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Research

Fine-root mortality rates in a temperate forest: estimates using radiocarbon data and numerical modeling

W. J. Riley[1], J. B. Gaudinski[1,2,3], M. S. Torn[1,5], J. D. Joslin[4] and P. J. Hanson[6]

[1]Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA; [2]Department of Environmental Studies, University of California, Santa Cruz, CA, USA; [3]Department of Integrative Biology, University of California, Berkeley, CA, USA; [4]Belowground Forest Research, Apartado 104-5655, Santa Elena de Monteverde, Puntarenas, Costa Rica; [5]Energy and Resources Group, University of California, Berkeley, CA, USA; [6]Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA

Author for correspondence:
W. J. Riley
Tel: +1 510 486 5036
Email: wjriley@lbl.gov

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Summary

- We used an inadvertent whole-ecosystem ^{14}C label at a temperate forest in Oak Ridge, Tennessee, USA to develop a model (*Radix*1.0) of fine-root dynamics. *Radix* simulates two live-root pools, two dead-root pools, non-normally distributed root mortality turnover times, a stored carbon (C) pool, and seasonal growth and respiration patterns.
- We applied *Radix* to analyze measurements from two root size classes (< 0.5 and 0.5–2.0 mm diameter) and three soil-depth increments (O horizon, 0–15 cm and 30–60 cm).
- Predicted live-root turnover times were < 1 yr and ~10 yr for short- and long-lived pools, respectively. Dead-root pools had decomposition turnover times of ~2 yr and ~10 yr. Realistic characterization of C flows through fine roots requires a model with two live fine-root populations, two dead fine-root pools, and root respiration. These are the first fine-root turnover time estimates that take into account respiration, storage, seasonal growth patterns, and non-normal turnover time distributions.
- The presence of a root population with decadal turnover times implies a lower amount of belowground net primary production used to grow fine-root tissue than is currently predicted by models with a single annual turnover pool.

Introduction

In a typical year, terrestrial plants assimilate about 20 times as much CO_2 as is emitted by fossil fuel combustion (Houghton *et al.*, 2001). Of the assimilated carbon (C), some is rapidly respired back to the atmosphere (Bowling *et al.*, 2001), but a substantial fraction is used to build plant tissues. In forest ecosystems, the production of fine roots is an important component of the overall forest C balance. Roots supply C to microorganisms and soil organic matter (SOM) through root mortality, sloughing, support of mycorrhizal fungi, and exudates. Over time, root-derived SOM is returned to the atmosphere via mineralization by soil microorganisms.

To characterize tree growth, models need to include representations of fine-root mortality turnover times, decomposition turnover times, and turnover times associated with other belowground C-cycle processes, such as respiration and exudation. The need to separately include these processes arises because their C fluxes depend differently on environmental factors, life histories, soil properties, and nutrient conditions. These basic components of the root C cycle remain uncertain (Trumbore & Gaudinski, 2003; Johnston *et al.*, 2004; Majdi *et al.*, 2005) and poorly characterized in models.

Recent studies using isotopic approaches have shown that root lifespans are very heterogeneous and range from months to more than a decade (Gaudinski *et al.*, 2001; Luo, 2003; Matamala *et al.*, 2003; Tierney *et al.*, 2003; Joslin *et al.*, 2006; Keel *et al.*, 2006). Fine roots have a positively skewed population age distribution, with young roots much more likely to die than older roots (Wells & Eissenstat, 2001; Tierney & Fahey, 2002). There is also a growing body of evidence that mortality turnover time depends on nitrogen (N) content and mycorrhizal association (Pregitzer *et al.*, 1997; Bidartondo *et al.*, 2001; Wells & Eissenstat, 2001; King *et al.*, 2002; Pregitzer, 2002; Guo *et al.*, 2004, 2008).

Most methods for calculating fine-root turnover have assumed uniform or normal, rather than positively skewed, age

distributions. Tierney & Fahey (2002) showed that using a normal age distribution underestimated mean root ages in minirhizotron applications and overestimated ages in isotopic applications. Guo *et al.* (2007) used a statistical model of fine-root populations that included root order and mortality probability distribution (e.g., lognormal or normal) to investigate differences between minirhizotron- and ^{14}C-based inferences of root turnover. They concluded that mortality estimates did not depend strongly on the turnover time distribution. Additionally, they concluded that the two main reasons for differences between minirhizotron and isotope-derived turnover time estimates were overemphasis of fast cycling roots by the root-number-based (minirhizotron) method, and underemphasis of fast cycling roots by the root-mass-based (isotope) method.

Root respiration is one of the largest C fluxes through roots, and may play a large role in controlling the isotopic composition of root tissue. Nevertheless, to our knowledge it has not been explicitly included in any root turnover models that use isotopes as constraints (Caldwell & Camp, 1974; Milchunas *et al.*, 1985; Gaudinski *et al.*, 2001; Luo, 2003; Matamala *et al.*, 2003; Trumbore *et al.*, 2006), at least partly because it is difficult to measure and therefore uncertain in magnitude and temporal variability.

Our goals in this study were: to estimate mortality and decomposition turnover times of live and dead roots, respectively; to estimate C fluxes out of the dead-root pool; and to characterize the sensitivity of predicted fine-root Δ^{14}C values to assumptions about root mortality turnover distributions, fine-root pool structure, and respiration. We developed a new model of fine-root C dynamics (*Radix1.0*), which accounts for: (1) short-lived and long-lived roots, each with right-skewed age populations; (2) stored-C and ^{14}C inputs to root growth and respiration; (3) seasonal variation in root respiration and growth rates; (4) structural versus nonstructural C in long-lived fine roots; (5) two dead-root pools; and (6) uncertainty in forcing variables and model parameters. We tested *Radix* using published ^{14}C data from live and dead roots from a mature deciduous forest (Joslin *et al.*, 2006) that was labeled with $^{14}CO_2$ in 1999 (Trumbore *et al.*, 2002). The site, on the Oak Ridge Reservation (ORR), Oak Ridge, Tennessee (USA), is part of the Enriched Background Isotope Study (EBIS; Joslin *et al.*, 2006) and provides a unique opportunity to quantify C cycling rates through mature trees on timescales ranging from months to decades.

Materials and Methods

In this section we describe the ORR site, ^{14}C data for fine-root biomass and respiration, and *Radix* model structure and parameter definitions; a series of sensitivity analyses used to improve our understanding of C cycling through fine roots is given in the supporting material. The definition of 'fine roots' varies in the literature, but for this paper we define fine roots as those < 2 mm in diameter. We define root mortality turnover time to be the annually averaged stock of C in the root pool divided by the annual C flux leaving the pool via mortality once the system has come to a steady annual biomass cycle. Analogously, the decomposition turnover time is defined to be the annually averaged stock of C in the dead-root pool divided by the C flux leaving the pool via decomposition (at a steady annual cycle). In this paper, unless otherwise noted, 'turnover time' refers to the turnover time associated with mortality for live roots and decomposition for dead roots. The turnover times of live-root pools estimated here are *not* equivalent to their mean residence time or age because we imposed a right-skewed turnover time distribution (Wells & Eissenstat, 2001; Tierney & Fahey, 2002).

