

Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration

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Abstract

Radiocarbon (^{14}C) provides a measure of the mean age of carbon (C) in roots, or the time elapsed since the C making up root tissues was fixed from the atmosphere. Radiocarbon signatures of live and dead fine (<2 mm diameter) roots in two mature Amazon tropical forests are consistent with average ages of 4–11 years (ranging from <1 to >40 years). Measurements of ^{14}C in the structural tissues of roots known to have grown during 2002 demonstrate that new roots are constructed from recent (<2-year-old) photosynthetic products. High $\Delta^{14}\text{C}$ values in live roots most likely indicate the mean lifetime of the root rather than the isotopic signature of inherited C or C taken up from the soil.

Estimates of the mean residence time of C in forest fine roots (inventory divided by loss rate) are substantially shorter (1–3 years) than the age of standing fine root C stocks obtained from radiocarbon (4–11 years). By assuming positively skewed distributions for root ages, we can effectively decouple the mean age of C in live fine roots (measured using ^{14}C) from the rate of C flow through the live root pool, and resolve these apparently disparate estimates of root C dynamics. Explaining the ^{14}C values in soil pore space CO_2 , in addition, requires that a portion of the decomposing roots be cycled through soil organic matter pools with decadal turnover time.

Keywords: belowground, carbon cycle, decomposition, fine root, radiocarbon, rhizosphere, root respiration, soil respiration, tropical forest, turnover

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Introduction

Roots are an essential yet poorly understood component of terrestrial ecosystems. They play an important role in the carbon (C) cycle by contributing a significant fraction of ecosystem net primary production (Nadelhoffer & Raich, 1992; Vogt *et al.*, 1996). In forest soils of eastern Amazonia, where this study was conducted, fine roots make up more than 50% of the total C found in the upper 10 cm (Silver *et al.*, 2000; Telles *et al.*, 2003). Although the highest density of root biomass is found close to the soil surface, roots extend to depths >15 m

in seasonally dry forests in eastern Amazonia (Nepstad *et al.*, 1994), where they are active in taking up water to sustain plant transpiration in the dry season (Jipp *et al.*, 1998).

Few data exist on the distribution and dynamics of fine roots in tropical forests. A recent review by Gill & Jackson (2000) cited only five studies of root dynamics from broadleaf tropical forests (precipitation >1000 mm yr⁻¹). Root lifetimes estimated in these studies ranged from 0.4 to 3.2 years. Methods of measuring fine root dynamics are hampered by large spatial variability and the difficulties of quantifying root biomass and turnover (reviewed by Aber *et al.*, 1985; Vogt *et al.*, 1998; Eissenstat *et al.*, 2000; Pregitzer, 2002).

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Recently, Gaudinski *et al.* (2001) used radiocarbon to estimate the mean age of fine root C in temperate ecosystems by comparing the radiocarbon (^{14}C) content of fine root structural material with the measured record of change for ^{14}C in atmospheric CO_2 . Radiocarbon values measured in live, dead, and mixed fine roots from temperate deciduous and coniferous forests corresponded to an average of 3–18 years elapsed since C was fixed from the atmosphere for three temperate forest sites, longer than estimates of root lifetime previously reported in the literature.

High ^{14}C values in roots could reflect one of several causes: (1) roots are long-lived and the ^{14}C content reflects the mean age of the root; (2) roots are constructed from C that is already high in ^{14}C because of recycling or storage within the plant; or (3) roots are constructed from C taken up from the soil. Gaudinski *et al.* (2001) tested hypothesis (2) by installing screens in the soil and found that the radiocarbon values of new roots growing through the screens had ^{14}C signatures close to contemporary carbon dioxide in the atmosphere, signifying that less than ~ 2 years had elapsed since C in new roots was fixed by photosynthesis. Tierney & Fahey (2002) also tested this hypothesis by measuring the radiocarbon content of a root that they had observed grow in a minirhizotron, and showed that the radiocarbon-derived age was in accord with the known root age. Matamala *et al.* (2003) reached a similar conclusion by contrasting the timing of the appearance of an isotopic tracer in root ingrowth cores vs. bulk roots at the Duke Free Air CO_2 enrichment experiment, and concluded that fine roots there had mean lifetimes of several years.

The observation that the majority of fine root biomass is long-lived has significant implications for the below-ground C cycle (Tierney & Fahey, 2002; Matamala *et al.*, 2003; Trumbore & Gaudinski, 2003). For example, the allocation of C belowground to support the growth of roots that persist for many years must be less than previously assumed. However, estimates of fine root production made with observations of root growth and death (for example through minirhizotrons) suggest that at least some of the fine root pool is much more dynamic (Pregitzer, 2002; Tierney & Fahey, 2002). Further, the amount of CO_2 respired from soil places a constraint on total belowground C allocation that requires more C to flow through short-lived pools if less C is used to grow longer-lived root structural material.

One additional constraint on belowground C dynamics arises from the isotopic composition of respired CO_2 , using radiocarbon to estimate the mean age of C in respiration sources. C used for root metabolism or derived from roots that live, die, and decompose in <1 – 2 years, should have ^{14}C values close to those of

contemporary photosynthetic products (i.e. close to current atmospheric $^{14}\text{CO}_2$ values). Decomposition of long-lived (>2 years but <50 years) root detritus and soil organic matter provides a source of more ^{14}C -enriched CO_2 , while decomposition of old (>50 years) soil organic matter will be depleted in ^{14}C .

Davidson & Trumbore (1995) reported that the radiocarbon signature of CO_2 in the pore space Amazonian soils is enriched in ^{14}C compared with recent photosynthetic products. They surmised that a component of the soil C with decadal turnover time must contribute significantly to CO_2 produced below 1 m depth in these forest soils. Trumbore *et al.* (1995) and Camargo *et al.* (1999) further estimated production rates of CO_2 as a function of depth based on the assumption that fine roots turn over annually, but could not identify the required pool of C with turnover times of decades in fractions isolated physically or chemically from soil organic matter. If roots in tropical forests are long-lived as in temperate forests, decomposition of dead fine roots may provide the source of ^{14}C -enriched CO_2 respired from tropical soils.

In this paper, we compare observations of fine root dynamics based on measures of root inventory and radiocarbon for mature and secondary forests and pastures from two locations in eastern Amazônia. Roots collected during the years 1993, 1996, and 1999 are compared with the time history of atmospheric ^{14}C change to estimate the mean age of C in fine roots. We also report measurements of ^{14}C in fine roots known to have grown through screens placed in the soil within a specific 6–11-month period, to test the hypothesis that tropical forest roots are constructed from recent photosynthetic products. We attempt to reconcile radiocarbon measurements of fine root age with other measures of fine root dynamics based on seasonal changes in root biomass and decomposition rates of dead root material. A model of root dynamics is constructed that can explain observations of fluxes of fine root production and decomposition and the mean age of C in roots. The model is compared with observations of CO_2 production rates and the radiocarbon content of pore space CO_2 in tropical forest soils.

