2 years in age. Leaf litter decomposing within 1-2 years of falling will be included in the Recent-C flux. This is largely why the leaf litter flux decreases from Howland (11-16%) to Walker Branch (2-4%) and the Recent-C flux increases from Howland (44-59%) to Walker Branch (61-73%).

Methods Comparison

Respiration partitioning using Incubations (method 1) requires no information about SOM ^{14}C stocks and their specific CO_2 fluxes, while method 2 requires a lot of information on C and ^{14}C stocks and C inputs. In method 1, breakdown into autotrophic and heterotrophic sources relies solely on the $^{14}CO_2$ measurements of total soil respiration, incubations to get the $^{14}CO_2$ of decomposing SOM and a measure of the annual soil CO_2 flux. As such, the quality of the input data are extremely important, but errors associated with calculation of SOM CO_2 and $^{14}CO_2$ fluxes are avoided.

In some cases for method 1, the mass balance does not work because Δ_{Het} is less than Δ_{Tot} (see **Table 8** and **Figure 18** which show negative values for heterotrophic production at the Howland NC site). Since Δ_{Tot} is a combination of Δ_{Het} and Δ_A, and ΔA is $<<\Delta_{Tot}$, Δ_{Het} must be greater than Δ_{Tot}. The fact that the mass balance does not work for the NC site could be because of uncertainties in calculating Δ_{Het} for the entire profile as discussed previously. Secondly, it also points to the limitation of using an annual flux weighted $\Delta^{14}C$ value for soil respiration (Δ_{Tot}) with an incubation value from one point in time. Multiple incubations should be performed throughout the year to get a better annual estimate for Δ_{Het}, or integration of fluxes and isotopic signatures should be performed over a shorter time step.

Calculation of the partitioning of soil respiration using method 2 requires making several assumptions. These are described in detail for Harvard Forest in Chapter 2. Briefly, while there are strictly two equations and two unknowns (F_{LR} and F_R) there are some components of the equation that are not known well and must be parameterized (i.e. running several scenarios with maximum and minimum values). For example the flux of CO_2 from leaf litter (F_{LL}) can be estimated by the stock of the Oi horizon divided by the ^{14}C derived turnover time assuming it is roughly at steady state. However as discussed in Chapter 3, ^{14}C measurements of SOM pools with components that cycle on timescales of 1-10 years are not useful for calculating a short timescale flux and thus F_{LL} is very uncertain. The amount of F_{LL} that leaves the system as CO_2 versus that going into other SOM pools (H and M) is also unknown and must be estimated. Additionally, ^{14}C and flux values for decomposing humified SOM (Δ_H, Δ_M, and F_H and F_M) must be estimated using ^{14}C-derived turnover times from the low and high density fractions (which represent decadal averages). Therefore, the actual decomposition fluxes from humified SOM in any one year may be significantly different than the ^{14}C-derived fluxes. For example, partitioning for the four years at Harvard Forest shows that the Recent-C contribution varies from 50-66% (**Figure 23**). However two of the three components (F_{LL} and F_{H+M}) do not vary. Clearly material in the O horizon, where all the leaf litter and 35% of the humified SOM stocks are located, will decompose at differential rates as a function of different moisture and temperature conditions. Thus method 2 can be improved with better parameterization of leaf decomposition rates from year to year and some way of allowing CO_2 flux from the humified components to vary as a function of climate.

Method 2 also requires explicit treatment of fine root decomposition, which is treated as an unknown and solved for. As discussed above, the SOM and ^{14}C of CO_2 in soil gas shown in **Figure 20** point to the importance of fine root decomposition and the fact that it must be explicitly included in any C and ^{14}C mass balance. One additional issue with the explicit inclusion of fine roots is that it requires fine root decomposition fluxes that when compared to fine root biomass, imply very rapid turnover times (i.e. one year or less). This is in direct contrast to the ^{14}C signature of fine roots that imply fine root lifetimes on the order of 5-10 years (see Chapter 4). It is possible some small fraction of the fine root stocks turns over quite quickly and a larger fraction of the stock turns over on decadal timescales as discussed in Chapter 4. However, then the fine roots with fast turnover should not have ^{14}C signatures elevated significantly relative to the atmospheric ^{14}C of CO_2. Yet, to have the mass balance work at all times all fine root turnover must have the elevated ^{14}C signature. Currently this is a problem that is still unresolved.

In short, to address annual or shorter time scale variability in respiration partitioning method 1 is the best option. The incubation (Δ_{Het}) signature will be sensitive to recent inputs of C and will therefore be most representative of dynamics happening in that given year. The best approach for implementing method 1 would be to do multiple incubations throughout the year so that partitioning of autotrophic and heterotrophic components of soil respiration could be estimated seasonally. To optimize method 1 for the whole soil profile it might be best to incubate a soil monolith at a carefully chosen temperature as opposed to incubating separate soil horizons. However if reliable CO_2 production numbers by horizon can be generated, then incubating by depth would yield valuable information on the depth distribution of partitioning. The utility of method 2 lies in its potential to characterize the general contribution of specific heterotrophic components to total soil respiration—something method 1 cannot do. Method 2 can be improved with better parameterization of leaf decomposition rates from year to year and some way of allowing CO_2 flux from the humified components to vary as a function of climate.

Respiration Partitioning: By Depth

It is theoretically possible to partition the fraction of soil respiration coming from autotrophic or heterotrophic sources with depth using the horizon specific incubations and profile $^{14}CO_2$ measurements. However actually doing this proved problematic especially in the deeper horizons. **Table 10** shows the results for depth partitioning at Howland and Harvard Forest and illustrates the problems. For the 1999 cases the values used for Δ_{Het} represent the site average for the two respective pits at each site. At Howland the partitioning works for the upper two horizons because Δ_{Het} is greater than Δ_{Tot}. However, in all of the B horizons ΔHet is less than Δ_{Tot} and the mass balance does not work.

The isotopic signature of heterotrophic respiration derived from incubations should theoretically be higher than that measured for the soil gas (since soil gas includes autotrophic respiration and is higher than atmospheric $\Delta^{14}CO_2$). This is true between 0-15 cm at Howland and Harvard Forest where we have useable incubation data, however not true below 15-20 cm at both sites (**Figure 20**). Disturbance effects such as the 3-5°C increase during the incubation period over normal summertime average temperatures at depth may account for this trend. Alternatively, there may be another C source with high ^{14}C in situ (such as DOC) that is not present in incubated soils.

Comparison of the results from respiration partitioning using method 1 at 6 cm (where the method did work) to those using method 1 for the whole soil shown in **Table 8** shows similar results and trends for both Howland and Harvard Forest. The percentage of soil respiration coming from heterotrophic sources at 6 cm in the soil profile at Howland and Harvard Forest are 71 and 48% respectively (**Table 10**) and the average whole profile partitioning (**Table 8**) is 64 to 84 and 46% for Howland and Harvard Forest respectively. The agreement between these two calculations lends confidence in this approach for two reasons. First, at six cm the values for $^{14}CO_2$ of soil gas are representative of production from all SOM below that point in the soil profile, thus only production in the top 6 cm is not represented. Secondly, the methods are independent in that Δ_{Het} and Δ_{Tot} are different with only Δ_A as a common value between the two equations. Mismatches between the depth intervals used in soil incubations and those monitored for ^{14}C of CO_2 in situ for soil profiles limit our attempts to calculate autotrophic and heterotrophic components of soil respiration by depth. Future efforts should consider monitoring the $^{14}CO_2$ of soil gas at shallower depths.

Latitudinal Trends

Surface Respiration

Elevated $\Delta\Delta^{14}CO_2$ at all sites (**Table 2**) in all years indicates that decadal cycling SOM is a very important decomposition source of CO_2. Based on the 1998 growing season, soil respiration at the Walker Branch site is composed of less decadal cycling material than the two northern sites (based on the lower $\Delta\Delta^{14}CO_2$). Comparison of the 1998-1999 $\Delta\Delta^{14}CO_2$ and CO_2 efflux records for Howland and Harvard Forest (**Figure 4**) indicates that Harvard Forest may show a greater degree of interannual variability in both total CO_2 production and its decomposition sources.

Profiles

Similar to surface fluxes, elevated $\Delta\Delta^{14}CO_2$ at all depths within the profile indicates the importance of decomposition of decadal cycling SOM at all sites. The annual concentration weighted average $\Delta\Delta^{14}C$ of soil CO_2 at 6-9 cm are elevated relative to the atmosphere by 17-28‰ in 1998 at Walker Branch (**Table 11**). This range is higher than the 1998 ranges for Howland (1-16‰) and Harvard Forest (9-25‰), indicating that at depth Walker Branch has decomposition sources with more bomb C.

Comparison of $\Delta\Delta^{14}C$ of CO_2 values at 6-9 cm relative to surface respiration shows differences of 3-14‰ with an average of 8 ±4 (**Table 11**) for all sites and indicate the upper 0-9 cm play a significant role in determining the final isotopic signature of soil respiration. The direction of isotopic change however is dependant on the site. In 1998 At Howland and Harvard Forest the profile $\Delta\Delta^{14}C$ of CO_2 is similar to or less than the surface $\Delta\Delta^{14}C$ of CO_2 while at Walker Branch the $\Delta\Delta^{14}CO_2$ in the soil profile is greater than the total $\Delta\Delta^{14}CO_2$ from the surface flux (**Table 11**). Thus in 1998, decadal cycling material in the top 6 cm at Harvard Forest and Howland are enriching the total soil respiration signature with bomb C, while at Walker Branch decomposition of litter in the top 8 cm is diluting the bomb C produced deeper in the profile. This is consistent with the fact that Walker Branch has much smaller stocks of humified C and ^{14}C stocks in the O and A horizons relative to the two northern sites. In 1999 however, unlike 1998, Harvard Forest shows the upper 6-9 cm adding younger C (which is also true for 1996). Climatically unusual conditions at Harvard Forest in 1999 (a very dry spring and extremely low CO_2 fluxes) may be responsible for this change in trend.

Incubations

The flux weighted heterotrophic $\Delta^{14}CO_2$ in 1999 for the entire soil profile shows a difference between the averages for Howland (122‰) and Harvard Forest (120‰) of only 2 ‰. Thus the ^{14}C signature of the heterotrophic component of soil respiration for the whole soil profile at Howland and Harvard Forest, incubated under conditions of adequate and constant moisture and the same temperature, were similar. This indicates a similar average age for both profiles of the SOM that was decomposing despite the fact that the SOM ^{14}C signatures in the Oe and Oa horizons of the Tower profile (see Chapter 3, Table 6) were 107 and 50‰ respectively. Variability in O horizon thickness and measured $\Delta^{14}C$ of SOM from O horizons between the two pits at Howland (Tower and NC) is significant (see Chapter 3). However, the $\Delta^{14}C$ of CO_2 from all O horizon incubations at both sites are similar (**Table 5**). Incubations of in-situ SOM from the two soils under different moisture and temperature conditions, might respond differently with SOM of different ages becoming decomposable.

Sampling of heterotrophic respiration 5-6 days after the beginning of the incubation and again 37 days later show the age of carbon contributing to decomposition did not change in the upper O horizon (Oi +Oe) at either Howland and Harvard Forest. (**Table 7**). However, in the lower part of the O horizon a shift was seen at both sites. At Howland the ^{14}C signature decreased from 99‰ (for the 0-6 day incubation period) to 72‰ (for the 6-43 day incubation period) indicating the carbon source overall became older. At Harvard Forest the ^{14}C of evolved CO_2 increased from 124‰ (for the 0-5 day incubation period) to 144‰ (for the 5-42 day incubation period). Despite the fact the direction of change is opposite relative to Howland, due to the curved nature of the atmospheric bomb $^{14}CO_2$ label, this still indicates a switch to an older source of SOM (see Chapter 2 figure 1) as the younger C sources became depleted and microbes were forced to decompose older C.

Respiration Partitioning

The results of both respiration partitioning methods generally show an increase in the contribution from autotrophic or Recent-C with latitude. The incubation method

(method 1) shows that for 1999, soil respiration at the Howland site is dominated less by autotrophic decomposition (16%) than at Harvard Forest (54%; **Table 8**). In 1998 method 2 shows the amount of total annual soil respiration coming from Recent-C increases from north to south (**Figure 19**) with an average 45, 58 and 67% at Howland, Harvard Forest and Walker Branch respectively. Taking the average coming from Recent-C at each site for all years with available data shows the same trend (Table 12 third row; note Reservoir-C is shown).

Variability at Harvard Forest

Harvard Forest is used as a case study in interannual variability of CO_2 and $^{14}CO_2$ fluxes as it is the only site studied here with a four year record of CO_2 and $^{14}CO_2$ data. The climate at Harvard Forest has already been discussed in the results section. Briefly, 1996 was wet and cool, 1997 was drier and cool though precipitation was fairly evenly spaced throughout the year. 1998 had a warm winter and a warm wet spring with some late season dry periods, however, significant late season rains as well. 1999 had a warm yet very dry spring followed by a warm wet summer (**Figure 5** and **Figure 6**).

The most dramatic effect of interannual climatic variation at Harvard Forest can be seen in the total CO_2 fluxes measured for each year (**Figure 4**). Despite the fact that 1999 actually received more total rainfall than 1997 or 1998, it has two thirds to one half the CO_2 flux compared to the three previous years on record. Much lower total CO_2 emission was observed in 1997 compared to 1998 though rainfall was similar in both years. Springtime moisture conditions seem to provide a good qualitative correlation to the magnitude of total annual CO_2 fluxes with winter and springtime air temperatures possibly being a factor as well.

Comparison of both total CO_2 fluxes and annual average $^{14}CO_2$ at Harvard Forest for 1996-1998 would lead one to think higher fluxes (1996 and 1998) correlate with lower $^{14}CO_{2,}$ and low fluxes (1997) correlate with higher $^{14}CO_2$ (**Figure 4**). Yet, this trend is not repeated in 1999 where very low fluxes combined with $\Delta\Delta^{14}CO_2$ values that were 14-21‰ lower than the previous three years (Table 2). Comparison of the 1997 $^{14}CO_2$ data with the other three years however, should be done with caution. 1997 is the year with greatest uncertainty in the annual flux weighted $^{14}CO_2$ value. $^{14}CO_2$ measurements were not taken during the peak of the growing season and there were some problems with our molecular sieve traps making for less useable sample replication when sampling did take place. Nevertheless, the 1996-1999 record implies that total annual precipitation is much less of a factor in controlling soil respiration and decomposition fluxes than timing and magnitude of precipitation events. Moisture and temperature conditions at specific time periods such as in the spring, may interact with phenological development of leaf-out and fine root growth, which may dramatically affect autotrophic fluxes throughout the rest of the season. Macro fauna populations and bacterial and fungal communities may also have been adversely affected by a dry spring in 1999 and been unable to recover completely.

The behavior of CO_2 and $^{14}CO_2$ at depth (below 6-9 cm) in the soil profiles differ from surface fluxes. Annual average CO_2 fluxes at Harvard Forest have varied by as much as a factor of two at Harvard Forest, however annually averaged profile concentrations do not vary significantly from year-to-year (**Figure 7**). Additionally, at Harvard Forest increased variability is seen in the total range of measured surface $^{14}CO_2$

values in 1996 and 1998 relative to 1997 and 1999 (**Figure 3** and **Figure 4**) however this is not seen for the profile $^{14}CO_2$ (**Figure 9**).

Variation in annual flux weighted $\Delta\Delta^{14}CO_2$ of soil respiration imply changes in the fraction of decadal cycling soil organic matter contributing to total CO_2 fluxes. Higher values imply that a greater amount of the decomposition flux is coming from SOM fixed from the atmosphere more than 1-2 years ago (Reservoir-C). Respiration partitioning using method 2 shows the overall average flux of Reservoir-C was 310, 325, 420 and 150 gC m^{-2} y^{-1} in 1996-1999 respectively (**Figure 23**). Compared to the total flux, these values correspond to 37, 50, 42 and 34% of the total soil CO_2 flux for 1996-1999 respectively. While the percentage difference in Reservoir-C fluxes is not striking, the magnitude of decomposition of Reservoir-C between the years is. Reservoir-C flux varies by a factor of 2.8 between 1998 and 1999 where the major climatic variation was the timing and distribution of rainfall in the spring and summer months (see **Figure 5** and **Figure 6**). Reservoir-C fluxes in 1996 are less than 75% of 1998 fluxes and the main climatic differences between the two years here are that 1996 was colder in winter and spring and received more rain in summer and fall. 1996 and 1997 have similar Reservoir-C fluxes, despite the fact that 1996 had higher total CO_2 fluxes. Despite the limitations to method 2 already discussed, it is a step forward in our ability to quantify variability in decomposition of SOM stocks from year to year and link this variability to climate anomolies.

Seasonal Variability

Seasonal variation in CO_2 fluxes can be seen at all three sites (**Figure 3**) with the spring season generally having higher ^{14}C than late summer and fall. This is particularly true for the NC site at Howland in 1998 where June and July $^{14}CO_2$ measurements range from 138-158‰ in contrast to 90-105‰ for August through October. Decreasing trends through the growing season can also be seen at Harvard Forest in 1996, 1998 and 1999 and at Walker Branch in 1999 (although comparison to later season measurements at this site cannot be made due to the unplanned ^{14}C release). It is possible Recent-C fluxes are less important in the early part of the growing season and increase as trees increase photosynthetic activity throughout the growing season.

Isotopic Disequilibrium

The average measured $\Delta\Delta^{14}C$ values of total soil respiration are 28, 25 and 13‰ (Table 12) for Howland, Harvard Forest and Walker Branch respectively. These values correspond to a mean residence time for C of 5±2, 4±2 and 5±4 years. This represents the time an average C atom spends in both the plant and soil since original photosynthetic fixation and includes both root respiration and all decomposition sources. The mean residence time (MRT) is calculated by plugging in values for MRT into our steady state model (see Chapter 2) until the appropriate $\Delta\Delta^{14}CO_2$ is reached. The MRT for Walker Branch is similar to the other two sites despite a $\Delta\Delta^{14}CO_2$ that differs by a factor of two because of the $^{14}CO_2$ releases beginning in 1995 which created an atmospheric $^{14}CO_2$ record that unlike the rest of the atmosphere did not decrease between 1995-1999 (which is also why the error term is greater; see Chapter 3). We also calculate the average value for $\Delta\Delta^{14}C$ of heterotrophic respiration to be 56, 61 and 38‰ for Howland, Harvard Forest and Walker Branch respectively, which corresponds to an average age of 8±2, 9±2 and 8±4 years respectively.

The lack of a significant difference between Howland and Harvard Forest is not too surprising. Even though Howland has larger C and ^{14}C stocks, both the $\Delta\Delta^{14}CO_2$ of soil respiration (**Table 2**) and heterotrophic signal from soil incubations (**Table 5**) indicate they are actually respiring C of similar ages. Given that Walker Branch has the smallest C and ^{14}C stocks (and lacks a large humified organic horizon) and has the smallest $\Delta\Delta^{14}CO_2$ we would expect the MRT of total and heterotrophic C to be less than the two more northern sites. The lack of such a decrease is likely due to the local $^{14}CO_2$ emissions at this site which make it difficult to obtain an accurate atmospheric $^{14}CO_2$ history. Moreover, if the atmospheric $^{14}CO_2$ has not been consistently decreasing, our modeling methods are less reliable.

The age of C respired from soil can be used to predict the ^{13}C isotope disequilibrium for all sites. The ^{13}C isotope disequilibrium is the difference between the ^{13}C signature of atmospheric CO_2 being fixed by plants and the ^{13}C respired from soils. A difference is expected because the ^{13}C in the atmosphere has been decreasing with time due to the addition of ^{13}C-depleted fossil fuels to the atmosphere (e.g. Ciais et al., 1995a, Fung et al., 1997). Using the $\delta^{13}C$ trend of –0.02‰ per year (Fung et al., 1997), and the average age of for heterotrophic respiration at each site, we estimate the ^{13}C isotope disequilibrium to be -0.16±.04, -0.18±.04, -0.16±.08‰ at Howland, Harvard Forest and Walker Branch respectively.

Global implications: temperate forest soils and atmospheric CO_2

The terrestrial biosphere and particularly temperate forests of the northern hemisphere have been shown to be important in the uptake of anthropogenic CO_2 from the atmosphere (Tans et al., 1990, Ciais et al., 1995b). In fact inter-annual variability in the rate of increase of global atmospheric CO_2 has been ascribed in part to inter-annual variation in NEP of the terrestrial biosphere (Keeling et al., 1995).

The three northern hemisphere temperate forest sites studied here have been shown to take up between 2-5 Mg C ha^{-1} y^{-1}. Chapter 3 shows that well drained soils are only responsible for 2-20% of this net uptake (as an integrated decadal scale average). Thus increases in forest biomass or more poorly drained soils and swamps must be responsible for the rest of the net terrestrial uptake on average. On an annual basis however, the heterotrophic component of soil respiration has been shown to be a large source of variation in NEP in forests (Goulden et al., 1996, Savage and Davidson, in Press). Indeed, variability in decomposition of Reservoir-C stocks at Harvard Forest in 1998 and 1999 correlate with preliminary results of net ecosystem uptake by Carol Barford, personal communication). In 1998 heterotrophic decomposition of Reservoir-C (according to respiration partition method 2) was 420 gC m^{-2} y^{-1} and net ecosystem uptake was 1.2 Mg C ha^{-1} y^{-1} (Carol Barford, personal communication). In 1999, decomposition fluxes of Reservoir-C were less by almost a factor of three at 150 gC m^{-2} y^{-1} and net ecosystem uptake was a factor of two larger at 2.3 Mg C ha^{-1} y^{-1} (Carol Barford, personal communication). While tree growth is estimated to be responsible for 60-70% of NEP, on average it shows little variation from year to year (Carol Barford, personal communication). Decomposition from coarse woody debris (not accounted for in Reservoir-C) will also vary from year to year and influence NEP.

The data presented in this thesis in concert with that of Carol Barford, personal communication) for the same site, strongly support the idea that decomposition fluxes from SOM fixed more than one to two years ago strongly impact NEP. Additionally, the average age of heterotrophic respiration at all three sites is estimated to be 8-9 years. Thus a significant time lag exists between initial C fixation and ultimate respiration by heterotrophs at all three sites. Therefore, consistent with the ideas discussed by Schimel et al., 1997 and Fung et al., 1997, variations in C storage or loss in any one year must partially reflect the net ecosystem uptake of previous years.

Conclusions

- At all three sites decomposition fluxes from decadal cycling SOM are an important component of total soil respiration and soil gas (to a depth of 80 cm) within the soil profile.
- Fine-root decomposition plays a very important role in decomposition fluxes, particularly at depth (below ~ 15 cm) where it is the dominant source of heterotrophic respiration.
- The amount of C fixed from the atmosphere >1-2 years ago contributing to soil respiration decreases from Maine to Tennessee. On average, C fixed >1-2 years ago makes up 50%, 41% and 33 % of soil respiration at Howland, Harvard Forest and Walker Branch.
- The average age of heterotrophic respiration is 8±2 years at both Harvard Forest and Walker Branch..
- Fluxes of CO_2 and $^{14}CO_2$ from soils are affected by interannual variability in climate.

- Variation in decomposition flux from decadal cycling SOM has a significant impact on net ecosystem productivity. Respiration partitioning using incubations is the best way to quantify this variability from year to year.

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Table 1. Annual soil respiration fluxes at all three sites.

Total Flux of CO_2 in gC m^{-2} yr^{-1}	1996	1997	1998	1999	Average[1]	±[2]
HOW-NC		483	698	669	617	117
HOW-TOW		674	836	800	770	85
HF-NWN	840	657	990	442	732	237
HF-SWF		882	900	644	809	143
WB-TDE	793	787	867	822	817	37

[1] Represents average for all years shown.

[2] Reprents standard deviation.

Table 2. The annual ΔΔ14CO_2 (‰) for all sites.

	1996	1997	1998	1999	avg[1]
Howland-NC			32	25	29 (3)
Howland-Tower			30	24	27 (3)
Harvard Forest	24	34	29	13	25 (9)
Walker Branch-P5			13		13
Walker Branch-TDE			12		12

[1] Values in parenthesis equal the range for (n = 2) or standard deviation for n >2. $\Delta^{14}C$ of atmospheric CO_2 in 1996, 1997 and 1999 is 104, 100, 96 and 92‰ except at Walker Branch where for 1998 117‰ is used. See text for details.

Table 3. CO_2 concentrations by depth for all three sites

Site (years monitored) Depth cm	Average %	± %	Max[1] %	Min %
Howland Tower (1997-1999)				
6	0.14	0.08	.61 (2.86)	0.03
10	0.18	0.08	.60 (2.98)	0.06
13	0.21	0.09	.63 (2.81)	0.07
15	0.23	0.10	.64 (3.07)	0.07
20	0.27	0.12	.65 (2.88)	0.08
32	0.39	0.16	1.02 (2.78)	0.12
51	0.49	0.17	0.96 (.96)	0.20
Harvard Forest 2W (1996-1999)				
6	0.17	0.09	0.42	0.06
10	0.22	0.12	0.63	0.07
33	0.36	0.21	1.23	0.11
60	0.48	0.32	2.42	0.14
Walker Branch P5 (1998-1999)				
3.5	0.15	0.07	0.31	0.06
8	0.15	0.09	0.36	0.06
14	0.35	0.27	1.06	0.10
24	0.57	0.48	1.79	0.14
36	0.64	0.47	1.80	0.14
61	0.86	0.53	2.04	0.29
Walker Branch TDE (1998-1999)				
3	0.11	0.08	0.33	0.05
8	0.29	0.35	1.39	0.07
14	0.36	0.40	1.62	0.10
21	0.50	0.47	1.80	0.13
37	0.59	0.47	1.85	0.17
52	0.72	0.45	1.87	0.22
68	0.91	0.52	2.02	0.28

[1] Values in parenthesis represent the maximum values measured February 4, 1997-April 29, 1997 and are. anomolously high; see text for discussion.

Table 4. Incubation information.

Site	Incubation Length (Days)	Field Sampling (Date)	Incubation Start (Date)	Soil Horizons Incubated	CO_2 Scrub (Day[1])	CO_2 Sampled (Day[1])	Isotopes Sampled (Day[1])
Howland	12	13-Jul-99	15-Jul-99	Oi+Oe, Oe+Oa, E, Bhs+Bh, Bs1	1	2,3,4,6,9,12	12
Howland	6 and 43	13-Jul-99	15-Jul-99	Oi+Oe, Oe+Oa	1, 6	2,3,4,5,6,9,12, 13,22,31,43	6, 43
Harvard Forest	12	17-Jul-99	19-Jul-99	Oi+Oe, Oe+A, Ap, Bw1	1	2,3,4,5,9,11,12	12
Harvard Forest	5 and 42	17-Jul-99	19-Jul-99	Oi+Oe, Oe+A	1,5	2,3,4,5,9,11,12, 22,31,39,42	5, 42
Harvard Forest[2]	10	11-Sep-97	18-Sep-97	O, A, Ap, Bw	1	10	10

[1] Day of Incubation from day one.

[2] Incubations performed by M. Torn (unpublished data)

Table 5. Results from 12 day incubations from Howland and Harvard Forest 1999. Values shown are from individual jar incubations.

Site	Horizon	Mid-point depth (cm)	Δ^{14}C (‰)	δ^{13}C (‰)	C evolved mg C g dry soil^{-1}	Bulk Density g cm^{-3}
Harvard Forest						
NWN 1	Oi + Oe	2.5	120.2	-27.61	3.47	0.08
	Oi + Oe	2.5	116.9	-28.56	5.33	0.08
	Oea + A	6.8	154.4	-26.84	0.80	0.23
	Oea + A	7.8	142.7	-27.75	0.82	0.23
	Ap	13.3	116.2	-26.92	0.13	0.54
	Bw1	27.0	75.8	-23.70	0.02	0.86
NWN 2	Oea + A	6.5	107.7	-26.39	2.51	0.23
	Ap	10.5	125.5	-26.47	0.22	0.54
	Bw1	32.0	73.1	-23.89	0.04	0.86
Howland						
NC	Oi+Oe	3.0	130.5	-27.20	5.53	0.09
	Oe+Oa	8.8	107.8	-26.01	1.10	0.13
	E	17.0	135.4	-25.82	0.03	1.10
	Bh	20.0	87.2	-26.05	0.08	0.65
	Bs1	33.0	74.9	-25.57	0.03	2.00
	Bs1	42.0	69.4	-24.23	0.02	2.13
Tower	Oi+Oe	3.0	153.5	-26.37	3.18	0.09
	Oe+Oa	7.3	116.3	-26.11	1.93	0.12
	Oe+Oa	8.3	139.9	-26.43	0.88	0.17
	E	12.8	118.7	-26.54	0.11	1.10
	Bh + Bhs	19.5	102.0	-26.84	0.14	0.65

Table 6. Results from 10 day incubations from Harvard Forest 1997.

