The Use of Stored Carbon Reserves in Growth of Temperate Tree Roots and Leaf Buds: Analyses Using Radiocarbon Measurements and Modeling

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Abstract

Characterizing the use of carbon (C) reserves in trees is important for understanding regional and global C cycles, stress responses, asynchrony between photosynthetic activity and growth demand, and isotopic exchanges in studies of tree physiology and ecosystem C cycling. Using an inadvertent, whole-ecosystem radiocarbon (^{14}C) release in a temperate deciduous oak forest and numerical modeling, we estimated that the mean age of stored C used to grow both leaf buds and new roots is 0.7 y and about 55% of new root growth annually comes from stored C. Therefore, the resultant mean age of C used to grow new root tissue is ~0.4 y. In short, new roots contain a lot of stored C but it is young in age. Additionally, the type of structure used to model stored C input is important. Model structures that did not include storage, or that assumed stored and new C mixed well (within root or shoot tissues) before being used for root growth, did not fit the data nearly as well as when a distinct storage pool was used.

Consistent with these whole-ecosystem labeling results, the mean age of C in new-root-tissues determined using "bomb-^{14}C" in three additional forest sites in North America and Europe (one deciduous, two coniferous) was less than 1-2 y. The effect of stored reserves on estimated ages of fine roots is unlikely to be large in most natural abundance isotope studies. However, models of root carbon dynamics should take stored reserves into account, particularly for pulse labeling studies and fast-cycling roots (< 1 y).

Introduction

Carbon reserves in plants play several roles in ecosystem C cycling. They are an important resource for mature trees under stressful conditions, such as after fire or pest outbreaks and they are also used on a routine basis, over a range of time scales (Chapin III *et al.* 1990), to moderate the effect of variations in C production. Photosynthate produced during the day may be used at night after stomates have closed. Seasonally, reserves are used to fuel initial bud break in the spring in both deciduous and coniferous forests (Hoch *et al.* 2003) and early wood growth in some oak species (Kramer and Kozlowski 1979; Barbaroux *et al.* 2003). New root growth is thought to be fueled primarily from recent photosynthate (Pregitzer and Friend 1996; Horwath *et al.* 1994). However, in deciduous species, winter and spring root growth can occur prior to canopy leaf out (Joslin *et al.* 2001) and thus must be fueled by reserves.

Little is known about the age of C in storage reserve pools of mature trees (Trumbore *et al.* 2002). Many tree physiology studies have observed a buildup of C reserves in the fall, and that these reserves are used for root and shoot growth in the spring (McLaughlin *et al.* 1980). However, neither the age of C in reserve pools nor the extent of its use in the growth of new leaf, wood, and root tissues have been well quantified for most mature tree species (Trumbore *et al.* 2002). Determining the mean age and amount of stored C used in tissue growth has become increasingly important in the last decade, because of new methods that rely on changing isotopic (^{13}C and ^{14}C) concentrations of atmospheric CO_2 to determine belowground C cycling rates (Gaudinski *et al.* 2001; Tierney and Fahey 2002; Trumbore *et al.* 2002; Matamala *et al.* 2003; Keel *et al.* 2006). Radiocarbon studies using the changing concentration of $^{14}CO_2$ in the atmosphere following thermonuclear weapons testing in the early 1960's ("bomb-^{14}C" technique; Trumbore 1993) have generally assumed that inputs to soil organic matter from roots and leaves

have the isotopic signature of the atmosphere at the time of their growth (Trumbore *et al.* 1995; Gaudinski *et al.* 2000; but for exceptions see Torn *et al.* 2005 and De Camargo *et al.* 1999). However, if storage C is used, then a mixture of recently fixed and previously stored C determines the isotopic composition of new tissues. Therefore, to accurately determine the turnover time of plant tissues and C exchanges with soil organic matter, the amount and mean age of stored C used in growth of new tissues may need to be taken into account.

The turnover time of a C pool (defined here as the ratio of annual average pool mass to cumulative annual flux leaving the pool) is equivalent to its mean age for pools that are well mixed and have a first order (exponential) loss process. This equivalence results because the C age and transit time distribution curves are equivalent (Rodhe 1992). The models used in this paper assume that the storage pool is well mixed and has a first-order loss process, thereby insuring that the mean age of C leaving the storage pool is equivalent to the storage pool turnover time. We note that this equivalence does *not* occur for C in the roots, since root populations have an age distribution curve different than their transit time distribution curve because younger roots tend to leave the fine root population more rapidly than older roots (Tierney and Fahey 2002; Trumbore and Gaudinski 2003;Wells and Eissenstat 2001).

Assessment of stored C inputs to new growth is particularly important for isotopic methods that estimate fine-root turnover time (Gaudinski 2001). Studies using isotopic methods have found that fine-roots (i.e., roots <2 mm in diameter) have turnover times ranging from 1 to longer than 20 y (Keel *et al.* 2006; Joslin *et al.* 2006; Trumbore *et al.* 2006; Matamala *et al.* 2003; Gaudinski *et al.* 2001; Tierney and Fahey 2002) and are challenging the assumption that fine roots, as a cohort, live for about one year (Jackson *et al.* 1997). Gaudinski *et al.* (2001) showed that in three temperate, deciduous forests of the United States, the mean age of C making

up new (<1 year old) root growth was less than the resolution of the studies' measurements using the bomb-^{14}C approach (1–2 y). Thus, storage C, if present, did not affect the ^{14}C-derived fine-root mean age of 3–18 y. These results, however, could not rule out the possibility of a significant use of C fixed in the previous 1 or 2 growing seasons. In fact, ~ 33% of the new root tissue of scrub oak in central Florida has been shown to be from stored C (Langley *et al.* 2002), and stored C was a significant component of autotrophic root respiration in boreal forests (Carbone *et al.* 2007; Czimczik *et al.* 2006; Schuur and Trumbore 2006), implying that stored C is allocated to roots for various functions. If stored reserves are used in new root growth, not accounting for them could cause large overestimation of root turnover time (e.g., as much as 31% and 293% if storage reserves have a mean age of 6 months or 2 y, respectively; Luo 2003).

Some plant tissues, such as leaf buds, and roots that develop in winter in deciduous species, grow entirely from stored C. Other tissues, such as wood, some leaf buds, and most fine roots, may grow from a combination of stored and recent photosynthate. The main goal of our research was to quantify the role of stored C in the new root and leaf-bud growth of mature, temperate forest trees. For a mature, deciduous forest in Oak Ridge Tennessee, we addressed the following questions: (1) What is the mean age of stored C reserves contributing to new leaf-bud and fine-root growth? (2) On an annual basis, how much new root growth comes from stored C reserves? To answer these questions, we took advantage of a whole-forest pulse label at the Oak Ridge Reservation (ORR), Tennessee, resulting from an unplanned ^{14}C release in 1999 (Trumbore *et al.* 2002). While the release was unplanned and not discovered until several months afterwards, we obtained time-series ^{14}C measurements in new roots, leaf buds, and parasitic plants growing between 1999 and 2002. We used the leaf-bud data with a one-pool model to determine the mean age of stored C used to grow leaf buds. Data from parasitic plants that grow only on root-derived

C were used as an additional proxy for the age of stored C supplying root growth. Data from new roots, in combination with a recently developed numerical root model (Radix; Riley *et al.* this issue), were used to quantify the amount and mean age of storage C used to grow new roots. In addition, the results from both modeling approaches were used to estimate the mean age of C used to grow new root-tissue from the mixture of stored and recently-fixed C.

We also investigated whether growth from stored C could affect previous results for three temperate forests, based on bomb-^{14}C, that fine roots have long lifetimes (Gaudinski *et al.* 2001). To do this, we used the bomb-^{14}C approach of Gaudinski *et al.* (2001) to estimate the mean age of C in new fine-root tissues in coniferous forests in Sweden and on the west coast of the United States, as well as a mixed deciduous forest at Harvard Forest, Massachusetts, previously studied in Gaudinski *et al.* (2001).

Site Descriptions

Locally Enriched ^{14}C Sites

This study was conducted at three sites on the Oak Ridge Reservation (ORR) in Tennessee, the site of Oak Ridge National Laboratory (36° N, 84° W; Figure 1). The local enrichment in atmospheric $^{14}CO_2$ at ORR was presumably from a nearby hazardous waste incinerator, and was discovered by $^{14}CO_2$ measurements in air and, soil respiration made in 1999. Subsequent measurements of tree-ring cellulose from white oak trees (Trumbore *et al.* 2002) showed East ORR received a large $^{14}CO_2$ pulse in 1999 (Appendix I, Trumbore *et al.* 2002 and http://ebis.ornl.gov/pretreat.html). The three sites studied here: Walker Branch (WB), Haw Ridge (HR), and the Throughfall Displacement Experiment site (TDE; adjacent to WB), are all located on East ORR (Figure 1). Although the ^{14}C pulse also affected the West ORR, only data from the eastern sites are used in the current analysis because root growth collection screens were in place

at TDE during the 1999 pulse, enabling collections of new roots that grew during and shortly after the labeling event. This work represents one component of a large multi-institution study of forest C cycling using radiocarbon labeling, called the Enriched Background Isotopic Study (EBIS; Joslin *et al.* 2006; Treseder *et al.* 2006; Hanson *et al.* 2005; Swanston *et al.* 2005; Cisneros-Dozal *et al.* 2006; Trumbore *et al.* 2002).

The sites are located in the upland oak forest type on ridge and upper slope positions. Vegetation is chiefly white oak (*Quercus alba* L.), chestnut oak (*Q. prinus* L.), and Red Maple (*Acer rubrum* L.), with scattered pine (*Pinus echinata* Mill. and P. *virginiana* Mill.), yellow poplar (*Liriodendron tulipifera* L.), black gum (*Nyssa sylvatica* Marsh.), and sourwood (*Oxydendron arboreum* L.). The age of overstory trees in all three sites is variable and ranges from 40 to 150 y (Hanson *et al.* 2005). Mean annual precipitation is 1,358 mm and mean annual temperature is 14.1°C (Johnson and Van Hook 1989). The soil at WB and TDE are ultisols, highly weathered Typic Paleudults developed over cherty dolomitic limestone parent material. At HR the soils are mostly Ultisols, inceptic Hapludults, mixed with some typic Dystrudepts developed over shale and/or sandstone parent material.

Bomb -^{14}C Sites

Harvard Forest is a mixed deciduous forest located near the town of Petersham in central Massachusetts (42.54°N, 72.18°W). The study area, located on the Prospect Hill Tract, was cleared in the mid-1800s and then plowed and used primarily for pasture until 1860–1880 (Foster 1992). The regrowing forest has been undisturbed since being leveled by a hurricane in 1938. The dominant tree species in the study area are northern red oak (*Quercus rubra* L.) and red maple (*Acer rubrum*) with some hemlock (*Tsuga canadensis* Carr.) and white pine (*Pinus*

strobes L.). Mean annual air temperature is 8.5°C, and mean annual precipitation is 1,050 mm. The soils developed on predominantly granitic glacial tills and are classified as Entisols.