The atmosphere near ORR was highly enriched in $^{14}CO_2$ sometime between 12 June and 22 August 1999, presumably from a hazardous waste incinerator near West ORR. In this analysis, we used previously published data on root biomass and ^{14}C content from before, during, and after this period in four upland oak forest sites on and near the ORR (Joslin *et al.*, 2006). Mean annual precipitation on ORR is 1358 mm and mean annual temperature is 14.1°C (Johnson & Van Hook, 1989). For further information on the site, ^{14}C measurements, and estimated local atmospheric ^{14}C content, see Supporting Information Methods S1 and Gaudinski *et al.* (2009).

Model description

We designed *Radix* to: represent processes and ecosystem characteristics important in root growth and function; interpret ^{14}C measurements in the context of fine-root C cycling rates; and have a sufficiently general structure that the model can be applied at other sites. *Radix* is a departure from previous fine-root models in that it explicitly includes two live- and two dead-root pools, each with their own turnover time distributions. To estimate turnover times and C fluxes, we run the model with root data sorted into depth intervals and two size classes (diameter < 0.5 and ≥ 0.5–2). Each modelled size class therefore has fast and slow cycling roots.

The development of models (like *Radix*) requires a balance between the desire to include all mechanisms hypothesized to be important and restrictions based on (1) uncertain parameter characterization; (2) uncertainty in boundary and initial conditions; (3) uncertainty in assumed system structure; (4) limited availability of measurements to test model predictions; and (5) computational resources. We attempted to balance these factors in the model development; however, we expect the model structure and parameterizations will improve as more information becomes available.

Model structure

Radix represents C flows through fine roots with the following pools (Fig. 1): storage (S), live roots with fast turnover (L_1),

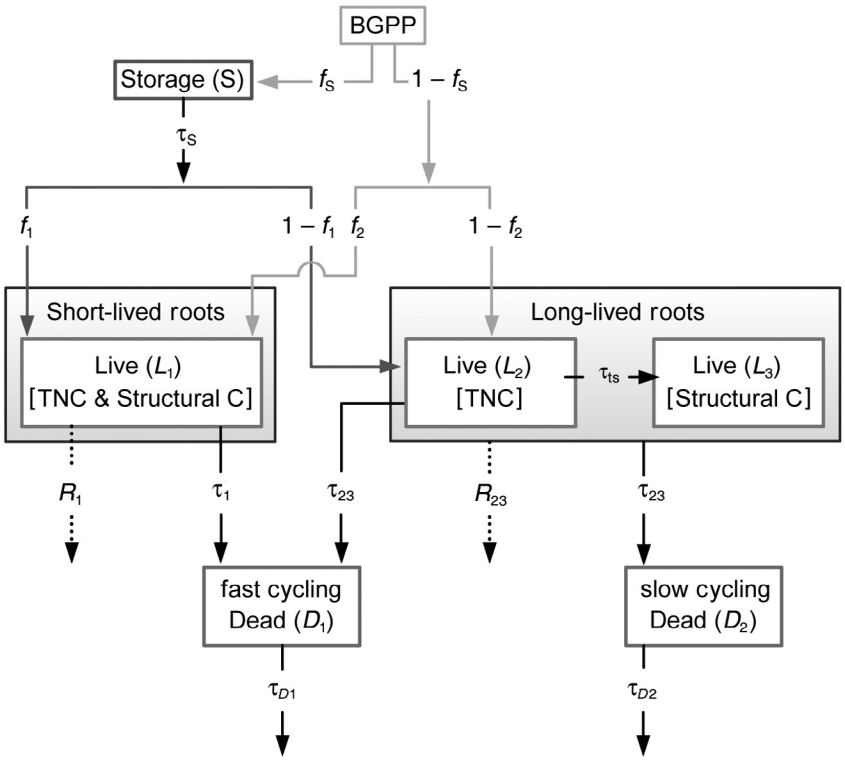

Fig. 1 Schematic structure of the *Radix* root model. Carbon (C) enters the root system and is allocated to storage (S) and live-root pools L_1 (short-lived) and L_2 (total nonstructural C (TNC) in longer lived roots). L_2 and L_3 (structural C) make up a single root but are considered as separate pools to distinguish nonstructural and structural C. C moves between L_2 and L_3 with turnover time τ_{ts} and all live pools respire and experience mortality. C flows into the fast-cycling dead roots from the L_1 and L_2 pools and into the slow-cycling dead roots from the L_3 pool.

live roots with slow turnover (divided into nonstructural (L_2) and structural (L_3) components), dead roots from the fast-turnover pool and nonstructural C in dead roots from the slow-turnover pool (D_1), and structural C from dead roots with slow turnover (D_2). A fraction (f_s) of recently fixed photosynthate is stored while the remainder ($1 - f_s$) is used immediately by roots (Fig. 1). The model conceptualizes storage as well-mixed carbohydrate pools of equal turnover times in one or more locations within the tree. While stored C is used in both aboveground and belowground growth, we assumed that the isotopic composition of the storage pool used to grow roots is controlled by C transfers to roots. However, in this forest the distinction is not critical because the turnover time of storage used to grow leaf buds, expanding leaves, and fine roots is similar (0.7 yr) (Gaudinski *et al.*, 2009). Carbon from recent photosynthate and storage is directed to live roots using the parameters f_1 and f_2 (Fig. 1); the effect of uncertainty in these parameters is explored in the sensitivity analyses described in the Results section.

In the model, C can exit the live-root pools via mortality, transfer to another live pool, and respiration. Carbon can exit the dead root pools via decomposition. Because they are extremely difficult to quantify (Hogberg & Read, 2006), we did not explicitly represent fluxes associated with exudation or mycorrhizal fungi. Mortality and decomposition losses are characterized in the model using turnover times. We assumed that turnover times for each of the pools (τ_{L1}, τ_{L23}, τ_{D1}, and τ_{D2}) are lognormally distributed (Tierney & Fahey, 2002) with geometric standard deviations (GSDs) of 2, thereby generating a right-skewed distribution. The turnover time distributions are limited to be within a factor of 3 of the geometric mean (GM). We imposed uncertainty on the mean and GSD of this distribution. As described in the sensitivity analysis, we also explored the effects of assuming normal turnover time distributions. Respiratory fluxes are notated with '*R*' (g C m^{-2} s^{-1}). Live roots grow from stored C, newly fixed C, or a mixture, depending on the season.