HORIZON	Δ^{14}C (‰)	δ^{13}C (‰)	C evolved mg C g dry soil^{-1}	Bulk Density g cm^{-3}
O	151	-28.73	5.16	0.08
A	140	-28.35	0.75	0.35
Ap	117	-28.73	0.14	0.54
B	85	-25.47	0.02	0.86

Table 7. Results from 5(6) and and 42(43) day incubations from Howland and Harvard Forest 1999.

SITE	HORIZON	Mid-point depth (cm)	Δ^{14}C (‰)	δ^{13}C (‰)	Δ^{14}C (‰)	δ^{13}C (‰)
Harvard Forest			**5 day**	**5 day**	**42 day**	**42 day**
NWN 1	Oi + Oe	2.5	123	-27.27	121	-27.60
	Oe+ Oa + A	8.0	123	-26.87	144	-27.46
Howland			**6 day**	**6 day**	**43 day**	**43 day**
NC	Oi+Oe	3.5	159	-26.61	157	-26.51
	Oe +Oa	8.0	99	-26.38	72	-26.39

Table 8. Results from respiration partitioning using Method 1. Highlighted values indicate situations where $\Delta_{Het} < \Delta_{Tot}$, leading to negative values for the fractional contribution of autotrophic respiration.

	Measured--				**Calculated--**			
Site	**F_{Tot}**	**Δ_{Het}**	**ΔA**	**Δtot**	**F_{Het}**	**F_{A}**	**F_{Het}**	**F_{A}**
	gC m^{-2} y^{-}	**‰**	**‰**	**‰**	**gC m^{-2} y^{-1}**	**gC m^{-2} y^{-1}**	**%**	**%**
Howland 1999								
Tower	800	129	92	116	516	284	64	36
NC	869	114	92	117	990	-121	114	-14
Average	735	121	92	117	619	116	84	16
Harvard Forest 1999								
NWN-1	442	121	92	105	195	247	44	56
NWN-2	442	114	92	105	258	184	58	42
Average	442	120	92	105	202	240	46	54
Harvard Forest 1997								
	657	141	100	134	544	113	83	17

Table 9. Values and ranges used for all sites to partition soil respiration into Recent-C and Reservoir-C sources using Method-2.

Site	Total Resp. F_T	Total Resp. ΔT	Leaf Litter max F_{LL}	Leaf Litter min F_{LL}	Leaf Litter max ΔL_L	Leaf Litter min ΔL_L	Root Litter max ΔL_R	Root Litter min ΔL_R	Humified F_{H+M}	Humified Δ_{H+M}
Howland NC										
1998	698	128	40	0	202	161	192	151	76	67
1999	669	117	40	0	195	161	192	151	76	67
Howland Tower										
1998	836	126	122	65	166	106	192	151	58	52
1999	800	116	142	85	158	106	192	151	58	52
Harvard Forest										
1996	840	128	95	25	132	113	214	180	68	132
1997	657	134	95	25	125	107	214	180	68	132
1998	990	125	95	25	119	102	214	151	68	132
1999	442	105	95	25	113	98	214	151	68	132
Walker Branch P5										
1998	867	138	39	0	132	121	224	173	84	110
Walker Branch TDE										
1999	867	129	72	0	132	121	224	173	77	118.3

Table 10. Results from respiration partioning based on depth (using Method 1). Highlighted values indicate situations where $\Delta_{Het} < \Delta_{Tot}$, leading to negative values for the fractional contribution of autotrophic respiration. see text for further discussion.

Site	Horizon	Δ_{Het} ‰	ΔA ‰	Δ_{tot} ‰	F_{Het} %	F_A %
Howland Tower 1999						
6 cm	Oe+Oa	121.3	92	113	0.71	0.29
15 cm	E	127.1	92	106	0.39	0.61
51 cm	Bs1	72.2	92	115	-1.12	2.12
Harvard Forest 1999						
6 cm	Oea + A	134.9	92	113	0.48	0.52
33 cm	Bw1	74.5	92	106	-0.76	1.76
60 cm	Bw1	74.5	92	93	-0.03	1.03
Harvard Forest 1997						
6 cm	O	151	92	no data		
33 cm	B	85	92	131	-5.22	6.22
60 cm	B	85	92	139	-6.30	7.30

Table 11. The annual ΔΔ14CO$_2$ (‰) for soil respiration and soil gas at all three sites.

Pit Depth (cm)	1996	1997	1998	1999
Howland, Tower				
soil respiration			30	24
6			16	21
15			14	14
51			1	23
Harvard Forest, 2W				
soil respiration	24	34	29	13
6	32		25	27
33	24	31	22	28
60	22	39	16	25
Walker Branch, P5				
soil respiration			13	
8			20	
24			23	
61			27	
Walker Branch, TDE				
soil respiration			12	
8			17	
14			17	
68			28	

Δ^{14}C of atmospheric CO$_2$ in 1996, 1997 and 1999 is 104, 100, 96 and 92‰ except at Walker Branch where for 1998 117‰ is used. See text for details.

Table 12. Isotopic summary, C residence times and $\delta^{13}C$ isotope disequilibrium. for all sites. Values in parentheses represent one standard deviation or the error based on modeling certainty.

	Howland 1998-1999	Harvard Forest 1996-1999	Walker Branch 1998
$\Delta\Delta^{14}CO_2$(‰) Total soil Respiration	28	25	13
Average Annual CO_2 Flux (mgC m^{-2} y^{-1})	695[1]	765[2]	820[2]
Average Fraction Reservoir-C	0.50(.07)	0.41(.07)	0.33(.08)
Mean Residence Time-All C (y)	5(2)	4(2)	5(4)
$\delta^{13}C$ Isotopic disequilibrium (‰)	-0.10(0.04)	-0.08(0.04)	-0.10(0.08)
Mean Residence Time-Reservoir-C (y)	8(2)	9(2)	8(2)
$\delta^{13}C$ Isotopic disequilibrium (‰)	-0.16(0.04)	-0.18(0.04)	-0.16(0.08)
Years of data	2	4	1

[1] 1997-1999

[2] 1996-1999

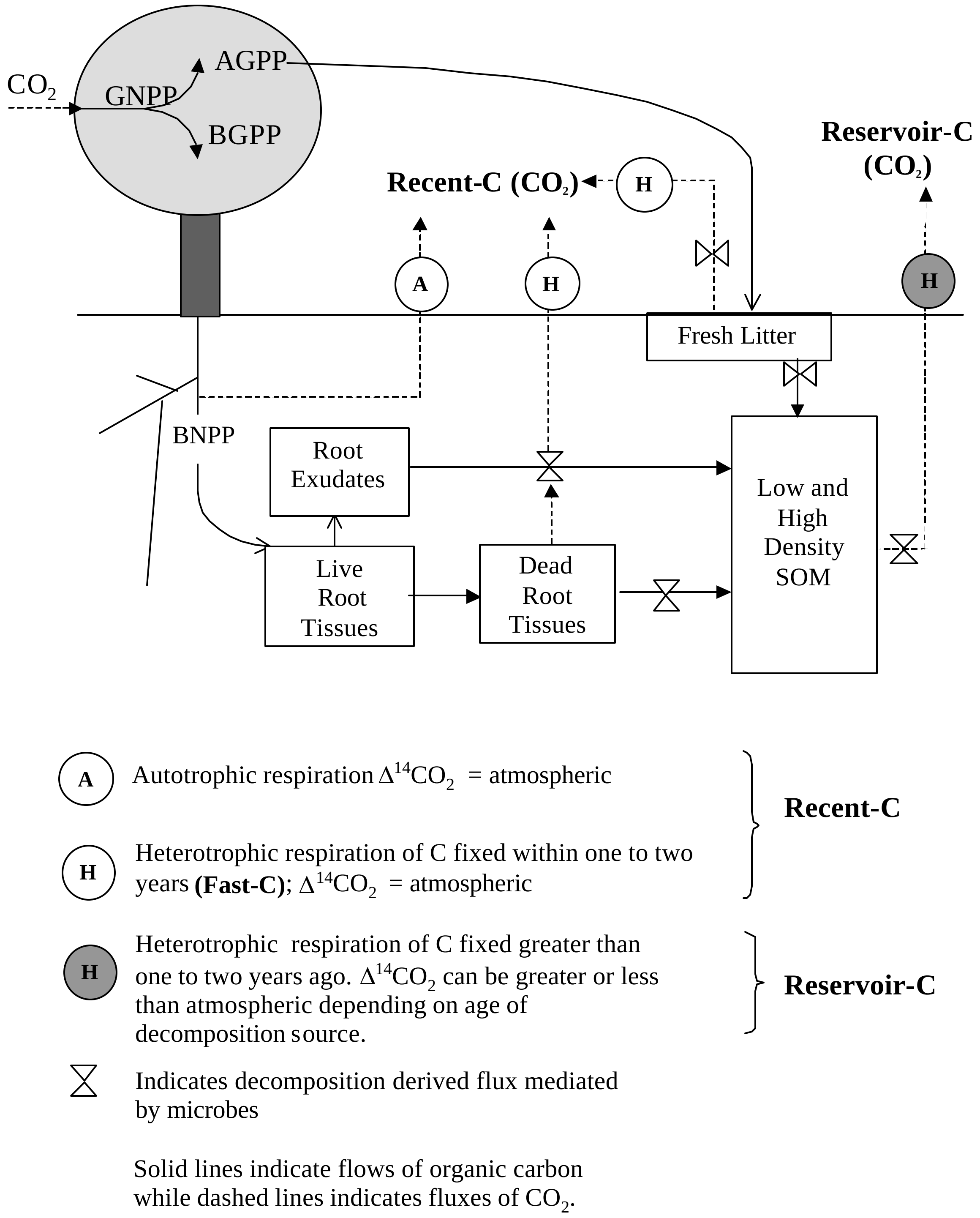


Figure 1. Forest carbon cycle and definition of terms and isotopic values. GNPP, ANPP and BNPP indicate gross, aboveground net and below ground net primary productivity respectively.

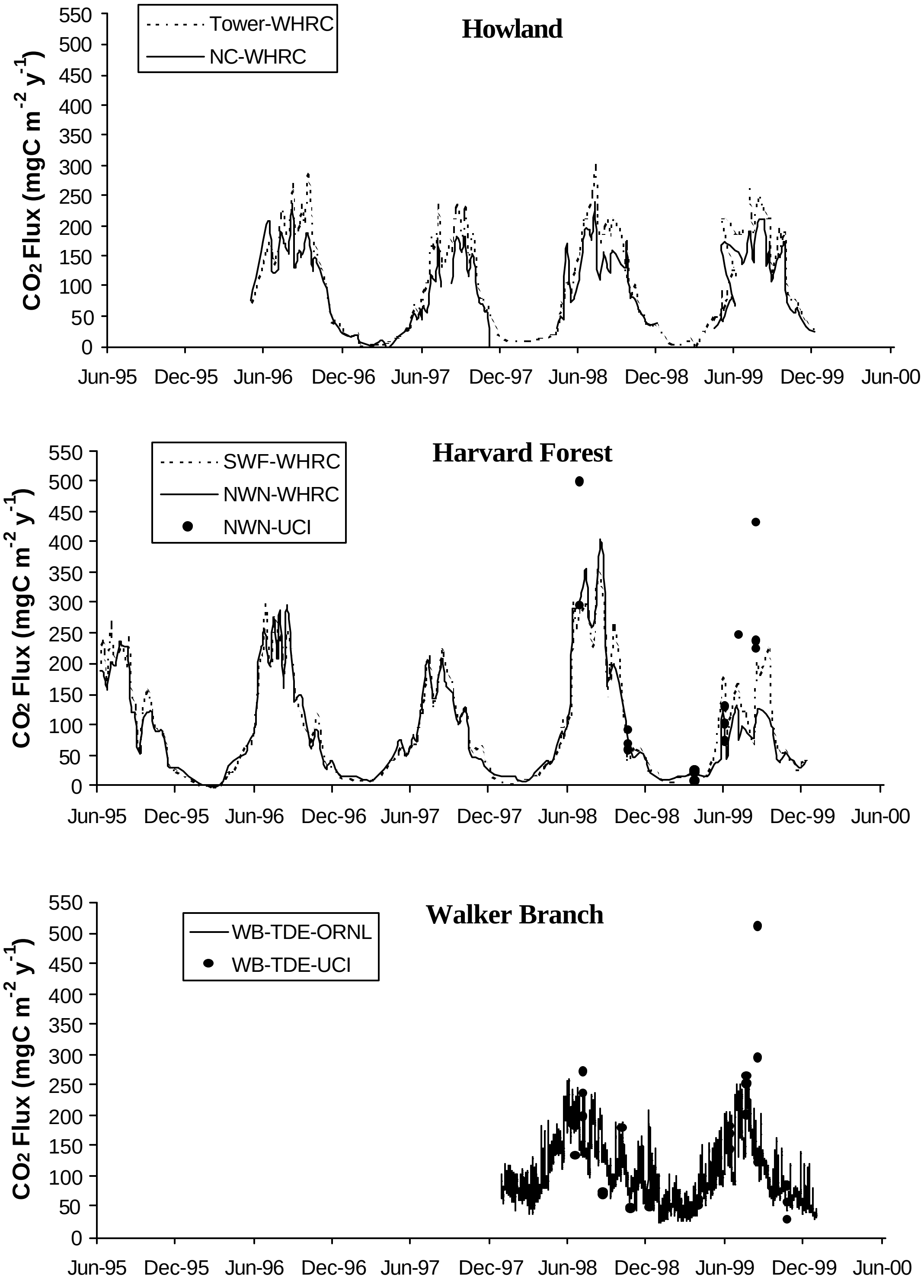


Figure 2. CO_2 fluxes for well drained soils at all three sites. See text for further details.

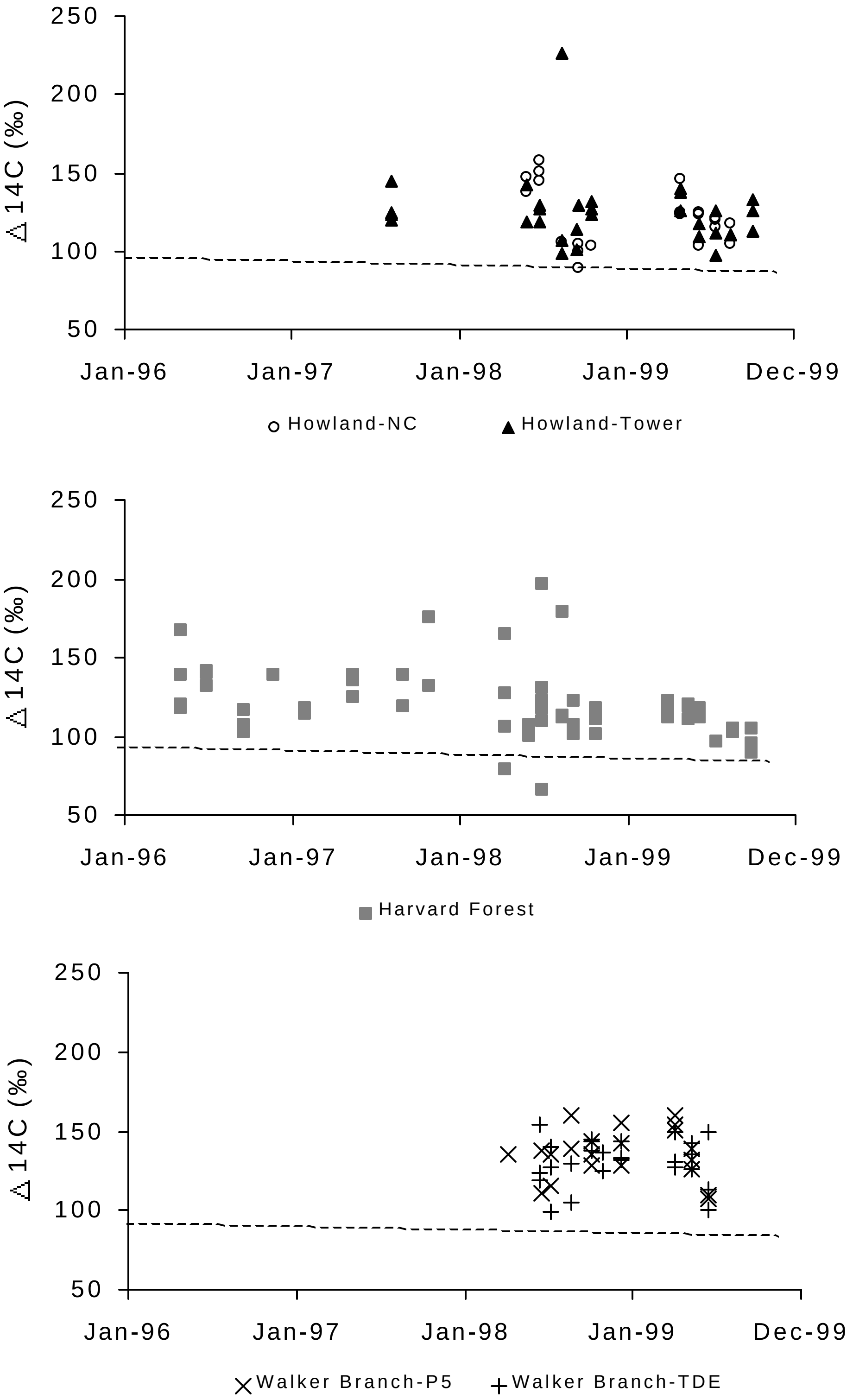


Figure 3. Time series of $\Delta^{14}C$ of CO_2 in soil respiration at all three sites. Dashed line represents the $\Delta^{14}C$ of atmospheric CO_2 (104-92‰). Values have all been corrected for any leaks during sampling using the measured $\delta^{13}C$ for each sample.

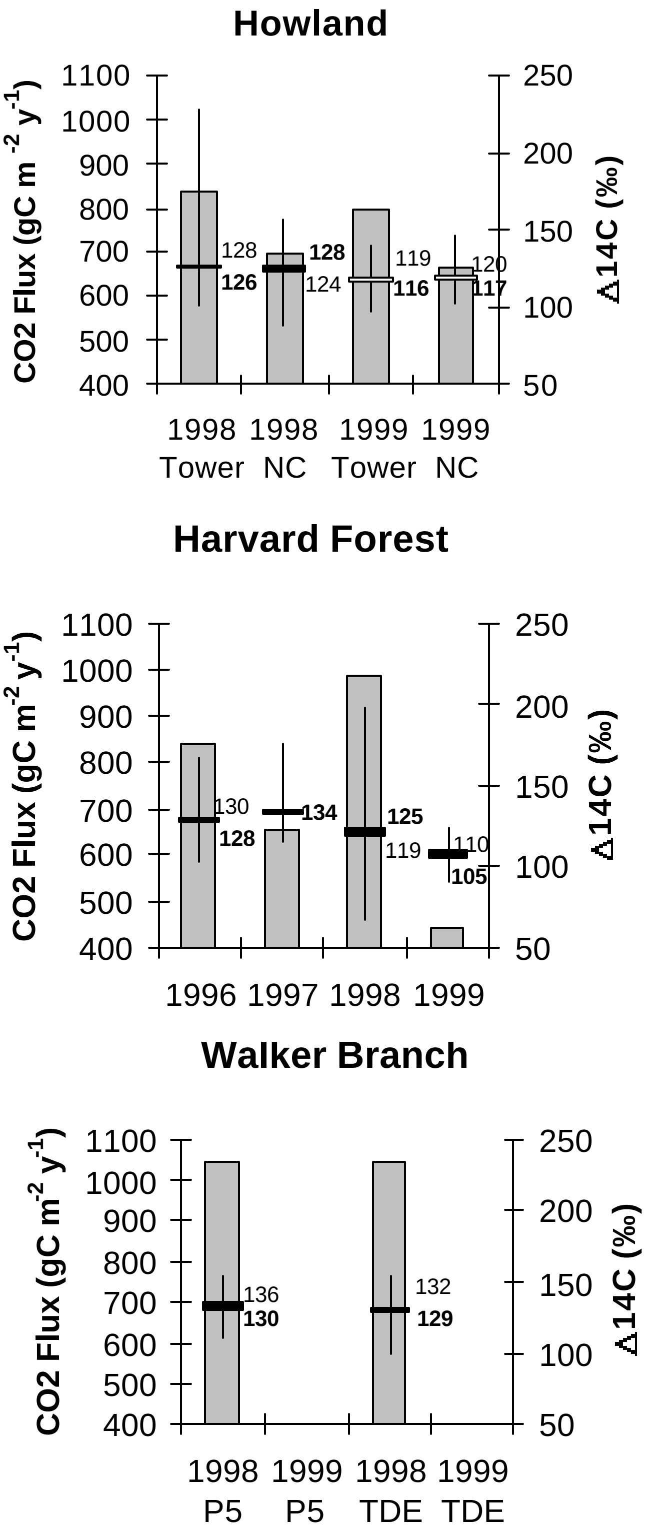


Figure 4. Annual average CO_2 flux and $\Delta^{14}CO_2$ values for all three sites. Grey bars are the CO_2 flux. The range of $\Delta^{14}CO_2$ values in a given year are shown by vertical lines. The horizontal line (or boxes) represent the range for an annual flux weighted average (bold values) versus a non-flux weighted average ^{14}C value (non-bold values).

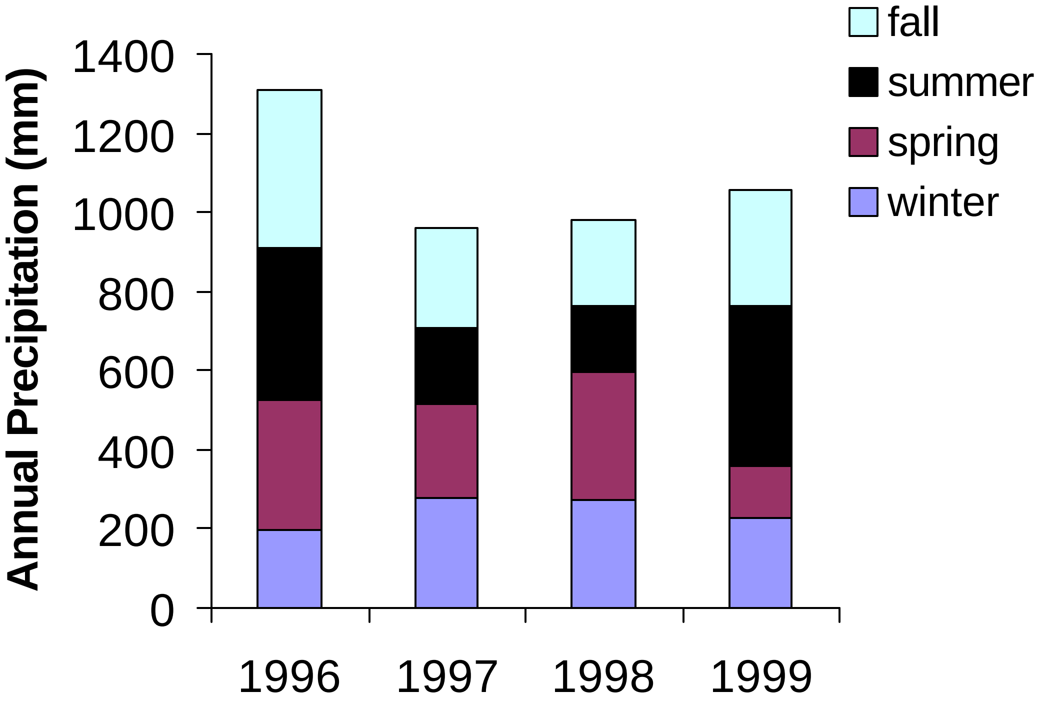


Figure 5. Annual precipitation at Harvard Forest by season.

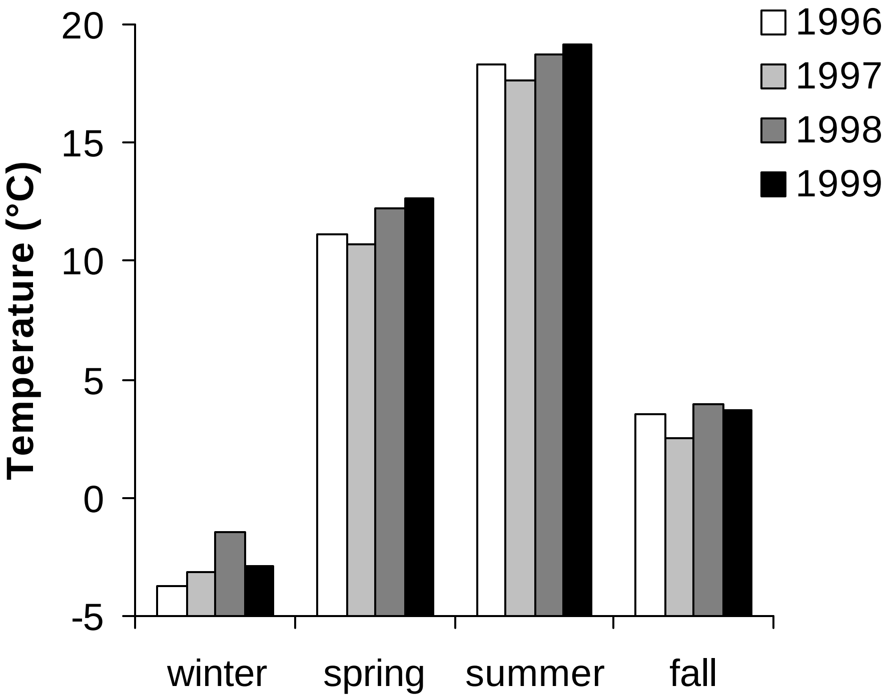


Figure 6. Harvard Forest, MA, average mean daily air temperature (°C) for winter (JD 1-90) spring (JD 91-180), summer JD (181-270) and fall (JD 271-365). Temperature data come from an environmental monitoring station at Harvard Forest roughly 2 km from our study area.