Methods

Study sites

Fine roots were collected at two sites in Eastern Amazônia: *Fazenda Vitória*, Paragominas, Pará State, Brazil ($2^\circ 59'S$, $43^\circ 31'W$), and the Tapajós National Forest, 83 km south of the city of Santarém, Para State, Brazil ($3^\circ 14'S$, $54^\circ 45'W$). Both sites have seasonally dry climates, with 1750 and 2000 mm of rain annually,

but averaging $\sim 1.5 \text{ mm day}^{-1}$ for the ~ 6 dry season months. Forests are deep rooted (Nepstad *et al.*, 1994), broadleaf evergreen tropical forest, on Oxisols or Ultisols (Nepstad *et al.*, 2002; Telles *et al.*, 2003). The water table at both sites is deep ($> 20 \text{ m}$).

Fazenda Vitória, *Paragominas, Pará*. For root inventory measures, soil cores were collected at four points in time corresponding to the end of the wet (Jun/July) and dry (December/January) seasons. Sampling began in June/July 92 and ended in December/January 94, with a total of four sampling periods used to determine the average live and dead root standing biomass as well as dynamics. While the sample dates match closely with the precipitation record, they do not correspond with the seasonal minimum and maximum values for volumetric water content at all depths because of time lags in the vertical transport of water in the 6 m soil column (Jipp *et al.*, 1998). We sampled three ecosystems, including mature forest (36 cores), secondary forest (~ 17 years old at the time of sampling; 20 cores), and pasture that was disked and planted with the C4 grass *Brachiaria brizantha* in 1987 (10 cores). Cores were taken along transects and were separated by 50 m.

The cores were subsampled for fine roots at 0–10, 40–60, 135–155, 285–305, 435–455, and 585–605 cm depth intervals. We obtained integrated biomass estimates for the profile by expanding those point estimates to half the distance above and below (for example, fine root biomass measured at 435–455 cm was applied to soil from 370 to 520 cm). The one exception to this procedure was for the upper 10 cm of the profile. Because fine root biomass drops off so quickly below that level, the estimate obtained for the 0–10 cm layer is only applied to that interval, and the sample taken at 40–60 cm extends from 10 to 97.5 cm.

Roots were separated from bulk soil by flotation (Nepstad *et al.*, 1994), and separated by hand into two size fractions (< 1 and 1–2 mm). Live and dead fine root pools were also separated by hand, using staining methods to train people to distinguish roots by texture and color criteria. Separated roots were weighed, and then stored in alcohol. We estimated C content as 45% of the biomass for all roots; results are reported as gC m^{-3} for biomass and gC m^{-2} for production estimates.

Samples for radiocarbon were taken from picked splits from cores collected in February 1993, as well as new cores taken using the same methods in January 1996 (early in the wet season), and June 1996 (early in the dry season). We analyzed roots from the < 1 mm pool for isotopes, but noted that (after drying) a few of the individual roots had diameters up to 2 mm in these samples. Samples from 1993, which had been stored in

alcohol, were washed thoroughly with water and dried to remove any remaining alcohol C. Samples from 1996 were rinsed, and air-dried and never exposed to alcohol. Radiocarbon was analyzed in roots from both the live and a subset of the dead root fractions.

Tapajós National Forest, Santarém, Pará. Samples from this site are for mature forests only. Live fine roots were separated from deep soil pits in 1999 from clay-rich Oxisols near 67 km of the BR 183 highway that borders the Tapajós National Forest (Nepstad *et al.*, 2002), using the same coring methods and employing some of the same people who worked to separate roots at the Paragominas sites. Also in 1999, we measured fine roots ($< 2 \text{ mm}$) hand picked from samples from various depths in loamy clay soil (Ultisol) described in Telles *et al.* (2003). These roots were not differentiated into live or dead pools.

At a site $\sim 15 \text{ km}$ away but also within the Tapajós National forest, Silver *et al.* (2000) conducted a study of fine ($< 2 \text{ mm}$) root biomass and dynamics (Silver *et al.* in press) along a soil textural gradient from very sandy (80% sand) to clay-rich (80% clay) surface (0–10 cm) soil. They provided us with hand-picked splits of live and dead fine roots isolated in 1995 from sand and clay soil end members. Details of sample collection and handling are given in Silver *et al.* (2000) and Silver *et al.* (2005).

Isotope measurements

To measure the isotopic signature of root structural tissues, and to facilitate comparison with published ^{14}C values for temperate forests, we used the chemical pretreatment applied by Gaudinski *et al.* (2001). Fine roots were washed sequentially in acid (1 N HCl), alkali solution (1 N NaOH), and again in 1 N HCl, with distilled water rinses after each step. Pretreated samples were oven-dried at 60°C and ground. We assume that this treatment removes all but the structural components of fine roots; comparisons of roots prepared this way with holocellulose show only small differences in radiocarbon signature (J. B. Gaudinski, personal communication).

Pretreated roots were combusted in quartz tubes with cupric oxide wire at 900°C for 2 h. The resulting CO_2 was cryogenically purified and subsampled for analysis of ^{13}C , while the remaining CO_2 was converted to graphite by sealed-tube zinc reduction (Vogel, 1992) and measured for radiocarbon using accelerator mass spectrometry (AMS, 1.5 SDH.1 Pelletron Accelerator, National Electrostatics Corporation, Middleton, Wisconsin, USA) at the Lawrence Livermore National Laboratory Center for AMS (LLNL CAMS) and the UC Irvine W. M. Keck Carbon Cycle AMS (KCCAMS) facility. The accuracy of radiocarbon measurements of

graphite made in our laboratory, estimated from repeated measures of secondary standards close in ^{14}C values to roots, was $\pm 3\text{--}6\text{‰}$ (depending on which facility made the measurement).

Stable C isotopes were measured using dual inlet isotope ratio mass spectrometry (Finnegan MAT 252, Bremen, Germany) in the CENA laboratory. The precision of ^{13}C analysis was $\pm 0.1\text{‰}$ (deviation in parts per thousand from the V-PDB standard).

Radiocarbon data are reported as $\Delta^{14}\text{C}$, the deviation (in ‰, or parts per thousand) of the ratio of $^{14}\text{C}/^{12}\text{C}$ in a sample divided by that of a standard of fixed isotopic composition. All $\Delta^{14}\text{C}$ data are corrected for the effects of mass-dependent isotope fractionation by correcting to a common $\delta^{13}\text{C}$ value (-25‰) and assuming that ^{14}C is fractionated twice as much as ^{13}C . The ^{14}C standard is the ^{14}C of atmospheric CO_2 in 1950. $\Delta^{14}\text{C}$ values >0 therefore reflect the influence of ^{14}C created by weapons testing, mostly in the 1960s, while $\Delta^{14}\text{C}$ values <0 indicate that C has resided in the system long enough for significant radioactive decay of ^{14}C .