L_1 can lose C via respiration (R_1) and mortality (τ_{L1}). Because these roots are short-lived, we assumed that there is no significant isotopic difference among nonstructural, structural, and respired C. Pools L_2 and L_3 collectively comprise living long-lived fine roots. L_2 represents total nonstructural carbohydrates (TNC; starch and sugar) while L_3 represents the structural (e.g., cellulose) portion. L_2 receives stored and new photosynthate and loses C via respiration (R_{23}), transfer of carbon to L_3 (characterized by the turnover time τ_{ts}), and mortality (τ_{L23}). We chose a value of τ_{ts} (0.5 yr) that produced average annual L_2 values that were within the range of published values for nonstructural carbohydrate concentrations for white oak roots (< 10 mm in diameter) growing in the Walker Branch Watershed (McLaughlin *et al.*, 1980). L_3 receives C from L_2, loses C via root mortality (τ_{L23}), and C associated with L_3 respiration is removed from L_2. The mortality turnover times for L_2 and L_3 are equivalent because when a root dies both TNC and structural pools are simultaneously lost. Pool D_1, comprised of the fast cycling component of dead roots, receives inputs

from L_1 and TNC from L_2 and loses C via decomposition. Pool D_2 receives only structural C (from L_3) and loses C via decomposition.

Model parameter determination

Values for model parameters (i.e., τ_{L1}, τ_{L23}, τ_{D1}, τ_{D2}) were estimated using a minimization of the squared differences between model predictions and observations, weighted by measurement uncertainty (Press *et al.*, 1989). The model was run from 1905 so that the inter-annual C pool size variations are steady by the time the elevated atmospheric ^{14}C event occurs in 1999.

To estimate the turnover times (τ_{L1}, τ_{L23}, τ_{D1}, and τ_{D2}) we used the live- and dead-root $\Delta^{14}C$ measurements from East and West ORR. The parameter fitting procedure sampled the following ranges of mortality turnover times: τ_{L1} = [0.1, 4] yr; τ_{L23} = [4, 19] yr; τ_{D1} = [0.1, 4] yr; and τ_{D2} = [4, 17] yr; and compared predictions averaged over a 30-d period surrounding the measurement time.

Storage

The size of the modeled storage pool is controlled by the fraction (f_s) of belowground gross primary productivity (BGPP) input to the storage pool during May–October and losses throughout the entire year. Values for f_s (0.55) and τ_s (0.7 yr) were estimated using measurements of new roots grown on the East ORR (Gaudinski *et al.*, 2009).

Root respiration

Fine-root respiration comes predominantly from recently assimilated C (Horwath *et al.*, 1994; Hogberg *et al.*, 2001; Keel *et al.*, 2006). Further, measured $\Delta^{14}C$ of root respiration at ORR had values similar to atmospheric $\Delta^{14}C$ (Trumbore *et al.*, 2002). Therefore, in *Radix*, respiration for short-lived roots (R_1) comes from the L_1 pool and respiration from long-lived roots (R_{23}) comes only from nonstructural C in the L_2 pool. The L_1 and L_2 pools are supplied by recently fixed and stored C (Fig. 1), with the relative amounts depending on the season. Evidence for autotrophic respiration containing some stored C, particularly in winter, has been found in some temperate and boreal forests (Gaudinski *et al.*, 2000; Schuur & Trumbore, 2006; Carbone *et al.*, 2007; Czimczik & Trumbore, 2007). As the mean age of stored C is young in this study (~0.7 yr; Gaudinski *et al.*, 2009), predicted $\Delta^{14}C$ values of L_1 and L_2 are always relatively close to the atmospheric value.

Total respiratory rates were estimated from field measurements of rhizosphere respiration (for roots < 1 mm (and primarily < 0.5 mm)) from four similar forests studied by Burton & Pregitzer (2002). In that study the roots were brushed, but not washed, so that some of the measured CO_2 emission may have included heterotrophic sources using labile C on the root surface. We used the average specific respiration for a mixed *Quercus* forest in Georgia, a *Quercus–Carya* and mixed hardwood forest in North Carolina, an *Acer saccharum* (sugar maple) forest in Michigan (adjusted to 18°C; 0.05 μg C g^{-1} s^{-1}), and an average temperature sensitivity factor (Q10) of 2.7 for the same four sites (Burton *et al.*, 2002) to calculate specific respiration rates for the four seasonal periods: November–March, April, May–July, and August–October. Mean 2000 and 2001 TDE soil temperatures at 10 cm depth for the four time periods were used for the Q_{10} conversions (14.0, 19.1, 20.7, and 8.6°C; Paul Hanson, unpublished data). With this method, estimated respiration rates for the four periods were 0.020, 0.033, 0.055, and 0.064 μg C g^{-1} root s^{-1}, respectively.

We note that these specific respiration rates are higher than measured rates for roots in some other forests (e.g., Majdi & Andersson, 2005; E. A. Davidson & K. Savage, unpublished data for Harvard Forest). However, root respiration rates varied by over a factor of 3 as a function of N content and diameter (Pregitzer *et al.*, 1998) in two sugar maple forests in Michigan. Use of these unscaled specific respiration rates led to unrealistically high predictions of R_{23} (i.e., larger than the proportion of C entering L_2). Therefore, we decreased the respiration rate for the long-lived roots (R_{23}) by a factor of 3 after consultation with A. J. Burton (pers. comm.) and comparison with other studies. We did not change R_1 because the L_1 root population is more representative of the types of roots measured by Burton & Pregitzer (2002). Finally, we investigated uncertainty and sensitivity of our predictions to respiration by varying the respiration rate via an adjustable scale factor (f_r).

Belowground biomass and productivity

Measured biomass values by live and dead status (live and dead categories were based on tensile strength, integrity, and color of the vascular tissue; Vogt & Persson, 1991), diameter size class, and depth interval are shown in Table 2 (see also Joslin *et al.*, 2006). Monthly, total soil column BGPP has been estimated for these sites (Hanson *et al.*, 2003b), but we were unable to directly apply these values because there was no method to partition BGPP by depth without first assuming turnover times (we used the Hanson *et al.* (2003b) estimate to partition BGPP over the year, as described two paragraphs hence). We therefore estimated BGPP by depth using measured live biomass and the best-fit turnover times as constraints.

We estimated annual BNPP* (belowground net primary productivity of new fine-root biomass) by subtracting predicted total annual respiration from predicted BGPP. We used the term BNPP* to distinguish it from total BNPP, which would also include production of exudates, fine-root hairs, and C export to mycorrhizal fungi (Clark *et al.*, 2001; Hanson *et al.*, 2003a). If root biomass is in an annual steady cycle (i.e., does not change year to year), then annual production is

equal to annual mortality, and BNPP* is equivalent to the annual fine-root mortality-derived C inputs to soil. Estimates of BGPP and BNPP* were made for each fine-root size class and depth interval.