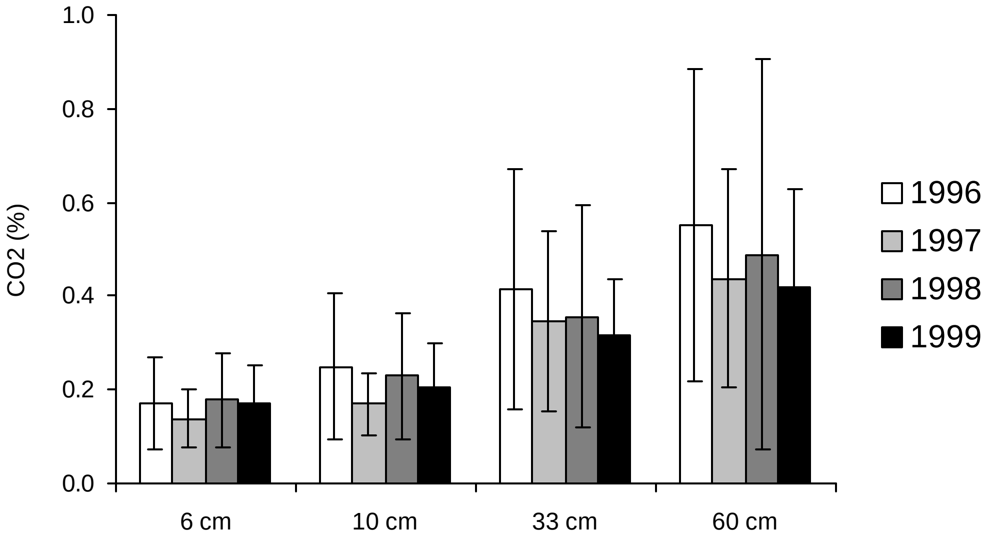
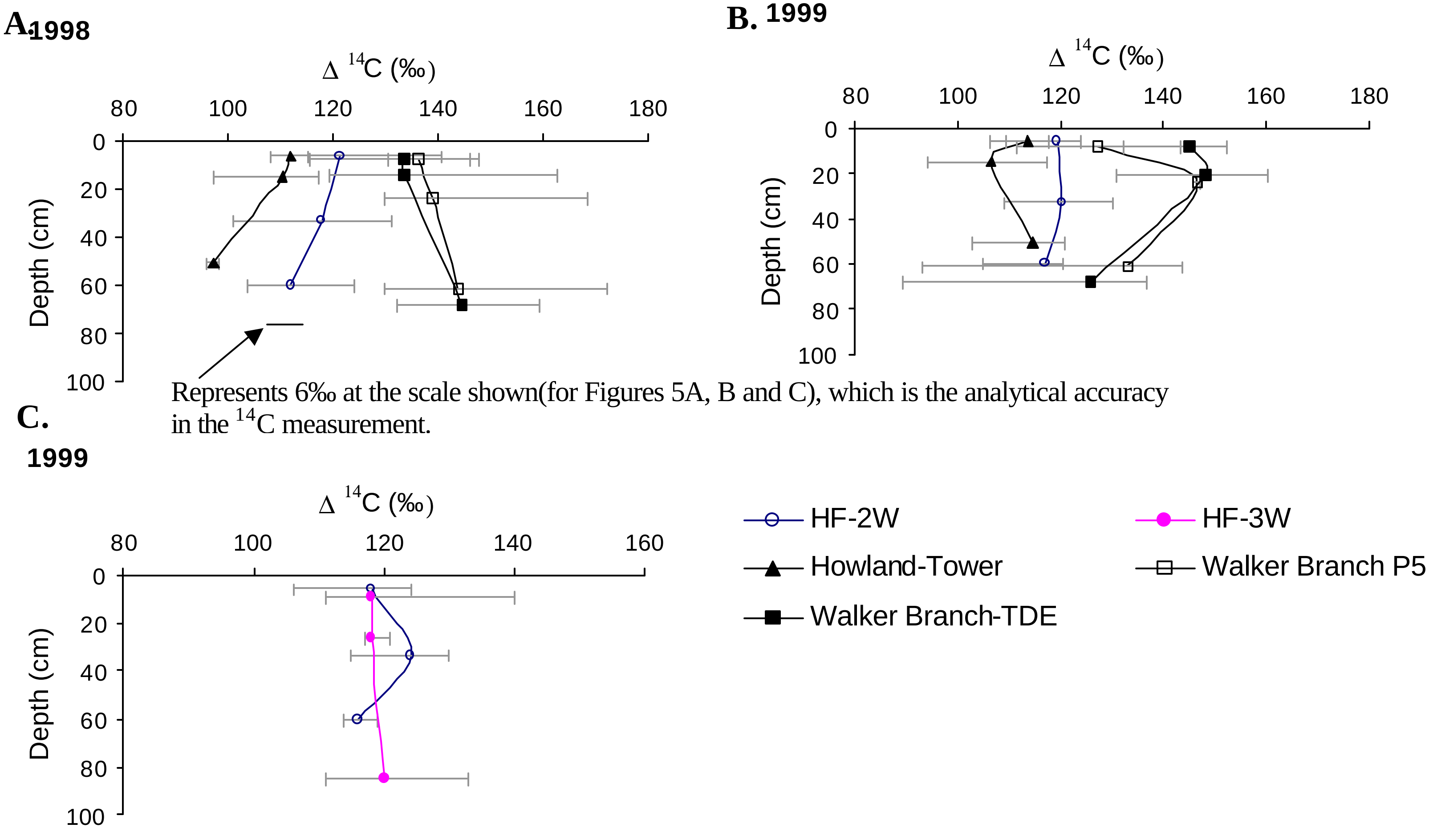


Figure 7. Annual average CO_2 concentrations for pit 2W at Harvard Forest by depth. Error bars represent one standard deviation.



Represents 6‰ at the scale shown(for Figures 5A, B and C), which is the analytical accuracy in the ^{14}C measurement.

Figure 8. Profile $^{14}CO_2$ concentrations. Figure 5A and B show annual concentration weighted average $^{14}CO_2$ at all three sites for 1998 (A) and 1999 (B). The 1999 Walker Branch data represent three samplings, April, May and June. Measurements after June are not comparable due to the unexpected ^{14}C release. Figure 5 C shows concentration weighted average $^{14}CO_2$ values for samples taken March , May, June and July, 1999 at Harvard Forest only. Error bars represent the total range of $^{14}CO_2$ measurements made at a given depth over the time interval shown. N equals one to six.

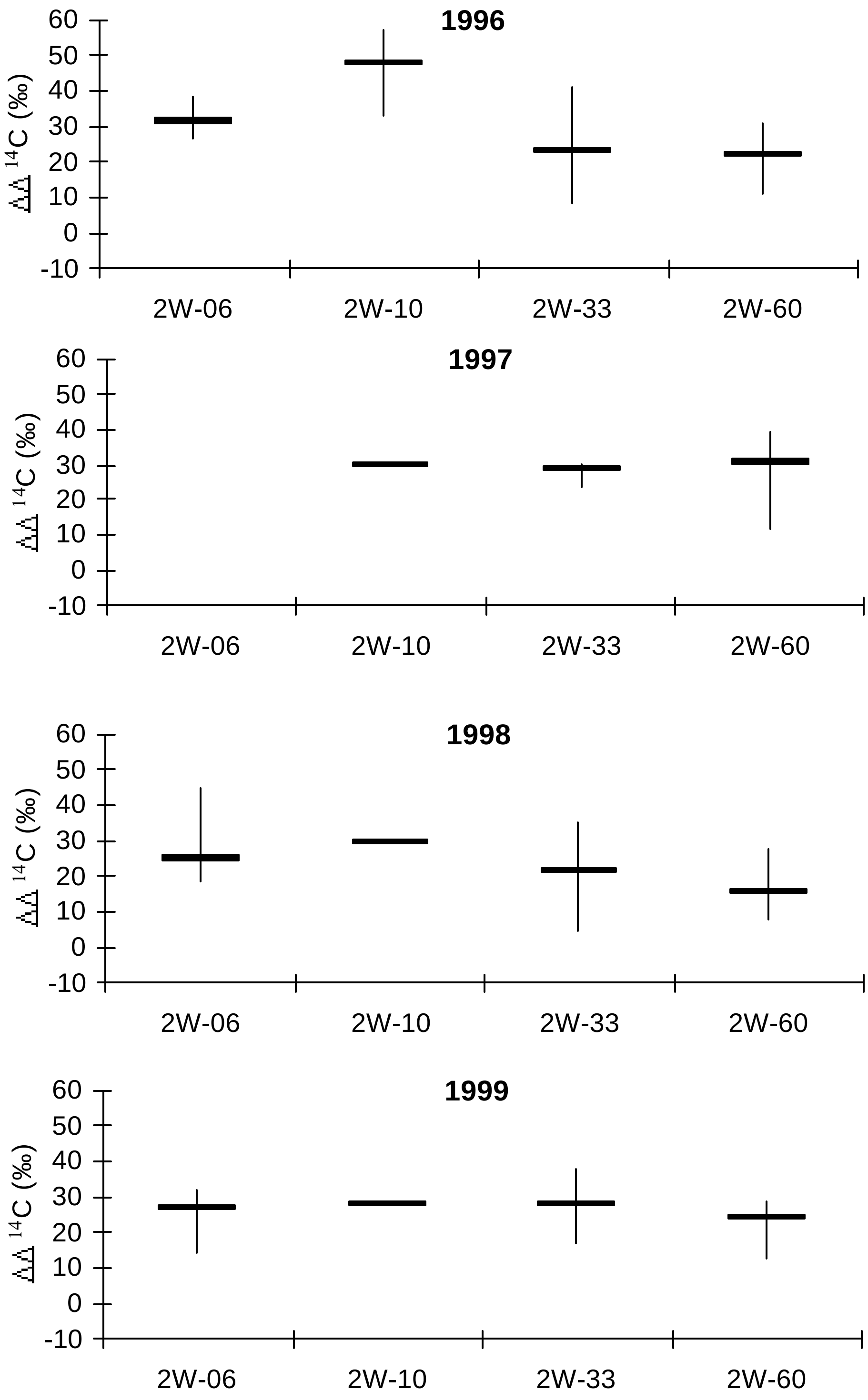


Figure 9. Annual concentration weighted average $\Delta\Delta^{14}CO_2$ of profile CO_2 samples for pit 2W at Harvard Forest. Depths in cm are also indicated. Horizontal bar indicates annual concentration weighted average $\Delta\Delta^{14}CO_2$ and vertical line represents range of all measured values.

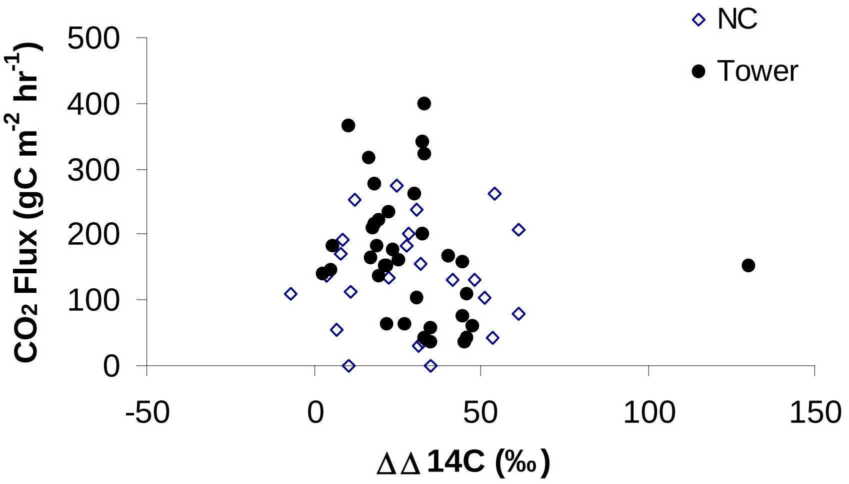


Figure 10. $\Delta\Delta^{14}CO_2$ plotted against the collar flux at or near the time of sampling was taken for both sites at Howland. The lack of correlation at Howland is similar for the other two sites as well.

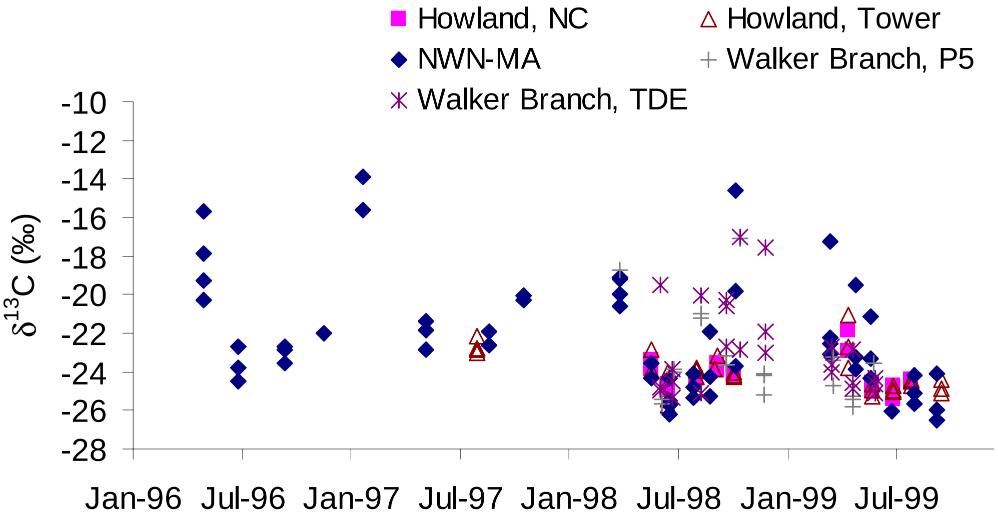


Figure 11. $\delta^{13}C$ of soil respiration through time for all sites.

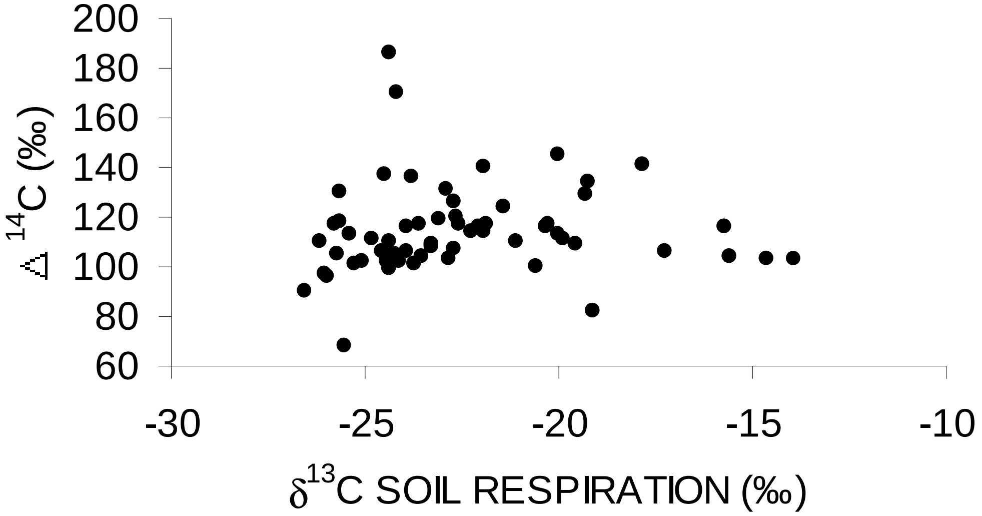


Figure 12. δ^{13}C of soil respiration vs. $\Delta^{14}CO_2$. The $\Delta^{14}CO_2$ plotted here does not reflect a correction for δ^{13}C.

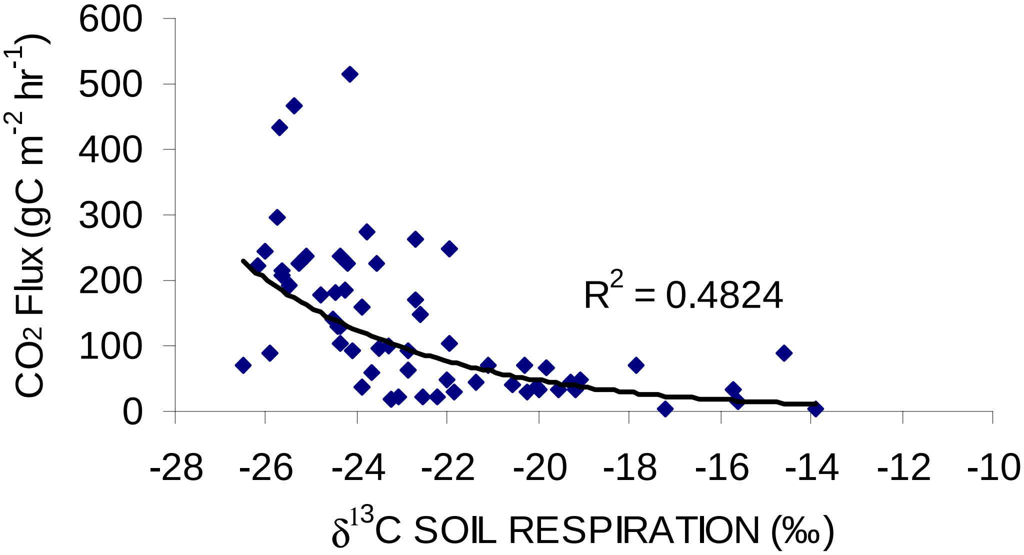
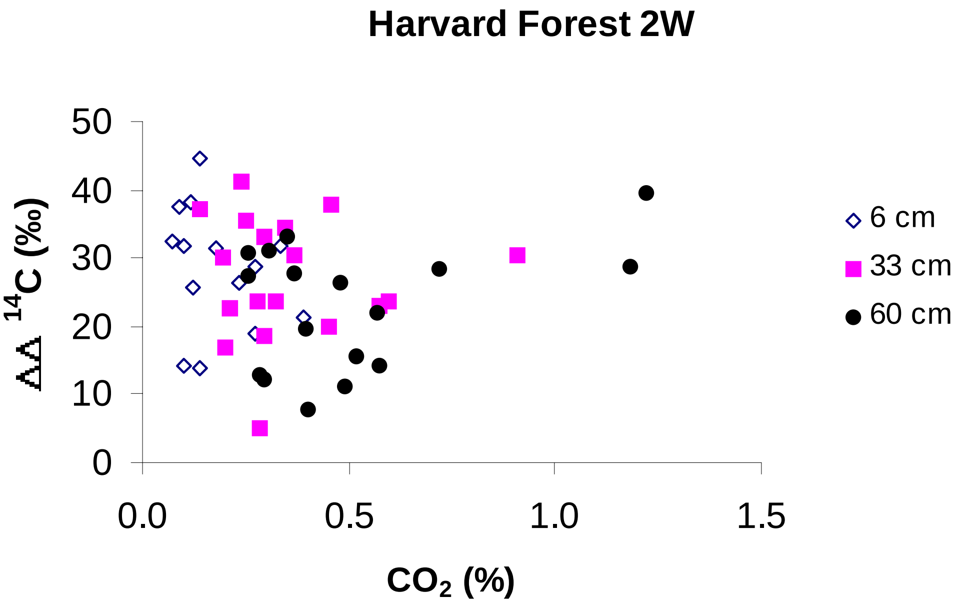


Figure 13. δ^{13}C of soil respiration vs. CO_2 flux. The flux shown is for the specific collar sampled.



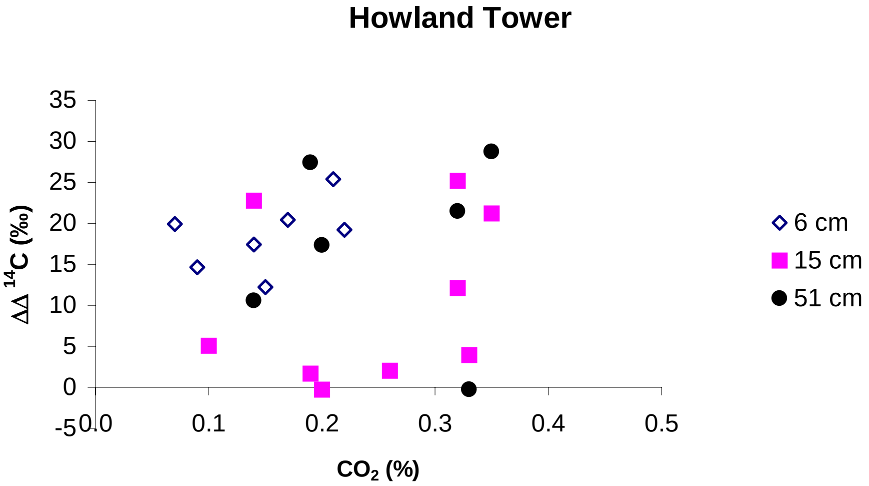
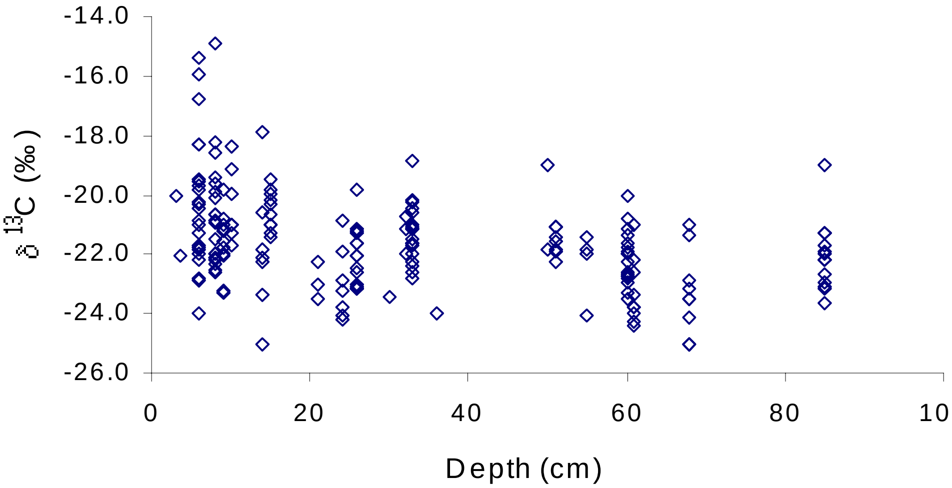


Figure 14. $\Delta\Delta^{14}$C of profile CO_2. Harvard Forest pit 2W (Top) and Howland Tower (bottom).



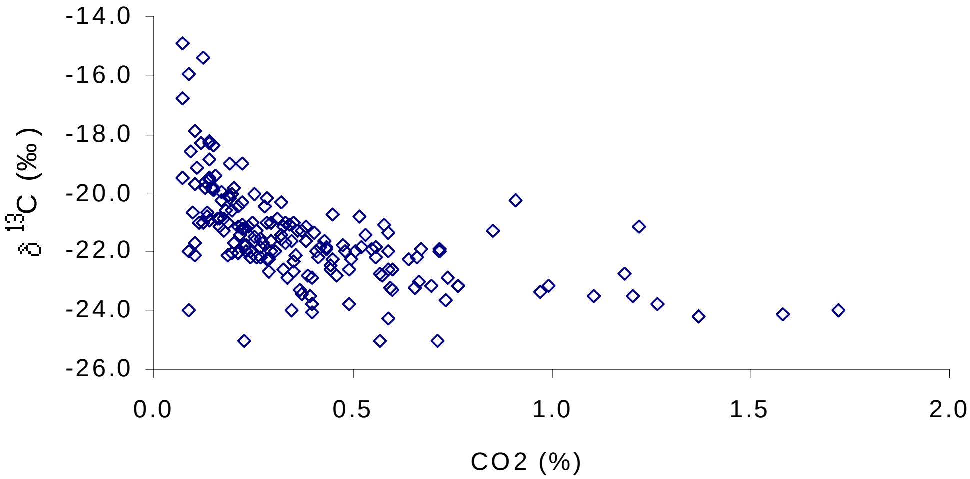


Figure 15. δ^{13}C versus depth (top) and profile CO_2 concentration (bottom) for all samples.

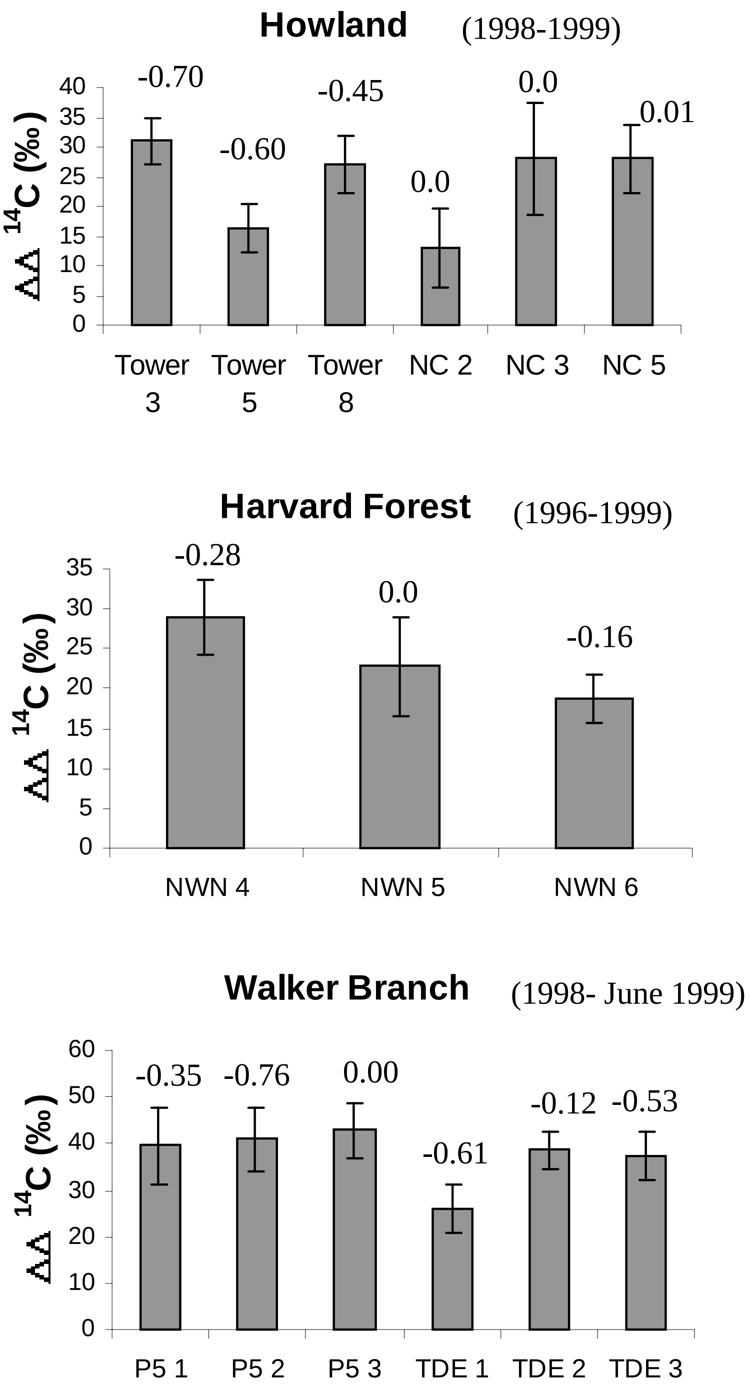


Figure 16. Variation in $^{14}CO_2$ signature for each specific collar. Error bars represent the standard error (n = 6 or more samples in all cases). Values above each collar represent the R^2 for the correlation between CO_2 flux and $\Delta\Delta^{14}CO_2$ for that given collar. Negative values indicate a negative trend (i.e. higher fluxes correlate with lower $\Delta\Delta^{14}CO_2$).

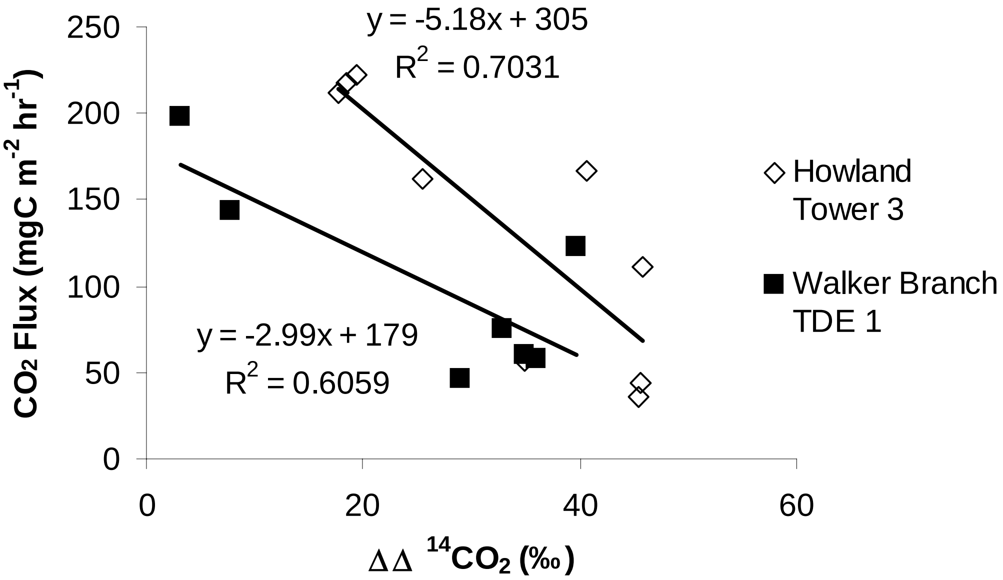


Figure 17. $\Delta\Delta^{14}CO_2$ versus CO_2 flux for two specific collars. Data for Howland are from 1998 and 1999 while data from Walker Branch are 1998 through June 1999.