The Blodgett Experimental Forest (Blodgett Forest) is a mixed coniferous forest located near the town of Georgetown in the Sierra Nevada, California (38.53°N, 128.30°W). The data presented here are from forest management unit 630, comprising trees that are about 90 y old. The dominant species is ponderosa pine (*Pinus ponderosa* Laws), with intermixed white fir (*Abies concolor* Lind. & Gord.*)*, douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Mean annual air temperature was 8.5°C in 2002 and 2003 (Jeff Bird unpublished data) and mean annual precipitation is 1,774 mm. The soils developed on granitic parent material and are classified as Alfisols.

Knotåsen is a coniferous forest located near the town of Jädraås in central Sweden. The study area (61.00°N 16.13°E) was clear-cut in 1963. Prior to that time, the forest comprised 120+ y old norway spruce. Present stands were planted in 1965, primarily with 2-year-old norway spruce (*Picea abies* (L.) Kars.) seedlings, with some scots pine (*Pinus sylvestris* L.) mixed in. Mean annual air temperature is 3°C and mean annual precipitation is 613 mm. The soils developed mainly on sandy glacial tills atop bedrock composed of granitic and volcanic sediments and are classified as Spodosols.

Methods

Site-Specific Atmospheric $^{14}CO_2$ Histories

This paper uses two types of atmospheric $^{14}CO_2$ enrichment to trace the time elapsed since C in plant tissues was fixed from the atmosphere by photosynthesis (i.e., its mean age). The first utilizes a local enrichment of $^{14}CO_2$ at ORR (Figure 2), the second uses the global enrichment in background atmospheric $^{14}CO_2$ caused by thermonuclear weapons testing (bomb-^{14}C) in the late

1950s and early 1960s (Figure 2). Both approaches require an accurate record of atmospheric $^{14}CO_2$ at the sites studied.

In the absence of direct atmospheric samples, tree rings can be used as a proxy for atmospheric $^{14}CO_2$ content (Hua *et al.* 1999). At each site, we assembled a local tree-ring record of atmospheric ^{14}C; additional proxy indicators that we used are discussed below. All tree cores were taken with a 4.35 mm Haglof increment borer and stored in a dry location until processed. Each core was separated into annual rings, and each ring was pretreated using the Jayme-Wise soxhlet extraction process and bleached to a final product that is operationally defined as holocellulose (Gaudinski *et al.* 2005).

Locally Enriched ^{14}C Sites at ORR

Because the local, 1999 ^{14}C release at ORR was unplanned, direct measurements of local atmospheric $^{14}CO_2$ content during and immediately after the release do not exist. Therefore, we relied on plant-based proxy records to estimate the atmospheric $^{14}CO_2$ inputs to the ORR ecosystem. Certain plant tissues or their respiration can be used as proxies because photosynthate, the organic substrate used in both tissue growth and autotrophic respiration, has the same $\Delta^{14}C$ value as the CO_2 from which it is derived (isotopic fractionation during photosynthesis does not alter the Δ unit; Stuiver and Polach 1977).

Two issues arise with this approach. First, these plant-based proxies are more representative of photosynthetic $^{14}CO_2$ uptake integrated over weekly to monthly time intervals, rather than actual atmospheric values at the time of the release, which probably varied dramatically on time scales of minutes to hours due to changing wind speed and direction. Therefore, we call our estimation of ^{14}C inputs to ORR the EBIS Atmospheric Radiocarbon Proxy Curve (ARPC). It should not be construed as an accurate reconstruction of atmospheric $^{14}CO_2$ over time.

Second, proxy measurement may not actually represent the atmospheric $^{14}CO_2$ concentration over the specified time interval due to use of stored C. For example, tissue that grew in 2000, but with stored C fixed after the 1999 pulse (entirely or in part), or newly-fixed CO_2 but from a re-respired 1999 source, would be more enriched in ^{14}C than if it grew from C fixed only in 2000. In fact it appears that the wood cellulose samples did indeed utilize stored C (see Appendix I). To address this issue, we use proxy measurements *only* to estimate local ^{14}C inputs prior to and during the 1999 pulse. After the 1999 pulse, atmospheric ^{14}C is assumed to return to a locally measured "background" and remain at that level through 2002. Details on the ARPC and the data utilized to create it are in Appendix I. The final values used for the ARPC are shown in Figure 3.

Bomb-^{14}C Sites Away from ORR

Atmospheric $^{14}CO_2$ content has been decreasing since the peak of the ^{14}C-bomb spike in the mid-1960s (Figure 2), because of dilution of ^{14}C through exchange with C in the oceans and terrestrial biosphere. The rate of decrease was rapid at first, but has slowed with time. In the northern hemisphere, the annual change in atmospheric $^{14}CO_2$ was roughly -8‰ y^{-1} in the 1980s and early 1990s, and roughly -6‰ y^{-1}in the late 1990s and early 2000s (Levin and Kromer 2004). The decrease will continue due to ^{14}C dilution by use of ^{14}C-free fossil fuels (aka the Suess Effect). The analytical error in ^{14}C measured with accelerator mass spectroscopy (AMS) reported here is 4–6‰, which is similar to the annual rate of $^{14}CO_2$ decrease over the time period of this study.

In the natural background sites, hereafter referred to as "bomb-^{14}C sites", use of stored C reserves will make the ^{14}C value of new root tissues higher than that of the current atmosphere because of the decreasing trend of atmospheric ^{14}C content. A significant, positive difference

between $\Delta^{14}C$ values in new root growth and atmospheric CO_2 allows us to calculate the influence of stored C reserves (Gaudinski *et al.* 2001). Negative differences indicate fossil fuel CO_2 incorporation into photosynthate. Positive differences, however, do not rule out the possibility of local atmospheric depressions in isotopic values due to fossil fuel contributions.

For the three bomb-^{14}C sites, annual atmospheric measurements or proxies are considered equivalent to plant ^{14}C uptake, because the annual rate of change in atmospheric $^{14}CO_2$ for the past two decades is small (< 8‰ per year) and known (Figure 2). Past studies have used hemispheric ^{14}C atmospheric records (i.e. Burchuladze *et al.* 1989; Levin and Kromer 1997; Levin and Hesshaimer 2000; Levin and Kromer 2004) as estimates of local atmospheric $^{14}CO_2$ (Gaudinski *et al.* 2001; Tierney and Fahey 2002; Trumbore *et al.* 2006). However, hemispheric $^{14}CO_2$ records by themselves do not account for local influences of fossil fuel and re-respired CO_2 within the forest canopy. Therefore, at each of our three sites, we compared three types of data that can be used to represent the atmospheric ^{14}C content. First, we used the ^{14}C signature of global background atmospheric CO_2 at Schauinsland, Germany, which is considered the most representative published record for both continental Europe and North America (Levin and Kromer 2004). Second, we sampled the ^{14}C content of local tree-ring cellulose at Blodgett Forest (1976-2004), Harvard Forest (1951-2003), and Knotåsen (1972-2003). Tree rings were analyzed from one tree core at each site and were measured at multi-year intervals prior to 1998 and annually after 1998. Tree species sampled were ponderosa pine, northern red oak, and norway spruce at Blodgett Forest, Harvard Forest, and Knotåsen, respectively. Finally, direct measurements of local air $^{14}CO_2$ were obtained at Harvard Forest in 2001, Knotåsen in 2001 and 2002, and Blodgett Forest in 2002 and 2003. Except at Harvard Forest, air samples were taken in evacuated 6 L stainless steel canisters (Scientific Instrumentation Specialists). Air was passed

through an inlet to restrict the fill rate and dry the air (using magnesium perchlorate). It took approximately 45 minutes to fill the canister. At Harvard Forest, air samples were collected through a molecular sieve trap as described in Gaudinski *et al.* (2000). Air samples were taken in an open location, at least 1 m off the ground, to obtain well-mixed air. The number of air sampling dates per year used in the calculation of the annual $\Delta^{14}CO_2$ value varied from 1 to 3 and the number of air samples taken on each date varied from 1 to 3 (see Supplemental Data).

Sampling of New Tissues

Roots

To investigate the magnitude of stored C reserves in new-root tissues, we collected new-root growth by slicing into the soil with a shovel and placing a nylon screen (1 mm mesh) stretched across a circular embroidery hoop (15 cm diameter) vertically into the soil so that the top of the hoop was 1-5 cm below the surface of the organic horizon. After placement, soil or organic horizon (as appropriate) was carefully packed around the entire screen. At ORR, roots that grew through the screen mesh were harvested and cleared multiple times between 1999 and 2002, to track the input of elevated ^{14}C to new root growth over time (Table 1). During 1999–2001, samples were collected at TDE, since screens to collect new-root growth were already in place (for another study) before the original 1999 release. In 2001 we collected new root growth at all three sites (TDE, WB, and HR) and in 2002 we sampled only WB and HR.

At the bomb-^{14}C sites, we collected new-root growth during only one time interval (Table 1), because the annual decrease in $\Delta^{14}C$ small and fairly constant. After collection, at both EBIS and bomb-^{14}C sites, roots were transported back to the laboratory and refrigerated or frozen until processed. EBIS roots were dried (50ºC for a minimum of 48 hours) and ground in a Spex Certprep 8000 M Mixer Mill to a fine homogeneous powder (5–10 minutes). Roots from bomb-

^{14}C sites were handled identically except that they underwent soxhlet extraction followedby bleaching (Gaudinski et al. 2005). At the Blodgett site, we also collected new roots from soil cores (from the O horizon and 0-10 cm) by selecting only the very fleshy white or very light colored unsuberized roots that were clearly the current year's growth. We used a stainless steel corer 5.35 cm in diameter. Once separated from the soil and other roots, the new roots were handled and processed as described above for bomb-^{14}C sites.

The non-structural C in new roots is derived mostly from recent photosynthate and is likely only days to weeks old (Horwath *et al.* 1994). In contrast, the structural component, such as cellulose, is not replaced over the root lifespan (Sternberg *et al.* 1986; Farquhar *et al.* 1998; Barbour *et al.* 2004). For roots from bomb-^{14}C sites, we pretreated tissue to isolate the cellulose by a soxhlet extraction, followed by bleaching (Gaudinski *et al.* 2005), thereby ensuring measurement of the oldest C making up the root. Root samples from ORR were not pretreated, because we wanted to compare the ^{14}C signature of bulk (i.e., not pre-treated) new root tissue with the ^{14}C content of leaf buds, expanding leaves, and parasitic plants which had already been measured for ^{14}C as bulk tissues. We also wanted to compare ^{14}C in new roots to that in mixed-age populations of roots sampled from cores (as bulk non-pretreated roots) for other aspects of the EBIS project. Given that the modeling approaches we applied to EBIS samples in this study are based on rates of decline in ^{14}C over time, and that the difference in age between structural and non-structural C is small for new roots because they are so young, the use of exclusively bulk tissues should not affect our results.