As long as a pool is not completely depleted of C, the predicted ^{14}C content of the roots does not depend on BGPP. Root ^{14}C content does, however, depend on seasonal BGPP partitioning because of its dependence on the timing of growth relative to the changing atmospheric ^{14}C content (in our case, primarily associated with the early summer 1999 ^{14}C pulse). We assumed that BGPP was zero between November and April, when the leaves have senesced or dropped. At Walker Branch, leaf expansion occurs between 10 April (5% completion) and 11 May (95% completion; Joslin *et al.*, 2001; Hanson *et al.*, 2003c). $^{14}CO_2$ labeling of mature white oaks (*Quercus alba*) on Walker Branch showed that leaves translocate C out of leaves in May through October (Edwards *et al.*, 1989). Therefore, we assumed that photosynthate produced in April is used for aboveground growth. The periods May–July and August–October receive 72 and 28% of annual BGPP, respectively, based on minirhizotron observations at ORR of < 2 mm diameter root-length growth during November–March (5%), April (10%), May–July (65%), and August–October (20%) (Joslin *et al.*, 2001). We divided the 15% of observed root-length growth occurring in November through April evenly among the 6 months between May and October. The resulting BGPP partitioning for May through October was: 0.24, 0.24, 0.24, 0.09, 0.09, and 0.09.

Uncertainty analysis

Each parameter and forcing variable used in the model is uncertain to some extent. We applied a Monte Carlo technique (Press *et al.*, 1989) to characterize the effect of these uncertainties on model predictions. For this analysis we assumed limited normal distributions for the following parameters: f_s, f_r, τ_{ts}, f_1, and f_2. The distributions were limited in that we enforced a limit of two standard deviations (SDs), thereby ensuring that unrealistic parameter values were excluded. We did not include the effects of parameter covariation in this analysis. For the model turnover times (τ_{L1}, τ_{L23}, τ_{D1}, τ_{D2}), the uncertainty in GM was normally distributed. For values that vary seasonally (e.g., BGPP), the annual value of the parameter changed between Monte Carlo simulations, but the relative monthly proportion did not. Because of the large uncertainty in atmospheric $\Delta^{14}C$ (Δ_{ARPC}), a scaling factor with a GM of 1 and GSD of 1.3 (East ORR) or 1.7 (West ORR) was applied to Δ_{ARPC} in each Monte Carlo simulation (Gaudinski *et al.*, 2009).

The Monte Carlo technique involved performing 300 simulations, each with a different set of parameters and boundary conditions based on the probability distributions described above. Mean and uncertainty ranges for the predicted quantity of interest (e.g., the $\Delta^{14}C$ value of pool L_1) were then computed from the ensemble simulation results.

Sensitivity analyses

Once the best-fit values for τ_{L1}, τ_{L23}, τ_{D1}, and τ_{D2} had been determined, we investigated model sensitivity to various model structures and parameters. We performed a series of six analyses (focusing on roots < 0.5 mm in the 0–15 cm depth interval) on the sensitivity of model predictions to: (1) live fine-root mortality turnover times (τ_{L1} and τ_{L23}); (2) the assumption of lognormally distributed turnover times; (3) the use of a simpler, one-pool model construct; (4) the distinction between structural and nonstructural C in live-root pools; (5) variations in seven critical model parameters; and (6) separating the East and West ORR ^{14}C observations (see Methods S1 for a more detailed description of these analyses).

Results

Predicted turnover times

Predicted and measured fine root $\Delta^{14}C$ values from East and West ORR were well above the atmospheric background during the entire 3-yr sampling period (2001–2003), demonstrating the substantial influence of the local ^{14}C release (Figs 2, 3). Best-fit turnover times for the three depth intervals (O horizon, 0–15 cm, and 30–60 cm), and two size classes of roots (< 0.5 and 0.5–2.0 mm diameter) were 0.1–0.3 yr for the fast-turnover root pool (τ_{L1}), 7–9 yr for the slower turnover live pool (τ_{L23}), 2 yr for the fast-turnover dead-root pool (τ_{D1}), and 9–10 yr for the slow-turnover dead-root pool (τ_{D2}) (Table 1). An example, best-fit turnover time distribution for τ_{L1} is shown in Fig. S1. We predicted no substantial differences in turnover time with depth or size class.

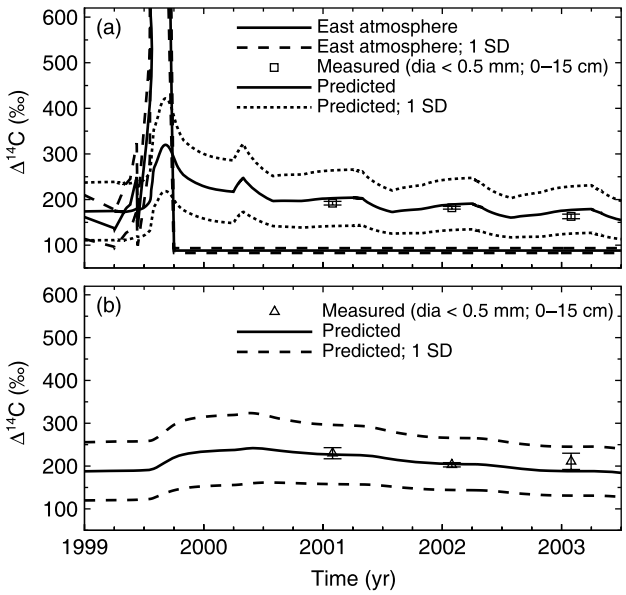

Fig. 2 Measured and predicted East Oak Ridge Reservation (ORR) $\Delta^{14}C$ values for roots from 0–15 cm depth and of < 0.5 mm diameter in (a) live and (b) dead roots.