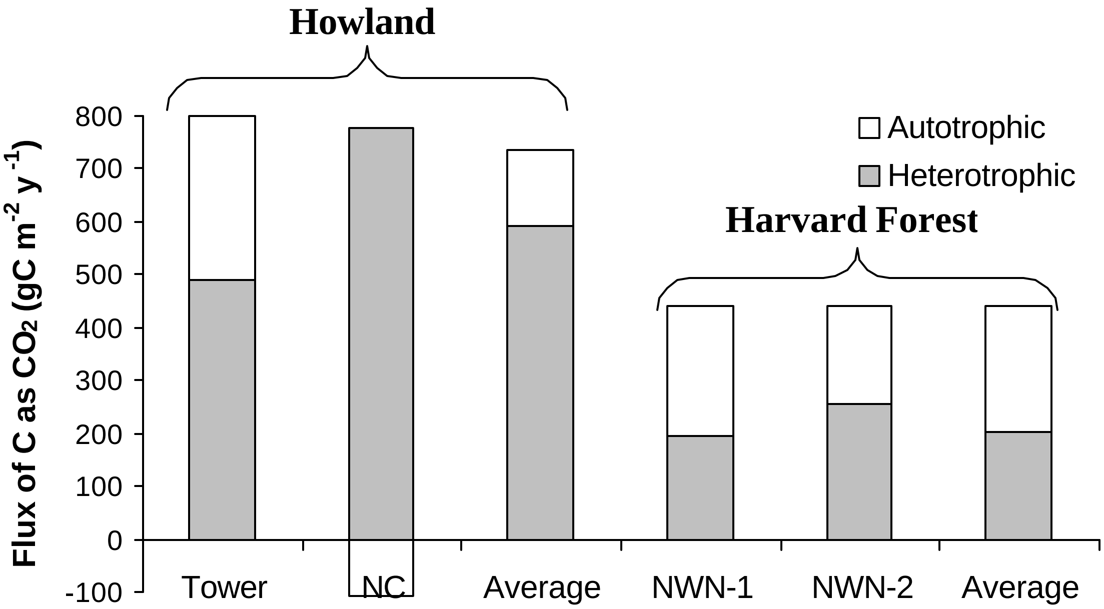


Figure 18. Results of partitioning soil respiration into autotrophic versus heterotrophic sources for the 1999 growing season. Numbers inside bars represent the percent of the total flux represented by each component. Error bars represent the range of isotopic values from the incubations for different ways of averaging the replicates within a pit.

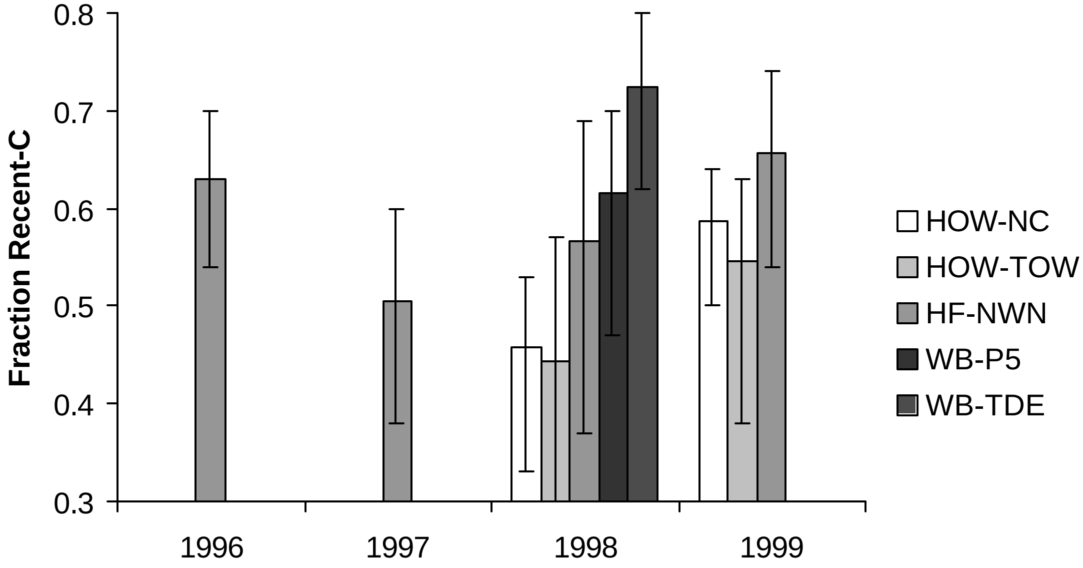


Figure 19. Fraction of total soil respiration coming from Recent-C for all sites and available years.

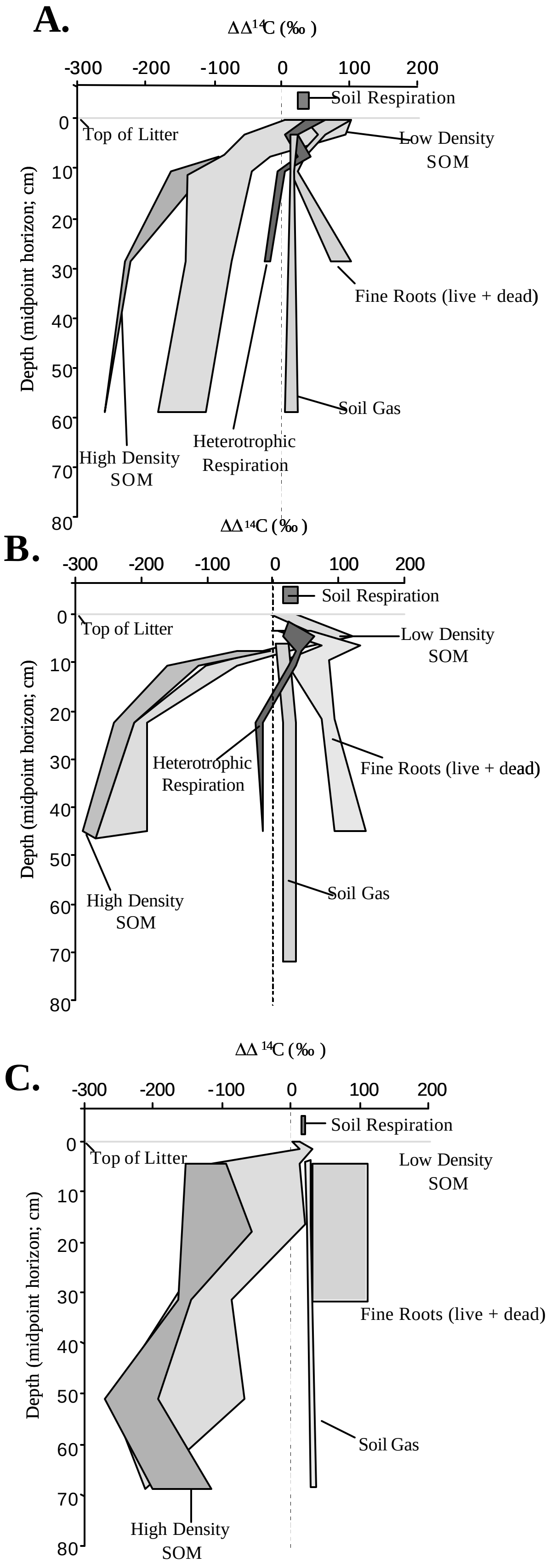


Figure 20. The $\Delta\Delta^{14}$C of all below ground components at all three sites. Plotting these data in this way allows for comparisons of soil gasses across different years (as atmospheric ^{14}C of CO$_2$ continues to decrease at a constant rate of 4‰ per year). Carbon fixed within one year (autotrophic respiration and C fixed within one year), will have a $\Delta\Delta^{14}$C equal to 0‰.
Filled parallelograms represent the entire range of measured values for high and low density soil organic matter; the range in annual flux or concentration weighted averages for soil respiration and soil gas; and the range in values obtained for heterotrophic respiration (from incubations) and for live+dead fine (< 1mm diameter) roots.
A. Howland. Gas samples taken during 1998 and 1999.
B. Harvard Forest. Gas samples taken during 1996-1999.
C. Walker Branch. Gas samples taken during 1998 only.

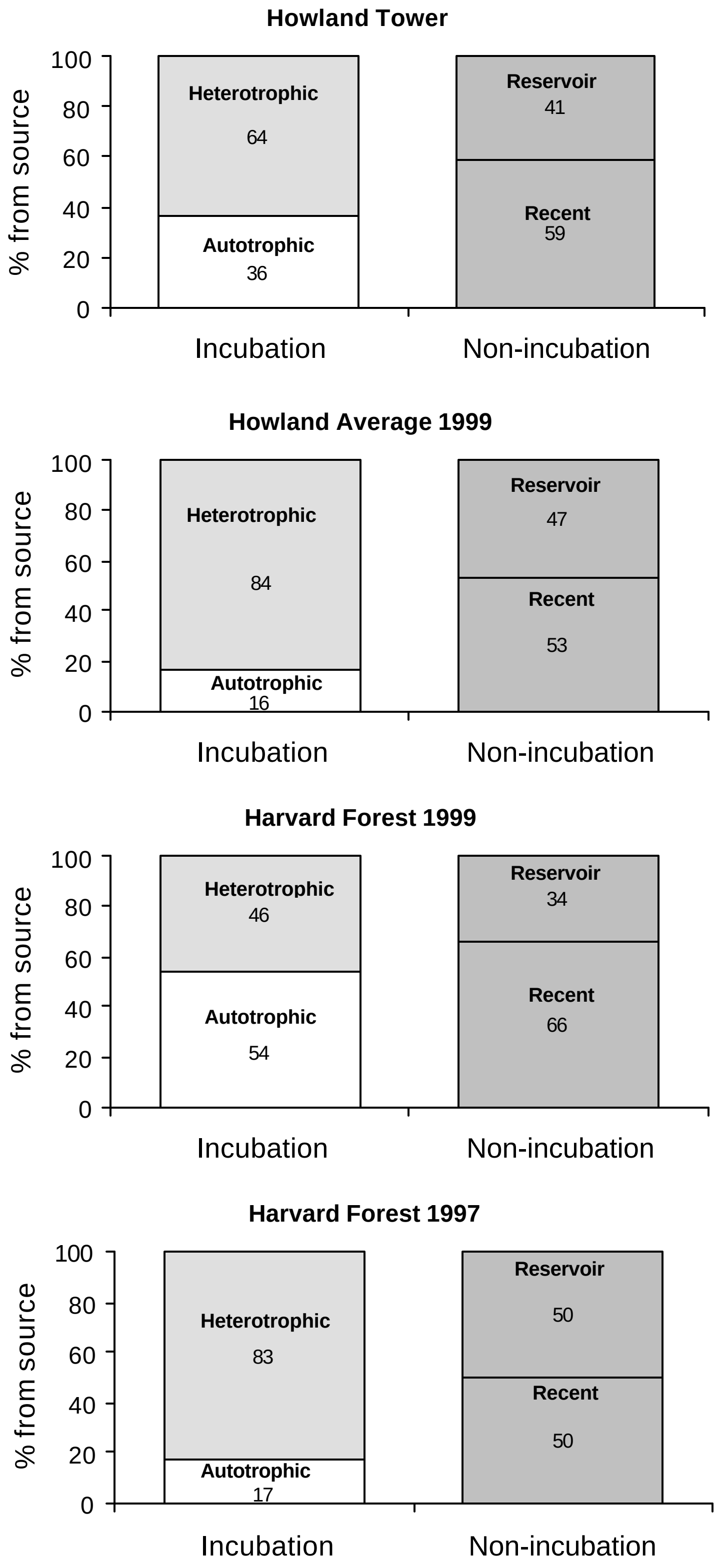


Figure 21. Respiration partitioning results for 1999 based on respiration partitioning methods that include incubations of SOM versus one that does not. The sum of Autotrophic plus Fast-C should theoretically equal Recent-C. Numbers indicate percentage contribution of each component to the total annual soil respiration.

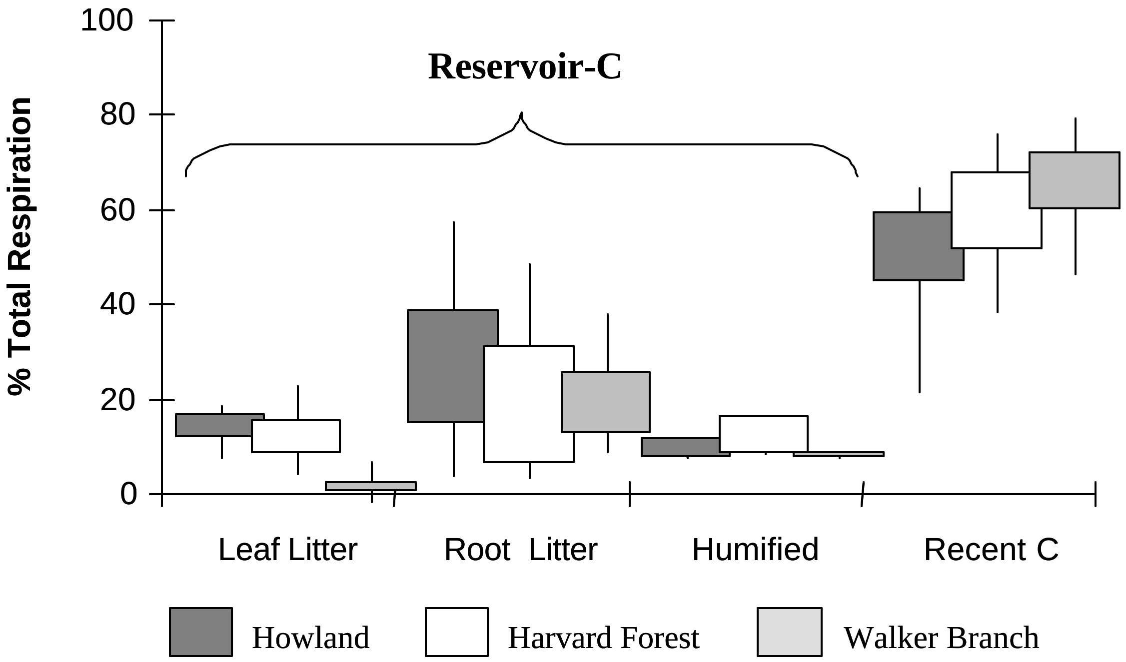


Figure 22. Percentage of total soil respiration coming from Reservoir-C sources and Recent-C sources. Boxes represent range of average values and lines represent maximum and minimum modeled values for all years with available data at a given site respectively.

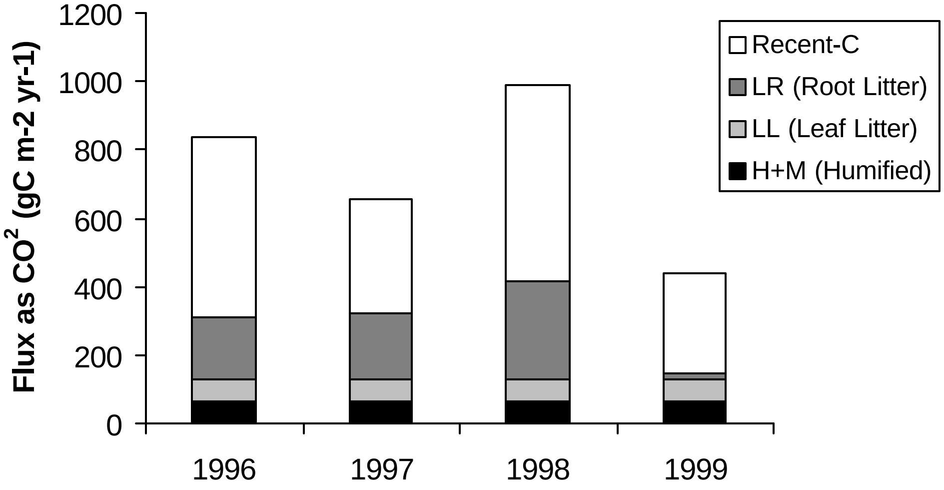


Figure 23. Estimated flux of CO_2 from each respiration source for the years 1996 through 1999 at Harvard Forest.

Chapter 6: Moisture manipulations at Harvard Forest

Introduction

As discussed in Chapter 5, the ^{14}C signature of CO_2 in soil respiration reflects the ^{14}C of both its autotrophic and heterotrophic sources. Inputs of bomb ^{14}C to atmospheric CO_2 began in the late 1950's, and largely ended in 1963 with the Nuclear Test Ban Treaty. As a result, $^{14}CO_2$ concentration in the atmosphere has been decreasing from a 1964 peak of ~900‰ (see Chapter 3: Radiocarbon Techniques). The radiocarbon content of atmospheric CO_2 during this study (1996-1999) was 104‰ in 1996 and 92‰ in 1999, with an annual rate of decrease of 4 ‰ (Levin and Hesshaimer, 2000). During photosynthesis, plants fix CO_2 from the atmosphere and will also fix $^{14}CO_2$ in proportion to its atmospheric concentration. Thus, after correction for isotopic fractionation during photosynthesis, the ^{14}C concentration of SOM, combined with the time record of atmospheric ^{14}C in CO_2, can be used to quantify carbon cycle dynamics.

Autotrophic respiration in any given year will have the same $^{14}CO_2$ as the atmosphere ($\Delta^{14}C$ = 92‰ in 1999), whereas decomposition of decadally cycling SOM will have $\Delta^{14}C > 92‰$ in 1999, and SOM cycling on centi-millenial timescales will be predominately made up of C fixed before 1950 (i.e. $\Delta^{14}C < 0$). Thus the ^{14}C content of soil respiration will fluctuate as 1) the partitioning between autotrophic and heterotrophic respiration varies, and 2) SOM sources with differing ages vary in their contributions of decomposition derived CO_2 in response to changes in soil temperature, moisture, and nutrient status throughout the profile.

The bulk of new C inputs to the soil profile come from leaf litter added to the top of the soil surface (O horizon) and fine root inputs which are greatest in the O and A horizons (McClaugherty and Aber, 1982). Thus the bulk of CO_2 production from both autotrophic and decomposition sources would logically come from these horizons. Indeed, based on CO_2 concentration profiles and diffusivity modeling, roughly two-thirds of CO_2 produced within the soil profile for the well-drained soils of Harvard Forest is estimated to come from the upper 10-15 cm, which comprise the O and A horizons (see Chapter 2 and (Davidson and Trumbore, 1995).

Two of the biggest influences on both autotrophic and heterotrophic respiration rates are soil temperature and soil moisture. Changes in soil temperature account for most variation in soil respiration fluxes (Davidson et al., 1998). Trumbore et al., (1996), extrapolating based on the temperature dependence of low density SOM, suggest a significant fraction of interannual variation in CO_2 accumulation in the atmosphere may derive from a temperature response of fast (decadal or faster) cycling SOM to temperature change. Davidson et al, (1998), reporting on work at Harvard Forest, show that a severe late summer drought in 1995 significantly decreased soil respiration rates, and discuss the need for including soil-moisture content (matric potential) as well as temperature in empirical models of soil respiration. Continuing their work at Harvard Forest since 1995, Savage and Davidson (in Press), found significant (though less extreme relative to 1995) decreases in soil respiration that do not correlate well with soil-moisture measurements made in the uppermost horizon of the mineral soil (A horizon). They hypothesize that varying moisture content in the 2-6 cm thick O horizon (litter layer), which is very responsive to short duration wet and dry periods, may be responsible for some of the variability in CO_2 fluxes.

This notion suggests that variations in $^{14}CO_2$ fluxes may also respond to moisture in the O horizon. The O horizon has a large stock of SOM with components that have $\Delta^{14}C$ values ranging from 92 to ~260‰ which are interpreted as turnover times of < 1 year to 40+ years (see Chapter 2). Calculated decomposition fluxes (based on inventory divided by turnover time) and the isotopic signature of these fluxes (based on ^{14}C measurements of low density SOM fractions) show that the low density SOM in the O and A horizons do in fact dominate both the total profile CO_2 production and isotopic signature of heterotrophic respiration relative to the deeper mineral horizons (Chapter 5).

In order to see the importance of moisture in the O and A horizons to both total CO_2 and $^{14}CO_2$ fluxes, we performed moisture manipulation experiments in well-drained soils at Harvard Forest, in both 1998 and 1999. In 1998 we performed both a wet-up and dry-down manipulations, while in 1999 we performed only a dry-down manipulation. For assessing the effect of the manipulations, monitoring moisture content is critical. Unfortunately, TDR methods (see Chapter 2) used in mineral horizons do not adequately track soil moisture in the surface organic horizons due to limitations imposed by probe length and area of influence. Low bulk density and textural heterogeneity of the O horizon make it extremely difficult to reliably monitor moisture content. In an effort to improve the ability to measure moisture content in this horizon, we also tested a DC half bridge measurement technique that will allow continuous monitoring of moisture content in the O horizon (**Figure 1**).

Methods

Moisture Manipulations

In both 1998 and 1999, the dry down was achieved by placing a 2m x 2m open PVC structure over the ground and covering the top with transparent plastic. A drain hole was cut in the plastic, sealed, drainage diverted into a bucket, and the run-off measured. The wet up was performed in 1998 only by watering a 2 m x 2 m plot with 5 gallons of water twice a week, simulating a 9.5 mm rain event twice a week. If it was raining on the day the watering was supposed to occur, no additional water was added to the plot. All experimental manipulations took place at two well-drained sites (NWN and SWF) and both sites were monitored for total CO_2 fluxes from soil respiration. However, only the NWN was monitored for $^{14}CO_2$ soil respiration fluxes and CO_2 and $^{14}CO_2$ concentrations. The dry down at NWN took place over an existing soil pit (3W) instrumented with soil gas tubes and TDR moisture measurements (see Chapter 2 for details) in the mineral soil horizons. A second pit (2W) provided the ambient or control soil profile, because it was not manipulated in any way. Craig Skipton took many of the measurements in 1998 for this experiment and we are deeply indebted to him for his dedication and enthusiasm.

Half Bridges

The half bridge measures the change in resistance across an object as a function of its water content. The design is based on one deployed by Dr. Paul Hanson to monitor the change in resistance of actual leaves in the litter layer at the Walker Branch Watershed

(Wilson et al., 2000) as shown in **1**A. We have modified his method to use a thin piece of porous Basswood (3 x 3 x 0.2 cm), which we insert at 3 depths into the O horizon (litter surface, 2 cm and 5 cm). The wood quickly equilibrates with the moisture content of the surrounding material and allows moisture measurements at and below the leaf litter surface. To obtain a calibration curve to convert from the measured voltage (resistance) to a moisture content, litter from 0-1, 1-2, and 2-5 cm depth (from an area approximately 4 cm x 4 cm) was placed in mesh bags in late July of 1999 and monitored with the DC half bridges (either the multimeter or data logger set up, **1**B and C), and also taken back to the lab periodically and weighed. In late August, the mesh bags were removed from the field and dried at 60 °C so that gravimetric moisture contents could be calculated and then correlated to the half-bridge readings.

Moisture content in the O horizon was measured gravimetrically in 1998 using a 10 cm x 10 cm wooden frame to collect litter samples at the same 3 depths as the half bridges. The samples were then weighed at field moisture, dried at 60 °C for 48 hours, and reweighed. In 1999, moisture was monitored by use of the DC half-bridge technique.

CO_2 and $^{14}CO_2$ fluxes and concentrations

Methods for sampling CO_2 and $^{14}CO_2$ fluxes and concentrations are described in detail in Chapter 2. With regard to the experimental set up for the moisture manipulations, surface CO_2 and $^{14}CO_2$ fluxes for the dry-down and wet-up sites were taken from 3 collars placed within the dry-down enclosures or wet-up plots respectively. For the ambient sites, CO_2 and $^{14}CO_2$ fluxes come from three of the existing 6 collars monitored by Eric Davidson’s research group, as described in Davidson et al., (1998). All pits and collars used in the experiment at the NWN site are within a 100 m^2 area. At the

SWN site, where only total CO_2 surface fluxes were measured, all collars are within a area roughly 300 m^2 area.

Respiration Partitioning

Partitioning of soil respiration into Recent-C (C fixed within one to two years) versus Reservoir-C (C fixed more than 1 to 2 years ago; see Chapter 5, Figure 1) sources during the period of the moisture manipulations was performed using Method 2 as described in Chapter 5. Parameters used to constrain leaf litter, soil organic matter C and ^{14}C fluxes and root isotopic signatures are the same as those shown in Chapter 5, Table 11.

Results

Half Bridges: monitoring moisture content of the O horizon

Gravimetric moisture contents from the ambient, wet and dry treatments in 1998 indicate drying of the O horizon relative to the ambient and wet-up sites after beginning of the moisture manipulation on July 8, 1998 (**Figure 2**). The average gravimetric moisture content for the dry-down, ambient, and wet-up treatments for the moisture manipulation beginning July 8, 1998 and ending October 28 was 0.49 ± 0.13, 0.89±0.55, and 0.97±0.49 g water per gram dry soil respectively. Only after one big rainstorm in early August did the O horizon in the dry down increase its moisture content, though still much less so than the other two treatments (**Figure 2**). In contrast, the wet-up treatment shows little difference in soil water content throughout the whole experiment relative to the ambient plot.

The DC half bridges used for the 1999 experiment qualitatively recorded moisture changes in their voltage response to rain events for locations under ambient conditions for the three different measurement depths (**Figure 3**). The sensors under the dry-down structure show generally damped or no response to rain events (**Figure 4**). However, during some of the large rain events (such as at JD 250 and 260) some wet up occurs at all depths beneath the dry-down enclosure. All half bridges in the same depth horizon show differences in water content (voltage), as would be expected, given that the O horizon wets or dries unevenly. The half bridge calibration curve between voltage (converted to resistance) and gravimetric water content is shown in **Figure 5** for all depths. The relation between resistance and gravimetric water content with a logarithmic fit has an R^2 of only 0.347. The least squares for specific depth intervals and mesh bags range from 0.913 to 0.001. In general, higher R^2 values are observed for the 0-1 and 1-2 cm interval than the 5-cm location. This may be because the deeper horizon tends to stay wetter, and shorting of the leads across the half bridge may give voltages close to zero, which translate to wet values when the sensor is not actually that wet. This phenomenon was a large problem in the very wet spring and summer of 2000 (data not included in this thesis) until the leads were insulated. Calibration should be performed again using insulated leads.

Surface CO_2 and $^{14}CO_2$ fluxes

In both 1998 and 1999, the dry-down plots had half the CO_2 flux observed in the ambient plots (**Figure 2** and **Figure 6**). During the roughly 4-month period of the manipulation experiments, the ambient plots respired 535 (1998) and 238 (1999) g C m^{-2} and the dry-down plots respired 250 (1998) and 90 (1999) g C m^{-2}. In 1998, the wet-up experiment actually had less total flux than the ambient plot (490 versus 530 g C m^{-2}). Based on the 1998 data, the wet up was not repeated in 1999, which is unfortunate because 1999 was such a dry year with lower overall fluxes. Despite such a dramatic difference in CO_2 fluxes created by the dry-down manipulation, no difference in $^{14}CO_2$ of the respiration was discerned in either year between the ambient and wet plots (**Figure 2** and **Figure 6**).

Depth profiles of H_20, CO_2 and $^{14}CO_2$

As stated earlier, the purpose of the wet-up and dry-down manipulations was to determine the effect of O horizon moisture content on total C and $^{14}CO_2$ fluxes. However, wetting/drying of the O horizon also affects the mineral horizons below. Therefore it is important to compare H_20, CO_2, and $^{14}CO_2$ within the mineral horizons of the ambient (2W) and dry-down pit (3W). The wet-up plot was not monitored in the mineral horizon. Differences in profile concentrations of both water and CO_2 can be seen between the ambient and dry-down pits in both years (**Figure 7** and **Figure 8**). However, most of the differences existed prior to the manipulation and persisted after the manipulation began. Unfortunately, on September 4,1998, the cable tester required to take soil moisture measurements at the dry-down plot broke and so moisture comparisons in the mineral horizons can only be made between July 8 and September 3 for 1998.

The volumetric water contents in the dry-down plot show little consistent effect of the dry down on comparable depths. There are a few exceptions, one of which is the 9 cm (dry down) and 10 cm (ambient) before and during the 1999 dry-down period (**Figure 7**). Interestingly, the difference is present well before the beginning of the dry down (July 19). In general, the two depths have similar CO_2 concentrations, and when they do differ at all the dry-down plot typically has a higher water content. At depth, the 26 cm (dry down) is often wetter than the 33 cm (ambient) when manipulations are not taking place. Concentrations are similar throughout the 1998 dry-down periods, and during the 1999 dry down the 26-cm (dry-down) depth remains a bit wetter than the 33 cm depth. The 52-cm (dry-down) concentration is typically wetter than the 60-cm (ambient) depths, both before and during the dry downs, except that from mid-August through mid-September 1999 the 52-cm (dry down) is about 30% drier than the 60-cm (ambient) location.

Similarly, consistent changes in CO_2 profile concentrations are not seen during the dry-down manipulations in 1998 or 1999 (**Figure 8**). All comparable depths show little difference throughout the dry down in 1998. However, in 1999 the 9-cm and deeper dry-down depths have a few tenths of a percent less CO_2 than the ambient plots. Two interesting exceptions to this during 1998 are July 9 (one day after the dry down started), when all CO_2 concentrations at depths at both treatments increased, and on July 23, where CO_2 concentrations at 33 and 60 cm depth in the ambient pit reached levels of 1.2 and 2.4%, while the comparable dry-down treatment did not.