Leaf Buds and Expanding Leaves

We sampled a time series of new leaf buds and expanding leaves from white and chestnut oak and red maple trees in East ORR between 2000 and 2003. New buds were collected in mid-

march of 2000 and 2001 and expanding leaf tips in early April of 2000 and 2001 (see Appendix I for sampling dates). Samples were kept cool and transported to the laboratory, where they were dried (50°C) and ground. Leaf buds and expanding leaves were assumed to grow entirely from stored C reserves (Kramer and Kozlowski 1979).

Parasitic plants

As an additional indicator of the isotopic signature of stored C fueling growth of new tissues, we collected samples of non-photosynthesizing perennial parasitic plants, which grow only on C originating from the root exudates of their tree hosts. Samples of the cone-shaped inflorescence of Squaw root (*Conopholis americana* (L.) Wallr) and Indian pipe (*Monotropa uniflora* L) were collected in East ORR during Spring 2000, 2001, 2002, and 2003. Samples were kept cool and transported to the laboratory, where they were dried (50ºC for a minimum of 48 hours) and ground. Squaw root is associated only with trees of the genus *Quercus* (Baird and Riopel 1986).

Radiocarbon Analysis

To determine ^{14}C content, we converted all samples (solids and atmospheric gas) to graphite by either sealed-tube zinc reduction (Vogel 1992) at Lawrence Berkeley National Laboratory or hydrogen reduction (Vogel *et al.* 1987) at the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratory. The graphite was measured for ^{14}C content at CAMS for all samples except tree rings from the bomb-^{14}C sites which were analyzed at the W.M. Keck-CCAMS facility at University of California, Irvine. Radiocarbon results are expressed as $\Delta^{14}C$ (‰) according to Stuiver and Polach (1977). The $\Delta^{14}C$ unit is normalized to a $\delta^{13}C$ value of –25‰, which removes the effects of mass-dependent isotopic fractionation, such as the discrimination against atmospheric ^{14}C during photosynthesis. The $\delta^{13}C$ values used to normalize $\Delta^{14}C$ for new roots, at the bomb-^{14}C sites, were measured in each sample after pre-

treatment. For EBIS samples, we used -25‰ for leaf buds, expanding leaves, and parasitic plants (-25.0 ±0.4‰ represents the mean of five measured parasitic plant samples); -28.1‰ for new root growth (-28.1 ±0.06‰ represents the mean of 113 fine root samples from EBIS root cores; Joslin *et al.* 2006); or sample-specific $\delta^{13}C$ values (see Supplemental Data).

Mean Age of Stored C in Leaf Buds, Expanding Leaves, and Parasitic Plants at East ORR (One-Pool Model)

Leaf buds and expanding leaves are made completely from C reserves stored in previous years (Kramer and Kzlowski 1979). We estimated the mean age of storage reserves used for leaf buds and expanding leaves at East ORR with a one-pool, donor-controlled model analogous to the approach described by Trumbore *et al.* (2002), except that we explicitly take into account the $\Delta^{14}C$ value of background atmospheric CO_2 (Joslin *et al.* 2006). In this model (hereafter referred to as the "one-pool model"), the C flux out of the pool is linearly proportional to pool size, inversely related to turnover time, and yields an exponential relationship for ^{14}C content with time:

$$N_i = (N_0 - A_b)e^{-t/\tau} + A_b \qquad (1)$$

where N is the measured $\Delta^{14}C$ value (‰) of the leaf buds, expanding leaves and parasitic plants (and represents the isotopic signature of the storage pool). The subscript $_0$ indicates the initial year of measurement, $_i$ indicates successive years of measurement, A_b is the background $\Delta^{14}C$ value of photosynthate fixed from atmospheric CO_2 before or after the pulse, t is time (y), and τ is the C pool turnover time (y). We took A_b to be constant (88‰ ± 13(SD)‰; see Appendix I) over the period after the pulse in 1999 through 2002, because we do not have accurate measurements of the local A_b during this time, and the standard deviation of the mean (for measurements taken in 1999 and spring/early summer 2000) encompasses the global background

measurements for 1999 through 2002 (90, 87, 81, and 75‰ respectively—Levin and Kromer (2004)). We estimated τ by exponential regression of the data (using equation 1), and the mean for A_b (88‰). We also calculated the range in τ given by using the mean A_b ± SD and the different plant tissue types. We assumed that the drop in $\Delta^{14}C$ value of N over time after the local 1999 pulse was caused by dilution of the storage pool by new photosynthetic inputs with a $\Delta^{14}C$ value of A_b. Radioactive decay of ^{14}C is not included in the model because, with a half-life of 5700 y, it is too slow to have an effect over the three-year time scale of this study.

Amount of Stored C used to Grow New Roots (One-Pool Model)

The amount of stored C contributing to new root growth (f_s) can be calculated using isotope mass balance, including the radiocarbon value of C supplying new tissue growth, which was estimated as the y-intercept of exponential curve fits to the ^{14}C data, of (1) leaf buds, expanding leaves, and parasitic plants (i.e. storage C growth), and (2) new root growth. The mass balance equation is:

$$\Delta_{ng} = \Delta_{nc} f_{nc} + \Delta_s f_s \qquad (2)$$

where Δ_{ng}, and Δ_s are the radiocarbon values at time zero of the C supplying new tissue growth for new root growth and storage C growth respectively. Δ_{nc} is the $\Delta^{14}C$ value for C fixed from new photosynthate (which is 0‰, because we subtract A_b from the initial data to perform the regressions). f_{nc} and f_s represent the fraction of new root growth coming from newly-fixed C or storage C, respectively.

Mean Age and Amount of Stored C Used in Fine-root Growth Annually at East ORR (Radix)

To calculate the mean age and amount of stored C supplying new root growth, we used the EBIS root-screen time-series data and a new model of fine-root dynamics (Radix1.0, Riley *et al.*

this issue). Similar to the model described above, Radix simulates donor-controlled fluxes. However, Radix has the following added components for simulating realistic physiological complexities: (1) short-lived (months) and long-lived (years to decades) roots, each with right-skewed age populations; (2) stored C inputs to new fine-root growth and fine-root respiration; (3) seasonal variation in fine-root respiration and growth rates; and (4) uncertainty in forcing variables and model parameters.

A simplified version of Radix was used for this paper which simulates only new root growth (Figure 4). In the model, fine roots grow using stored and/or newly photosynthesized C and are represented by one pool (New Roots; L_1). L_1 loses C via respiration (R_1). Mortality turnover of L_1 was not simulated because the roots were sampled (harvested) after less than one year so that mortality turnover was assumed to have small influence on the results. A fraction of new photosynthate (f_s) is allocated to the storage pool; the remainder (1- f_s) goes directly into L_1 (see Figure 4). Losses from the storage pool result from transfer to L_1. The transfer is controlled by the storage-pool turnover time (τ_s) and size. The goal of the Radix modeling was to estimate values of f_s and τ_s that best fit the time series of new-root ^{14}C measurements. The best fit was achieved with a chi-square (χ^2) analysis which minimizes the squared difference between model predictions and measured $\Delta^{14}C$ values, weighted by measurement uncertainty (Press *et al.* 1989). The relative χ^2 values indicate how well predictions using a particular combination of f_s, and τ_s fit the ^{14}C data. The smaller the χ^2 value, the better the fit. The model inputs and constraints are described in more detail in the companion paper by Riley *et al.* (this issue).

Model Inputs and Constraints

Between November and April, when tree leaves in the ORR deciduous forest have senesced or dropped, there is no gross primary productivity. There can, however, be new root growth and

respiration from stored C reserves. At WB, leaf expansion occurs on average between April 10 (5% completion) and May 11 (95% completion; Joslin *et al.* 2001; Hanson *et al.* 2003). Previous radiocarbon labeling of mature white oaks at Walker Branch showed that in April leaves are accumulating C (much of it from stored reserves) and not translocating C out of the leaf (Edwards *et al.* 1989). However, during May through October, leaves translocate a large part of the newly photosynthesized C (Edwards *et al.* 1989). Thus, we assume all new photosynthate produced in April is used for aboveground leaf growth (and not used belowground).

In the model, the periods of May-July and August-October receive 72 and 28%, respectively, of annual belowground primary productivity (BGPP). This partitioning is estimated from minirhizotron observations at TDE of growth in the length of fine roots (< 2 mm diameter), in November–March (5%), April (10%), May–July (65%), and August–October (20%; Joslin *et al.* 2001and Joslin unpublished data). Since none of the C used between November and April (when 15% of root growth occurs) is recently fixed, we divide the remaining 15% BGPP evenly between the 6 months of May–October (i.e., 2.5% of the annual new-root growth occurs each month, May-October).

We assumed a lower bound for the fraction of BGPP allocated to the storage pool (f_s) of 0.15, because 15% of new fine-root growth occurs between November and April, when no new photosynthate is being generated. To impose seasonality in use of storage reserves, we set the C fluxes out of the storage pool explicitly, such that 10% occurs in April, and 1% occurs in each of the 5 months between November and March. These partitions are based on data from Joslin *et al.* (2001) and Joslin (unpublished data). Any growth from storage C above 15% of BGPP (i.e., $f_s >$ 0.15) is partitioned equally among the remaining six growing season months.

The model prescribes a steady annual oscillation in storage pool size (i.e., the annual variation in storage pool size is identical between years). The turnover time of the storage pool (τ_s) reported here is the annual flux-weighted value, calculated as the ratio of the annual mean storage pool size, S_m (g C m^{-2}), and the cumulative C flux out of the storage pool. S_m is an important determinant of τ_s but was not constrained by available data. Instead, S_m is imposed (as an initial condition), and we varied S_m (instead of τ_s directly) to generate a range of τ_s values for the χ^2 simulations. We used 20 y as an upper bound on τ_s (Gaudinski *et al.* 2001).

Values for root respiration (R_1; maintenance + growth) were set at 0.020, 0.033, 0.055, and 0.064 μg C g (root) s^{-1} for the four seasonal periods (November–March, April, May–July and August–October, respectively; see Riley *et al.* this issue). Harvest of L_1 roots was prescribed based on actual harvest dates for the root screens, and grouped into five root cohorts labeled A-E (see Table 1; Figure 3).

Once we determined the best fit values for f_s and τ_s, we defined this to be our "nominal" case and investigated the sensitivity of model predictions to several different parameterizations (Table 3). First, we investigated the impact of our parameterization of seasonality in use of storage C by running the model with no seasonality in storage use (i.e., an equal proportion of the total annual growth from storage is used in each of the twelve months; Run 2). Second, we investigated the sensitivity of χ^2 values to f_s and τ_s by running Radix with the minimum observed value of f_s (0.15; Run 3) and values of τ_s that were much longer than the nominal τ_s (5 y, Run 4 and 10 y, Run 5). Finally, we investigated the sensitivity to use of stored C by assuming (1) that all new photosynthate and stored C mix together in one pool before, rather than being stored or moved separately (f_s = 1; Run 6) or (2) that there is no use of stored reserves (f_s = 0; Run 7). For Run 6, we determined the best fit τ_s that went with f_s = 1.