Table 1 Predicted turnover times for two root size classes at three depth intervals using 3 yr of root ^{14}C data from the Oak Ridge Reservation sites

Diameter (mm)	τ_{L1}		τ_{L23}		τ_{D1}		τ_{D2}	
	< 0.5	0.5–2	< 0.5	0.5–2	< 0.5	0.5–2	< 0.5	0.5–2
Horizon								
O	0.2	0.1	7	8	2	2	10	9
0–15 cm	0.2	0.3	8	9	2	2	10	9
30–60 cm	0.2	0.2	9	9	2	2	9	9

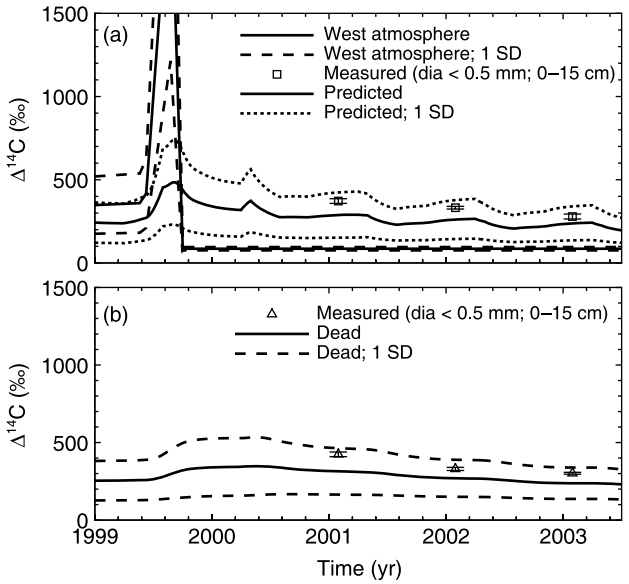

Fig. 3 Measured and predicted West Oak Ridge Reservation (ORR) $\Delta^{14}C$ values for roots from 0–15 cm depth and of < 0.5 mm diameter in (a) live and (b) dead roots.

Comparison of measured and predicted $\Delta^{14}C$ values

Predicted mean $\Delta^{14}C$ values of live roots < 0.5 mm from the 0–15 cm depth interval were slightly higher than those measured on the East ORR (Fig. 2a) and somewhat lower than those measured on the West ORR (Fig. 3a). All the live-root measurements fell within the 1 SD uncertainty bounds of the predicted $\Delta^{14}C$ values. The peak in live-root $\Delta^{14}C$ at the beginning of 2000, and all subsequent peaks, resulted from seasonal increases in use of storage C.

Predicted dead-root $\Delta^{14}C$ values on the East ORR matched measurements relatively well (Fig. 2b). Most predicted West ORR (Fig. 3b) dead-root $\Delta^{14}C$ values were lower than measurements, although again within the 1 SD uncertainty bounds. Differences between measured and predicted $\Delta^{14}C$ values were similar to those shown in Fig. 3 for the other depth intervals and size classes.

The uncertainty ranges in predicted $\Delta^{14}C$ values for the live pools were large and dominated by uncertainty in local atmospheric $^{14}CO_2$ (Δ_{ARPC}). The uncertainty bounds were largest when Δ_{ARPC} was largest, and declined after the peak values in 1999. To illustrate the effect of uncertainty in Δ_{ARPC} on live-pool $\Delta^{14}C$ values, we performed simulations that eliminated uncertainty in Δ_{ARPC}. In these simulations, the 1 SD uncertainty bounds in live-root ^{14}C content were reduced by about one-third compared with simulations including Δ_{ARPC} uncertainty.

Belowground biomass and productivity

We predicted large seasonal variability in the biomass of short-lived roots (L_1): a factor of about 3 between minimum (early spring) and maximum (mid-summer) values (Fig. S2a). Because $L_2 + L_3$ are long-lived, the overall $L_2 + L_3$ biomass was less variable than L_1 biomass (Fig. S2a). Predicted variation in root biomass between summer and winter was similar to that observed in other temperate hardwood forests for which monthly or bimonthly sampling of live- and dead-root biomass has been performed (McClaugherty *et al.*, 1982; Aber *et al.*, 1985).

For the combined O horizon, 0–15 cm, and 30–60 cm depth intervals, 35 and 65% of predicted BGPP were associated with roots < 0.5 and 0.5–2 mm, respectively (Table 2). Total mortality-derived C input to soils (BNPP*) for the three depth intervals combined was 30% of BGPP, with 40 and 60% of that derived from roots < 0.5 and 0.5–2 mm, respectively. To estimate BGPP and BNPP* in the 15–30 cm and 60–90 cm intervals (which were not simulated because ^{14}C data were unavailable, although biomass data were available), we assumed that the ratio of production to biomass was the same in these depth intervals as in the 30–60 cm interval. Including the values estimated in this way, BGPP and BNPP* to 90 cm depth were 360 and 110 g C m^{-2} yr^{-1}, respectively.

Sensitivity analyses

The sensitivity analyses were designed to probe important aspects of the model structure and parameterization, to aid in understanding which system components most strongly affect fine-root C exchanges, and inform future experimental and observational work. Results for the first sensitivity analysis (varying the live fine-root short- and long-lived mortality turnover times; τ_{L1} and τ_{L23}) showed that, as τ_{L1} increased, the L_1 pool size increased and its response rate to the input ^{14}C pulse decreased, as did the rate of subsequent ^{14}C loss (Fig. 4a). Predicted $\Delta^{14}C$ values for L_1 using $\tau_{L1} = 0.2$ and 2 yr differed by > 100‰ and *c.* 50‰ immediately following the atmospheric pulse and 1 yr later, respectively. The effect of these

Table 2 Predicted belowground gross primary productivity (BGPP), predicted belowground net primary productivity of new fine-root biomass (BNPP*), and measured biomass for two root size classes at three depth intervals

	Predicted BGPP (g C m^{-2} yr^{-1})		Predicted BNPP* (g C m^{-2} yr^{-1})		Measured live biomass (g C m^{-2})		Measured dead biomass (g C m^{-2})	
Diameter (mm)	< 0.5	0.5–2	< 0.5	0.5–2	< 0.5	0.5–2	< 0.5	0.5–2
Horizon								
O	20	12	7	5	10 ± 1	6 ± 1	4 ± 1	2 ± 0
0–15 cm	66	134	21	35	34 ± 3	71 ± 5	44 ± 4	43 ± 5
15–30 cm					13 ± 3	16 ± 2	18 ± 4	13 ± 2
30–60 cm	14	38	5	12	7 ± 0	20 ± 1	12 ± 2	17 ± 3
60–90 cm					8 ± 2	10 ± 4	11 ± 4	10 ± 3
0–90 cm					71 ± 6	123 ± 4	89 ± 7	85 ± 13
Total								

Measured values are from data collected at all four enriched background isotope study (EBIS) sites over 3 yr of sampling.