Because our samples were collected over a period spanning 10 years, during which the radiocarbon signature of atmospheric CO_2 dropped more than 50‰, we report the difference in $\Delta^{14}\text{C}$ between the sample and the $\Delta^{14}\text{C}$ of atmospheric CO_2 of the year it was collected, which we refer to as $\Delta\Delta^{14}\text{C}$.

Soil CO_2 isotopes and soil organic matter

In Paragominas and Santarém sites, we sampled gas tubes installed at depths from 1 to 11 m into the wall of an open pit (Davidson & Trumbore, 1995). Radiocarbon in CO_2 was sampled, purified, and measured for ^{13}C and ^{14}C isotopes as described in Davidson & Trumbore (1995). Samples from Paragominas date from 1993 and 1996, the year when live roots were collected; samples from Santarém were taken in 2003.

Measurements of the isotopic signature of soil organic matter at the Paragominas and Santarém sites are published in Camargo *et al.* (1999) and Telles *et al.* (2003), respectively.

Estimates of fine root lifetimes

Methods based on root inventory

Paragominas. We used four methods to determine fine root turnover, which we will refer to as the min-max method, the decision matrix method, the compartment-flow method, and the decay rate method (Pulitzer & Vogt, 1993). For the min-max method, production of live roots was estimated as the difference in biomass between the end of wet season 1993 and the end of the dry season 1993 values. Turnover for the live

root pool is calculated as the mean standing stock of live roots divided by the inferred rate of production. The decision-matrix method considers significant changes in both live and dead roots between sample dates, while the compartment-flow method uses live and dead root measurements and a decomposition factor. Large spatial variation generally exceeded temporal (wet/dry season) variation in root abundance except for the 0–10 cm depth interval, and temporal differences between coring intervals were significant only in the 0–10 cm interval for mature forest and the two pasture types. Only those values are reported here.

The decay-rate method is based on data collected on the rate of root decomposition using litter bags buried at different depths in the soil. Dead fine root decomposition rate is calculated as the product of the first-order rate constant for root decomposition multiplied by the mean dead root biomass. At steady state (stocks of live and dead fine roots do not change from year to year), live fine root production will equal dead root decomposition. Our estimate of root litter decomposition rate for Paragominas comes from a litter bag experiment, with litter bags placed at 20 and 500 cm depths in three mature forest and three pasture ecosystems in January 1993. On average, 50% of the root biomass was lost in the 18 months (D. C. Nepstad, unpublished data). Normally, decomposition rates slow over time. Since our experiment lasted only 18 months, our use of a single rate constant may result in overestimation of root production rates required to sustain the fine root pool.

Santarém. Estimates of root turnover and fine root decomposition rate are derived from the compartment-flow method using fine root inventory sampled multiple times per year in the 0–10 cm depth interval (Silver *et al.*, 2005).

Estimate of the mean age of C in fine roots. The amount of radiocarbon in atmospheric CO_2 increased sharply in the late 1950s and early 1960s because of ^{14}C production by atmospheric nuclear weapons testing. The ^{14}C signature of CO_2 in the atmosphere nearly doubled in the northern hemisphere, where most of these tests took place. When combined with the approximately 1-year time period required to mix air from one hemisphere to another, the record for ^{14}C in the southern hemisphere shows maximum ^{14}C values of $\sim +600\text{‰}$, with a 1-year delay in the occurrence of maximum ^{14}C values (Fig. 1). By 2000, the $\Delta^{14}\text{C}$ values for atmospheric CO_2 had dropped below $+100\text{‰}$.

In any given year, the $\Delta^{14}\text{C}$ signature of new photosynthetic products will equal that of the carbon dioxide source; mass-dependent isotope fraction (which would discriminate twice as much for radiocarbon as

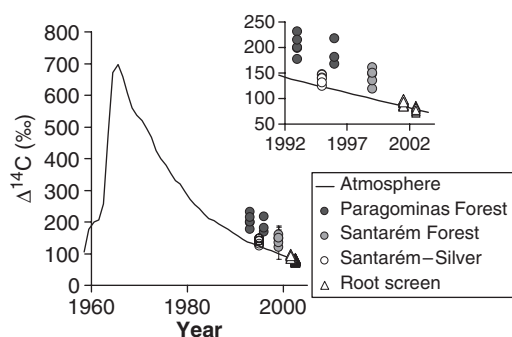


Fig. 1 Comparison of radiocarbon in root structural material collected from soil and growing through root screens with that of atmospheric CO_2 in the tropics.

for ^{13}C) is corrected for in the $\Delta^{14}\text{C}$ notation. For an individual root, the average time elapsed since the material from which it was constructed was fixed from the atmosphere by photosynthesis may be estimated simply as the year when atmospheric $\Delta^{14}\text{C}$ values were equal to those observed in fine root structural material (see Fig. 1). For populations of roots, the mean age of roots is determined using a steady-state homogeneous pool model (Gaudinski *et al.*, 2001). Ages determined using either method give very similar results for radiocarbon-based ages of less than 15 years (Gaudinski *et al.*, 2001).

We used data from Levin *et al.* (2000) for the record of $\Delta^{14}\text{C}$ in atmospheric CO_2 in tropical latitudes (30°N to 30°S) for the period 1900–1996, and our own measurements of clean marine air in the tropics for 2002 ($80 \pm 4\%$). We assumed that $\Delta^{14}\text{C}$ values for CO_2 in air over the intervening years decreased at a rate of $5.5\% \text{ yr}^{-1}$ to fill in between the two records; clean air samples taken at the field sites in Brazil during 1996–2002 are in accord with these estimates.

Age of C in recently grown fine roots

To determine whether or not the C in root structural material is derived from recent photosynthetic products, we measured the radiocarbon content of roots known to have grown within a specific 6-month period at the Santarém sand and clay soil sites. In March 2001, we placed mesh screens (8–10 per site) at the soil–litter interface, subsequently covering the screens with litter. Screens were collected in November 2001, and fine ($<1 \text{ mm}$) roots obviously growing through them were picked out by hand and processed (acid–base–acid treatment), combusted, and converted into graphite targets as described above. A second set of root screens were installed in the Paragominas mature and secondary forest and managed pasture sites and at the Santarém forest sites in March 2002. These were sampled in February 2003.

Results

Fine root inventory

Total (live + dead) fine ($<2 \text{ mm}$) root biomass to 6 m depth was similar in mature and secondary forests and degraded pasture in Paragominas, ranging from 366 to 387 g C m^{-2} (3.7 – 3.9 Mg C ha^{-1} ; Table 1). In these three ecosystem types, 30–42% of the total fine root biomass was found in the 0–10 cm depth interval; 60–74% of the total biomass was in the top meter. The managed pasture (planted with *Brachiaria brizantha*) differed in both total fine root biomass (584 g C m^{-2} ; 5.8 Mg C ha^{-1}), and its vertical distribution (58% in the top 10 cm; 92% of roots in the top meter; Table 1).