The flux-weighted average $\Delta^{14}C$ of CO_2 in soil gas shows some consistent trends in both dry-down manipulations. **Figure 9** shows the $^{14}CO_2$ for the periods prior to and after the dry downs for both the 2W (ambient) and 3W (dry-down) pits. In both 1998 and 1999, the $^{14}CO_2$ of the ambient pit increased at 6- and 60-cm depths, whereas it decreased at 33 cm depth pre- vs. post-dry down. At the dry down, all depths had a decrease in $^{14}CO_2$ signature pre- vs. post-dry down, the decreases being most extreme in 1999 (the driest year).

Respiration Partitioning

In 1998, we estimate the fractions of total CO_2 respiration fluxes from Reservoir-C components were 0.52 (280 g C m^{-2}), 0.45 (220 g C m^{-2}), and 0.64 (160 g C m^{-2}) over the manipulation period for the ambient wet-up and dry-down sites respectively. In 1999, respiration partitioning with Method 2 did not work because the low total CO_2 fluxes combined with $\Delta^{14}CO_2$ values were very close to atmospheric $^{14}CO_2$ values. For example, in 1999 at the dry-down pit (3W), the total measured CO_2 flux and $^{14}CO_2$ content over the experimental period was 90 g C m^{-2}, with $\Delta^{14}CO_2$ = 98‰. However, using Method 2, the combined flux and isotopic signature from F_{LL} and F_{H+M} is constrained to be 129 g C m^{-2}, with $\Delta^{14}C$ of 120‰. Thus the total measured C flux and ^{14}C signature is less than that of just the F_{LL} and F_{H+M} components of Reservoir-C, and negative values for the Recent-C component ($\Delta^{14}C$ = 92‰) are produced. Such results point to problems in the fixed values used to constrain F_{LL} and F_{H+M} in Method 2 (see Chapter 5 for further discussion).

Discussion

Using DC half-bridge sensors to estimate continuous moisture content of the O horizon in 1999 shows promising results. Voltage readings track dry periods and rain events in the uppermost (0-1 cm) of the O horizon (litter), and show damped responses at 2- and 5-cm depth, as would be expected (**Figure 3**). For example, during a warm dry spell between Julian Days (JD) 241 and 249, the 0-1 cm sensors dry within a day, the 2 cm sensors take 3 –4 days, and the 5 cm sensors dry to only the middle of the measurement range over the entire 8-day dry period. At JD 250, when it rains the sensors at all levels respond relatively quickly to the wet-up event. But again, the sensors at 0-1 cm respond the fastest, and those at 5 cm the slowest. The slow drying during long dry periods (JDs 202 to 210, 211-223, and 241 to 249), and relatively fast wetting following rain events, is consistent throughout the season.

Conversion of voltage readings to an actual moisture measurement via a calibration curve (**Figure 5**) can likely be improved by insulation of the half-bridge leads. Also, calibration might improve further if smaller amounts of soil are used relative to the roughly 4 cm x 4 cm area used within the mesh bags in 1999. The wetness of the litter within the mesh bags from the 1-2 and 5 cm depths was sometimes variable. And from visual inspection, the moisture content of the wood did not always appear to be in equilibrium with the moisture content of part of the litter in the mesh bag. In fact, not using a mesh bag at all, destructively sampling the organic matter around the wood and replacing the wood in a new location, may be the best way to calibrate. Finally, the very inexpensive half-bridge instrumentation permits their wider deployment (important for very variable horizons).

During both 1998 and 1999, drying of the O horizon showed dramatic decreases in total CO_2 fluxes and no significant difference in the $\Delta^{14}CO_2$ signature. CO_2 fluxes in untreated controls in 1999 were in general much reduced relative to 1998, effectively making 1999 a natural dry down and NOT the best year to artificially dry down the O horizon.

Vertical profiles of H_20 content and CO_2 concentration in the mineral horizons did not show marked changes from the manipulation. However, the $\Delta^{14}CO_2$ produced at depth tended to decrease during the dry down in comparison to the ambient plot. One possible explanation for the lack of difference in total $^{14}CO_2$ production between treatments is that decomposition derived CO_2 production did shift lower in the O horizon, accessing older, more bomb ^{14}C enriched C sources. However, this was offset by decreases in the ^{14}C signature of CO_2 at depth, suggesting that decomposition of decadal-cycling material (fine root and/or DOC inputs from above) decreased at depth. In order to test this theory, CO_2 production modeling with depth is needed in combination with the isotopic $^{14}CO_2$ data to calculate a C and ^{14}C mass balance. Work is currently underway to improve this approach but will not be completed in time to be part of this thesis.

Results of respiration partitioning in 1998 show little difference between the wet-up and ambient site, matching the lack of differences in moisture, CO_2, and $^{14}CO_2$ between the two treatments. Respiration partitioning at the dry-down site shows that 64% of total respiration came form Reservoir C, in contrast to 45-52% at the other two treatments. The larger percentage of decomposition flux at the dry-down site suggests that respiration of Recent-C sources decreased relative to Reservoir-C sources. As discussed above, the depth profile data show a decrease in $\Delta^{14}CO_2$ at the dry-down versus the ambient site, suggesting an increase in relative contribution of Recent-C sources at depth. Thus the increase in percentage of the total flux coming from Reservoir-C for the total profile would have to come from decomposition in the O horizon (again, likely the deeper part of the O horizon as it dried out the least). An alternative explanation is that the higher estimate for Reservoir-C contribution is simply an artifact from the constraints placed on F_{LL} and F_{H+M} fluxes in Method 2, which fixes their total flux at a given value. As such, if total fluxes are lower, a higher percentage of the total must come from F_{LL} and F_{H+M}.

Conclusions

Drying of the organic horizon by rainfall exclusion created a dramatic decrease in soil respiration fluxes, but not the ^{14}C signature of these fluxes. The $\Delta^{14}C$ of CO_2 in the soil profile show a decrease between 9-85 cm, which suggests a decrease in decomposition in the mineral horizons offset an increase in the $\Delta^{14}C$ of CO_2 within the O horizon. In order to determine the changes in decomposition sources vertically within the soil profile, depth measurements of CO_2 and $^{14}CO_2$ are required. Estimates of CO_2 production with depth are needed to complete the C and ^{14}C mass balance and test the hypothesis of changing production with depth.

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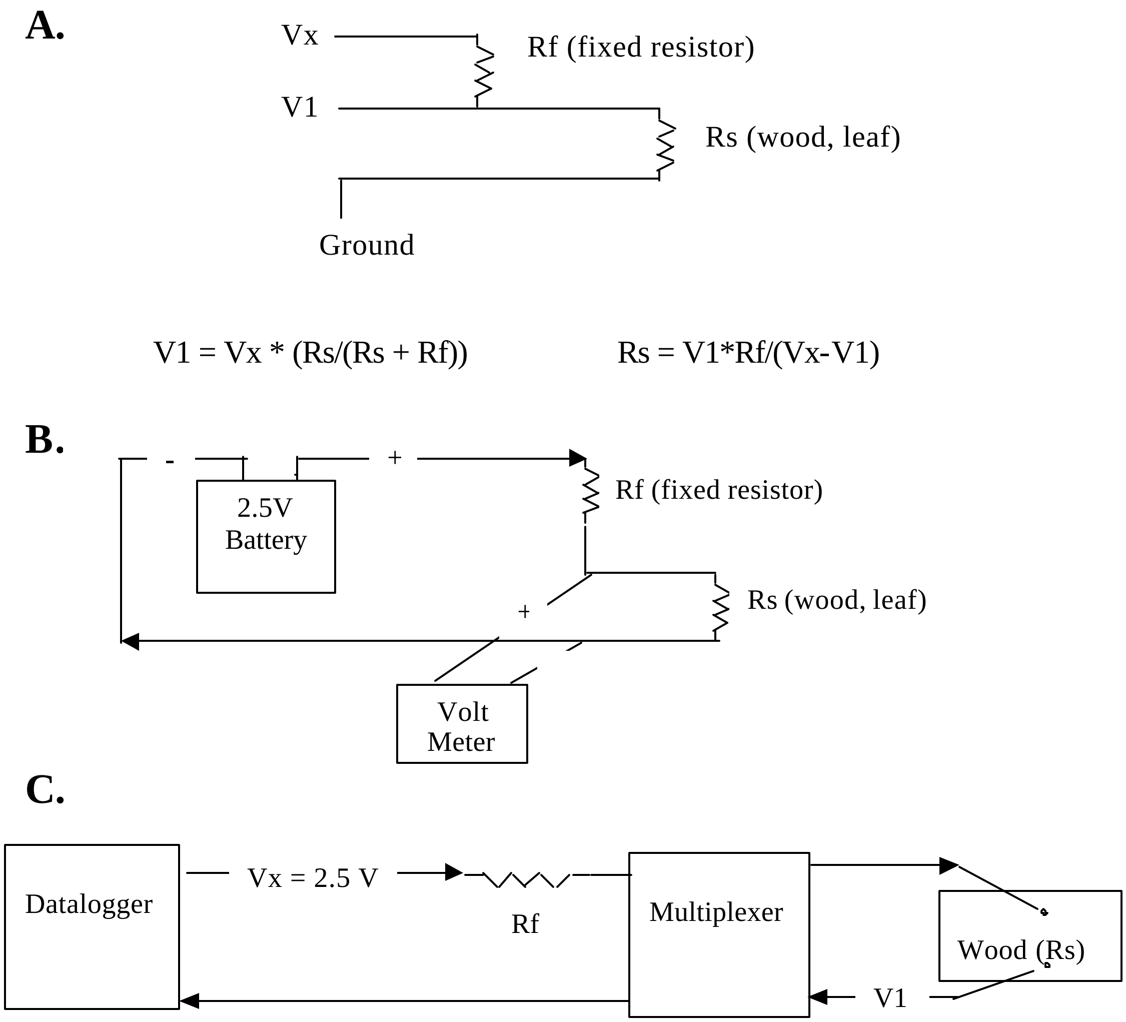


Figure 1. DC half-bridge sensor.
A. General description. A DC voltage of 2.5 volts (Vx) is applied across the half-bridge circuit and the return signal (V1) is related to the resistance of (Rs). Rf is a fixed resistor.
B. Diagram of the experimental set up when using a multimeter to measure voltage at a given point in time.
C. Diagram of the data logger and multiplexer used to monitor the change in resistance of a piece of wood placed in the O horizon as a function of variable moisture content. As moisture increases in the O horizon, the wood quickly equilibrates and its resistance decreases, thereby causing a decrease in V1. Rf is a fixed resistor (390 Kohm). Metal alligator clips are attached to the wood (Rs) 2 cm apart.

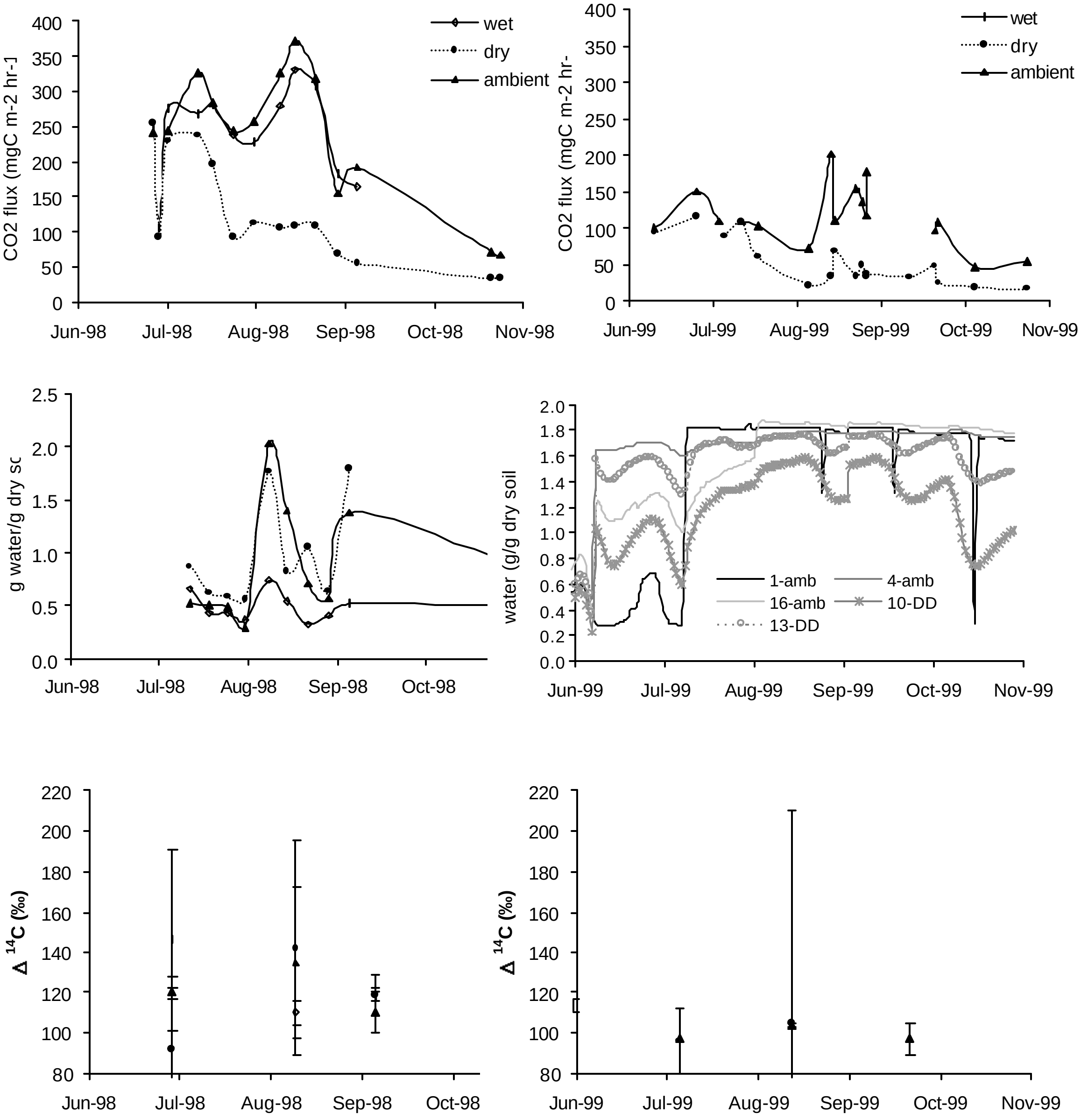


Figure 2. 1998 and 1999 moisture manipulations.
Top: CO_2 fluxes for 1998 (left) and 1999 (right). The wet-up experiment was performed in 1998 only.
Middle: Field measured gravimetric water content for 1998 (left) and DC half-bridge results converted to gravimetric water content at 2 cm depth for 1999 (right). The half bridges in the dry-down enclosure are dryer than the ambient half bridges, although they do experience some wetting.
Bottom: ^{14}C of soil respiration during 1998 (left) and 1999 (right).

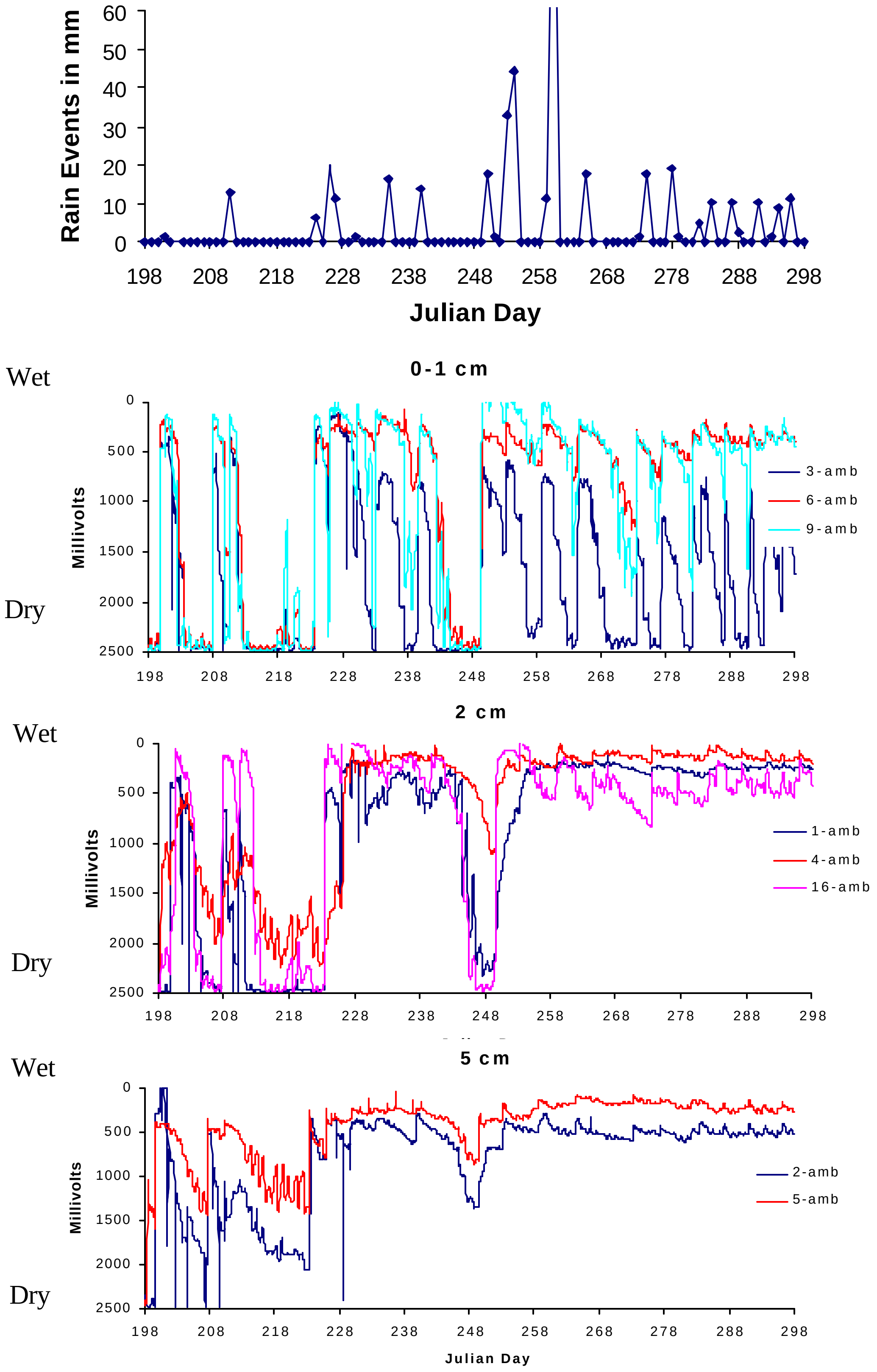


Figure 3. 1999 rainfall data and half-bridge voltage readings for the ambient site during the moisture-manipulation experiment.

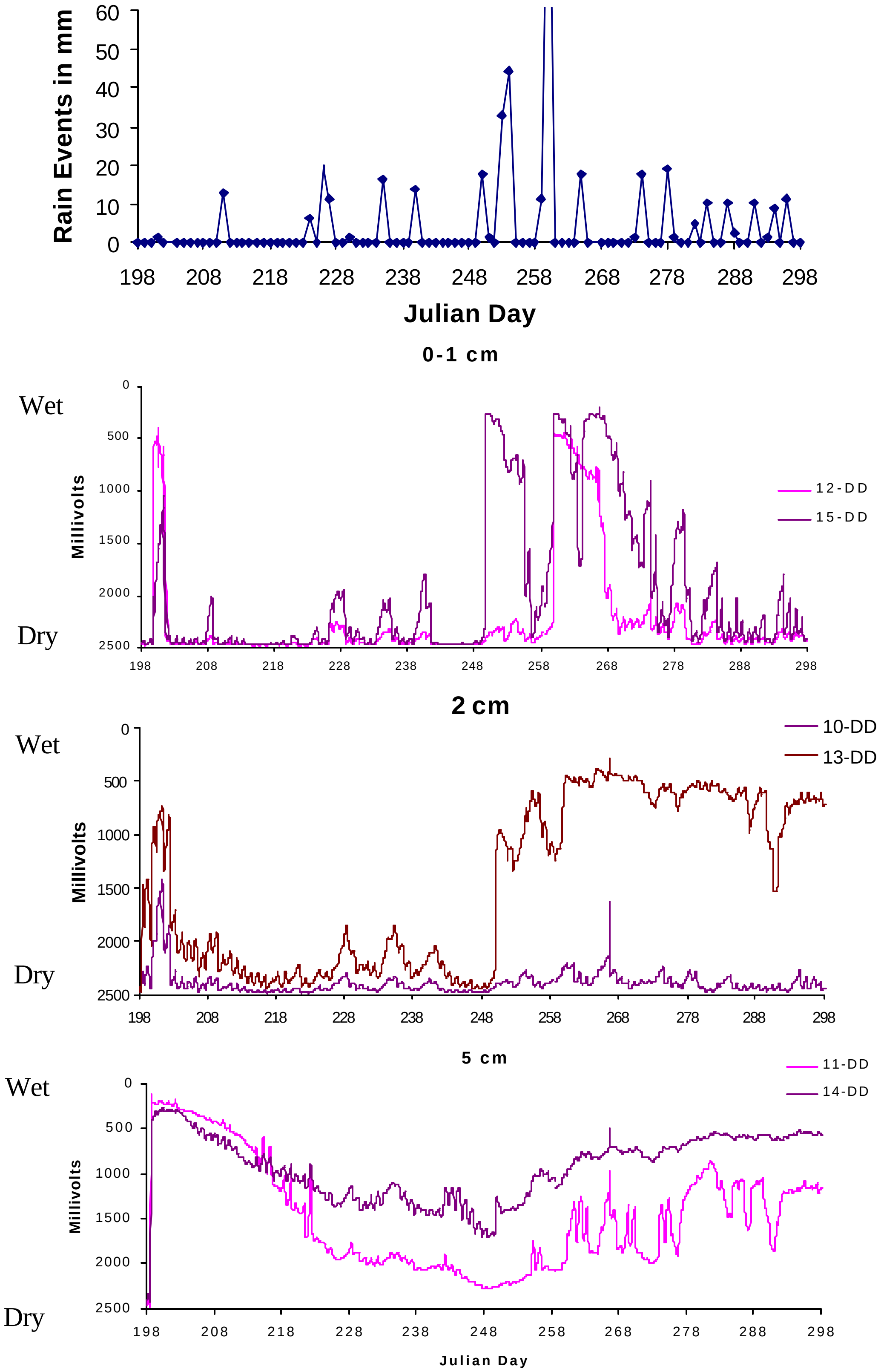


Figure 4. 1999 rainfall data and half-bridge voltage readings for the dry-down exclosure during the 1999 moisture-manipulation experiment.

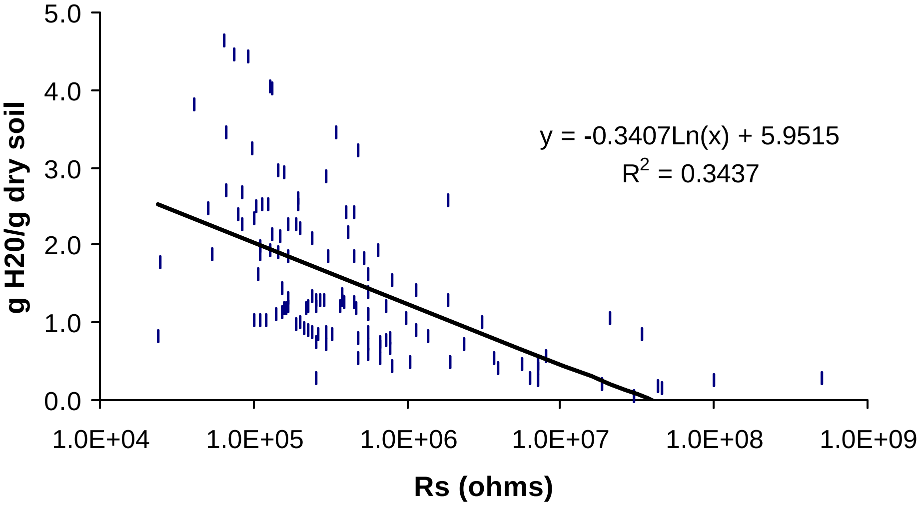


Figure 5. DC half-bridge calibration.
Calibration curve used to convert DC half-bridge measurements from resistance to a gravimetric water content. Note: The X axis is a log scale. Data were taken during the summer of 1999 at Harvard Forest.

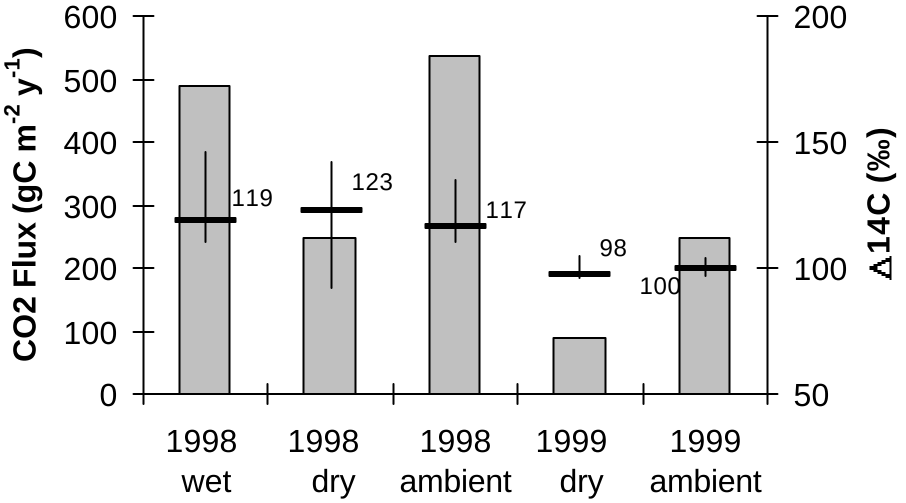


Figure 6. Moisture-manipulation CO_2 and $^{14}CO_2$ data.
Total CO_2 flux and flux-weighted $^{14}CO_2$ values for the time period of the two moisture-manipulation experiments in 1998 and 1999.

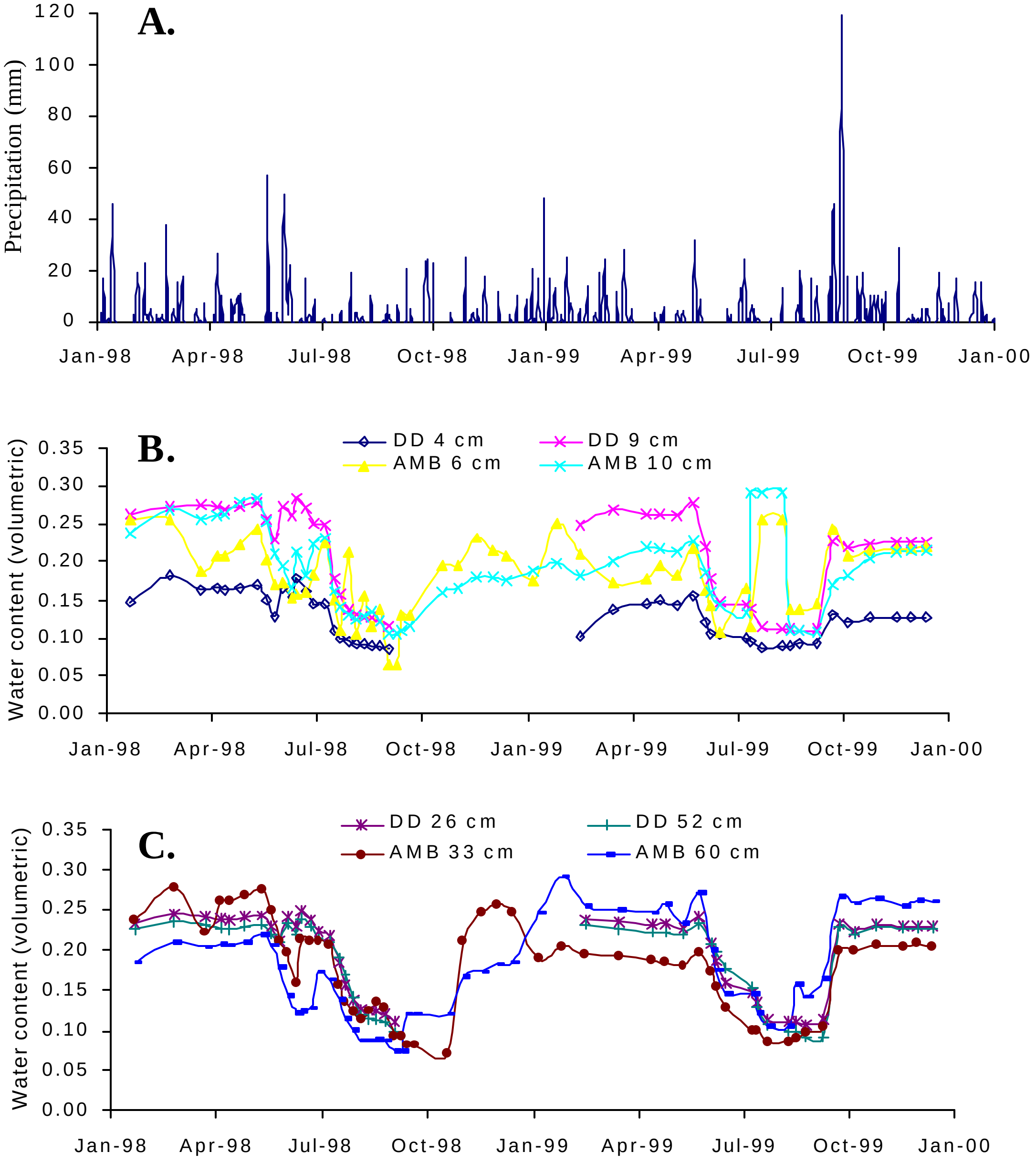


Figure 7. 1998 and 1999 dry-down vs. ambient CO_2.
Rainfall events and moisture conditions for the dry-down (3W) and ambient pit (2W). In 1998, the dry down went from July 8 to October 28. In 1999, the dry down went from July 21 to October 28.