Mean Age of C Used to Grow New Root Tissue

Root tissues grow using C from storage and/or newly-fixed photosynthate. Using the best-fit values of f_s and τ_s derived from the *Radix* and one-pool models, we estimated the mean age of C used to grow new roots (C_r) for both modeling approaches. Using equation 3, we average the mean ages of the two sources of C supplying root growth:

$$C_r = \tau_s f_s + \tau_{rf}(1 - f_s) \qquad (3)$$

where τ_{rf} is the turnover time of new photosynthate (assumed to be one week). We note that C_r represents the mean age of tissues in "new roots" as well as "new tissue" growing on existing roots that may be several years in age.

Results

Mean Age of Stored Carbon Used to Grow Leaf Buds, Expanding Leaves, and Parasitic Plants

Leaf-Bud, New-Leaf, and Parasitic-Plant ^{14}C Content at East ORR

Isotopic signatures of leaf buds and expanding leaves at East ORR showed a significant degree of ^{14}C incorporation, from the 1999 release, in 2000, followed by rapid return to background atmospheric ^{14}C levels in 2001 (Figure 5). Compared to leaf buds and expanding leaves of maple, leaf buds and expanding leaves of oak had a higher peak ^{14}C value and more rapid return to background levels—indicating a faster turnover time of the storage pool in oak. In March 2000, oak buds ranged between 332 and 521‰, whereas maple buds ranged from 364 to 382‰. In March 2001, ^{14}C levels had dropped to 132–148‰ for oak, but only to 192‰ for maple (note there was only one maple-leaf sample in 2001 (Figure 5)). Parasitic plants sampled in summer 2000 had values between 406 and 516‰ in June and between 320 and 419‰ in August (Figure 5 and Appendix I). These values dropped to less than 100‰ by late April 2003.

The mean ages of C in leaf-bud growth, as estimated from an exponential fit to the data (equation 1), are 0.5 and 1.0 y for oak and maple, respectively (Table 2; Figure 5). The shorter mean age for oak derives from the faster decline in $\Delta^{14}C$ values and implies that its reserve pool cycles more quickly relative to maple. The mean age of C fueling leaf bud and leaf growth, combining data for both species, was 0.6 y (Table 2). The mean age of C in parasitic plants was 0.7 y (Figure 5, Table 2), based on samples from early spring only, when we are sure that their growth represents only stored C, as well as when using data from all measurement periods. This concurrence may be due to the fact that the curve fit is strongly influenced by the three measurements in April 2003 (Figure 5). The mean age of C used in new growth as calculated from all leaf-bud and parasitic plant data was also 0.7 y. We note that the sample sizes of the different data sets (oak, maple, and parasitic plants) are not equal and the curve fitting is strongly influenced by a few points at the tail end of the data sets. Therefore, interpretations of inter-species differences should be used with caution. Additionally, the parasitic plants are perennials with a subterranean plant body (Baird and Riopel 1986). Therefore it is possible that stored C from the subterranean plant body, fixed prior to the 1999 pulse, was used in the growth of the flowering stalk. However given the high $\Delta^{14}C$ values measured in spring 2000, and their rapid decline, it is unlikely that a large amount of "pre-pulse" stored C was used.

Using the range in A_b of ±13‰ changed the mean age of any given tissue by ± 0.1 to 0.3 y, yielding a range in mean C storage age of 0.4 – 1.10 y (Table 2). Our estimates differ from the 4–6 y reported by Trumbore *et al.* (2002) because there was an error in their calculation of τ (Sue Trumbore personal communication).

Mean Age and Amount of Stored C Reserves Used in Root Growth

Root ^{14}C Content at East ORR

The isotopic content of new roots that grew into root screens at ORR between April 2 and August 20, 1999 showed a large degree of label incorporation (Figure 3), with values ranging from 306 to 864‰. The large variability was likely due to different periods of root growth relative to the $^{14}CO_2$ atmospheric pulse as well as to species differences in C allocation to various pools. Because roots could have grown into the screen at any time after emplacement, we do not know the precise time of growth. Samples with higher ^{14}C values may have accumulated a larger fraction of their mass closer to the ^{14}C release.

Roots that grew in fall 1999 or the 2000 growing season (August 20, 1999, through September 10, 2000) have $\Delta^{14}C$ values between 149 and 197‰. Roots that grew during the 2001 growing season at TDE showed declines in isotopic signatures, with an average of 91 ± 5‰ in 2001; (Figure 3). Roots that grew in 2001 at HR and WB (data pooled to calculate one mean; n = 5 or 6 in all cases) had $\Delta^{14}C$ values similar to TDE, but slightly higher means and standard errors (125 ± 23‰). Subsequent, minor ^{14}C releases or plumes from fossil fuel sources could explain such differences. Variability was greatest at WB, with one particularly high value (237‰) in 2001. In 2002, roots were measured only at HR and WB, and showed no significant decline in ^{14}C relative to the 2001 growing season, whether they grew in the early half of the growing season (108 ± 9‰; March 26–May 16 2002) or the latter half of the growing season (114 ±14‰; May 16–Nov 6 2002).

Storage C Use in Roots Estimated Using One-Pool Model

New-root $\Delta^{14}C$ values were lower than those of leaf bud, new leaf, and parasitic plants (Figure 5a). This pattern is consistent with new root growth being a mixture of stored C and newly-fixed

photosynthate, where the ^{14}C signature of the latter is the same as the background atmosphere (Figure 5b). Using equation 2, and the y-intercept values for new root growth (402‰; Table 2), and storage C (780‰; Table 2 equation for all leaf buds, expanding leaves, and parasitic plants) we estimate that 52% of the C in new roots comes from storage with a range of 35-64% given ±13‰ in the value of background atmospheric $^{14}CO_2$. The range was 32-79% if the minimum (maple) and maximum (oak) y-intercept values were used.

We investigated the affect of our assumption of a constant A_b on our results for the one-pool model by forcing A_b to decrease 5‰ per year (Levin and Kromer 2004; Supplemental Data for tree-ring cellulose from Blodgett Forest, Harvard Forest and Knotåsen sites) beginning in 2001. The $\Delta^{14}CO_2$ values for 1999 and 2000 came from observations (see Appendix I and Supplemental Data) and the $\Delta^{14}CO_2$ values we used for 1999, 2000, 2001, 2002, and 2003 were 90, 86, 81, 76, and 71‰ respectively. The resulting τ's were all within the range of those predicted using a constant A_b. However, they were all at the highest end of the range. Given the lack of data for 2001-2003, the enriched local $^{14}CO_2$ history, and the potential for use of re-respired $^{14}CO_2$, we contend the use of a higher constant A_b with the large error (±13‰; resulting from the standard deviation of the 1999-2000 data) is the better approach.

Radix Predictions

We estimated the fraction of new photosynthate (f_s) allocated to the storage pool and its turnover time (τ_s) by determining the values that gave the best fit (lowest χ^2) to the time-series of measurements of $\Delta^{14}C$ in new roots. If we define the range of best fit values as the region in Figure 6 with χ^2 values < 2.0, then the range of best fit values for f_s 0.5–0.6, and for τ_s is 0.5–1.2 y. The best χ^2 value (1.3) occurs for $f_s = 0.55$ and $\tau_s = 0.7$ y.

The sensitivity of Radix predictions to seasonality of C inputs was minimal. Using the previously calculated best-fit values of f_s and τ_s, simulations with and without seasonality showed a very similar fit to the data and χ^2 values that were almost identical (Table 3 and Figure 7 compare Runs 1 and 2). Based on these comparisons we conclude that the model is not sensitive to the prescribed seasonal parameterization in the region where the best fit occurs.

Radix is sensitive to the values of f_s and τ_s. The sensitivity occurs primarily with fitting the last four data points. All values of f_s and τ_s predict highly enriched root $\Delta^{14}C$ values in 1999 (Figure 7). Beginning May 1, new photosynthate began to be generated and most of the growth was from this newly produced and highly enriched C source. Thus, the $\Delta^{14}C$ value of the storage pool, and the amount of it used had little impact on root $\Delta^{14}C$ values in early 1999. Post 1999, the low values for f_s (0.15; Run 3 and 0.0; Run 7) produced the poorest fit to the data because the storage pool did not supply enough ^{14}C to sustain the enrichment at the measured levels. For simulations where $f_s = 0.55$, the effect of varying τ_s was not large, (compare Runs 1, 4 and 5), although the longer τ_s values produced a poorer fit. Run 6 ($f_s = 1$), which simulated the mixing of stored and recently fixed C in one pool, matched the first and second data points well, but could not reproduce the higher $\Delta^{14}C$ values measured in 2001 and 2002.

Mean Age of New Root Tissues at East ORR

We calculated the mean age of C making up new root tissues (C_r) using equation 3 and f_s and τ_s calculated from both the one-pool and Radix models. For the former, mean values for f_s and τ_s were 52% and 0.7 y, respectively and C_r was 0.4 y (with a range of 0.2 to 0.8 y due to range in A_b and all non-root values of τ_s in Table 2). For Radix, mean values for f_s and τ_s were 55% and 0.7 y, respectively and C_r was 0.4 y (with a range of 0.3 to 0.7 y if the range in best fit f_s and τ_s were used). In the one-pool analysis, we assumed that the age of storage C used for

aboveground growth—in other words from leaf buds--was the same as that fueling new root growth. We did not use the storage-pool τ calculated from new roots (i.e., τ = 0.8 y; Table 2) because new roots may contain a mixture of stored and recently fixed C (unlike leaf buds and expanding leaves which are grown entirely from stored C). The calculation was not sensitive to T_{rf} (turnover time of new photosynthate); doubling T_{rf} from one to two weeks increased C_r by only 0.01 y in each case.

Mean age of New Roots Using the Bomb-^{14}C Technique

At the three bomb-^{14}C sites, mean Δ^{14}C values of new roots differed from Δ^{14}C values of (1) local air by 2–7‰ and (2) tree-ring cellulose by 0–4‰ (Table 4). There were no significant differences between ^{14}C content of new roots and of either air or tree-ring cellulose samples (α=0.05; see Table 4) in any case. Therefore, storage inputs to new fine-root growth were undetectable using the bomb-^{14}C approach. The age of C used in new fine-root growth must be less than 1-2 y, which is the limit of the technique, given our AMS analytical error of 4–6‰, a decline in northern hemisphere atmospheric $\Delta^{14}CO_2$ between 1998 and 2003 of ~6‰ y^{-1} (Levin and Kromer 2004), and a decline of ~ 5‰ y^{-1} in tree-ring Δ^{14}C values for 1998–2003 (based on measured tree-ring values at each site; Supplemental Data). More samples with higher precision AMS measurements of ^{14}C would be required for a more accurate determination of the mean age of new root tissues using the bomb-^{14}C signal. *In situ* ^{13}C or low-level ^{14}C labeling experiments (Carbone *et al.* 2007) may be a more cost-effective approach for more precise quantification of C storage, if labeling could be accomplished on mature trees.

Summary of Storage Contributions

Analysis of $\Delta^{14}C$ values for leaf buds and expanding leaves using the one-pool model showed that aboveground tree tissues were grown using stored reserves with mean age that ranged between 0.5 and 1.0 y (Table 2).