The total fine root C in the 0–10 cm interval for Santarém forest clay soils was similar to forests in Paragominas (Silver *et al.* in press; Table 1). However, in Paragominas live roots were $\sim 40\%$ of the total fine root biomass in mature and secondary forests, while Silver *et al.* (2004) found that live roots represented only 16% of the total fine root biomass.

Estimates of fine root lifetime from seasonal changes in biomass

Changes in fine root inventory between wet and dry seasons at the Paragominas sites were only significant for the 0–10 cm depth interval. Estimates of root lifetimes using the min–max, decision matrix, and compartment-flow methods range from 1.0 to 3.4 years for mature and secondary forest, and 0.4–1.3 years for grass roots in pastures (Table 2). Given the estimates of standing biomass in Table 1, these correspond to annual fine root production rates for the 0–10 cm interval of 16 – $53 \text{ g C m}^{-2} \text{ yr}^{-1}$ for forests and 25 – $91 \text{ g C m}^{-2} \text{ yr}^{-1}$ for pastures.

Silver *et al.* (2005) used the compartment-flow model and more frequent sampling of root biomass in the 0–10 cm interval to estimate the annual fine root production in the Santarém sites at $77 \pm 18 \text{ g C m}^{-2} \text{ yr}^{-1}$ (in 1999–2000) to $115 \pm 14 \text{ g C m}^{-2} \text{ yr}^{-1}$ (in 2001–2002). Turnover times for live fine roots estimated by Silver *et al.* (2005) are 1.4–1.7 years, within the range of estimates from Paragominas sites (Table 2).

The decay rate method to estimate fine root production and lifetime is the only one available to estimate production for roots $>10 \text{ cm}$ depth (Table 3). Multiplying the decomposition rate derived from the root litter bag experiment in Paragominas ($\ln(2)/1.5$ years or 0.46 yr^{-1} ; Nepstad, unpublished data) by the inventory of dead roots in Table 1 yields an estimate of annual live fine root production (assumed to equal annual loss of dead fine root biomass at steady state) of

Table 1 Fine root inventory (in g C m^{-2})

Depth (cm)	Mature forest ($n = 4$)						Secondary forest ($n = 2$)					
	Dead	±	Live	±	Total	±	Dead	±	Live	±	Total	±
<i>Paragominas</i>												
0–10	63	22	54	16	117	27	104	27	50	22	154	35
10–97.5	74	27	54	26	128	37	71	18	36	22	107	28
97.5–220	25	32	20	33	44	46	21	32	15	45	35	55
220–370	22	72	18	70	40	100	14	20	14	46	28	50
370–520	13	89	13	56	27	105	12	65	11	59	23	88
520–670	13	45	11	60	24	75	9	54	11	35	20	64
Total (to 600 cm)	209		170		379		230		136		366	
% of total in 0–10 cm	29.9		31.8		30.8		45.0		36.9		42.0	
% in the top meter	65.3		63.6		64.5		76.1		63.2		71.3	
<i>Santarém</i> [†]												
Clay (0–10)	103	10	20	5	123	9						
Sand (0–10)	124	7	24	7	148	9						
Depth (cm)	Degraded pasture ($n = 4$)						Reformed pasture ($n = 4$)					
	Dead	±	Live	±	Total	±	Dead	±	Live	±	Total	±
<i>Paragominas</i>												
0–10	96	20	34	35	131	40	246	14	93	76	339	78
10–97.5	85	33	38	34	124	48	125	33	72	70	197	
97.5–220	20	73	25	84	44	111	17	19	12	54	30	
220–370	21	117	25	108	46	159	8	49	2	64	11	
370–520	13	120	11	123	24	172	3	49	1	72	4	
520–670	11	166	8	161	19	232	3	9	0	85	3	
Total (to 600 cm)	245		142		387		402		182		584	
% of total in 0–10 cm	39.3		24.1		33.7		61.1		51.3		58.1	
% in the top meter	74.0		51.1		65.7		92.3		90.7		91.8	

*Assumes 45% of fine root dry biomass weight is C.

[†]Values are from Silver *et al.* (2005), assuming 50% of root biomass is C; values given are from 1999–2000.

Table 2 Estimates of fine root longevity for 0 to 10 cm depth interval based on seasonal changes in inventory

	Mature forest		Secondary forest		Degraded pasture		Reformed pasture	
	Production ($\text{g C m}^{-2} \text{yr}^{-1}$)	Lifetime (yr)	Production ($\text{g C m}^{-2} \text{yr}^{-1}$)	Lifetime (yr)	Production ($\text{g C m}^{-2} \text{yr}^{-1}$)	Lifetime (yr)	Production ($\text{g C m}^{-2} \text{yr}^{-1}$)	Lifetime (yr)
<i>Paragominas, roots < 2 mm diameter</i>								
Min–max method	15.9	3.4	na	na	64.9	1.43	25.4	1.43
Decision matrix method	41.3	1.3	na	na	71.8	0.48	64.9	0.48
Compartment flow	53.2	1.0	na	na	na	na	80.6	0.42
Decomposition model	23.2	2.3	38.3	1.2	35.7	1.0	91.0	1.0
<i>Santarém, roots < 2 mm diameter Silver et al. (in press)</i>								
Clay compartment flow	77–115	1.4						
Sand compartment flow	77–115	1.7						

23–91 $\text{g C m}^{-2} \text{yr}^{-1}$. Dividing the observed live fine root biomass by the annual fine root production estimate yields estimates of fine root lifetimes of 1–3 years for

ecosystems dominated by tree or shrub roots (mature and secondary forest and degraded pasture >3 m depth; Table 3). Shorter lifetimes, and higher production

Table 3 Calculation of fine root production and decomposition using root decomposition data and mean standing dead root biomass

Depth (cm)	Mature forest		Secondary forest		Degraded pasture		Reformed pasture	
	Production (g C m ⁻² yr ⁻¹)	Lifetime (yr)	Production (g C m ⁻² yr ⁻¹)	Lifetime (yr)	Production (g C m ⁻² yr ⁻¹)	Lifetime (yr)	Production (g C m ⁻² yr ⁻¹)	Lifetime (yr)
0–10	23.2	2.3	38.3	1.2	35.7	1.0	91.0	1.0
10–97.5	27.4	2.0	26.4	1.4	31.5	1.2	46.4	1.5
97.5–220	9.1	2.1	7.6	1.9	7.2	3.4	6.5	1.9
220–370	8.1	2.2	5.0	2.8	7.7	3.3	3.0	0.8
370–520	4.9	2.7	4.5	2.5	4.7	2.3	0.9	1.6
520–670	4.8	2.3	3.3	3.3	3.9	2.1	1.1	0.4
Total (to 600 cm)	77.5		85.1		90.7		148.9	
% of total in 0–10 cm	30.0		45.0		39.3		61.1	
% of total in the top meter	65.3		76.1		74.0		92.3	

rates, are estimated for pasture grass roots (top 3 m of degraded pasture and managed pasture). Estimated fine root turnover showed no relation with depth for forests, but turnover times increase with depth for other ecosystems. As with root stocks, 30–45% of total (to 6 m) fine root production is in the top 10 cm (65–76% in the top meter) for forest and degraded pasture ecosystems, while the managed pasture has a much higher proportion of fine root production near the soil surface (61% in the top 10 cm, 92% in the top meter; Table 3). Potential errors in these estimates are difficult to assess; if we change the time required for 50% of root decomposition to be ± 6 months, the resulting change in fine root production is $\pm 30\%$. Significant slowing of root decomposition rates beyond the 18 months of the litter bag deployment would indicate that we are overestimating fine root production rates; alternatively, artifacts associated with litter bags may have slowed decomposition to an unknown degree. Adopting the faster root decomposition rates estimated by Silver *et al.* (2005) would approximately double our estimates of fine root production for Paragominas.