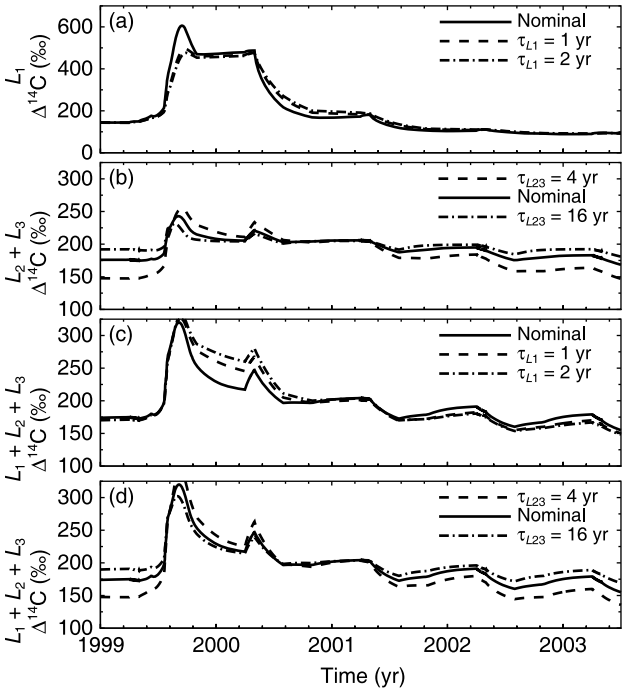

Fig. 4 Sensitivity analysis of live root Δ^{14}C values to mortality turnover times of short- and long-lived roots (τ_{L1} and τ_{L23}). Nominal values for τ_{L1} and τ_{L23} are 0.2 and 8 yr. (a) L_1 Δ^{14}C value for the nominal case and τ_{L1} = 1 and 2 yr. (b) $L_2 + L_3$ Δ^{14}C values for the nominal case and τ_{L23} = 4 and 16 yr. (c) $L_1 + L_2 + L_3$ Δ^{14}C value for the nominal case and τ_{L1} = 1 and 2 yr. (d) $L_1 + L_2 + L_3$ Δ^{14}C value for the nominal case and τ_{L23} = 4 and 16 yr.

differences in τ_{L1} on the total live fine-root pool ($L_1 + L_2 + L_3$) Δ^{14}C value was *c.* 50‰ in spring 2000, very small in spring 2001, and *c.* 20‰ thereafter (Fig. 4c).

The response of the long-lived fine-root ($L_2 + L_3$) pool to changing τ_{L23} was complicated by the fact that the predicted Δ^{14}C value of the pool at the beginning of the atmospheric pulse depends on τ_{L23} (Fig. 4b). This difference is not seen for the effect of τ_{L1} on the Δ^{14}C of L_1 because τ_{L1} (~0.2 yr) is small relative to the characteristic time of variability in background atmospheric Δ^{14}C. Analogous to the response of L_1 to changes in τ_{L1}, the Δ^{14}C of the long-lived pool responded most rapidly to the pulse when τ_{L23} was smallest (~100‰ and ~40‰ changes when τ_{L23} = 4 and 16 yr, respectively), reflecting the relative rates at which the atmospheric ^{14}C pulse was assimilated into $L_2 + L_3$. The ^{14}C content of the entire live-root pool ($L_1 + L_2 + L_3$) was sensitive to variations in both τ_{L1} and τ_{L23} (Fig. 4c,d).

The second sensitivity analysis assumed normal distributions for the mortality turnover times (τ_{L1} and τ_{L23}) instead of lognormal distributions. The effect on the mean predictions over time was between 5 and 20‰, with the normal turnover time distributions resulting in more enriched values than the lognormal distributions. This result is consistent with the lognormal distributions resulting in higher flux-weighted turnover times than the normal distributions when using the same values for GMs and means. Therefore, the live pools with the lognormal distribution acquired relatively less of the ^{14}C pulse in 1999, but had a relatively smaller decline over time. Given the uncertainty ranges in the data, these differences were not significant enough to distinguish which turnover time distribution type was more appropriate for this system.

Our third sensitivity analysis tested whether using only one live pool, one dead pool, and a storage pool (compared to the nominal structure of two live and two dead populations with different turnover times) changed the model's ability to match the observations. For this scenario, the best-fit turnover times were 2 and 1 yr for the live and dead pools, respectively. The fit to the data was substantially worse for both live and dead roots (Fig. 5), and the amounts of BGPP and BNPP* both increased substantially (factors of 4 and 10 for BGPP and BNPP*, respectively). The fits to the biomass data, however, were about the same for both cases. This sensitivity analysis demonstrates that conceptualizing live and dead fine roots as single pools can lead to substantial errors in C transfers from roots to soil.

Table 3 Sensitivity of annual averaged live ($L_1 + L_2 + L_3$) and dead ($D_1 + D_2$) biomass and $\Delta^{14}C$ values (before the large 1999 pulse) to 50% increases and decreases in model parameters

	$L_1 + L_2 + L_3$ (%)		$D_1 + D_2$ (%)		$\Delta^{14}C$ of $L_1 + L_2 + L_3$ (‰)		$\Delta^{14}C$ of $D_1 + D_2$ (‰)	
Parameter	Reduce	Increase	Reduce	Increase	Reduce	Increase	Reduce	Increase
f_r	**72**	**–28**	**51**	**–21**	2	–1	**10**	–5
f_1	**20**	**–20**	0	2	0	–4	**18**	**–17**
τ_{ts}	4	–4	5	–4	1	–1	3	–1
τ_1	–4	0	11	–7	1	–1	–5	4
τ_{L23}	–16	8	**32**	–14	**–30**	**13**	2	**–10**
τ_{D1}	0	0	**–23**	**25**	0	0	**16**	**–7**
τ_{D2}	0	0	**–26**	**26**	0	0	**–23**	**6**

Values shown are either per cent or per mil (‰) changes from the nominal case. Parameters causing a > 20% change in biomass or a > 6‰ (the analytical error in the ^{14}C measurement) change in $\Delta^{14}C$ value are shown in bold. The largest effects on live biomass were from f_r; those on dead biomass were from f_r, τ_{L23}, τ_{D1}, and τ_{D2}; those on live $\Delta^{14}C$ values were from τ_{L23}, and those on dead $\Delta^{14}C$ values were from f_r, f_1, τ_{D1}, and τ_{D2}.

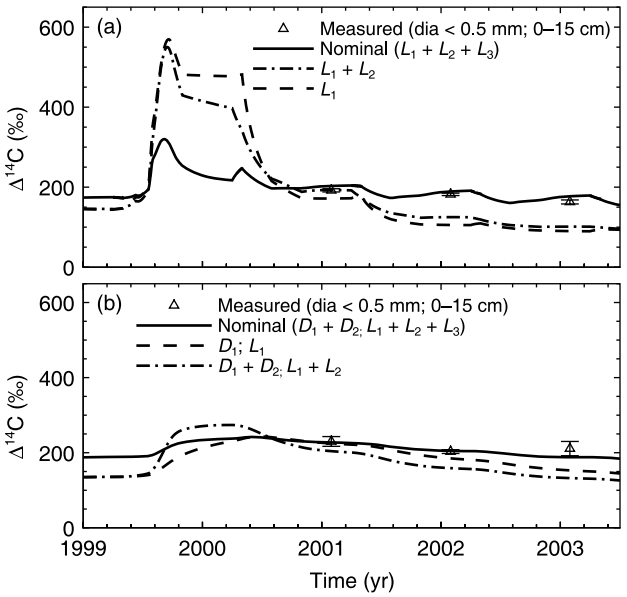

Fig. 5 East Oak Ridge Reservation (ORR) measured $\Delta^{14}C$ for (a) live and (b) dead roots from 0–15 cm depth and of < 0.5 mm diameter and model predictions using the nominal model construct (three live- and two dead-root pools) and two simplified model constructs.