We estimated that the mean age of C reserves contributing to new fine-root growth (τ_s) was 0.7 y by two approaches. First, Radix had best fit τ_s of 0.7 y with a range of 0.5-1.2 y. Second, the one-pool model, using the ^{14}C content of parasitic plants growing on root exudates prior to full canopy leaf out, showed a mean age of stored C of 0.7 y with a range 0.5-1.0 y (Table 2).

The fraction of new fine-root C coming from stored reserves annually was calculated to be 55% with a range of 50-60% using Radix, and 52% with a range of 32-79% using τ estimated from the one-pool model.

We calculated the annually averaged mean age of C in new root-tissues (after stored-C and newly-fixed C mix), C_R, at ORR to be 0.4 y (range 0.3 to 0.7 y) using Radix and 0.4 y (range 0.2 to 0.8 y) using the one-pool model. At the three bomb-^{14}C sites, the mean age of C in new root tissues was less than 1-2 y.

Discussion

Despite uncertainties in ^{14}C inputs to the ORR ecosystem, we are confident in our estimates of both the mean age of C reserves used to grow leaf buds and new roots, and the amount of new root growth coming from stored C reserves annually. This is because our two independent model approaches, the one-pool model (for which we did not need to quantify ^{14}C inputs) and Radix (for which we estimated ^{14}C inputs via East ORR ARPC), gave very similar results.

The use of storage C may be different in other ecosystem types such as boreal forests which tend not to be water limited or Mediterranean scrublands or woodlands where there is typically no summer rain. For example, three studies in boreal black spruce forests in Alaska and Canada found the mean age of stored C pools supplying root respiration, and therefore presumably root growth, to be >3-5 y (Czimczik *et al.* 2006; Schuur and Trumbore 2006; Carbone *et al.* 2007). Additionally, in a seasonally-dry scrub oak system of central Florida, one-third of the C in new-root tissues came from photosynthate fixed before the year of the study. However, a mean age for this C could not be estimated (Langley *et al.* 2002). Further work is needed, particularly in non-temperate ecosystems, to understand the amount and seasonal timing of stored C use in mature forests.

Isotopic studies of fine-root dynamics and patterns of C allocation, particularly ^{13}C or low-level ^{14}C pulse-chase studies (e.g., Carbone *et al.* 2007), could be used to investigate the influence of stored carbohydrate on time scales less than 1-2 y. In past isotopic studies, in-growth cores (used to sample new root growth) have typically been sampled at annual intervals or longer (Langley *et al.* 2002; Matamala *et al.* 2003) or not placed in the soil until several months after labeling began (Matamala *et al.* 2003). As such, they miss information on seasonal use of stored carbohydrate. In this study, for example, the influence of storage is most clear in

the isotopic measurements of roots sampled in the year immediately after the ^{14}C release. For our study, time-series measurements of root ^{14}C content in April, May–July, and August–September of 2000, as well as in April 2001, would have helped constrain seasonal patterns of storage use and improved confidence in model estimates of f_s and τ_s. Labeling studies are also needed to investigate the amount and age of stored reserves used under varying types and degrees of plant stress.

In the deciduous forest at ORR, the storage C used to grow new above- and belowground plant tissue was fixed 0.7 y ago and the mean age of C in new root-tissues is 0.4 y. At the three other forests studied here (one deciduous, two coniferous), and in two broadleaf tropical forests in the Eastern Amazon of Brazil (Trumbore *et al.* 2006); the mean age of storage C used to grow new roots was < 1-2 y. Taken together, the seven sites span a broad range of forest and ecosystem types and suggest that in several different forest types, storage reserves generally turn over quickly (are used quickly relative to stock). This implies that storage C may provide limited capacity to buffer tissue growth from stress or periods of low productivity that last more than one year.

It is possible, however, that trees have other storage pools with longer turnover times that were not accessed during these studies. The results reported here represent storage C use during years without anomalous environmental stress. None of the sites studied here experienced acute climatic stress, pest outbreaks, or fire during our study. The amount and age of C reserves used might vary under different degrees of stress such as mild versus intense fires or droughts. Under extreme conditions plants might access different reserve pools that could be older. Once photosynthate is converted to storage materials (primarily starch), it is commonly deposited into parenchyma cells where it stays until remobilized and transported outward radially toward the

cambium. The starch is available along deep-to-shallow radial axes from the inside of the tree, outwards, and therefore the sink organs very likely use the nearest (and therefore youngest) carbohydrate available (Kagawa *et al.* 2006).

Implications for Fine-root Modeling

Isotopic methods for estimating mean ages of roots compare measured isotopic values of roots, to a known and changing record of isotope values in the atmosphere (Gaudinski *et al.* 2001; Tierney and Fahey 2002; Trumbore *et al.* 2002; Matamala *et al.* 2003; Keel *et al.* 2006). These previous studies assumed plant tissues grow entirely from new photosynthesis and have the same isotopic signature as the atmosphere at the time of their growth (Trumbore *et al.* 1995; Gaudinski *et al.* 2000), and thus have a mean age of 0 y. Our work shows that this assumption is not entirely correct (for roots or leaves). For roots specifically, given that we estimated an age of the C in new root tissues of 0.4 y, this error will make up a large proportion of the estimated mean age only for fast (≤1 y) cycling roots. The error associated with this assumption decreases as the turnover time of roots increase.

To test the impact of our findings, on published estimates of fine-root lifetimes, we modified the model published in Gaudinski *et al.* (2001) to include reserve use of 55%, with a mean age of storage C of one year. The resulting root mean ages decreased by 0-2 y in all cases, with a new range of 1-17 y. Although this change is within the error of their method, it is a systematic bias and future applications of the technique should account for storage C use whenever possible.

Root populations comprise roots that cycle on time scales ranging from months to several years (Gaudinski *et al.* 2001; Tierney and Fahey 2002; Trumbore and Gaudinski 2003; Majdi and Andersson 2005). Therefore, models of fine-root dynamics (with or without an isotopic component) need to be able to handle this complexity by using, for example, multiple pools

and/or specified age distributions within a pool (Majdi and Andersson 2005; Joslin *et al.* 2006; Trumbore *et al.* 2006). This study shows that inclusion of a storage pool is also important for models of fine-root dynamics. Additionally, because the amount of storage C used to grow new roots is significant (~55%), it should be accounted for in ecosystem C budgets. For example, including stored C would be important in reconciling above and belowground net primary productivity in periods when primary production is not constant across years.

Models of root dynamics vary in their assumptions about how is stored and utilized. Radix assumes that storage exists as a distinct pool and that C used for root growth or maintenance comes either from this storage pool, or from the new photosynthate pool, or both (Figure 4). However, there are other possible model constructs. Luo 2003; Luo *et al.* 2004) assumed that stored non-structural C and new non-structural C are always mix well and are contained in the same pool before being used to drive root growth (Figure 4; analogous to our simulation with f_s = 1). Matamala *et al.* 2003; Matamala *et al.* 2004) assumed that all new growth is supported by recent C assimilation with no storage input (Figure 4; analogous to our simulation with $f_s = 0$ and $\tau_s = 0$).

We used the ORR new-root time-series data, and Radix to test which of these three constructs-- distinct as done with Radix; inclusive as in Luo (2003) and Luo *et al.* (2004); or no-storage as in Matamala *et al.* (2003; 2004)—best fit the ORR data (Table 3 and Figure 7). In the *distinct* and *inclusive* cases we used the value for τ_s that gave the smallest χ^2 in each case (0.70 and 0.35 respectively). The *distinct* construct produced the best fit to the data with a χ^2 of 1 (Run 1). The simulations with the *inclusive* storage pool (in which all new and old C mix well prior to use for growth) had a best fit χ^2 of 9 (Run 6). The inclusive simulation under-predicted $\Delta^{14}C$ values in summer 1999 (Figure 7) and appears to be less responsive to the isotopic pulse relative

to the *distinct* construct. The no-storage-pool χ^2 best fit value was 154 (Run 7). The large difference between the *no-storage-pool* construct and both of the other two constructs supports the interpretation that storage is significant for new root growth in the ORR forest. We conclude that the best framework to model C storage use has a distinct storage C pool and allows C for root growth or respiration to be drawn from both storage and new photosynthate.

Conclusion

In a deciduous forest in Tennessee, in years when trees are not under acute stress, the age of storage reserves contributing to both above and belowground tissue growth is young (0.7 y) and the mean age of C used to grow new root-tissue is 0.4 y. In three additional temperate forests (two coniferous, one deciduous), the mean age of C in new roots was less than 1-2 y. Thus C reserves appear to cycle quickly and their impact on calculation of fine-root lifetimes is small particularly for roots that live for many years. However, a significant percentage of stored C is used to grow root tissues (~55%) and this should be considered in future modeling efforts (both isotopic and non-isotopic). Research is needed on the seasonal and interannual variability in stored C use, as well as to evaluate the use of stored C as a function of ecosystem stress. These would allow us to learn more about impacts of asynchrony between photosynthetic activity and growth demand on seasonal and annual timescales.

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Table 1. Sampling and processing information for new-root samples.

	Screens Emplaced	Screens Harvested	# Screens w/ Roots[1]	# ^{14}C Samples Measured[2]	Pretreatment Method[3]	δ^{13}C Range[4] ‰	Graphing Cohort[5]
EBIS Sites[6]							
TDE	4/2/99	8/20/99	3/3	3	none	-28.1	A
	6/12/99	8/20/99	6/6	5	none	-28.1	A
	8/20/99	9/10/00	10/10	3	none	-28.1	B
	4/30/00	9/10/00	3/3	2	none	-28.1	B
	5/1/01	11/7/01	12/12	2	none	-28.1	C
Walker Branch	7/20/01	11/11/01	9/12	3	none	-28.1	C
	03/26/02	5/15/02	9/12	2	none	-28.1	D
	5/15/02	11/6/02	8/12	3	none	-28.1	E
Haw Ridge	7/20/01	11/11/01	10/12	3	none	-28.1	C
	03/26/02	5/15/02	10/12	3	none	-28.1	D
	5/15/02	11/5/2002	8/12	3	none	-28.1	E
Bomb-^{14}C Sites							
Harvard Forest	04/08/01	10/25/8/01	12	5	sox/bleach	-26.8 to -27.6	none
Blodgett	04/09/02	06/07/02	4	2	sox/bleach	-24.5	none
Knotåsen	09/03/01	8/12/2002	8	4	sox/bleach	-23.7 to -24.5	none

[1] Top number represents the amount of screens put in the field. Bottom number represents the number of screens that had roots growing through them.
[2] Samples represent roots from one screen or a composite of roots from two screens.
[3] Pretreatment was via a soxhlet/bleaching (sox/bleach) method (Gaudinski *et al.* 2005).
[4] Each sample measured individually on bomb-^{14}C samples, for EBIS sites a value of -28.1‰ was assumed (see text for details).
[5] Roots were grouped and graphed in 5 different cohorts (A-E) depending on when they grew.
[6] The large ^{14}C release at ORR occurred sometime between June 12 and July 22, 1999.