Silver *et al.* (2005) report the results of root decomposition experiments based on trenching in Santarém forest sites. They found decomposition rate constants of 0.96 yr^{-1} in clay soils and 0.61 yr^{-1} for sand soils. These are faster decomposition rates than observed in Paragominas (0.46 yr^{-1}). Using the compartment-flow method, the rate of fine root production would be calculated (in 1999–2000) as $76\text{--}99 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is within the range of what was estimated by the other methods (Table 2). However, the live fine root pool measured in the Santarém forest is small compared with those found in the Paragominas mature forest (Table 1), so fine root lifetimes estimated in this way are shorter, 0.2–0.3 years.

Age of C in roots known to have grown in 2002–2003

Roots growing through the mesh of screens placed in the soil showed much less variation in $\Delta^{14}\text{C}$ ($\pm 5\text{--}6\%$) than was found in live roots sampled from soils ($\pm 20\text{--}36\%$; Fig. 1, Table 4). The $\Delta^{14}\text{C}$ values observed in roots that grew between March 2002 and February 2003 ($+79.4 \pm 4.5\%$ in all ecosystems in Paragominas ($n = 12$) and $+80.6 \pm 6.1\%$ ($n = 9$) in Santarém sand and clay soils) are in accord with the $\Delta^{14}\text{C}$ value of atmospheric CO_2 measured in October, 2003 ($79.9 \pm 2.1\%$) in the tropical Pacific (Xu *et al.*, 2004). Roots sampled from screens deployed between May 2001 and March 2002 averaged $+92.5 \pm 4.9\%$. We do not have good atmospheric ^{14}C data for comparison, but the assumption that the atmosphere is dropping at a rate of $\sim 6\%$ per year yields an estimate of $\sim 86\%$ for C fixed in 2001 and $\sim 92\%$ for 2000. While we cannot entirely exclude the possibility that some inherited C is used to grow fine roots, we can say that new root C is overwhelmingly derived from C fixed within the past 1–2 years. $\delta^{13}\text{C}$ values for forest roots growing through root screens were the same as those measured in hand-picked live root samples, averaging -27% . We observed no difference in the isotopic signature of roots sampled using root screens between sand and clay sites in forest; roots from C4 grasses were clearly dominating in both pasture sites near the surface.

Estimates of root C age from radiocarbon

Fine roots in mature and secondary forest soils in both areas had $\Delta^{14}\text{C}$ values ranging from $+85$ to $+285\%$, greater than expected for recent photosynthetic products in the year they were sampled in all ecosystems (Fig. 1 and Table 4). Estimates of the mean time since photosynthesis for C in fine roots averaged 2–6 years in

Table 4 Mean age of live fine root structural C derived from radiocarbon

Site	Ecosystem	<i>n</i>	$\delta^{13}\text{C}^*$	SD	$\Delta\Delta^{14}\text{C}^\dagger$	SD	Mean age (yr) (range)
Paragominas (dead)	Mature forest-1993	5	na	na	73	20	8 (6–10)
Paragominas (dead)	Managed pasture-1993	2	na	na	17	2	2 (1–3)
Paragominas (live)	Mature forest-1996	7	-28.5	0.8	95	44	11 (7–15)
Paragominas (live)	Secondary forest-1996	9	-27.8	1.0	52	22	9 (6–12)
Paragominas (live)	Degraded pasture-1996	4	na	na	9	26	2 (<1 to >40)
Paragominas (live)	Managed pasture-1996	5	-12.1	0.3	46	27	6 (3–11)
Santarém (live)	Mature forest-clay-1999	24	-28.5	1.5	40	36	7 (<1–11)
Santarém (mixed)	Mature forest-sand-1999	8	na	na	39	24	7 (3–9)
Santarém [‡] (live)	Mature forest-sand-1995	3	na	na	-12	4	na (<1)
Santarém [‡] (dead)	Mature forest-sand-1995	3	na	na	10	16	2 (0–4)
Santarém [‡] (live)	Mature forest-clay-1995	3	na	na	22	4	4 (3–5)
Santarém [‡] (dead)	Mature forest-clay-1995	3	na	na	14	11	2 (1–4)
Root Screens							
Santarém	Mature forest	10	-27.9	0.3	8	5	1 (<1 to 3)
Paragominas	All ecosystem types	12	§		1	5	<1 (0 to 2)

**n* is < *n* for ^{14}C .

[†]The difference in per mil between the mean $\Delta^{14}\text{C}$ of fine roots and the $\Delta^{14}\text{C}$ of atmospheric CO_2 for the year of sampling (1993, 1996; 120 per mil, or 1999; 96.5 per mil).

[‡]Samples from Silver *et al.* (2000).

[§]-27.1 (forest), -28.6 (SF), -11.9 (MP).

pasture ecosystems, and 7–11 years in mature and secondary forests. Several individual samples had $\Delta^{14}\text{C}$ values less than that of the current years' atmospheric CO_2 , indicating dilution of ^{14}C by C fixed prior to the peak of atmospheric $^{14}\text{CO}_2$ in 1963, or at least 35 years ago.

Live <2 mm diameter roots sampled from 0 to 10 cm depth in Paragominas mature forest had $\Delta\Delta^{14}\text{C}$ values of $+58 \pm 16\%$ ($n=4$), while roots sampled from depths of 50–600 cm had $\Delta\Delta^{14}\text{C}$ of $79 \pm 33\%$ ($n=10$). However, the two sets of samples were taken in different years (1996 and 1993, respectively), so the significance of these differences is unclear. Any depth dependence is far smaller than the difference between live roots and the $\Delta\Delta^{14}\text{C}$ of roots known to have grown in the last 6–11 months; $0 \pm 5\%$.

Dead roots had ^{14}C ages similar to or less than live roots, although the variability in both cases is large enough that these differences are not significant except for the managed pasture site in Paragominas. Although in some cases ^{14}C values in roots in the 0–10 cm interval are lower compared with deeper roots, we report ^{14}C values averaged over all depths in Table 4.