The fourth sensitivity analysis investigated the need for both the L_2 and L_3 pools (in addition to L_1). In the scenario that excluded L_3, the best-fit turnover times changed only for τ_{L23}, which was reduced from 8 to 6 yr. Additionally, there was a substantially worse match with the observations (Fig. 5). In the nominal scenario (which included L_2 and L_3), most of the ^{14}C variability in the long-lived roots occurred in L_2, which made up a relatively smaller fraction of the biomass. Therefore, the total live pool ^{14}C content in the scenario that did not include L_3 responded more strongly to the atmospheric ^{14}C pulse than in the case where L_3 was included. This sensitivity analysis demonstrates that, for pulse label experiments, separating TNC and structural C in the long-lived roots is critical for accurate prediction of fine-root ^{14}C content.

As a general sensitivity analysis for eight important model parameters, we imposed variations of ± 50% on the parameters and evaluated changes during 1998, the year before the ORR ^{14}C pulse (Table 3). The largest effects on live biomass were from perturbations to respiration (f_r) and the partitioning of C leaving the storage pool (f_1). The largest effects on dead biomass were from f_r, the slow pool mortality turnover time (τ_{L23}), and the decomposition turnover times of the two dead pools (τ_{D1} and τ_{D2}). Overall, the largest changes in live plus dead fine-root biomass occurred with perturbations in the magnitude of respiration (f_r). The largest effects on live $\Delta^{14}C$ values were from τ_{L23}, and the largest effects on dead $\Delta^{14}C$ values were from f_r, f_1, τ_{L23}, τ_{D1}, and τ_{D2}.

For our sixth sensitivity analysis we tested whether different turnover times would be predicted if separate East and West ORR analyses were performed instead of the nominal analysis, which combined observations from both sides of ORR into a single data set. Both East and West ORR best-fit turnover times were within the ranges shown in Table 1. This result implies that the predicted mortality turnover times were robust for two very different atmospheric ^{14}C pulses and that the forests behaved similarly on the two different ORR ridges.

Discussion

We used an inadvertent whole-ecosystem ^{14}C label at a temperate forest in Oak Ridge, Tennessee to develop, test, and apply a model (*Radix*1.0) of fine-root dynamics. The model simulates two live-root populations, two dead-root pools, non-normally distributed root mortality turnover times, a stored C pool, and seasonal growth and respiration patterns. After using the model to estimate turnover times for two size classes and three depths, we performed sensitivity analyses to elucidate mechanisms responsible for C exchanges through the fine-root system.

While root lifetimes undoubtedly span a continuum, we found that fine roots were well described as comprising a short-lived and a long-lived population with turnover times at ORR of < 1 yr and ~10 yr, respectively (Fig. 5). Our results also indicated that it is important to distinguish structural from nonstructural components. Without the physiologically realistic separation of nonstructural and structural C in the long-lived root pool, the $\Delta^{14}C$ value of root respiration is significantly different from that of atmospheric C and forces predicted root $\Delta^{14}C$ values to be overly enriched following the atmospheric ^{14}C pulse.

Joslin *et al.* (2006) reported that roots < 0.5 mm in diameter had more rapid turnover than roots 0.5–2 mm, and that roots in the O horizon had more rapid turnover than deeper roots. We did not predict similar trends in this study, although uncertainty in predicted turnover times might have obscured such differences. Although this study used measurements of the ^{14}C content of bulk roots, better characterization of live-root turnover times could be achieved by measuring the ^{14}C content of root cellulose and TNC separately.

The *Radix* model structure and predictions are consistent with a growing body of literature arguing that roots vary widely in probability of mortality and that including this variation is necessary to model root dynamics accurately (Wells & Eissenstat, 2001; Pregitzer, 2002; Tierney & Fahey, 2002; Trumbore & Gaudinski, 2003; Majdi *et al.*, 2005; Joslin *et al.*, 2006). Our results also support the idea that the large differences in fine-root mortality turnover times derived from minirhizotrons (3 months to < 1 yr; Hendrick & Pregitzer, 1992; Jackson *et al.*, 1997; Fahey *et al.*, 1999) versus isotopic techniques (1.2–18 yr; Gaudinski *et al.*, 2001; Matamala *et al.*, 2003; Keel *et al.*, 2006) occur because these approaches are sensitive to different ends of the fine-root mortality turnover time spectrum. In other words, the minirhizotron results are strongly influenced by the short-lived roots, while results from the isotopic approaches are influenced predominantly by the long-lived roots, which have more biomass.

Uncertainty in our turnover time predictions was dominated by uncertainty in local atmospheric $^{14}CO_2$ and the lack of live-root ^{14}C measurements immediately following the ^{14}C pulse enrichment. In particular, constraints on the turnover time of the short live-root pool (τ_{L1}) would have improved markedly if we had fine-root $\Delta^{14}C$ measurements in spring 2000, because root ^{14}C content during this period strongly reflects variations in the fast-turnover pool. These observations highlight the fact that, although isotopes are useful tracers of ecosystem C fluxes, frequent sampling in the months and years immediately after any pulse labeling is required to obtain the most useful information.

Assuming that the two depth intervals for which we did not have ^{14}C data (15–30 and 60–90 cm) had BGPP and BNPP* that scaled with live biomass, we estimated column BGPP and BNPP* to be 360 and 110 g C m^{-2} yr^{-1}, respectively, for roots < 2 mm in diameter. Previous BGPP estimates (Curtis *et al.*, 2002; Hanson *et al.*, 2003b; Joslin & Wolfe, 2003) from sites on the ORR using a C budget approach were *c.* 30–70% larger than our estimate (478–619 g C m^{-2} yr^{-1}). This previous carbon budget approach may overestimate BGPP because it used: the fine-root production estimate of Joslin & Wolfe (2003); measurements of total soil respiration which included respiration by larger roots; and assumptions about the mix of heterotrophic versus autotrophic respiration. In contrast, our measured live-root biomass may be an underestimate given our root sorting protocol (see Supporting Information), which could lead to an underestimate of BGPP. Improved measurements of biomass, autotrophic respiration, and exudation, coupled with root models such as *Radix*, could help reduce uncertainty in predicted BGPP.