Table 2. Exponential curve fitting parameters for one-pool model.

Tissues	Equation[1]	τ (y)[2]	Time interval[3] (y)	r^2	n
Oak Buds/Expanding Leaves	$1265e^{-0.0057x}$	0.5 (0.4-0.6)	1	0.9287	10
Maple Buds/Expanding Leaves	$511e^{-0.0028x}$	1.0 (0.9-1.1)	1	0.9668	5
All Leaf Buds/Expanding Leaves[4]	$925e^{-0.0047x}$	0.6 (0.4-0.6)	1	0.8585	15
Parasitic Plants[5]	$1190e^{-0.0040x}$	0.7 (0.5-1.0)	3	0.9467	10
All Leaf Buds, Expanding Leaves and Parasitic Plants	$780e^{-0.0037x}$	0.7 (0.5-1.0)	3	0.9300	25
New Roots	$402e^{-0.0036x}$	0.8 (0.7-1.1)	3	0.5553	32

[1] The equation is $y=N_i-A_b=(N_o-A_b)e^{(-x/\tau)}$ where the background value (A_b) has been subtracted from the input data and is thus equivalent to 0‰; x is equivalent to time and τ is one divided by the exponent. See text for further explanation of symbols.

[2] Values in parenthesis represent range of results based on running the curve fit for background (88‰ ±13‰ ; i.e. 101 or 75‰). The smallest value of τ is associated with A_b of 101‰ and the highest value of τ with A_b of 75‰.

[3]Represents the period of time from the first tissue sampling to the last tissue sampling.

[4] Includes data for leaf buds and expanding leaves for both oak and maple trees.

[5]Data included are for all sampling dates (see text for details). The same A_b was also applied to parasitic plant measurements taken in April 2003 because the tissues grew from stored C fixed in the previous growing seasons over which A_b applies (i.e. 1999-2002).

Table 3. Simulations run as part of a sensitivity analysis for fraction of new photosynthate allocated to the storage pool (f_s) and the turnover time of the storage pool (τ_s) in Radix.

Run #	Run Description	f_s	τ_s [1] (y)	Seasonality	χ^2
1	Nominal	0.55	0.7	Yes	**1.3**
2	No Seasonality	0.55	0.7	No	**1.5**
3	Min f_s	0.15	0.7	Yes	**30**
4	5 year τ_s	0.55	5	Yes	**15**
5	10 year τ_s	0.55	10	Yes	**21**
6	Inclusive Storage	1	0.35	Yes	**9**
7	No storage	0	0	Yes	**154**

[1]Annually flux-weighted value.

Table 4. $\Delta^{14}C$ values for new roots, local air, local tree-ring cellulose, and global background air. Units are $\Delta^{14}C$‰ and values in parenthesis represent standard error.

Site	Blodgett Forest		Harvard Forest		Knotåsen		Harvard Forest	
Year	**2002**	**n**	**2001**	**n**	**2002**	**n**	**1999**	**n**
New Roots	63 (5)	9	77 (1)	5	81 (3)	4	90 (2)[1]	5
Local Air	69 (2)	9	75 (1)[2]	2	74 (2)	3	93 (3)[3]	3
Local Tree-Ring Cellulose	62 (2)	1	80 (2)	1	77 (2)	1	90 (2)	1
Global Background Air[4]	75 (2)		81 (2)		75 (2)		90 (2)	
New Roots minus Local Air	-6		2		7		-3	
New Roots minus Tree-Ring Cellulose	-1		-3		4		0	
P value New Roots/Local Air[5]	0.1468		0.1675		0.0546		not done	
P value New Roots/Local Tree-Ring Cellulose[6]	0.8640		0.1070		0.3070		not done	

[1] Gaudinski *et al.* 2001.

[2] Air samples collected in 2002, we added 4‰ to average value to estimate 2001.

[3] Gaudinski and Trumbore unpublished data.

[4] Levin and Kromer 2004.

[5] *P* value obtained from Student's *T*-Test (2 sample assuming unequal variance).

[6] *P* value obtained from Student's *T*-Test (1 sample assuming known value-i.e. wood value).

Figure Legends

Figure 1. Location map for the Oak Ridge Reservation. Shown are all four sites that are part of the EBIS project (WB, HR, TVA and PR) as well as TDE which was originally developed for a separate experimental program (see text for more details).

Figure 2. $\Delta^{14}C$ values for background northern hemispheric air and local East ORR tree rings (n = 1 in each case). Northern hemispheric air values (straight line) come from Levin and Hessheimer (2000) for 1950-1976 and Levin and Kromer (2004) for 1977-2003. The tree-ring cellulose data from 1950-1975 (filled circles) come from one white oak on TDE; data from 1976-2002 (open circles) come from 4 different trees (3 white oaks, one Chestnut oak) from WB and HR. They are separated into annual increments except during 1999 and 2000 were they were separated into 3 increments per year. The elevated tree-ring values in 1999 and 2000 show clear influence of a strong local ^{14}C pulse at ORR. See Appendix I, Figure 1 for smaller scale presentation of post 1998 tree-ring data.

Figure 3. Atmospheric radiocarbon proxy curve (ARPC) for East ORR and $\Delta^{14}C$ values of new roots over time. Dashed lines represent one standard deviation of the ARPC curve. Letters indicate the "cohort" to which roots belong and key them to information in Table 1. For the new root values, the horizontal line and the placement of each data point constrain the time interval during which the root tissues could have grown.

Figure 4. Modified Radix model (see Riley et al. (this issue) for full model description). In Radix, new photosynthate (f_s) is represented by belowground primary productivity, τ_s represents the steady state turnover time of the storage pool, and R_1 is respiration from the live root pool (L_1). For this study, root death is assumed to occur only at root harvest (See Table 1 for root harvest dates).

Figure 5. (a) The local EBIS pulse of ^{14}C was released at some time between June 12 and July 22, 1999 (represented by vertical dashed lines). Data are plotted along the x-axis at the date of tissue harvest. (b) The same data as 5a, except all values have had the $\Delta^{14}C$ value of newly-fixed photosynthate (i.e. A_b or background; 88‰) subtracted so that the y-intercept values can be used in equation 2. Therefore, A_b is represented by 0‰ on this graph. The x-axis represents the number of days since harvest of the first root samples.

Figure 6. Contour plot of χ^2 values, using East ORR ARPC over the space of f_s and τ_s showing the entire range evaluated. The lower the χ^2 value the better a particular f_s, τ_s combination fits the time series ^{14}C data measured from new root screens. These simulations were performed with seasonal use of storage reserves. White areas indicate the storage pool size is unable to supply the required C throughout the year and thus are not valid combinations of f_s and τ_s.

Figure 7. Predicted $\Delta^{14}C$ values for new roots grown in root screens for seven scenarios (Runs 1-7; see Table 3) using East ORR ARPC. For the new root values, the horizontal line and the placement of each data point constrain the time interval during which the measured root tissues could have grown. The root mass at the beginning of any growth interval is zero. Sharp changes in $\Delta^{14}C$ values indicate either root harvest or the turning on or off of new photosynthate as a source for new root growth, or both.