Overall, live fine roots from the Santarém forest sites had significantly (5% significance level using a Student's *t*-test) lower $\Delta\Delta^{14}\text{C}$ values ($40 \pm 36\%$; $n=24$) than those from Paragominas ($85 \pm 40\%$; $n=12$), and correspondingly shorter lifetimes (averaging 7 vs. 11 years; Table 4). Fine roots picked by Silver *et al.* (2000)

had the smallest differences from atmospheric ^{14}C values (Fig. 1 and Table 4). Ages estimated from radiocarbon were <1 year for sand soils and 3–5 years for clay soils in the 0–10 cm interval.

The $\delta^{13}\text{C}$ values for fine roots in forests ranged from -26‰ to -31‰ in mature forest sites, with no apparent trends with depth, except in pastures. In the managed pasture, $\delta^{13}\text{C}$ values reflected the influence of C4 grasses, with values between -11‰ and -12.5‰. The degraded pasture had root $\delta^{13}\text{C}$ values reflecting those of C4 grasses in the upper meter, but showed the influence of C3 vegetation at greater depths. Degraded pastures contain living shrubs that can supply living C3 roots.

Discussion

Reasons for high ^{14}C values in living fine roots

The $\Delta^{14}\text{C}$ values observed for live fine roots in Amazonian forests are very similar to those measured in temperate forests (Gaudinski *et al.*, 2001). As in temperate forests, several hypotheses may explain the fact that the $\Delta^{14}\text{C}$ values of live fine roots are much greater than expected: (1) roots may live a long time; (2) roots may grow from C that has been stored in the tree for some time; (3) roots may take up C from the soil subsequent to or during initial growth; and (4) the separation of live roots from dead roots may err and

include old, dead roots within what is identified as the live root pool.

Although our root screens were placed at the bottom of the litter layer and therefore do not directly test the soil uptake hypothesis (3), the lack of a depth trend in root radiocarbon outside of the 0–10 cm interval leads us to reject it as an important determinant of root ^{14}C values. Live fine roots from Paragominas forest sampled in 1993 averaged $+207\text{‰}$ for depths from 450 to 600 cm, while roots from 50 to 300 cm averaged $+201\text{‰}$. The $\Delta^{14}\text{C}$ of soil organic matter over the same depth range decreases from $\sim +180\text{‰}$ to $< -800\text{‰}$. If uptake of organic matter from the soil was an important process, we would expect the $\Delta^{14}\text{C}$ signatures of roots to decrease rapidly with depth along with the bulk (and hydrolysable) components of soil organic matter (Telles *et al.*, 2003); instead, root $\Delta^{14}\text{C}$ values remain constant or increase.

The root screen data provide a test of the second hypothesis. Roots known to have grown in the previous year uniformly had $\Delta^{14}\text{C}$ values equal to the $\Delta^{14}\text{C}$ of atmospheric CO_2 within the last 1–2 years, and hence cannot explain ^{14}C ‘ages’ of nearly a decade. The small degree of variation in ^{14}C values for roots sampled from screens may indicate that either all roots formed about the same time, or that changes in structural tissue ^{14}C over a period of up to a year are not significant. We cannot absolutely rule out subsequent use of stored material to ‘thicken’ the root following 6–11 months of growth; however, this implies a storage pool with very high ^{14}C values. If thickening doubled structural root biomass, the $\Delta\Delta^{14}\text{C}$ value for added C would have to be $+100\text{‰}$ (roughly 20-year-old C) to yield the observed root $\Delta\Delta^{14}\text{C}$ value of $+50\text{‰}$.

The separation of live and dead root material during root picking is highly subjective, and some dead material may be included in with the live roots measured here. This would influence the radiocarbon content of the live root pool, and might explain why we observed no consistent differences (at the 5% significance level) in radiocarbon between live and dead root pools in forest ecosystems in clay soils. However, the mean time it takes for fine roots to decompose (based on the litter bag experiments), is ~ 2 years – not long enough to explain the ^{14}C ages of >7 years observed in the live root pool. While we cannot rule out the presence of some older, dead roots in the live root pool, the presence of those dead roots alone cannot explain the observed radiocarbon values. We conclude that the much greater and more variable $\Delta^{14}\text{C}$ values measured in live roots picked from the soil must therefore be associated with the time elapsed since the root grew, as has been observed in temperate forests (Gaudinski *et al.*, 2001).

Differences in fine root lifetimes for roots sampled by different groups may be because of how roots were

separated from soil and into live and dead pools. While the total root biomass was similar among forest sites, Silver *et al.* (2005) assigned about half as much root C to the live root pool. This may partly be because of the sampling interval involved (0–10 cm for Silver *et al.* vs. the average of all depth intervals to 290 cm in Table 4 for other Santarém forest sites), or because of real differences in root dynamics between sites. Different groups may also have a different ‘cutoff’ for the smallest root that gets picked from a sample, which could influence the age of C if very small roots (e.g. <0.5 mm) have different dynamics than larger ones (1–2 mm).

Differences among forest, secondary forest, and managed pasture

We observed no significant ($\alpha < 0.05$) differences in the mean age of roots from mature or secondary forests sampled for this study. Pasture roots, however, had radiocarbon values closer to those of recent photosynthetic products. Stable C isotope data show that roots in the upper 2 m are derived from the C4 grass (*Brachiaria brizanthus*) that dominates the pasture vegetation, while roots from 6 m depth show evidence of C3 plant material, likely roots belonging to shrubs that grow in pastures. Higher $\Delta^{14}\text{C}$ values in roots sampled deeper in the soil, therefore, reflect the influence of nongrass vegetation. Given the 1–3-year lifetimes of grass roots, and the relatively short period of time since this pasture had been reformed, the steady-state assumptions used to estimate decay-rate-based root production rates may be inaccurate, especially for roots sampled in 1993 when the pasture was only 5-year old. This may also explain problems that Camargo *et al.* (1999) had in modeling the managed pasture soil organic matter changes over the same period. Estimated lifetimes increased for roots from 1993 to 1996, which could indicate increases in the mean age of C in accumulating root stocks over time as the grasses mature.

Vandam *et al.* (1997) used ^{14}C pulse labeling to estimate the residence time of C in fine roots of *Axonopus compressus* grass in Costa Rica. For equivalent depths (50–300 cm), they estimated fine root lifetimes of 2–3 years, in accord with the values we derived from the managed pasture sampled in 1993.