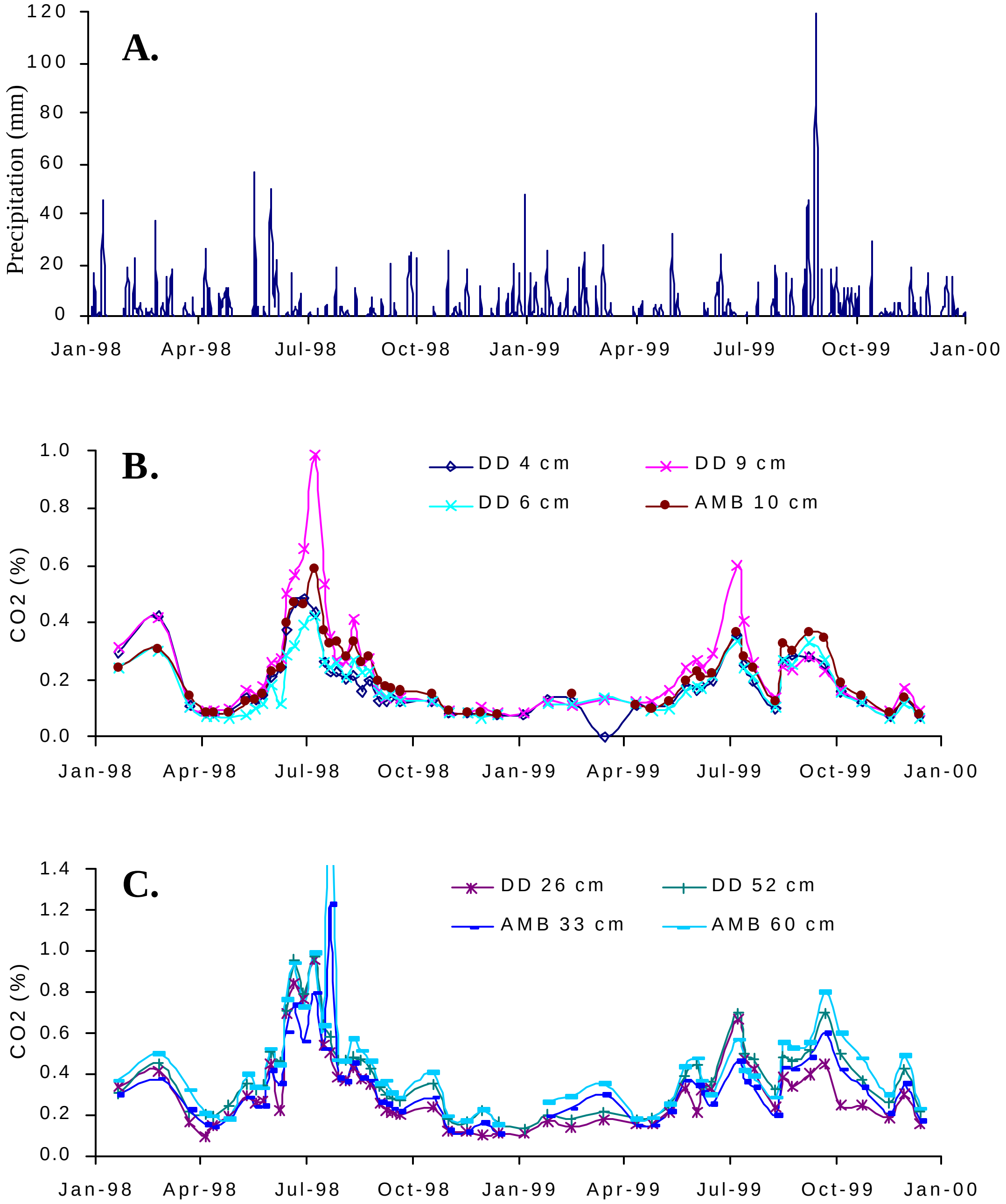
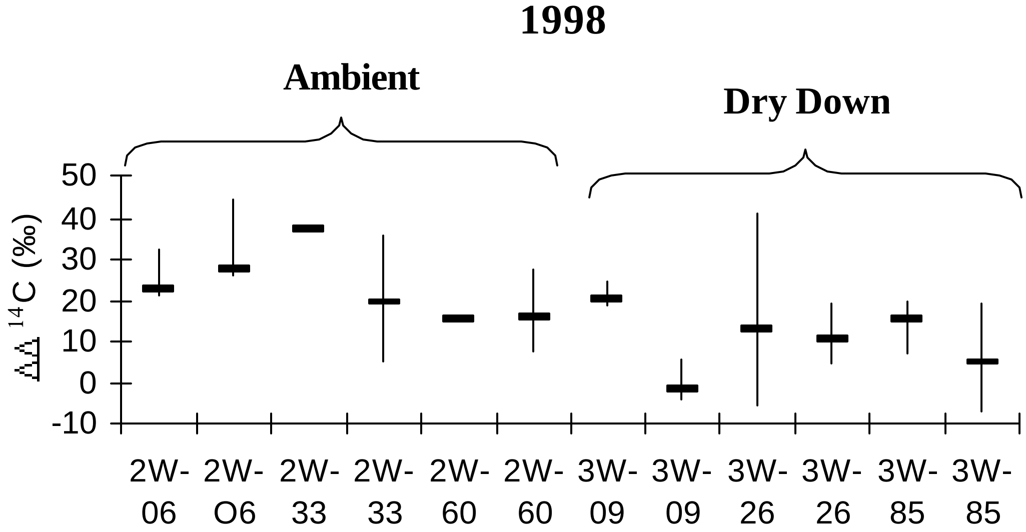


Figure 8. Rainfall events and CO_2 concentrations for the dry down (3W) and ambient pit (2W) for 1998 and 1999. In 1998, the dry down went from July 8 to October 28. In 1999, the dry down went from July 21 to October 28.



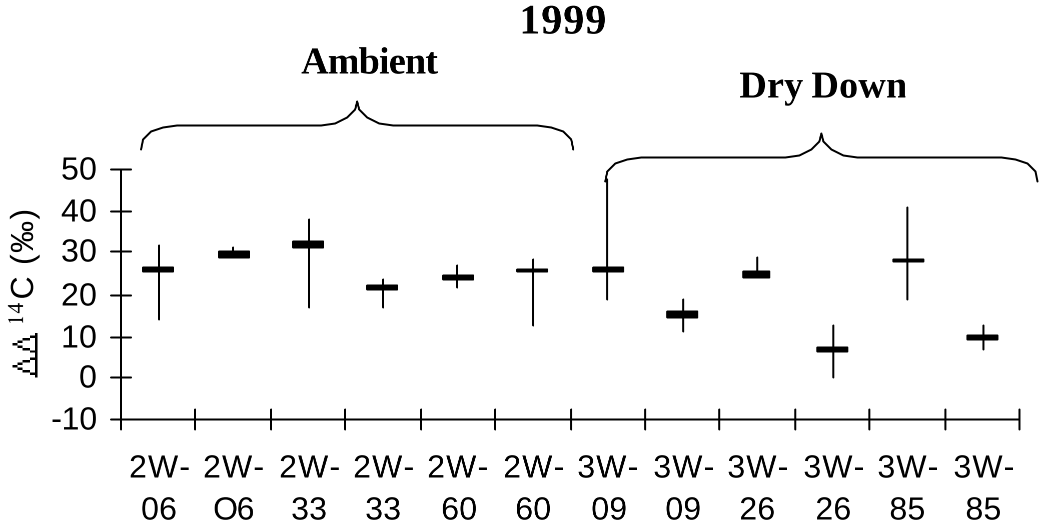


Figure 9. Dry-down vs ambient $^{14}CO_2$.
Flux-weighted $\Delta\Delta^{14}CO_2$ values by depth for the time period pre- and post- moisture manipulations for both the dry-down (3W) and ambient (2W) pits. The first number in a pair represents the pre-manipulation value and the second number the post-manipulation value. Depths in cm are indicated after the dashes. Vertical bars represent the entire range of values measured.

Appendices

Key to terms:

UCIT	Tracking number used by Dr. Susan Trumbore's laboratory.
B.D.	Bulk density
z	Number used in calculation of bulk density that accounts for waviness of horizon boundary
HOW	Abbreviation for the Howland site in Howland, ME
HF	Abbreviation for the Harvard Forest site in Petersham, MA
OR	Abbreviation for the Walker Branch site in Oak Ridge, TN
Length	Number of days the incubation was performed
^{14}C	^{14}C numbers represent the $\Delta^{14}C$ value in parts per thousand (per mil or ‰)
^{13}C	^{13}C numbers represent the $\delta^{13}C$ value in parts per thousand (per mil or ‰)
^{14}C corrected	Means the $\Delta^{14}C$ value has been corrected for leaks within the flux chamber/sampling system by using the $\delta^{13}C$ number (see Chapter 2: methods).
Flux	Refers to the flux of CO_2 in mgC m^{-2} hr^{-1}

Note:

Values for $\delta^{13}C$ numbers are measured with an analytical accuracy of ± 0.10‰. If no number to the right of the decimal is shown, the $\delta^{13}C$ value is assumed.

APPENDIX 1. Air sample data (samples generally taken at roughly 10 cm off ground surface).

TYPE	Date	SITE	AREA	UCIT	^{13}C	^{14}C	+/-
	Sampled				‰	‰	‰
air	15-May-96	HF	NWN	1817	-9.2	113	6
air	11-Jul-96	HF	NWF	1897	-9	98	7
air	11-Jul-96	HF	NWM	1898	-8.6	96	6
air	02-Dec-96	HF		2083	-10.4	47	6
air	06-Feb-97	HF		2242	-12.1	100	8
air	06-Feb-97	HF		2236	-10.3	100	8
air	22-May-97	HF		2533	-8.9	94	6
air	05-Sep-97	HF		2664	-9.4	-10	5
air	02-Nov-97	HF	SWN	2845	-8.8	81	6
air	02-Nov-97	HF	SWN	2846	-9	83	6
air	02-Nov-97	HF		2839	-9	94	6
air	12-Apr-98	HF		3107	-8.4	72	6
air	12-Apr-98	HF		3108	-6.8	183	7
air	12-Apr-98	HF		3113	-8.5	98	6
air	12-Apr-98	HF	P5	3118	-8.1	98	5
air	12-Apr-98	HF	P5	3119	-8.6	121	7
air	02-Jun-98	HF		3282	-8	83	5
air	02-Jul-98	HF		3650	-10.7	94	5
air	02-Jul-98	HF		3651	-9	109	5
air	13-Aug-98	HF	NWN	3473	-9	90	6
air	14-Aug-98	HF	SWN	3670	-8.6	85	5
air	08-Sep-98	HF	NWN	3565	-9.7	87	6
air	26-Oct-98	HF		3629	-9.9	99	5
air	29-Mar-99	HF	NWN	4546	-9.0	99	5
air	12-May-99	HF		4651	-9.3	91	5
air	05-Jun-99	HF	NWN	4664	-8.8	88	4
air	10-Jul-99	HF	SWN	4794	-10.4	92	4
air	16-Aug-99	HF	NWN	4195	-12.6	94	6
air	24-Sep-99	HF	NWN	4877	-10.7	79	5
air	21-May-00	HF		5424	-8	62	5
air	16-Aug-97	HOW	TOWER	2659	-9	106	6
air	03-Jun-98	HOW		3289	-8.2	127	6
air	03-Jun-98	HOW		3290	-8.5	97	5
air	01-Jul-98	HOW		3334	-8	109	5
air	01-Jul-98	HOW		3335	-8	94	5
air	18-Aug-98	HOW		3477	-9.5		
air	21-Sep-98	HOW		3577	-8.8	79	6
air	19-Oct-98	HOW		3617	-12.3	99	7
air	29-Apr-99	HOW		4634	-9.3	79	6
air	08-Jun-99	HOW	TOWER	4685	-10.7	83	5
air	12-Jul-99	HOW	TOWER	4804	-9.5	67	4
air	13-Aug-99	HOW		4207	-9.7	53	4
air	01-Oct-99	HOW		4370	-8.4	81	6
air	20-May-00	HOW		5432	-9.3	78	5
air	19-Jun-98	OR		3306	-8	85	6
air	19-Jun-98	OR		3307	-7.4	96	6
air	19-Jun-98	OR		3308	-8	92	6
air	09-Jul-98	OR	TDE	3461	-8	81	5
air	09-Jul-98	OR	P5	3463	-8	77	4
air	06-Oct-98	OR	P5	3614	-10.4	72	4
air	30-Oct-98	OR		3626	-8.7	102	5
air	10-Dec-98	OR	TDE	3621	-8	55	5
air	10-Dec-98	OR	TDE	3622	-8	47	5
air	10-Dec-98	OR	TDE	3623	-8	52	5
air	01-Apr-99	OR	TDE	4557	-9.5	75	6
air	07-May-99	OR	P5	4618	-9.0	80	5
air	07-May-99	OR	TDE	4622	-9.2	96	5
air	11-Jun-99	OR	P5	4676	-14.5	90	6
air	12-Jun-99	OR	TDE	4673	-9.9	72	6
air	22-Jul-99	OR	P5	4183	-10.3	436	7
air	19-Aug-99	OR	P5	4223	-9.5	116	5

APPENDIX 1. Air sample data (samples generally taken at roughly 10 cm off ground surface).

TYPE	Date Sampled	SITE	AREA	UCIT	^{13}C ‰	^{14}C ‰	+/- ‰
air	24-Oct-99	OR	TDE	4380	-9.1	80	5
air	29-Apr-00	OR	AIR	5401	-9.4	89	5
air	10-Jun-00	OR	TDE	5490	-9.6	87	5
air	12-Dec-97	HOW		3006	-10.2	106	5

Appendix 2. Soil pit bulk density by horizon.					
			Layer	**Grav-free**	**All soil**
			z	**B.D.**	**B.D.**
Site	**Pit**	**Horizon**	**cm**	**Mg/m3**	**Mg/m3**
NWN	1	Oi	1.2	0.07	0.47
NWN	1	Oe	2.7	0.10	0.64
NWN	1	A	1.3	0.41	1.06
NWN	1	Ap	8.6	0.67	1.19
NWN	1	Bw1	7.3	0.79	1.24
NWN	1	Bw2	9.6	0.89	1.16
NWN	1	Bw3	16.8	1.13	1.54
NWN	1	Bw4	not completed		
NWN	2	Oi	1.1	0.08	0.08
NWN	2	Oae	1.4	0.13	0.13
NWN	2	A	2.3	0.32	0.34
NWN	2	Ap	7.5	0.41	0.46
NWN	2	Bw1	8.1	0.92	1.07
NWN	2	Bw2	8.5	0.97	1.57
NWN	2	Bw3	not completed		
NWN	3	Oi	2.0	0.03	0.03
NWN	3	Oea	6.4	0.07	0.08
NWN	3	A	4.0	0.30	0.31
TDE	1	Oi	1.6	0.05	0.05
TDE	1	Oe	3.6	0.02	0.02
TDE	1	A	2.8	0.44	0.64
TDE	1	E1	34.9	1.01	1.28
TDE	1	Bt1	25.1	1.18	1.33
P5	1	O	1.4	0.10	0.10
P5	1	A	2.9	0.52	0.45
P5	1	min2	17.7	1.01	1.49
P5	1	min3	19.2	1.13	1.73
P5	1	min4	17.4	0.92	1.60

Organic Matter Samples									
Type	**SUB-TYPE**	**DATE**	**SITE**	**AREA**	**DESCRIPTION**	**UCIT**	**^{13}C**	**^{14}C**	**+/-**
		SAMPLED					**‰**	**‰**	**‰**
SOM	HD	1996	HF	hem	HEM-AHD	2160	-25	-19	
SOM	HD	1996	HF	hem	HEM-AEHD	2161	-25	-43	
SOM	HD	1996	HF	hem	HEM-Bw1HD	2162	-25	-88	
SOM	HD	1996	HF	hem	HEM-Bw2aHD	2163	-25	-160	
SOM	HD	1996	HF	hem	HEM-Bw2bHD	2164	-25	-197	
SOM	HD	1996	HF	nwn	N1-AHD	2165	-25	42	
SOM	HD	1996	HF	nwn	N1-ApHD	2166	-25	-11	
SOM	HD	1996	HF	nwn	N1-Bw1aHD	2167	-25	-88	
SOM	HD	1996	HF	nwn	N1-Bw1bHD	2168	-25	-121	
SOM	HD	1996	HF	nwn	N1-Bw2HD	2169	-25	-168	
SOM	HD	1996	HF	swn	S1-AHD	2157	-25	2	
SOM	HD	1996	HF	swn	S1-Bg1HD	2158	-25	-103	
SOM	HD	1996	HF	swn	S1-Bg2HD	2159	-25	-201	
SOM	HD	1979	HF		HF_0-15 cm HD	4442	-26	43	5
SOM	HD	1979	HF		HF_15-30cm HD	4443	-26	191	4
SOM	HD	1979	HF		HF_30-45cm HD	4444	-26	7	3
SOM	HD	1996	HOW	tower	HOW-EHD	2175	-25	7	
SOM	HD	1996	HOW	tower	HOW-BhsHD	2177	-25	-14	
SOM	HD	1996	HOW	tower	HOW-Bs1HD	2178	-25	-124	
SOM	HD	1996	HOW	tower	HOW-Bs2HD	2179	-25	-119	
SOM	HD	1996	HOW	tower	HOW-BCHD	2180	-25	-161	
SOM	HD	24-Apr-98	OR	P5	HD P5-A1-1998	4756	-25	22	5
SOM	HD	24-Apr-98	OR	P5	HD P5-E1 7-24cm-1998	4757	-25	59	6
SOM	HD	24-Apr-98	OR	P5	HD P5-E2 24-40cm-1998	4758	-25	-25	4
SOM	HD	24-Apr-98	OR	P5	HD P5-E2 40-63cm-1998	4759	-25	-80	5
SOM	HD	24-Apr-98	OR	P5	HD P5-B2-65-75cm-1998	4760	-25	-90	5
SOM	HD	1972	OR	P5	HD P5-A1-1972	4745	-25	56	5
SOM	HD	1972	OR	P5	HD P5-A2(E)-1972	4746	-25	107	4
SOM	HD	1972	OR	P5	HD P5-B1-1972	4747	-25	-38	5
SOM	HD	1972	OR	P5	HD P5-B21T-1972	4748	-25	-67	5
SOM	HD	21-Apr-98	OR	TDE	HD TDE-A 3-8cm	4773	-25	37	5
SOM	HD	21-Apr-98	OR	TDE	HD TDE-E 18-23cm	4774	-25	19	5
SOM	HD	21-Apr-98	OR	TDE	HD TDE-E 223-50cm	4775	-25	-53	5
SOM	HD	21-Apr-98	OR	TDE	HD TDE-BT1	4776	-25	-156	4
SOM	LD	1996	HF	hem	HEM-OILD	2128	-25	138	
SOM	LD	1996	HF	hem	HEM-ALD	2129	-25	29	
SOM	LD	1996	HF	hem	HEM-Bw1LD	2131	-25	-30	
SOM	LD	1996	HF	hem	HEM-Bw2aLD	2132	-25	-59	
SOM	LD	1996	HF	hem	HEM-Bw2bLD	2133	-25	-109	
SOM	LD	1996	HF	hem	MOD-HEM	2181	-25	120	
SOM	LD	1996	HF	hem	Mbd-Hem(groundneedle	2181	-25	110	
SOM	LD	1996	HF	hem	MOD-HEM	2181	-25	120	
SOM	LD	1996	HF	hem	Mbd-Hem(groundneedle	2181	-25	110	
SOM	LD	1996	HF	hem	HEM-AEL.D.	2130	-25	6	
SOM	LD	1996	HF	nwf	MOD-SPHAG	2183	-25	114	
SOM	LD	1996	HF	nwn	N1-OiLD	2134	-25	140	
SOM	LD	1996	HF	nwn	N1-OeLD	2135	-25	234	
SOM	LD	1996	HF	nwn	N1-ALD	2136	-25	138	
SOM	LD	1996	HF	nwn	N1-ApLD	2137	-25	52	
SOM	LD	1996	HF	nwn	N1-Bw1aLD	2138	-25	-72	
SOM	LD	1996	HF	nwn	N1-Bw1bLD	2139	-25	-100	
SOM	LD	1996	HF	nwn	N1-Bw2LD	2140	-25	-169	
SOM	LD	1996	HF	nwn	N2-OiLD	2141	-25	124	
SOM	LD	1996	HF	nwn	N2-OeLD	2142	-25	165	
SOM	LD	1996	HF	nwn	N2-ALD	2143	-25	211	
SOM	LD	1996	HF	nwn	N2-ApLD	2144	-25	-3	
SOM	LD	1996	HF	nwn	N2-Bw1bLD	2146	-25	-129	
SOM	LD	1996	HF	nwn	N2-Bw2LD	2147	-25	-88	
SOM	LD	1996	HF	nwn	N2-ALD	2170	-25	94	
SOM	LD	1996	HF	nwn	N2-ApLD	2171	-25	-51	
SOM	LD	1996	HF	nwn	N2-Bw1aLD	2172	-25	-116	
SOM	LD	1996	HF	nwn	N2-Bw1bLD	2173	-25	-149	
SOM	LD	1996	HF	nwn	N2-Bw2LD	2174	-25	-176	
SOM	LD	1996	HF	nwn	MOD-LEAV	2182	-25	92	
SOM	LD	1996	HF	nwn	N2-Bw1AL.D.	2145	-25	-86	
SOM	LD	1996	HF	nwn	N2-Bw2L.D.	2147	-25	-94	
SOM	LD	1996	HF	nwn	N2-Bw2LD	2147	-25	-88	
SOM	LD	1996	HF	nwn	N2-Bw2L.D.	2147	-25	-94	

Organic Matter Samples									
Type	**SUB-TYPE**	**DATE**	**SITE**	**AREA**	**DESCRIPTION**	**UCIT**	**^{13}C**	**^{14}C**	**+/-**
		SAMPLED					**‰**	**‰**	**‰**
SOM	LD	1996	HF	swn	S1-OiLD	2123	-25	141	
SOM	LD	1996	HF	swn	S1-OeLD	2124	-25	206	
SOM	LD	1996	HF	swn	S1-ALD	2125	-25	152	
SOM	LD	1996	HF	swn	S1-Bg1LD	2126	-25	12	
SOM	LD	1996	HF	swn	S1-Bg2LD	2127	-25	-87	
SOM	LD	1996	HF	swn	S1-Bg1L.D.	2126	-25	-14	
SOM	LD	1996	HF	swn	S1-Bg1LD	2126	-25	12	
SOM	LD	1996	HF	swn	S1-Bg1L.D.	2126	-25	-14	
SOM	LD	1979	HF		HF_0-15 cm LD	4437	-26.3	-47	5
SOM	LD	1979	HF		HF_15-30cm LD	4438	-26.5	80	5
SOM	LD	1979	HF		HF_30-45cm LD	4439	-26.4	-30	5
SOM	LD	1979	HF		HF_45+ LD	4440	-26.7	1116	10
SOM	LD	1979	HF		HF_Charcoal	4441	-25	-222	4
SOM	LD	1996	HOW	tower	HOW-OiLD	2148	-25	183	
SOM	LD	1996	HOW	tower	HOW-OeLD	2149	-25	107	
SOM	LD	1996	HOW	tower	HOW-OaLD	2150	-25	51	
SOM	LD	1996	HOW	tower	HOW-ELD	2151	-25	94	
SOM	LD	1996	HOW	tower	HOW-BhLD	2152	-25	-35	
SOM	LD	1996	HOW	tower	HOW-BhsLD	2153	-25	20	
SOM	LD	1996	HOW	tower	HOW-Bs1LD	2154	-25	-34	
SOM	LD	1996	HOW	tower	HOW-Bs2LD	2155	-25	-8	
SOM	LD	1996	HOW	tower	HOW-BCLD	2156	-25	-79	
SOM	LD	1996	HOW	tower	HOW-BhH.D.	2176	-25	-61	
SOM	LD	24-Apr-98	OR	P5	LD P5-01-1998	4749	-25	127	5
SOM	LD	24-Apr-98	OR	P5	LD P5-02-1998	4750	-25	144	6
SOM	LD	24-Apr-98	OR	P5	LD P5-A->80u-1998	4751	-25	45	5
SOM	LD	24-Apr-98	OR	P5	LD P5-A-<80u-1998	4752	-25	0	5
SOM	LD	24-Apr-98	OR	P5	LD P5-E1 7-24cm-1998b	4753	-25	21	6
SOM	LD	24-Apr-98	OR	P5	LD P5-E2 24-40cm-1998b	4754	-25	31	5
SOM	LD	24-Apr-98	OR	P5	LD P5-E2 40-63cm-1998	4755	-25	-139	4
SOM	LD	1972	OR	P5	LD P5-01-1972	4739	-25	550	8
SOM	LD	1972	OR	P5	LD P5-02-1972	4740	-25	373	7
SOM	LD	1972	OR	P5	LD P5-A1->80u-1972	4741	-25	195	6
SOM	LD	1972	OR	P5	LD P5-A1-<80u-1972	4742	-25	73	6
SOM	LD	1972	OR	P5	LD P5-A2(E)-1972	4743	-25	138	6
SOM	LD	1972	OR	P5	LD P5-B1-1972	4744	-25	157	5
SOM	LD	21-Apr-98	OR	TDE	LD TDE-Oi least decomp	4761	-25	130	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-OEA-V very decomp	4762	-25	136	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-OEA-MATRIX	4763	-25	135	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-A1->80u:undif.	4764	-25	130	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-A1-<80u:undif.	4765	-25	36	5
SOM	LD	21-Apr-98	OR	TDE	LD TDE-A1-fineroots	4766	-25	152	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-A1-sheaths	4767	-25	207	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-E1->80u	4768	-25	143	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-E1-<80u	4769	-25	55	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-E2->80u	4770	-25	89	6
SOM	LD	21-Apr-98	OR	TDE	LD TDE-E2-<80	4771	-25	49	4
SOM	LD	21-Apr-98	OR	TDE	LD TDE-BT1	4772	-25	113	6
SOM	LD <80	1996	HF	hem	HEM-A	2541	-25	-11	
SOM	LD <80	1996	HF	hem	HEM-AE	2542	-25	-29	
SOM	LD <80	1996	HF	hem	HEM-Bw1	2543	-25	-39	
SOM	LD <80	1996	HF	hem	HEM-Bw2a	2544	-25	-95	
SOM	LD <80	1996	HF	hem	HEM-Bw2b	2545	-25	-130	
SOM	LD <80	1996	HF	nwn	N1-A	2546	-25	48	
SOM	LD <80	1996	HF	nwn	N1-AP	2547	-25	3	
SOM	LD <80	1996	HF	nwn	N1-Bw1a	2548	-25	-66	
SOM	LD <80	1996	HF	nwn	N1-Bw1b	2549	-25	-108	
SOM	LD <80	1996	HF	swn	S1-A	2550	-25	104	
SOM	LD <80	1996	HF	swn	S1-Bg1	2551	-25	-81	
SOM	LD <80	1996	HF	swn	S1-Bg2	2552	-25	-282	
SOM	LD >80	1996	HF	hem	HEM>63-1	2607	-25	153	
SOM	LD >80	1996	HF	hem	HEM>63-4	2609	-25	69	
SOM	LD >80	1996	HF	hem	HEM>63-5	2610	-25	210	
SOM	LD >80	1996	HF	nwn	NWN1LD>63-1	2604	-25	266	
SOM	LD >80	1996	HF	nwn	NWN1LD>63-2	2605	-25	231	
SOM	LD >80	1996	HF	nwn	NWN1LD>63-4	2606	-25	130	
SOM	LEAVES	01-Jun-96	HF	NWN	MOD-LEAV	2182	-25	92	7
SOM	LEAVES	14-Aug-98	HF	NWN	Leaves: NWN: 8/14/98	5063	-28	102	4