Figures

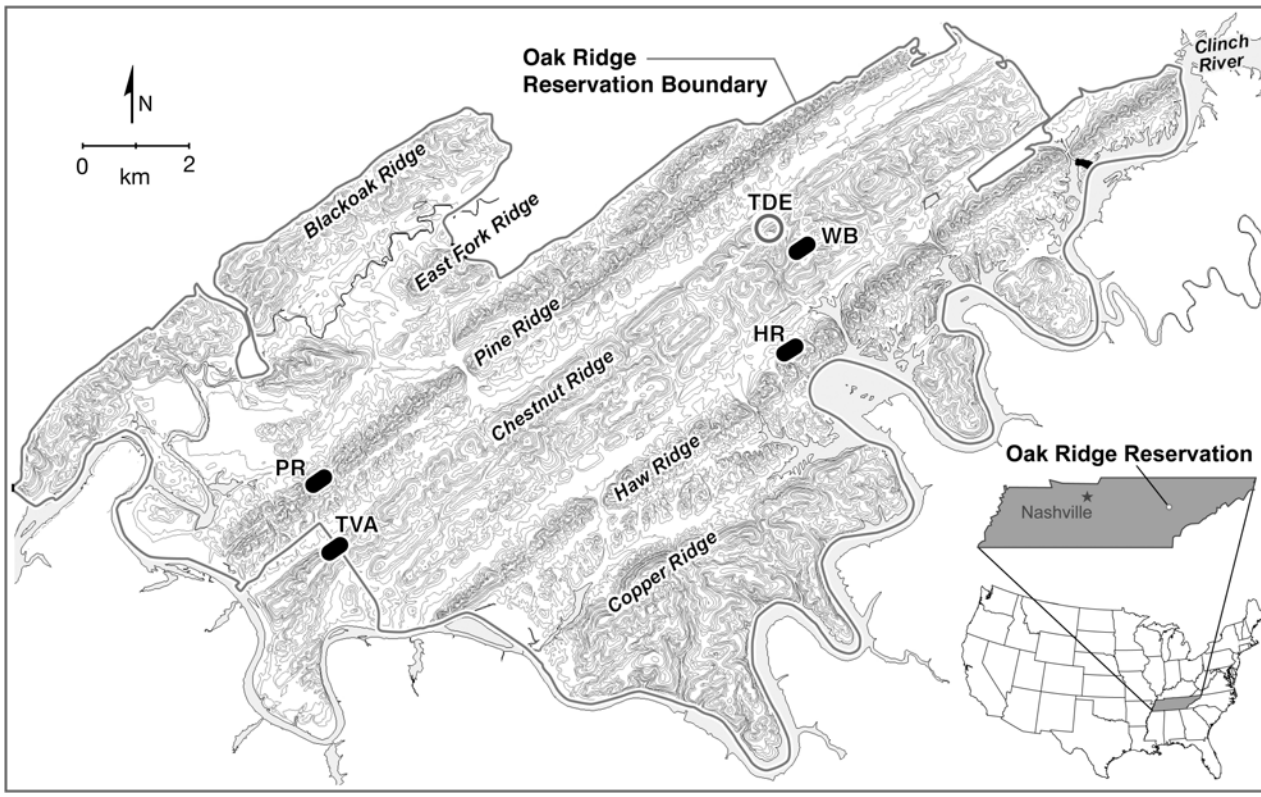


Figure 1

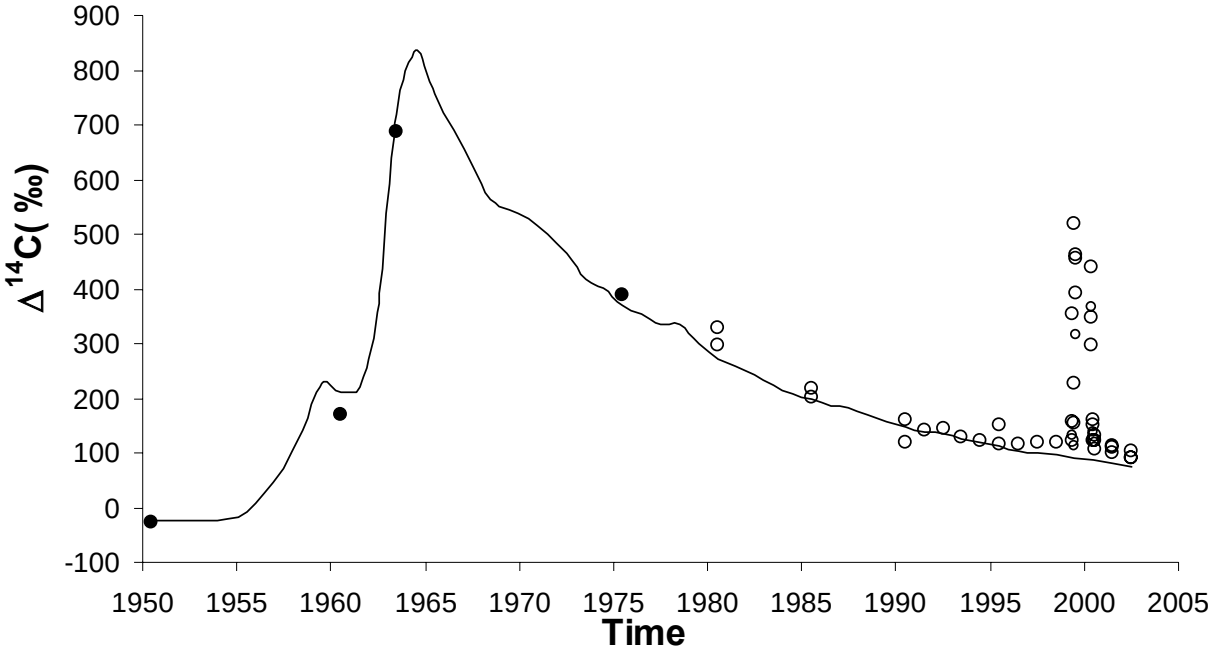

900
800
700
600
500
400
300
200
100
0
-100
Δ14C(‰)
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
Time

Figure 2

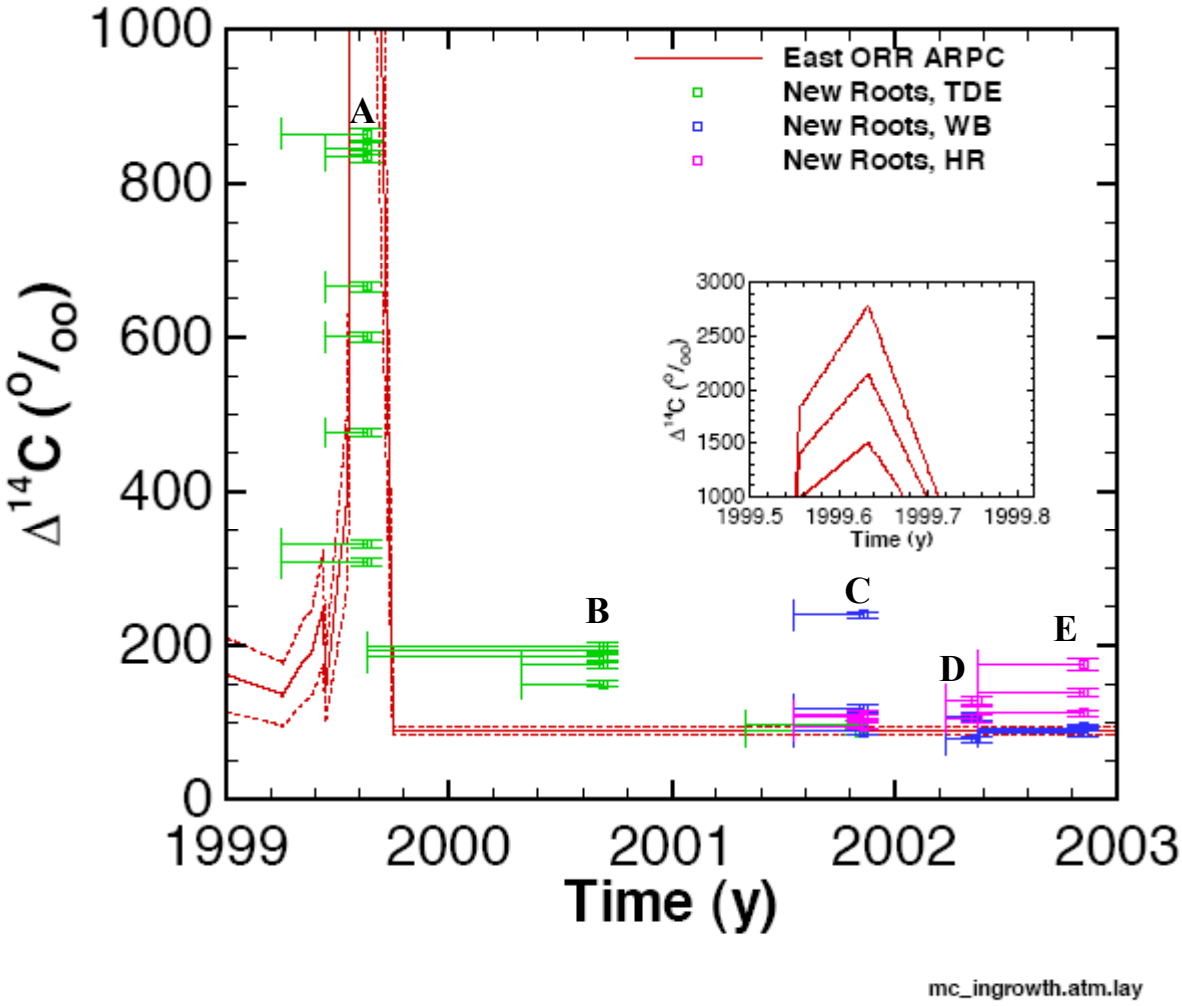

East ORR ARPC
New Roots, TDE
New Roots, WB
New Roots, HR
A
B
C
D
E
Δ14C (o/oo)
Time (y)
mc_ingrowth.atm.lay

Figure 3

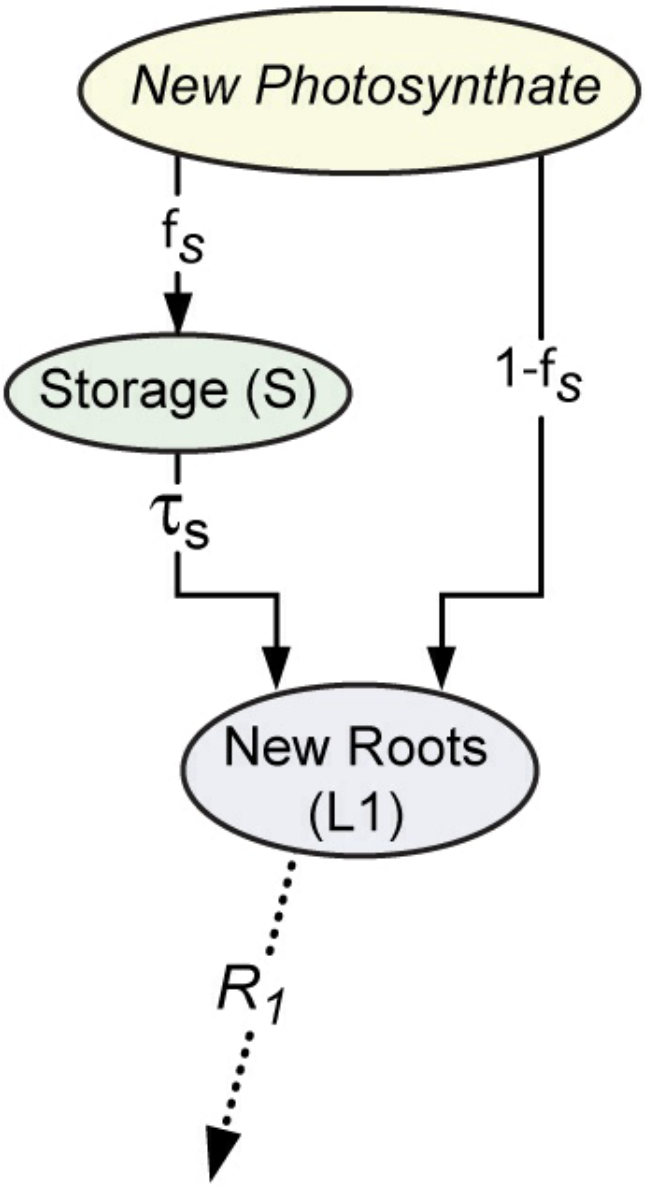
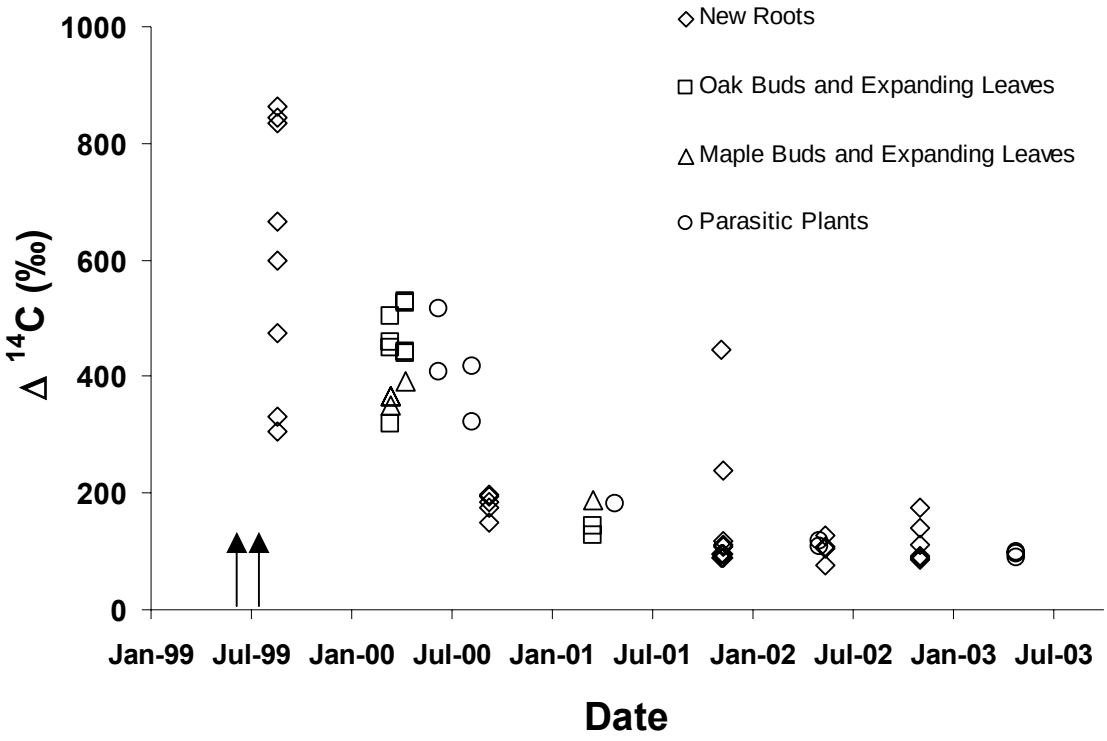