Comparison of roots with soil CO_2 and soil organic matter

The radiocarbon signature of CO_2 measured in soil air space reflects a combination of sources: (1) root respiration, which should reflect the isotopic signature of recent photosynthetic products ($\Delta\Delta^{14}\text{C} = 0$; Fig. 2); (2) decomposition of dead roots (in forests, $\Delta\Delta^{14}\text{C}$ values of dead roots were $+20$ to $+95$; Table 4); and (3) decom-

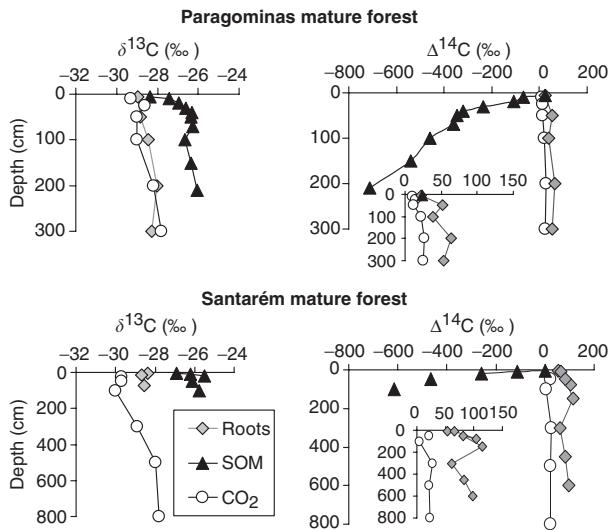


Fig. 2 Comparison of the isotopic signatures of CO_2 in soil air pore space with carbon in bulk soil organic matter and live fine roots. The $\delta^{13}\text{C}$ of soil pore space CO_2 have been corrected for the 4.4‰ enrichment expected from diffusion (Cerling, 1984). Radiocarbon data are given as $\Delta\Delta^{14}\text{C}$; using this notation, the radiocarbon signature of autotrophic respiration (or recent photosynthetic products) should be zero.

position of soil organic material (SOM), which has $\Delta\Delta^{14}\text{C} > 0$ between the surface and ~ 50 cm, but has $\Delta\Delta^{14}\text{C} < 0$ at greater depths (Trumbore *et al.*, 1995; Camargo *et al.*, 1999; Telles *et al.*, 2003). When the isotopic signature of these three sources is compared with CO_2 measured in the soil atmosphere (Fig. 2), it is clear that the two most important contributors to CO_2 production at depths > 20 cm in soil are root respiration and root decomposition. Old organic matter deep in these soils contributes almost nothing to CO_2 efflux.

The importance of fine roots as sources of soil respiration may also be observed by comparing the $\delta^{13}\text{C}$ signature of soil CO_2 with those of root and SOM sources. Fractionation of C isotopes during diffusion increases the $\delta^{13}\text{C}$ of soil CO_2 by ~ 4.4 ‰ compared with the CO_2 sources (Cerling, 1984). Once this correction is made, it is clear that the ^{13}C signature of root material is closer to the $\delta^{13}\text{C}$ of soil CO_2 than is that of soil organic matter (Fig. 2). Because radiocarbon data as reported have been corrected for mass-dependent isotopic fractionation, the $\Delta\Delta^{14}\text{C}$ of soil CO_2 does not reflect this fractionation because of diffusion.

Reconciling different observations of root turnover

The turnover times (< 1 – 3 years) that we derive for mature tropical forests and pastures are in accord with observations of fine root inventory change using a variety of methods (e.g. Gill & Jackson, 2000). The fact

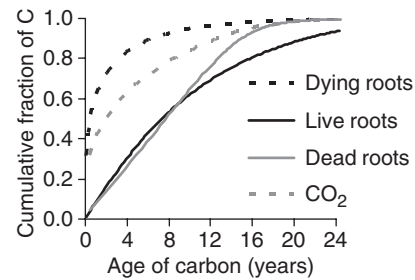


Fig. 3 Hypothetical models of root dynamics that reproduce observed turnover times and mean ages of C in live and dead root pools (Paragominas). Comparison of the age distribution of C assigned to live and dead root pools with the age of C exiting each pool (dying roots and decomposition-derived CO_2).

that the radiocarbon-derived mean age of C in fine roots (7–11 years for forests) is longer than the turnover time (1–3 years) can be explained if fine root lifetimes have a positively skewed distribution (Pregitzer, 2003; Tierney & Fahey, 2003).

Figure 3 shows hypothetical distributions of root lifetimes that roughly match the observed mean ages of live (10 years) and dead (8.5 years) forest root pools in Paragominas, as well as the turnover times that we deduce by comparing the fluxes of C with the inventories in these pools (~ 2.2 years for both live and dead roots). These modeled age distributions yield a ratio of live:dead root inventory of ~ 1 , also in accord with our observations in Paragominas (Table 1). Because the models do not assume that the root pools are homogeneous, the mean age of dying roots (2.2 years) is younger than the age of the standing live root biomass (Fig. 3), and the age of CO_2 resulting from decomposition of dead roots (4.4 years) is younger than the mean age of C in the dead root pool. Using this model, we predict that $\sim 75\%$ of dying roots are < 2 years old, and the shape of the live root age distribution is consistent with survivorship curves published based on long-term deployments of minirhizotrons in temperate ecosystems (e.g. Pregitzer *et al.*, 2002; Tierney & Fahey, 2003). While the details of these hypothetical age distributions can vary, the overall requirement – that most of the C allocated for root growth pass through shorter lived pools while most of the biomass is in longer-lived pools – is clear. A second requirement is that shorter-lived roots decompose faster than longer-lived roots, although decomposition rates overall are fast enough so that dead roots do not persist as long as living roots (Fig. 3).

Sources of CO_2 produced between 1 and 6 m depth

Davidson & Trumbore (1995) used a one-dimensional diffusion model to estimate the rate of production of

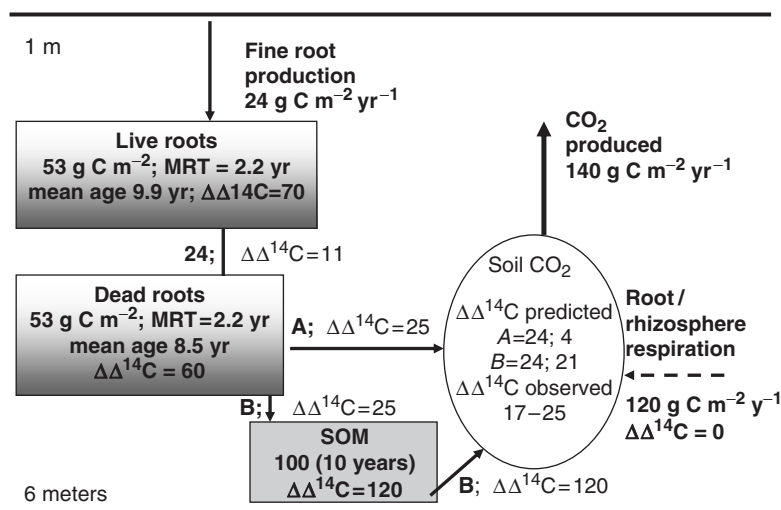


Fig. 4 Belowground carbon cycle for the depth interval from 1 to 6 m in mature forest, Paragominas, Para. CO_2 production rates between 1 and 6 m depth were estimated from Davidson & Trumbore (1995). Fine root production between 1 and 6 m depth is taken from Table 3; root/rhizosphere respiration is calculated as the difference between this and total CO_2 production. Root dynamics are from the model represented in Fig. 3. The range in predicted values for the radiocarbon content of pore space CO_2 derive from assuming either that all of the C from the dead root pool is decomposed directly to CO_2 (pathway A; $\Delta\Delta^{14}\text{C}_{\text{CO}_2}$ predicted = 4) or that all dead root C resides in a soil organic matter pool before being decomposed (pathway B; $\Delta\Delta^{14}\text{C}_{\text{CO}_2}$ = 21). Note that the $\Delta\Delta^{14}\text{C}_{\text{CO}_2}$ of CO_2 derived from decomposition of the dead root pool is lower (25) than that of the standing dead root biomass (60). This is a result of the assumption that fast-dying roots decompose more quickly (see Fig. 3).