Organic Matter Samples									
Type	**SUB-TYPE**	**DATE**	**SITE**	**AREA**	**DESCRIPTION**	**UCIT**	**^{13}C**	**^{14}C**	**+/-**
		SAMPLED					**‰**	**‰**	**‰**
SOM	LEAVES	14-Aug-98	HF	NWN	Live decid. leaves 8/14	5067	-31.3	89	5
SOM	LEAVES	16-Jul-99	HF	NWN	HFLVS-UNDER:7-16-99	4270	-27.1	83	7
SOM	LEAVES	17-Aug-99	HF	NWN	HFLVS-UNDER:8-17-99	4272	-31.4	89	6
SOM	LEAVES	22-May-97	HF		Leaves-GREEN FRESH	2540	-29.5	105	6
SOM	LEAVES	07-Jun-99	HF		Leaves HF-6/7/99-Upper canopy	4779	-27.5	96	5
SOM	LEAVES		HF		Leaves: Harvard Forest	5064	-29.1	87	7
SOM	LEAVES	02-Jun-98	HF?		Fresh leaves 6/2/98	3298	-25	89	7
SOM	LEAVES	12-Jul-99	HOW		HOWLVS-UNDER:7-12-99	4268	-32.7	97	5
SOM	LEAVES	13-Aug-99	HOW		HOWLVS-UNDER:8-13-99	4269	-31.3	109	6
SOM	LEAVES	10-Jul-98	OR	P5	Fresh leaves:P5 OR:7/1	5068	-31.3	105	5
SOM	LEAVES	25-Aug-98	OR	P5	Leaves OR Plot5: 8/25/9	5066	-30.3	121	5
SOM	LEAVES	06-Oct-98	OR	P5	Leaves ORP5-10/6/98understory	4777	-30.5	118	6
SOM	LEAVES	23-Jul-99	OR	P5	ORLVS-UNDER:7-23-99	4274	-31.0	173	7
SOM	LEAVES	19-Aug-99	OR	P5	ORLVS-UNDER:8-19-99	4275	-31.0	198	6
SOM	LEAVES	19-Jun-98	OR	TDE	Leaves:TDE OR8 15?:6/1	5065	-31.9	104	7
SOM	LEAVES	12-Jun-99	OR	TDE	Leaves ORTDE-6/12/99Understory	4778	-31.1	117	6
SOM	MUSHROOMS	1997	HF		HF-HORN	2734	-25	97	
SOM	MUSHROOMS	1997	HF		HF-YELSTK	2735	-25	99	
SOM	MUSHROOMS	1997	HF		HF-FUNNEL	2736	-25	98	
SOM	MUSHROOMS	1997	HOW		HOW-COINCAP	2737	-25	144	
SOM	MUSHROOMS	1997	HOW		HOW-FALSEFUN	2738	-25	108	
SOM	MUSHROOMS	1997	HOW		HOW-GBOLEK	2739	-25	103	
SOM	MUSHROOMS	1997	HOW		HOW-MYRENA	2740	-25	131	
SOM	O horizon	1996	HF	hem	Hem OM-top	2601	-25	232	
SOM	O horizon	1996	HF	hem	Hem OM-mid	2602	-25	292	
SOM	O horizon	1996	HF	hem	Hem OM-bot	2603	-25	80	
SOM	O horizon/leaves	1997	HF	nwn	NWNOi	2909	-25	113	
SOM	O horizon/leaves	1997	HF	nwn	NWNZero	2910	-25	113	
SOM	O horizon/leaves	1997	HF	nwn	NWN>0-3.5	2911	-25	126	
SOM	O horizon/leaves	1997	HF	nwn	NWN3.5-6.6	2912	-25	132	
SOM	O horizon/leaves	1997	HF	nwn	NWN1FF_OTH	2919	-25	220	
SOM	O horizon/leaves	1997	HF	nwn	NWN2OEA_OTH	2920	-25	182	
SOM	O horizon/leaves	1997	HF	swn	SWN+4-+2.9	2913	-25	105	
SOM	O horizon/leaves	1997	HF	swn	SWN+2.9-1.9	2914	-25	103	
SOM	O horizon/leaves	1997	HF	swn	SWN+1.9-0	2915	-25	123	
SOM	O horizon/leaves	1997	HF	swn	SWN0-3.1	2916	-25	158	
SOM	O horizon/leaves	1997	HF	swn	SWN3.1-5.2	2917	-25	148	
SOM	O horizon/leaves	1997	HF	swn	SWNBR#3_OTH	2918	-25	265	
SOM	ROOTS	1997	HF	hem	HEM-1P	2730	-27.0	398	
SOM	ROOTS	1997	HF	hem	HEM-1S	2731	-27.0	169	
SOM	ROOTS	1997	HF	hem	HEM OiHomo live	2565	-27.0	-986	
SOM	ROOTS	1996	HF	hem	HemlockPit1BW2 (live)	2815	-27.0	180	
SOM	ROOTS	1996	HF	hem	HEMAHomoLive	2567	-26.9	271	
SOM	ROOTS	1996	HF	hem	HEMAHomodead	2568	-26.9	221	
SOM	ROOTS	1996	HF	hem	HEMOE/splitlive	2569	-27.0	201	
SOM	ROOTS	1996	HF	hem	HEMOE/splitdead	2670	-27.0	196	
SOM	ROOTS	1996	HF	hem	HEMOE/alive	2571	-26.9	244	
SOM	ROOTS	1996	HF	hem	HEMOE/adead	2572	-26	246	
SOM	ROOTS	1996	HF	hem	HEM1BW1-homolive	2577	-27.0	242	
SOM	ROOTS	1996	HF	hem	HEM1BW1-homodead	2578	-27.0	177	
SOM	ROOTS	1996	HF	nwn	NWnearForestfloor#2l	2563	-29.0	157	
SOM	ROOTS	1996	HF	nwn	NWnearforestfloor#2D	2564	-27.8	188	
SOM	ROOTS	1997	HF	nwn	NWN-1P	2725	-27.0		
SOM	ROOTS	1997	HF	nwn	NWN-1S	2726	-27.0	116	
SOM	ROOTS	1997	HF	nwn	NW near#2 BW2 live	2575	-28.4	199	
SOM	ROOTS	1997	HF	nwn	NW core#2 live	2579	-27	186	
SOM	ROOTS	1997	HF	nwn	NW core#2 dead	2580	-27	214	
SOM	ROOTS	1997	HF	nwn	NW2 of 2 BW3 live	2581	-27	310	
SOM	ROOTS	1996	HF	nwn	Pit1FF#1NWN (live)	2809	-27	156	
SOM	ROOTS	1996	HF	nwn	Pit2OaeNWN (live)	2810	-27	148	
SOM	ROOTS	1996	HF	nwn	Pit2BW1NWN (live)	2811	-27	170	
SOM	ROOTS	1996	HF	nwn	Pit2BW2NWN (live)	2812	-27	237	
SOM	ROOTS	1996	HF	nwn	Pitcore1NWN (live)	2813	-27	174	
SOM	ROOTS	1996	HF	nwn	Pit2ApNWN (live)	2814	-27	188	
SOM	ROOTS	1997	HF	swamp	SP-1P	2732	-27	177	
SOM	ROOTS	1997	HF	swamp	SP-1S	2733	-27	116	
SOM	ROOTS	1996	HF	swn	SWN#2Live	2557	-27.2	100	
SOM	ROOTS	1996	HF	swn	SWN#2Dead	2558	-27.0	291	

Organic Matter Samples									
Type	**SUB-TYPE**	**DATE**	**SITE**	**AREA**	**DESCRIPTION**	**UCIT**	**^{13}C**	**^{14}C**	**+/-**
		SAMPLED					**‰**	**‰**	**‰**
SOM	ROOTS	1996	HF	swn	SWN#1Live	2559	-28.3	129	
SOM	ROOTS	1996	HF	swn	SWN#1Dead	2560	-27.2	219	
SOM	ROOTS	1996	HF	swn	SWN#3Live	2561	-27.6	172	
SOM	ROOTS	1996	HF	swn	SWN#3Dead	2562	-27.0	227	
SOM	ROOTS	1996	HF	swn	SWN1ALive	2573	-27.7	191	
SOM	ROOTS	1996	HF	swn	SWN1ADead	2574	-27.4	244	
SOM	ROOTS	1997	HF	swn	SWN-1.5P	2727	-27.0	113	
SOM	ROOTS	1997	HF	swn	SWN-1P	2728	-27.0	115	
SOM	ROOTS	1997	HF	swn	SWN-1S	2729	-27.0	105	
SOM	ROOTS	1996	HF	swn	SWNPit1BG1 (live)	2816	-27.0	190	
WOOD	ALPHA-C	Oct-99	OR	TDE	1999 TDE_Oakridge wood	4446	-26	426	7
WOOD	ALPHA-C	Oct-99	OR	TDE	1998 TDE_Oakridge wood	4447	-26	117	5
WOOD	ALPHA-C	Oct-99	OR	TDE	1997 TDE_Oakridge wood	4448	-26	119	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1996 TDE_Oakridge wood	4449	-26	114	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1995 TDE_Oakridge wood	4450	-26	107	5
WOOD	ALPHA-C	Oct-99	OR	TDE	1994 TDE_Oakridge wood	4451	-26	121	5
WOOD	ALPHA-C	Oct-99	OR	TDE	1993 TDE_Oakridge wood	4452	-26	125	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1992 TDE_Oakridge wood	4453	-26	124	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1991 TDE_Oakridge wood	4454	-26	135	7
WOOD	ALPHA-C	Oct-99	OR	TDE	1990 TDE_Oakridge wood	4455	-26	126	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1985 TDE_Oakridge wood	4456	-26	185	6
WOOD	ALPHA-C	Oct-99	OR	TDE	1975 TDE_Oakridge wood	4457	-26	389	7
WOOD	ALPHA-C	Oct-99	OR	TDE	1963 TDE_Oakridge wood	4458	-26	686	13
WOOD	ALPHA-C	Oct-99	OR	TDE	1960 TDE_Oakridge wood	4459	-26	170	7
WOOD	ALPHA-C	Oct-99	OR	TDE	1950 TDE_Oakridge wood	4460	-26	-27	6
WOOD	ALPHA-C	Oct-99	OR		1999 Gap_Oakridge wood	4461	-26	454	8
WOOD	ALPHA-C	Oct-99	OR		1999 Yard_Oakridge wood	4462	-26	1068	13
WOOD	ALPHA-C	Oct-99	OR		1999 TCSA Top_Oakridge	4463	-26	1882	16
WOOD	ALPHA-C	Oct-99	OR		1999 TCSA Mid_Oakridge	4464	-26	1123	12

APPENDIX 4. Soil Respiration CO_2 data

Type	DATE SAMPLED	SITE	AREA	COLLAR	UCIT	^{13}C ‰	^{14}C ‰	+/- ‰	^{14}C (corrected) ‰	FLUX mg C m^{-2} hr^{-1}	FLUX DATE
Surface	03-Jun-98	HOW	nc	5	3285	-23.9	135	6	138	132	27-May-98
Surface	03-Jun-98	HOW	nc	3	3286	-23.4	142	5	148	104	27-May-98
Surface	01-Jul-98	HOW	nc	3	3328	-25.0	154	6	158	208	01-Jul-98
Surface	01-Jul-98	HOW	nc	4	3329	-24.7	141	6	144	132	01-Jul-98
Surface	01-Jul-98	HOW	nc	5	3330	-24.9	147	5	150	264	01-Jul-98
Surface	18-Aug-98	HOW	nc	5	3478	-24.3	105	5	105	192	19-Aug-98
Surface	21-Sep-98	HOW	nc	3	3574	-23.6	101	5	104	169	23-Sep-98
Surface	21-Sep-98	HOW	nc	2	3575	-24.0	88	5	89	109	23-Sep-98
Surface	21-Sep-98	HOW	nc	5	3576	-23.9	98	6	100	136	23-Sep-98
Surface	19-Oct-98	HOW	nc	2	3625	-24.2	102	6	103	54	
Surface	29-Apr-99	HOW	nc	2	4628	-21.8	113	5	125	36	28-Apr-99
Surface	29-Apr-99	HOW	nc	3	4629	-21.8	129	6	146	43	28-Apr-99
Surface	29-Apr-99	HOW	nc	5	4630	-22.9	116	5	124	30	28-Apr-99
Surface	08-Jun-99	HOW	nc	3	4682	-24.6	120	6	124	155	08-Jun-99
Surface	08-Jun-99	HOW	nc	2	4683	-25.0	102	6	103	112	08-Jun-99
Surface	08-Jun-99	HOW	nc	5	4684	-24.8	120	6	123	239	08-Jun-99
Surface	12-Jul-99	HOW	nc	2	4801	-25.4	113	4	115	135	12-Jul-99
Surface	12-Jul-99	HOW	nc	5	4802	-24.8	117	4	121	201	12-Jul-99
Surface	12-Jul-99	HOW	nc	3	4803	-24.7	116	4	120	184	12-Jul-99
Surface	13-Aug-99	HOW	nc	5	4206	-24.6	111	5	117	273	13-Aug-99
Surface	13-Aug-99	HOW	nc	3	4208	-24.4	100	7	105	252	13-Aug-99
Surface	20-May-00	HOW	nc	2	5429	-21.5	93	6	99	NA	20-May-00
Surface	20-May-00	HOW	nc	3	5430	-23.1	115	5	123	NA	20-May-00
Surface	20-May-00	HOW	nc	5	5434	-23.4	139	6	150	78	20-May-00
Surface	16-Aug-97	HOW	tower	2	2658	-22.2	136	6	145	160	16-Aug-97
Surface	16-Aug-97	HOW	tower	1	2660	-22.9	117	6	120	136	16-Aug-97
Surface	16-Aug-97	HOW	tower	7	2661	-22.8	120	7	123	236	16-Aug-97
Surface	16-Aug-97	HOW	tower	6	2662	-23.0	121	6	124	177	16-Aug-97
Surface	03-Jun-98	HOW	tower	2	3283	-22.9	117	7	118	64	27-May-98
Surface	03-Jun-98	HOW	tower	3	3284	-24.0	139	5	142	111	27-May-98
Surface	01-Jul-98	HOW	tower	7	3325	-25.4	126	6	127	261	01-Jul-98
Surface	01-Jul-98	HOW	tower	6	3326	-25.8	129	6	130	324	01-Jul-98
Surface	01-Jul-98	HOW	tower	2	3327	-24.0	116	6	118	152	01-Jul-98
Surface	18-Aug-98	HOW	tower	5	3479	-24.2	99	4	99	140	19-Aug-98
Surface	18-Aug-98	HOW	tower	8	3480	-23.8	107	5	107	365	19-Aug-98
Surface	18-Aug-98	HOW	tower	3	3481	-23.9	227	6	227	153	19-Aug-98
Surface	17-Sep-98	HOW	tower	3	3571	-23.9	110	5	114	212	14-Sep-98
Surface	17-Sep-98	HOW	tower	5	3572	-23.9	99	5	101	146	14-Sep-98
Surface	21-Sep-98	HOW	tower	8	3570	-23.2	121	6	129	201	23-Sep-98
Surface	19-Oct-98	HOW	tower	8	3618	-24.2	124	5	127	105	22-Oct-98
Surface	19-Oct-98	HOW	tower	5	3619	-24.0	120	7	123	63	22-Oct-98
Surface	19-Oct-98	HOW	tower	3	3620	-24.3	127	6	131	57	22-Oct-98
Surface	29-Apr-99	HOW	tower	3	4631	-22.7	126	5	138	36	28-Apr-99
Surface	29-Apr-99	HOW	tower	5	4632	-21.1	112	5	126	44	28-Apr-99
Surface	29-Apr-99	HOW	tower	8	4633	-23.8	132	6	140	61	28-Apr-99
Surface	08-Jun-99	HOW	tower	5	4686	-24.7	107	6	110	166	08-Jun-99
Surface	08-Jun-99	HOW	tower	8	4687	-25.3	108	6	109	317	08-Jun-99
Surface	08-Jun-99	HOW	tower	3	4688	-25.0	115	5	118	162	08-Jun-99
Surface	12-Jul-99	HOW	tower	3	4798	-24.8	108	4	112	222	12-Jul-99
Surface	12-Jul-99	HOW	tower	5	4799	-25.0	96	5	98	182	12-Jul-99
Surface	12-Jul-99	HOW	tower	8	4800	-25.0	122	5	126	401	12-Jul-99
Surface	13-Aug-99	HOW	tower	8	4210	-24.5	105	7	110	277	13-Aug-99
Surface	13-Aug-99	HOW	tower	3	4211	-24.5	105	6	111	218	13-Aug-99
Surface	13-Aug-99	HOW	tower	5	4212	-24.7	106	7	111	182	13-Aug-99
Surface	01-Oct-99	HOW	tower	8	4371	-25.1	123	6	125	342	29-Sep-99
Surface	01-Oct-99	HOW	tower	5	4372	-24.4	110	6	113	153	29-Sep-99
Surface	01-Oct-99	HOW	tower	3	4373	-24.9	130	6	133	167	29-Sep-99
Surface	19-May-00	HOW	tower	3	5425	-23.1	124	6	134	44	19-May-00
Surface	19-May-00	HOW	tower	5	5426	-23.7	117	6	123	38	19-May-00
Surface	20-May-00	HOW	tower	8	5427	-23.7	125	5	133	77	20-May-00
Surface	15-May-96	HF	nwn	5	1820	-15.7	116	7	120	32	13-May-96
Surface	15-May-96	HF	nwn	2	1823	-20.3	116	7	118	71	13-May-96
Surface	15-May-96	HF	nwn	4	1824	-19.3	129	7	140	46	13-May-96
Surface	15-May-96	HF	nwn	2	1825	-17.8	141	7	167	71	13-May-96
Surface	11-Jul-96	HF	nwn	3	1887	-23.8	136	7	141	273	10-Jul-96
Surface	11-Jul-96	HF	nwn	4	1888	-22.7	126	7	132	169	10-Jul-96
Surface	11-Jul-96	HF	nwn	6	1889	-24.5	137	10	140	182	10-Jul-96
Surface	29-Sep-96	HF	nwn	3	1945	-23.6	117	6	117	225	21-Sep-96

APPENDIX 4. Soil Respiration CO$_2$ data											
Type	**DATE**	**SITE**	**AREA**	**COLLAR**	**UCIT**	**^{13}C**	**^{14}C**	**+/-**	**^{14}C (corrected)**	**FLUX**	**FLUX**
	SAMPLED					**‰**	**‰**	**‰**	**‰**	**mg C m^{-2} hr^{-1}**	**DATE**
Surface	29-Sep-96	HF	nwn	5	1946	-22.9	103	7	103	92	21-Sep-96
Surface	29-Sep-96	HF	nwn	6	1947	-22.7	107	7	107	261	21-Sep-96
Surface	02-Dec-96	HF	nwn	6	2076	-22.0	116	6	139	50	03-Dec-96
Surface	06-Feb-97	HF	nwn	1	2234	-13.9	103	7	118	4	06-Feb-97
Surface	06-Feb-97	HF	nwn	3	2243	-15.6	104	9	114	16	06-Feb-97
Surface	22-May-97	HF	nwn	6	2527	-22.9	131	6	140	64	22-May-97
Surface	22-May-97	HF	nwn	5	2529	-21.9	117	6	125	31	22-May-97
Surface	22-May-97	HF	nwn	3	2531	-21.4	124	6	136	45	22-May-97
Surface	04-Sep-97	HF	nwn	5	2674	-22.6	120	6	120	147	08-Sep-97
Surface	05-Sep-97	HF	nwn	4	2669	-22.0	140	6	140	105	08-Sep-97
Surface	02-Nov-97	HF	nwn	5	2840	-20.0	145	5	176	38	12-Nov-97
Surface	02-Nov-97	HF	nwn	6	2841	-20.3	117	5	133	30	12-Nov-97
Surface	12-Apr-98	HF	nwn	6	3111	-20.6	100	6	107	41	13-Apr-98
Surface	12-Apr-98	HF	nwn	4	3112	-20.0	113	6	127	32	13-Apr-98
Surface	12-Apr-98	HF	nwn	5	3114	-19.2	134	6	166	33	13-Apr-98
Surface	12-Apr-98	HF	nwn	2	3115	-19.1	82	6	79	49	13-Apr-98
Surface	02-Jun-98	HF	nwn	6	3278	-24.4	99	5	100	103	03-Jun-98
Surface	02-Jun-98	HF	nwn	4	3279	-23.5	104	5	108	98	03-Jun-98
Surface	03-Jul-98	HF	nwn	J1	3652	-26.2	110	5	110	222	03-Jul-98
Surface	03-Jul-98	HF	nwn	J2	3653	-24.4	186	5	197	237	03-Jul-98
Surface	03-Jul-98	HF	nwn	J3	3654	-25.7	130	5	131	208	03-Jul-98
Surface	03-Jul-98	HF	nwn	J5	3655	-25.5	68	5	67	191	03-Jul-98
Surface	03-Jul-98	HF	nwn	J6	3656	-25.7	118	6	118	216	03-Jul-98
Surface	03-Jul-98	HF	nwn	6	3657	-25.7	117	6	118	296	03-Jul-98
Surface	03-Jul-98	HF	nwn	4	3336		123	5	123	499	03-Jul-98
Surface	13-Aug-98	HF	nwn	5	3471	-25.4	113	5	113	466	13-Aug-99
Surface	13-Aug-98	HF	nwn	4	3476	-24.1	170	5	179	514	13-Aug-99
Surface	13-Aug-98	HF	nwn	6	3665	-24.8	111	5	113	176	13-Aug-99
Surface	08-Sep-98	HF	nwn	4	3567	-21.9	114	5	123	249	08-Sep-98
Surface	08-Sep-98	HF	nwn	5	3568	-25.3	101	5	101	226	08-Sep-98
Surface	08-Sep-98	HF	nwn	6	3529	-24.3	105	5	108	185	08-Sep-98
Surface	23-Oct-98	HF	nwn	4	3634	-19.8	111	5	118	68	23-Oct-99
Surface	23-Oct-98	HF	nwn	5	3637	-14.6	103	5	111	89	23-Oct-99
Surface	23-Oct-98	HF	nwn	6	3636	-23.7	101	4	101	57	23-Oct-99
Surface	28-Mar-99	HF	nwn	4	4542	-17.2	106	6	113	5	28-Mar-99
Surface	28-Mar-99	HF	nwn	6	4543	-22.3	114	4	118	23	28-Mar-99
Surface	29-Mar-99	HF	nwn	5	4544	-22.6	117	6	122	21	29-Mar-99
Surface	29-Mar-99	HF	nwn	6	4545	-23.1	119	6	124	22	29-Mar-99
Surface	12-May-99	HF	nwn	4	4646	-19.5	109	5	121	32	11-May-99
Surface	12-May-99	HF	nwn	5	4647	-23.3	108	5	111	18	11-May-99
Surface	12-May-99	HF	nwn	6	4648	-23.9	116	5	119	37	11-May-99
Surface	05-Jun-99	HF	nwn	4	4667	-21.1	110	6	118	71	05-Jun-99
Surface	05-Jun-99	HF	nwn	5	4666	-24.4	110	6	112	129	05-Jun-99
Surface	05-Jun-99	HF	nwn	6	4665	-23.3	109	7	113	100	05-Jun-99
Surface	10-Jul-99	HF	nwn	6	4787	-26.0	97	5	97	246	10-Jul-99
Surface	16-Aug-99	HF	nwn	4	4197	-24.2	104	5	105	224	16-Aug-99
Surface	16-Aug-99	HF	nwn	5	4193	-25.7	105	6	105	433	16-Aug-99
Surface	16-Aug-99	HF	nwn	6	4199	-25.1	102	7	103	235	16-Aug-99
Surface	24-Sep-99	HF	nwn	6	4880	-25.9	96	5	96	91	23-Sep-99
Surface	24-Sep-99	HF	nwn	5	4882	-26.5	90	5	90	69	23-Sep-99
Surface	24-Sep-99	HF	nwn	4	4883	-24.1	102	4	105	92	23-Sep-99
Surface	13-Aug-98	HF	nwn	J1	3474	-25.2	104	6	104	128	13-Aug-99
Surface	08-Sep-98	HF	nwn	J1	3523	-28.5	117	6	117	115	08-Sep-98
Surface	13-Aug-98	HF	nwn	J2	3666	-24.8	108	5	109	244	13-Aug-99
Surface	08-Sep-98	HF	nwn	J2	3531	-23.6	115	4	119	151	08-Sep-98
Surface	13-Aug-98	HF	nwn	J3	3475	-25.0	114	4	115	246	13-Aug-99
Surface	08-Sep-98	HF	nwn	J3	3532	-24.1				105	08-Sep-98
Surface	08-Sep-98	HF	nwn	J4	3526	-22.9	107	5	112	79	08-Sep-98
Surface	28-Oct-98	HF	nwn	J4	3630	-21.0	100	4	100	46	27-Oct-98
Surface	16-Aug-99	HF	nwn	j4	4198	-24.2	98	5	98	126	16-Aug-99
Surface	24-Sep-99	HF	nwn	j4	4881	-25.2	103	5	105		23-Sep-99
Surface	13-Aug-98	HF	nwn	J5	3669	-24.0	169	6	180	87	13-Aug-99
Surface	08-Sep-98	HF	nwn	J5	3521	-20.8	114	5	126	57	08-Sep-98
Surface	28-Oct-98	HF	nwn	J5	3631	-21.1	109	5	113	36	27-Oct-98
Surface	16-Aug-99	HF	nwn	j5	4196	-24.1	109	6	111	112	16-Aug-99
Surface	24-Sep-99	HF	nwn	j5	4878	-25.3	106	5	107	55	23-Sep-99
Surface	13-Aug-98	HF	nwn	J6	3668	-24.0	103	4	105	136	13-Aug-99
Surface	08-Sep-98	HF	nwn	J6	3528	-21.2				61	08-Sep-98