Estimates of annual fine-root production with root length observations (via minirhizotrons), measured biomass (from soil cores), and an implicit one-pool model for live roots on the ORR (110–140 g C m^{-2} yr^{-1}; Joslin & Wolfe (2003) and reported in Curtis *et al.* (2002)) were closer to our estimate (110 g C m^{-2} yr^{-1}). We expected our BNPP* estimate to be lower than estimates based on a one-pool model because we accounted for a large portion of fine-root biomass with decadal turnover times. Our third sensitivity analysis illustrated that using one live-root pool with a fast turnover time can accurately predict the biomass but will overestimate fine-root production. We predict that root production estimates will in general decrease as models begin to account for short- and long-lived fine roots.

Root decomposition rates are a critical component of ecosystem C modeling. We predicted that two pools are required to simulate dead root decomposition: a rapidly decomposing pool with turnover time ~2 yr and a slower pool with turnover time ~10 yr (Fig. 5). This conclusion is consistent with previous litter bag and litter recovery studies (Bird & Torn, 2006). Similar to the live-root pools, we did not predict a consistent trend of turnover time with either depth or size class. Dead-root biomass was approximately equally divided between D_1 and D_2, yet their turnover times were substantially different (Table 1, SM Fig. 2). Therefore, we predict that more of the organic C entering soil organic matter is coming from the shorter decomposition turnover time pool.

Effect of root respiration on predicted ecosystem parameters

Previous studies have ignored the effects of respiration when using isotopic measurements to infer C turnover times (e.g., Luo, 2003; Gaudinski *et al.*, 2001). To illustrate the effect of respiration on transient $\Delta^{14}C$ values (and therefore on inferred turnover times) we performed two simulations for the East ORR using the best-fit parameters (Fig. 6). The simulations differ only in that one has respiration from all the live pools forced to zero. For the live-root pools, ignoring respiration led to a substantially lower predicted peak $\Delta^{14}C$

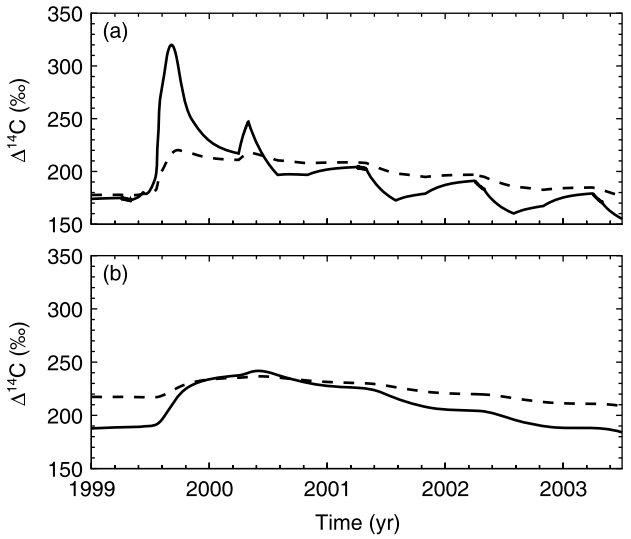

Fig. 6 Effect of ignoring respiratory CO_2 fluxes on the $\Delta^{14}C$ value of (a) live and (b) dead fine roots for Oak Ridge Reservation (ORR) following the 1999 pulse. Solid line, with respiration; dashed line, without respiration. Parameters used are the same as the nominal case discussed in the text. Predicted $\Delta^{14}C$ values of live-root pools after mid-2000 are larger and have smaller seasonal cycles in the absence of respiration. Dead-root pools in the absence of respiration also have larger $\Delta^{14}C$ values.

value (by ~100‰), higher subsequent values, and much lower seasonal variability. For the dead-root pools, ignoring respiration led to more enriched predictions after about 1 yr following the pulse.

The effects of respiration can be important for studies using ^{14}C even in the absence of a large ^{14}C pulse like that at ORR. To illustrate these effects, we performed two simulations (one with and one without respiration) using the background atmospheric ^{14}C record (i.e., the 'bomb spike') (Fig. S3). A more pronounced seasonal cycle in live-root ^{14}C content is predicted when respiration is included. In this sensitivity analysis, ignoring respiration led to differences in $\Delta^{14}C$ values of the total live- and dead-root pools of *c*. 20 and 40‰ in 2000, respectively, which would affect a ^{14}C-derived mortality turnover time by ~3 yr for live roots and ~7 yr for dead roots. These analyses demonstrate that ignoring respiration when using an isotopic label to trace C exchanges to the root system can lead to errors in estimated mortality turnover times. The errors will be larger for $^{14}CO_2$ pulse labeling experiments but are potentially significant when using more gradual changes in input ^{14}C values, such as the bomb spike.

Implications

The results of this study have important implications for ecosystem models that include C transfers through tree root systems. A large portion of live fine roots live much longer (~10 yr) than previous approaches (i.e., minirhizotron) have indicated. We demonstrated that the use of two pools to represent live roots and two pools to represent dead roots, and inclusion of root respiration are critical for accurate characterization of fine-root C fluxes. The typical ecosystem model assumption that live roots turn over annually will lead to large over-predictions of root inputs to soil organic matter. Even a model with an accurate flux-weighted turnover time, but that still treats roots as a single pool, will predict very different responses to changes (e.g., in net primary production) than would a model with two pools with distinct turnover times.

Our results highlight the need for research to understand the complexities of fine-root dynamics, including: the controls on the proportion of roots with different lifetimes; the plasticity of root growth and mortality as a function of species and environmental conditions; and the magnitude and variability of autotrophic root respiration and heterotrophic respiration of recently fixed, root-derived C. Simplifications to the *Radix* model structure should be investigated, including omitting seasonal variability in respiration and BGPP if the model is being used in scenarios not including an isotopic pulse label.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Methods S1 Site description, root data, characterizing $\Delta^{14}C$ values of carbon (C) inputs to the fine-root system, and sensitivity analysis.

Fig. S1 Frequency (from the Monte Carlo simulations) of best-fit turnover time for L_1 (τ_{L1}) for roots < 0.5 mm diameter in the 0–15 cm depth interval.

Fig. S2 Predicted biomass for roots from 0–15 cm depth and of < 0.5 mm diameter in the (a) live-root pools and (b) dead-root pools.

Fig. S3 Effect of ignoring respiratory CO_2 fluxes on the $\Delta^{14}C$ value of (a) live and (b) dead fine roots for the background atmosphere (i.e., no pulse) using the nominal best-fit turnover times for roots from 0–15 cm depth and of < 0.5 mm diameter.

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