Figure 4

(a)


New Roots
Oak Buds and Expanding Leaves
Maple Buds and Expanding Leaves
Parasitic Plants
Δ 14C (‰)
1000
800
600
400
200
0
Jan-99
Jul-99
Jan-00
Jul-00
Jan-01
Jul-01
Jan-02
Jul-02
Jan-03
Jul-03
Date

(b)

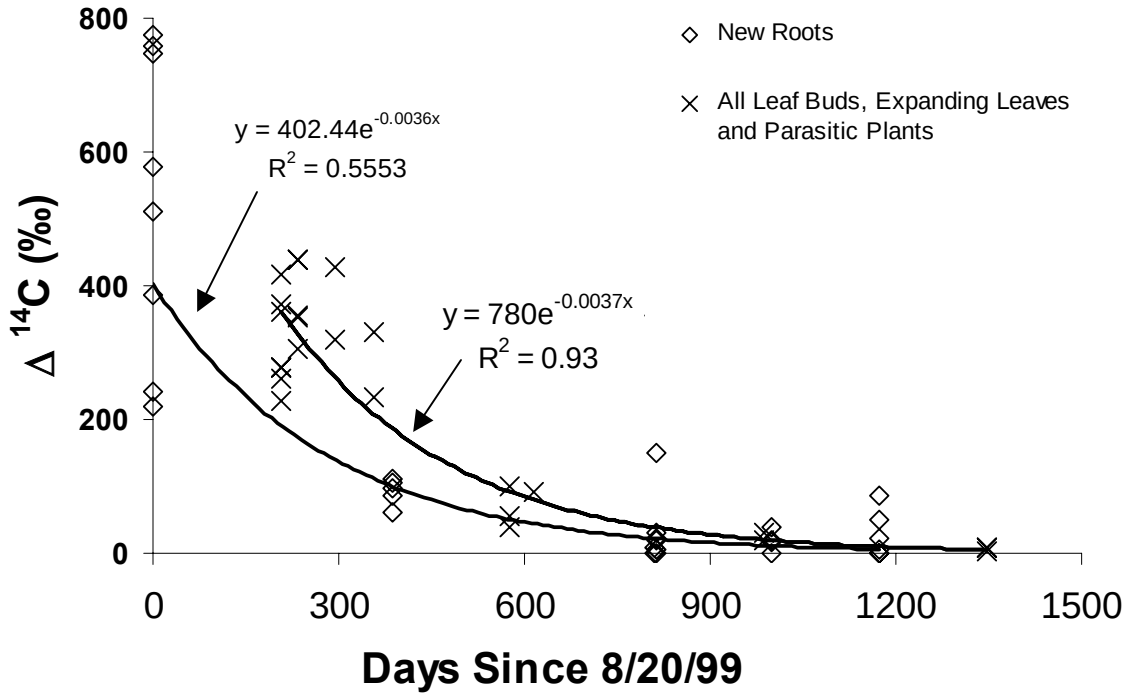

New Roots
All Leaf Buds, Expanding Leaves and Parasitic Plants
y = 402.44e-0.0036x
R2 = 0.5553
y = 780e-0.0037x
R2 = 0.93
Δ 14C (‰)
800
600
400
200
0
0
300
600
900
1200
1500
Days Since 8/20/99

Figure 5

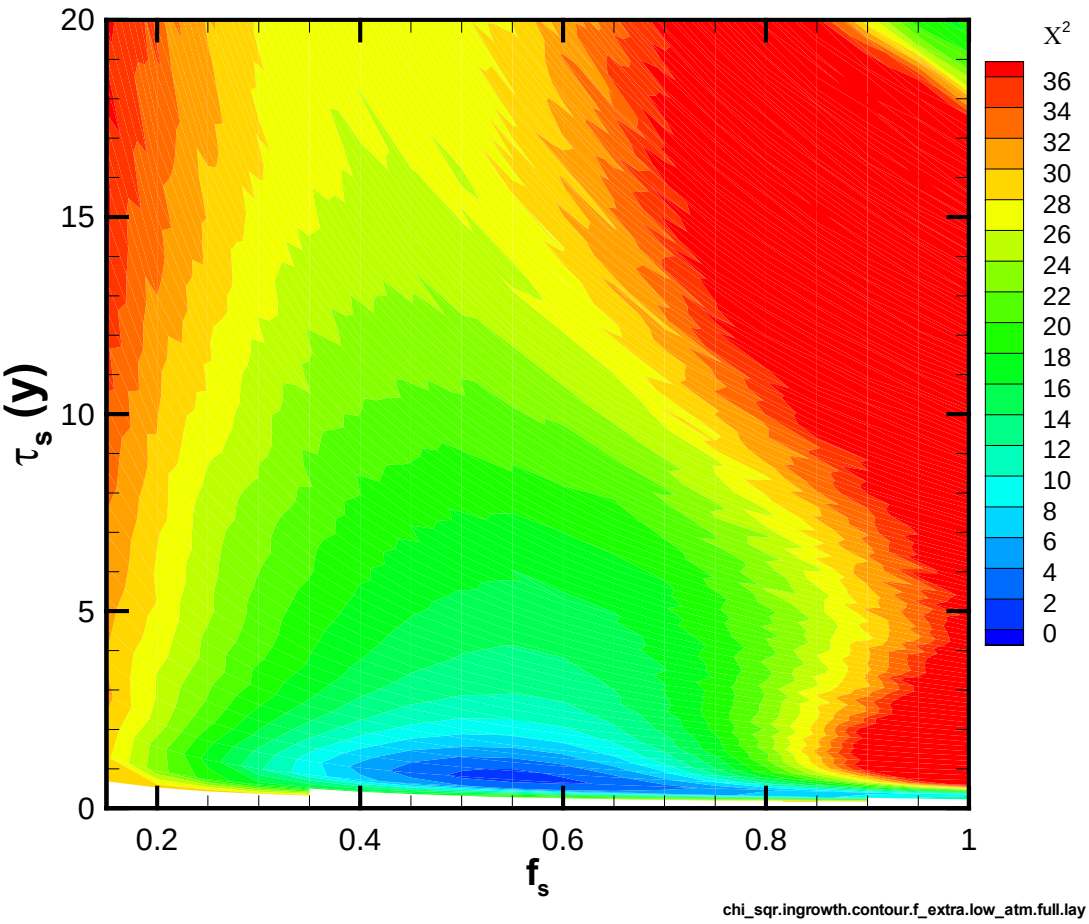

20
15
10
5
0
τs (y)
0.2
0.4
0.6
0.8
1
fs
X2
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
chi_sqr.ingrowth.contour.f_extra.low_atm.full.lay

Figure 6

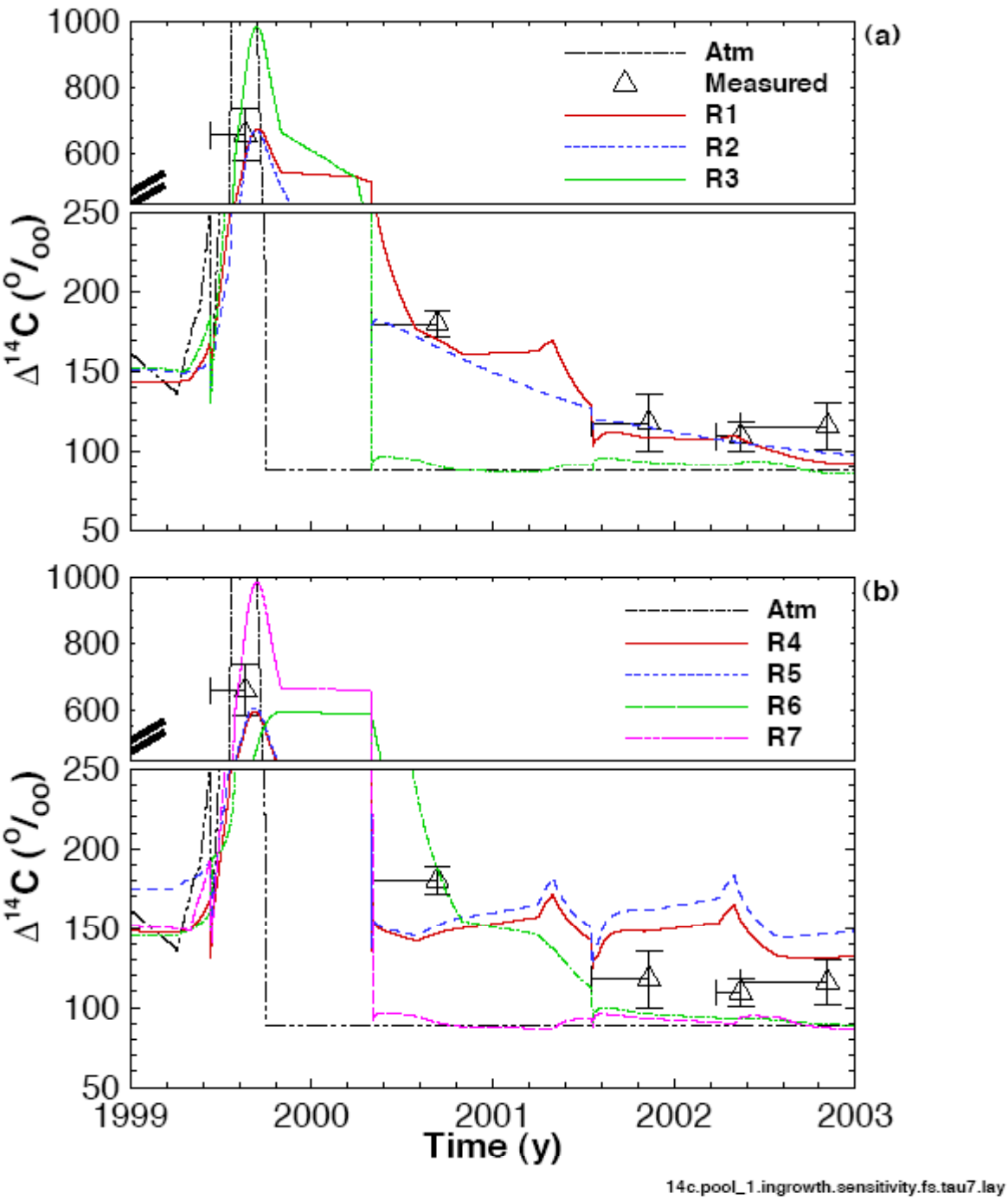

(a)
Atm
Measured
R1
R2
R3
(b)
Atm
R4
R5
R6
R7
Δ14C (o/oo)
1000
800
600
250
200
150
100
50
1999
2000
2001
2002
2003
Time (y)
14c.pool_1.ingrowth.sensitivity.fs.tau7.lay

Figure 7