APPENDIX 4. Soil Respiration CO$_2$ data

Type	DATE SAMPLED	SITE	AREA	COLLAR	UCIT	^{13}C ‰	^{14}C ‰	+/- ‰	^{14}C (corrected) ‰	FLUX mg C m^{-2} hr^{-1}	FLUX DATE
Surface	16-Aug-99	HF	nwn	j6	4194	-24.1	82	6	80	111	16-Aug-99
Surface	24-Sep-99	HF	nwn	j6	4879	-23.9	100	5	103	43	23-Sep-99
Surface	12-Apr-98	OR	P5	1	3117	-18.7	136	5	136		
Surface	20-Jun-98	OR	P5	2	3313	-25.4	110	6	111	178	20-Jun-99
Surface	20-Jun-98	OR	P5	3	3314	-25.7	137	6	138	276	20-Jun-99
Surface	10-Jul-98	OR	P5	1	3464	-24.0	111	5	115	313	10-Jul-98
Surface	10-Jul-98	OR	P5	1	3468	-23.8	128	6	135	313	10-Jul-98
Surface	24-Aug-98	OR	P5	2	3485	-21.2	123	6	139	88	24-Aug-98
Surface	25-Aug-98	OR	P5	3	3489	-21.0	137	6	160	98	25-Aug-98
Surface	06-Oct-98	OR	P5	2	3581	-23.2	124	5	136	159	06-Oct-98
Surface	06-Oct-98	OR	P5	1	3615	-23.6	120	5	129		06-Oct-98
Surface	06-Oct-98	OR	P5	3	3616	-23.7	133	5	143	159	06-Oct-98
Surface	30-Oct-98	OR	P5	2	3639	-17.1	224	6		44	30-Oct-98
Surface	09-Dec-98	OR	P5	1	3647	-24.2	144	5	155	79	09-Dec-98
Surface	09-Dec-98	OR	P5	2	3648	-24.1	133	5	143	77	09-Dec-98
Surface	09-Dec-98	OR	P5	3	3649	-25.2	125	5	128	65	09-Dec-98
Surface	02-Apr-99	OR	P5	1	4554	-23.3	146	6	160	78	02-Apr-99
Surface	02-Apr-99	OR	P5	2	4555	-23.4	141	6	154	59	02-Apr-99
Surface	02-Apr-99	OR	P5	3	4556	-24.8	145	6	151	91	02-Apr-99
Surface	07-May-99	OR	P5	1	4619	-25.5	124	5	126		
Surface	07-May-99	OR	P5	2	4620	-25.3	137	5	139		
Surface	07-May-99	OR	P5	3	4621	-25.8	131	5	132		
Surface	11-Jun-99	OR	P5	1	4677	-23.6	104	5	107	138	11-Jun-99
Surface	11-Jun-99	OR	P5	3	4678	-23.6	106	6	110	102	11-Jun-99
Surface	22-Jul-99	OR	P5	3	4180	-27.3	775	8	749	612	22-Jul-99
Surface	22-Jul-99	OR	P5	2	4181	-26.2	616	6	614	406	22-Jul-99
Surface	22-Jul-99	OR	P5	1	4182	-26.2	712	7	708	484	22-Jul-99
Surface	19-Aug-99	OR	P5	1	4220	-23.6	915	10	1052	218	19-Aug-99
Surface	19-Aug-99	OR	P5	3	4222	-23.6	1017	10	1171	114	19-Aug-99
Surface	23-Oct-99	OR	P5	1	4377	-21.2	218	6	271	55	23-Oct-99
Surface	23-Oct-99	OR	P5	2	4378	-20.1	167	7	213	52	23-Oct-99
Surface	23-Oct-99	OR	P5	3	4379	-21.4	233	8	290	40	23-Oct-99
Surface	12-Apr-98	OR	TDE		3173	-19.5	119	7	119		
Surface	18-Jun-98	OR	TDE	2	3310	-24.8	151	7	155	133	18-Jun-99
Surface	18-Jun-98	OR	TDE	3	3311	-24.9	122	5	124	182	18-Jun-99
Surface	18-Jun-98	OR	TDE	3	3312	-25.3	138	6	140	182	18-Jun-99
Surface	09-Jul-98	OR	TDE	2	3462	-24.5	123	5	127	236	09-Jul-98
Surface	09-Jul-98	OR	TDE	1	3465	-23.8	97	6	100	198	09-Jul-98
Surface	09-Jul-98	OR	TDE	3	3466	-25.1	103	6	105	272	09-Jul-98
Surface	24-Aug-98	OR	TDE	1	3486	-20.1	112	4	129	75	24-Aug-98
Surface	24-Aug-98	OR	TDE	2	3488	-20.6	123	6	143	69	24-Aug-98
Surface	06-Oct-98	OR	TDE	2	3586	-20.3	118	6	145	122	06-Oct-98
Surface	06-Oct-98	OR	TDE	3	3589	-22.7	124	5	138	180	06-Oct-98
Surface	06-Oct-98	OR	TDE	1	3613	-22.9	123	6	136	123	06-Oct-98
Surface	30-Oct-98	OR	TDE	1	3641	-17.0	113	5	125	46	30-Oct-98
Surface	30-Oct-98	OR	TDE	3	3643	-17.6	123	5	143	48	30-Oct-98
Surface	10-Dec-98	OR	TDE	1	3644	-23.0	119	4	132	58	10-Dec-98
Surface	10-Dec-98	OR	TDE	2	3645	-22.0	115	5	134	50	10-Dec-98
Surface	10-Dec-98	OR	TDE	3	3646	-22.7	131	5	150	69	10-Dec-98
Surface	01-Apr-99	OR	TDE	1	4551	-23.6	120	6	127	61	01-Apr-99
Surface	01-Apr-99	OR	TDE	2	4552	-24.1	124	6	130	52	01-Apr-99
Surface	01-Apr-99	OR	TDE	3	4553	-22.9	116	6	126	60	01-Apr-99
Surface	07-May-99	OR	TDE	1	4623	-24.9	140	5	143		
Surface	07-May-99	OR	TDE	2	4624	-24.6	132	5	136		
Surface	07-May-99	OR	TDE	3	4625	-25.1	147	5	149		
Surface	12-Jun-99	OR	TDE	1	4671	-24.4	97	5	100	144	12-Jun-99
Surface	12-Jun-99	OR	TDE	2	4672	-24.6	110	5	113	169	12-Jun-99
Surface	12-Jun-99	OR	TDE	3	4674	-24.6	113	5	117	181	12-Jun-99
Surface	22-Jul-99	OR	TDE	3	4184	-26.1	875	8	874	249	22-Jul-99
Surface	22-Jul-99	OR	TDE	2	4185	-25.9	710	9	713	198	22-Jul-99
Surface	22-Jul-99	OR	TDE	1	4186	-26.1	752	9	751	264	22-Jul-99
Surface	19-Aug-99	OR	TDE	1	4217	-24.5	853	9	925	294	19-Aug-99
Surface	19-Aug-99	OR	TDE	3	4218	-25.1	2009	21	2117	509	19-Aug-99
Surface	19-Aug-99	OR	TDE	2	4219	-23.4	1109	11	1295	122	19-Aug-99
Surface	24-Oct-99	OR	TDE	2	4381	-20.4	570	8	810	29	24-Oct-99
Surface	24-Oct-99	OR	TDE	1	4382	-22.8	472	6	565	83	24-Oct-99
Surface	24-Oct-99	OR	TDE	3	4383	-20.8	420	7	570	56	24-Oct-99

APPENDIX 5. Soil Profile CO_2 data

TYPE	DATE	SITE	AREA	DEPTH	UCIT	^{13}C	^{14}C	CO_2	DATE
	SAMPLED			cm		‰	‰	%	CO_2
Profile	01-Jul-98	HOW	tower	6	3699	-20.34	115	0.22	30-Jun-98
Profile	18-Aug-98	HOW	tower	6	3697	-19.81	108	0.15	21-Aug-98
Profile	19-Oct-98	HOW	tower	6	3598	-15.96	111	0.09	20-Oct-98
Profile	08-Jun-99	HOW	tower	6	4717	-20.21	112	0.17	09-Jun-99
Profile	12-Jul-99	HOW	tower	6	4818	-20.46	117	0.21	13-Jul-99
Profile	13-Aug-99	HOW	tower	6	4228	-19.45	112	0.07	12-Aug-99
Profile	01-Oct-99	HOW	tower	6	4392	-19.52	109	0.14	05-Oct-99
Profile	20-May-00	HOW	tower	6	5445	-23.98	109	0.09	16-May-00
Profile	03-Jun-98	HOW	tower	10	3295	-18.36	98	0.15	09-Jun-98
Profile	16-Aug-97	HOW	tower	15	2642	-21.02	104	0.33	12-Aug-96
Profile	01-Jul-98	HOW	tower	15	4151	-21.00	117	0.35	30-Jun-98
Profile	17-Sep-98	HOW	tower	15	3593	-19.80	96	0.20	15-Sep-98
Profile	19-Oct-98	HOW	tower	15	3681	-20.19	98	0.19	20-Oct-98
Profile	29-Apr-99	HOW	tower	15	4626	-19.46	115	0.14	27-Apr-99
Profile	08-Jun-99	HOW	tower	15	4718	-20.30	104	0.32	09-Jun-99
Profile	12-Jul-99	HOW	tower	15	4819	-21.45	117	0.32	13-Jul-99
Profile	13-Aug-99	HOW	tower	15	4230	-20.63	97	0.10	12-Aug-99
Profile	01-Oct-99	HOW	tower	15	4391	-21.30	94	0.26	05-Oct-99
Profile	16-Aug-97	HOW	tower	32	2641	-20.73	90	0.45	12-Aug-96
Profile	03-Jun-98	HOW	tower	32	3296	-21.11	119	0.38	09-Jun-98
Profile	01-Jul-98	HOW	tower	32	3700	-21.98	122	0.72	30-Jun-98
Profile	03-Jun-98	HOW	tower	50	3297	-21.87	99	0.56	09-Jun-98
Profile	19-Oct-98	HOW	tower	51	3682	-21.86	96	0.52	20-Oct-98
Profile	29-Apr-99	HOW	tower	51	4627	-21.55	121	0.32	27-Apr-99
Profile	08-Jun-99	HOW	tower	51	4719	-21.10	109	0.34	09-Jun-99
Profile	12-Jul-99	HOW	tower	51	4820	-21.88	119	0.67	13-Jul-99
Profile	13-Aug-99	HOW	tower	51	4229	-21.07	103	0.22	12-Aug-99
Profile	01-Oct-99	HOW	tower	51	4394	-22.28	113	0.64	05-Oct-99
Profile	15-May-96	HF	nwn	6	1826		141	0.09	14-May-96
Profile	11-Jul-96	HF	nwn	6	1902	-21.80	130	0.23	08-Jul-96
Profile	29-Sep-96	HF	nwn	6	1977	-21.00	142	0.12	22-Sep-96
Profile	11-Apr-98	HF	nwn	6	3097	-16.76	128	0.07	13-Apr-98
Profile	03-Jul-98	HF	nwn	6	3689	-22.83	117	0.39	30-Jun-98
Profile	13-Aug-98	HF	nwn	6	3693	-21.84	115	0.27	12-Aug-98
Profile	08-Sep-98	HF	nwn	6	3580		141	0.14	09-Sep-98
Profile	23-Oct-98	HF	nwn	6	3596	-15.39	122	0.12	19-Oct-98
Profile	29-Mar-99	HF	nwn	6	4558	-18.31	106	0.14	16-Mar-99
Profile	12-May-99	HF	nwn	6	4652	-19.68	106	0.10	11-May-99
Profile	05-Jun-99	HF	nwn	6	4704	-20.85	123	0.18	04-Jun-99
Profile	10-Jul-99	HF	nwn	6	4812	-22.89	124	0.33	09-Jul-99
Profile	13-Aug-99	HF	nwn	6	4232	-21.72	124	0.10	10-Aug-99
Profile	24-Sep-99	HF	nwn	6	4390	-22.18	121	0.27	22-Sep-99
Profile	05-Sep-97	HF	nwn	9	2678	-21.22	106	0.23	09-Sep-97
Profile	11-Apr-98	HF	nwn	8	3100	-18.60	121	0.09	13-Apr-98
Profile	02-Jun-98	HF	nwn	8	3534	-22.17	114	0.26	02-Jun-98
Profile	03-Jul-98	HF	nwn	9	3691	-23.24	116	0.66	30-Jun-98
Profile	13-Aug-98	HF	nwn	9	3674	-21.98	92	0.41	12-Aug-98
Profile	08-Sep-98	HF	nwn	9	3578	-20.77	102	0.14	09-Sep-98
Profile	30-Mar-99	HF	nwn	9	4561	-19.84	140	0.13	16-Mar-99
Profile	12-May-99	HF	nwn	9	4655	-21.17	111	0.17	11-May-99
Profile	05-Jun-99	HF	nwn	9	4701	-21.55	128	0.27	04-Jun-99
Profile	10-Jul-99	HF	nwn	9	4815	-23.28	111	0.60	09-Jul-99
Profile	16-Aug-99	HF	nwn	9	4237	-20.98	103	0.25	17-Aug-99
Profile	24-Sep-99	HF	nwn	9	4385	-21.79	111	0.23	22-Sep-99
Profile	11-Jul-96	HF	nwn	10	1903	-21.30	113	0.37	08-Jul-96
Profile	29-Sep-96	HF	nwn	10	1978	-21.00	161	0.19	22-Sep-96
Profile	02-Dec-96	HF	nwn	10	2090	-19.10	137	0.11	02-Dec-96

APPENDIX 5. Soil Profile CO_2 data

TYPE	DATE	SITE	AREA	DEPTH	UCIT	^{13}C	^{14}C	CO_2	DATE
	SAMPLED			cm		‰	‰	%	CO_2
Profile	02-Nov-97	HF	nwn	10	2837	-21.00	130	0.12	11-Nov-97
Profile	13-Aug-98	HF	nwn	10	3694	-21.72	126	0.33	12-Aug-98
Profile	29-Mar-99	HF	nwn	10	4559	-19.96	120	nd	16-Mar-99
Profile	11-Apr-98	HF	nwn	26	3101	-19.80	137	0.14	13-Apr-98
Profile	02-Jun-98	HF	nwn	26	3291	-22.48	90	0.44	02-Jun-98
Profile	03-Jul-98	HF	nwn	26	3535	-23.16	117	0.77	30-Jun-98
Profile	03-Jul-98	HF	nwn	26	3690	-23.15	115	0.77	30-Jun-98
Profile	13-Aug-98	HF	nwn	26	3676	-21.64	106	0.43	12-Aug-98
Profile	08-Sep-98	HF	nwn	26	3582	-21.22	115	0.22	09-Sep-98
Profile	27-Oct-98	HF	nwn	26	3686	-21.14	101	0.24	19-Oct-98
Profile	30-Mar-99	HF	nwn	26	4563	-21.26	121	0.18	16-Mar-99
Profile	12-May-99	HF	nwn	26	4656	-22.02	117	0.21	11-May-99
Profile	05-Jun-99	HF	nwn	26	4702	-22.02	119	0.21	04-Jun-99
Profile	10-Jul-99	HF	nwn	26	4816	-23.03	117	0.67	09-Jul-99
Profile	16-Aug-99	HF	nwn	26	4239	-21.63	92	0.38	17-Aug-99
Profile	24-Sep-99	HF	nwn	26	4387	-22.59	105	0.44	22-Sep-99
Profile	15-May-96	HF	nwn	33	1827		145	0.24	14-May-96
Profile	11-Jul-96	HF	nwn	33	1904	-21.10	127	0.58	08-Jul-96
Profile	29-Sep-96	HF	nwn	33	1979	-21.12	128	0.32	22-Sep-96
Profile	02-Dec-96	HF	nwn	33	2091	-20.60	134	0.20	02-Dec-96
Profile	06-Feb-97	HF	nwn	30	2245	-23.44	131	0.37	05-Feb-97
Profile	22-May-97	HF	nwn	33	2522	-20.23	131	0.91	21-May-97
Profile	02-Nov-97	HF	nwn	33	2838	-20.44	124	0.28	11-Nov-97
Profile	11-Apr-98	HF	nwn	33	3098	-18.87	133	0.14	13-Apr-98
Profile	13-Aug-98	HF	nwn	33	3695	-22.25	116	0.45	12-Aug-98
Profile	08-Sep-98	HF	nwn	33	3520	-21.48	131	0.25	09-Sep-98
Profile	23-Oct-98	HF	nwn	33	3683	-20.16	101	0.29	19-Oct-98
Profile	28-Mar-99	HF	nwn	33	4560	-21.65	125	0.30	16-Mar-99
Profile	28-Mar-99	HF	nwn	33	4560*	-21.00	111	0.30	16-Mar-99
Profile	12-May-99	HF	nwn	33	4653	-21.17	115	0.21	11-May-99
Profile	05-Jun-99	HF	nwn	33	4705	-21.64	127	0.35	04-Jun-99
Profile	10-Jul-99	HF	nwn	33	4813	-22.84	130	0.46	09-Jul-99
Profile	13-Aug-99	HF	nwn	33	4233	-21.72	109	0.20	10-Aug-99
Profile	24-Sep-99	HF	nwn	33	4389	-22.63	116	0.60	22-Sep-99
Profile	06-Feb-97	HF	nwn	55	2240	-24.07	112	0.40	05-Feb-97
Profile	05-Sep-97	HF	nwn	55	2676	-21.84	109	0.43	09-Sep-97
Profile	11-Apr-98	HF	nwn	55	3099	-19.02	94	0.19	13-Apr-98
Profile	29-Mar-99	HF	nwn	55	4564	-21.43	111	0.22	16-Mar-99
Profile	16-Aug-99	HF	nwn	55	4240	-21.96	102	0.48	17-Aug-99
Profile	15-May-96	HF	nwn	60	1828		135	0.31	14-May-96
Profile	11-Jul-96	HF	nwn	60	1905	-21.90	132	0.72	08-Jul-96
Profile	29-Sep-96	HF	nwn	60	1980	-22.60	115	0.49	22-Sep-96
Profile	02-Dec-96	HF	nwn	60	2092	-21.60	135	0.25	02-Dec-96
Profile	06-Feb-97	HF	nwn	60	2246	-23.49	120	0.40	05-Feb-97
Profile	22-May-97	HF	nwn	60	2523	-21.12	139	1.22	21-May-97
Profile	02-Nov-97	HF	nwn	60	2836	-22.00	112	0.30	11-Nov-97
Profile	02-Jun-98	HF	nwn	60	3294	-20.79	112	0.52	02-Jun-98
Profile	13-Aug-98	HF	nwn	60	3696	-22.78	110	0.57	12-Aug-98
Profile	08-Sep-98	HF	nwn	60	3522	-23.27	124	0.37	09-Sep-98
Profile	23-Oct-98	HF	nwn	60	3684	-21.38	104	0.40	19-Oct-98
Profile	28-Mar-99	HF	nwn	60	4562	-22.70	125	0.35	16-Mar-99
Profile	12-May-99	HF	nwn	60	4654	-20.00	119	0.26	11-May-99
Profile	05-Jun-99	HF	nwn	60	4706	-21.79	118	0.48	04-Jun-99
Profile	10-Jul-99	HF	nwn	60	4814	-22.76	114	0.57	09-Jul-99
Profile	13-Aug-99	HF	nwn	60	4231	-22.24	105	0.29	10-Aug-99
Profile	24-Sep-99	HF	nwn	60	4388	-22.73	121	1.18	22-Sep-99
Profile	11-Apr-98	HF	nwn	85	3103	-19.02	103	0.22	13-Apr-98

APPENDIX 5. Soil Profile CO_2 data

TYPE	DATE SAMPLED	SITE	AREA	DEPTH cm	UCIT	^{13}C ‰	^{14}C ‰	CO_2 %	DATE CO_2
Profile	02-Jun-98	HF	nwn	85	3292	-22.92	115	0.50	02-Jun-98
Profile	13-Aug-98	HF	nwn	85	3677	-21.93	89	0.55	12-Aug-98
Profile	08-Sep-98	HF	nwn	85	3585	-21.30	102	0.36	09-Sep-98
Profile	27-Oct-98	HF	nwn	85	4162	-22.19	115	0.41	19-Oct-98
Profile	29-Mar-99	HF	nwn	85	4565	-22.67	123	0.29	16-Mar-99
Profile	12-May-99	HF	nwn	85	4657	-21.71	116	0.28	11-May-99
Profile	05-Jun-99	HF	nwn	85	4703	-21.98	133	0.51	04-Jun-99
Profile	10-Jul-99	HF	nwn	85	4817	-23.63	111	0.73	09-Jul-99
Profile	16-Aug-99	HF	nwn	85	4238	-22.19	99	0.56	17-Aug-99
Profile	24-Sep-99	HF	nwn	85	4386	-23.15	105	0.70	22-Sep-99
Profile	25-Aug-98	OR	P5	61	3533	-22.16	149	0.66	25-Aug-98
Profile	06-Oct-98	OR	P5	61	3587	-22.60	145	0.59	06-Oct-98
Profile	29-Oct-98	OR	P5	61	3679	-21.01	130	0.29	29-Oct-98
Profile	09-Dec-98	OR	P5	61	4158	-24.27	172	0.59	09-Dec-98
Profile	02-Apr-99	OR	P5	61	4571	-23.75	93	0.49	01-Apr-99
Profile	07-May-99	OR	P5	61	4614	-24.39	144	0.97	07-May-99
Profile	11-Jun-99	OR	P5	61	4716	-23.37	143	0.97	11-Jun-99
Profile	22-Jul-99	OR	P5	61	4190	-24.33	569	2.04	22-Jul-99
Profile	19-Aug-99	OR	P5	61	4221	-23.42	830	1.12	19-Aug-99
Profile	23-Oct-99	OR	P5	61	4396	-23.46	325	0.34	23-Oct-99
Profile	29-Apr-00	OR	P5	61	5407	-25.38	382	0.96	28-Apr-00
Profile	09-Jun-00	OR	P5	61	5500	-24.71	258	1.31	09-Jun-00
Profile	18-Jun-98	OR	TDE	3	3316	-20.02	120	0.20	19-Jun-98
Profile	18-Jun-98	OR	TDE	8	3317		130	0.59	19-Jun-98
Profile	09-Jul-98	OR	TDE	8	4154	-20.88	130	0.31	09-Jul-98
Profile	24-Aug-98	OR	TDE	8	3514	-18.24	148	0.14	25-Aug-98
Profile	10-Dec-98	OR	TDE	8	4161	-20.96	140	0.14	10-Dec-98
Profile	01-Apr-99	OR	TDE	8	4566	-20.12	132	0.19	01-Apr-99
Profile	07-May-99	OR	TDE	8	4615	-22.53	152	0.23	07-May-99
Profile	12-Jun-99	OR	TDE	8	4711	-21.95	141	0.23	11-Jun-99
Profile	22-Jul-99	OR	TDE	8	4188	-24.16	977	1.39	22-Jul-99
Profile	19-Aug-99	OR	TDE	8	4224	-20.78	1279	0.20	19-Aug-99
Profile	23-Oct-99	OR	TDE	8	4400	-17.83	268	0.07	23-Oct-99
Profile	18-Jun-98	OR	TDE	14	3318	-23.33	120	0.70	19-Jun-98
Profile	09-Jul-98	OR	TDE	14	4155	-21.87	142	0.42	09-Jul-98
Profile	06-Oct-98	OR	TDE	14	3591	-20.60	163	0.18	06-Oct-98
Profile	30-Oct-98	OR	TDE	14	3678	-17.90	129	0.10	29-Oct-98
Profile	10-Dec-98	OR	TDE	14	3688	-25.00	158	0.23	10-Dec-98
Profile	01-Apr-99	OR	TDE	14	4567	-22.23	135	0.29	01-Apr-99
Profile	18-Jun-98	OR	TDE	21	3319	-23.50	122	1.21	19-Jun-98
Profile	07-May-99	OR	TDE	21	4616	-23.00	160	0.50	07-May-99
Profile	12-Jun-99	OR	TDE	21	4712	-22.27	131	0.50	11-Jun-99
Profile	22-Jul-99	OR	TDE	21	4192	-24.49	942	1.80	22-Jul-99
Profile	19-Aug-99	OR	TDE	21	4226	-21.47	1577	0.49	19-Aug-99
Profile	23-Oct-99	OR	TDE	21	4398	-20.62	322	0.13	23-Oct-99
Profile	18-Jun-98	OR	TDE	68	3320	-24.11	132	1.58	19-Jun-98
Profile	09-Jul-98	OR	TDE	68	4156	-23.52	148	1.11	09-Jul-98
Profile	24-Aug-98	OR	TDE	68	3524	-21.37	149	0.59	25-Aug-98
Profile	06-Oct-98	OR	TDE	68	4163		159	0.57	06-Oct-98
Profile	30-Oct-98	OR	TDE	68	3675	-21.01	141	0.28	29-Oct-98
Profile	10-Dec-98	OR	TDE	68	3687		154	0.71	10-Dec-98
Profile	01-Apr-99	OR	TDE	68	4568	-22.85	89	0.74	01-Apr-99
Profile	07-May-99	OR	TDE	68	4617	-23.47	137	1.00	07-May-99
Profile	12-Jun-99	OR	TDE	68	4713	-23.19	136	0.99	11-Jun-99
Profile	22-Jul-99	OR	TDE	68	4189	-24.69	678	2.02	22-Jul-99
Profile	19-Aug-99	OR	TDE	68	4227	-22.67	1113	0.91	19-Aug-99
Profile	23-Oct-99	OR	TDE	68	4399	-22.04	349	0.34	23-Oct-99

APPENDIX 6. Soil incubation data

TYPE	DATE SAMPLED	SITE	AREA	Horizon	UCIT	^{13}C ‰	^{14}C ‰	+/- ‰	Total Flux	LENGTH DAYS
INCUB	17-Jul-99	HF	NWN-1	Oi +Oe	5483	-27.3	123	5	3.055	5
INCUB	17-Jul-99	HF	NWN-1	Oe + Oa	5484	-26.9	123	5	0.253	5
INCUB	17-Jul-99	HF	NWN-1	Oi +Oe	5485	-27.6	121	5	14.638	37
INCUB	17-Jul-99	HF	NWN-1	Oe + Oa	5486	-27.5	144	5	1.143	37
INCUB	17-Jul-99	HF	NWN-1	Oi +Oe	5454	-27.6	120	6	5.328	12
INCUB	17-Jul-99	HF	NWN-2	Oi +Oe	5455	-27.5	117	5	5.748	12
INCUB	17-Jul-99	HF	NWN-1	Oea+ A	5456	-26.8	154	5	0.797	12
INCUB	17-Jul-99	HF	NWN-1	Oea+ A	5457	-27.8	143	5	0.821	12
INCUB	17-Jul-99	HF	NWN-2	Oea+ A	5458	-26.4	108	6	2.506	12
INCUB	17-Jul-99	HF	NWN-2	Ap	5459	-26.5	125	5	0.217	12
INCUB	17-Jul-99	HF	NWN-1	Ap	5460	-26.9	116	5	0.129	12
INCUB	17-Jul-99	HF	NWN-1	Bw1	5461	-23.7	76	5	0.018	12
INCUB	17-Jul-99	HF	NWN-2	Bw1	5462	-23.9	73	5	0.035	12
INCUB	17-Jul-99	HF	NWN-2	Bw1+dark layer	5463	-27.2	139	5	0.048	12
INCUB	13-Jul-99	HOW	NC	Oe	5466	-26.0	108	5	1.103	12
INCUB	13-Jul-99	HOW	TOWER	Oe + Oa	5467	-26.4	140	5	0.878	12
INCUB	13-Jul-99	HOW	TOWER	Oe + Oa	5468	-26.1	116	5	1.932	12
INCUB	13-Jul-99	HOW	NC	Bh	5469	-26.1	87	5	0.074	12
INCUB	13-Jul-99	HOW	TOWER	Bhs + Bh	5470	-26.8	117	5	0.211	12
INCUB	13-Jul-99	HOW	TOWER	Bhs + Bh	5471	-26.8	87	4	0.077	12
INCUB	13-Jul-99	HOW	TOWER	E	5472	-26.5	119	4	0.109	12
INCUB	13-Jul-99	HOW	NC	Bs1	5474	-25.6	75	5	0.034	12
INCUB	13-Jul-99	HOW	NC	Bs2	5475	-24.2	69	5	0.018	12
INCUB	13-Jul-99	HOW	NC	Oe	5479	-26.4	99	4	1.918	6
INCUB	13-Jul-99	HOW	NC	Oi +Oe	5480	-26.6	159	5	0.458	6
INCUB	13-Jul-99	HOW	NC	Oe	5481	-26.4	72	5	2.091	37
INCUB	13-Jul-99	HOW	NC	Oi +Oe	5482	-26.5	157	5	9.825	37
INCUB	13-Jul-99	HOW	NC	E	5810	-25.8	136	4	0.03	12
INCUB	13-Jul-99	HOW	TOWER	Oi +Oe	5464	-26.4	153	5	3.182	12
INCUB	13-Jul-99	HOW	NC	Oi +Oe	5465	-27.2	130	5	5.525	12
INCUB	23-Jul-99	OR	P5	A	5476	-27.0	355	7	0.139	11
INCUB	23-Jul-99	OR	P5	A (?)	5477	-26.8	354	6	0.127	11
INCUB	23-Jul-99	OR	P5	B1	5478	-26.7	257	6	0.01	11
INCUB	23-Jul-99	OR	P5	O	5487	-28.5	330	6	2.072	4
INCUB	23-Jul-99	OR	P5	O	5488	-27.9	177	5	18.77	42
INCUB	7/23/99	OR	P5	Bt	4355	-27.1	204	4	0.007	11
INCUB	7/23/99	OR	TDE	O	4356	-28.4	188	6	3.576	11