CO_2 as a function of depth in Paragominas mature forest soils. Scaling their results to the depth interval from 1 to 6 m, we estimate the total rate of CO_2 production to be between ~ 100 (dry season value) and ~ 300 (wet season value) $\text{g C m}^{-2} \text{yr}^{-1}$. For purposes of illustration, we have assumed a value of $140 \text{ g C m}^{-2} \text{yr}^{-1}$ (Fig. 4). We estimate the annual fine root production for the same depth interval to be $\sim 24 \text{ g C m}^{-2} \text{yr}^{-1}$ (Table 3). Assuming roots are the only source of decomposable organic matter at this depth (i.e. inputs from downward transport of dissolved organic C are negligible), we estimate that $\sim 17\%$ of the CO_2 in the 1–6 meter depth interval is derived from heterotrophic decomposition of roots. The remaining $\sim 83\%$, therefore, comes from root and rhizosphere metabolism. Does this partitioning match our observations of the radiocarbon signature of pore space CO_2 ?

Carbon dioxide respired by living roots has the radiocarbon signature of recent photosynthetic products (i.e. $\Delta\Delta^{14}\text{C} = 0$; Trumbore & Camargo, unpublished data). Rhizosphere respiration derived from root exudates presumably also is from recently fixed C sources. The $\Delta\Delta^{14}\text{C}$ value observed for soil CO_2 is between 17% and 25% in both Paragominas and Santarém forest sites (Fig. 2). While it is tempting to look at Fig. 2 and use the radiocarbon value of standing root biomass as the end member for root decomposition (i.e. $\Delta\Delta^{14}\text{C}$ averaging ~ 70), the mass balance in that case would require a decomposition source of roughly

$40 \text{ g C m}^{-2} \text{yr}^{-1}$, or nearly double what we estimate from dead root biomass and decomposition rate. Further, our positive skew model, which explains decomposition dynamics, biomass, and mean age of fine root C for both live and dead fine roots, requires that the age of C being decomposed to be less than that of the standing stock (Fig. 3); the $\Delta\Delta^{14}\text{C}$ estimated for decomposing dead roots by that model is 25% (Fig. 4). If there is no additional time lag and all dead roots decompose directly to CO_2 (pathway A in Fig. 4), the $\Delta\Delta^{14}\text{C}$ predicted for pore space CO_2 is too low: only 4% . Satisfying all constraints of root inventory, age, and turnover as well as the isotopic signature of pore space CO_2 requires that a major fraction of root C pass through a soil organic matter pool with a residence time of ~ 10 years (Fig. 4, pathway B).

Several other explanations are still possible and require further investigation. First, we have assumed roots grow from C that has not aged in the plant, while some of our root screens indicate that there could be up to a 1–2-year lag between C fixation and allocation to root growth. An additional year would add 5–6% to the $\Delta\Delta^{14}\text{C}$ value estimated for decomposing dead roots (i.e. 10 or 30 instead of 4 or 24%). Second, we have ignored the role played by roots $> 2 \text{ mm}$ in diameter, which presumably would have ^{14}C values greater than or similar to fine roots and might significantly increase the estimated fine root production rates. Third, our estimates of root production are based on a single

decomposition experiment that is itself based on roots picked from the soil.

There is likely some conceptual overlap in Fig. 4 between roots that die young and decompose rapidly and root/rhizosphere respiration, since both would have identical ^{14}C signatures; in effect, this could mean we are underestimating fine root production rates and overestimating root/rhizosphere respiration. Radiocarbon isotopes cannot be used to distinguish these sources effectively; field pulse labeling studies would be required to constrain belowground C cycling on <2-year timescales.

Finally, we have ignored other potential processes that may be adding C that decomposes in the 1–6 m depth interval. Although little of the dissolved organic C observed near the soil surface is observed at depth, transport of DOC to deeper layers cannot be ruled out as a source of C that could have higher ^{14}C values. Similarly, soil fauna (leaf cutter ants, termites) may transfer C from one depth interval to another in soils.

Conclusions

Estimates of the turnover time of C in forest fine roots (inventory divided by loss rate) are substantially shorter (1–3 years) than the age of standing fine root C stocks obtained from radiocarbon (4–11 years). By assuming positively skewed distributions for root ages, we can effectively decouple the mean age of C in live fine roots (measured using ^{14}C) from the rate of C flow through the live root pool (Tierney & Fahey, 2002), and resolve these apparently disparate estimates of root C dynamics. Root dynamics in secondary forests are similar to those of primary forests, while there is less of a difference in the turnover time and the mean age of C in C4 grass roots in pastures. We found a large spatial variation of $\Delta^{14}\text{C}$ values in live and dead fine roots sampled over a number of vegetation types and years.

Further progress on root dynamics will require better approaches to sampling that link root architecture and function to root dynamics (Pregitzer, 2002). It is likely that much of the variation in ^{14}C values observed for roots in the same diameter class arises from mixing different species, and different types of roots (e.g. root tips with mature roots). Radiocarbon results are likely very dependent on the lower limit size cutoff for picking roots. Our observation that dead roots often have slightly lower $\Delta^{14}\text{C}$ values than live roots supports the hypothesis that most of the flux of C through roots is likely in shorter-lived components like root tips. While root death is likely not a random process, we still know very little about what causes roots to die (Pregitzer, 2002).

Similarly, in order to explain the radiocarbon signature of dead roots and the CO_2 produced by decomposition of dead roots, we must infer skewed distributions for root decay, with shorter-lived roots decomposing faster than longer-lived roots. However, measures of root decomposition by litter bags have not been accompanied by studies of changes in ^{14}C content that might elucidate whether or not decomposition depends on root age or other factors that may covary, such as nutrient content.

Root dynamics must be evaluated in the context of other C fluxes in the ecosystem. Both radiocarbon and stable isotope data indicate that root decomposition must be a major source of CO_2 respired from soils and found in the soil pore space below ~ 1 m depth in mature forests. Our estimates of root production suggest that $\sim 80\%$ of the CO_2 produced between 1 and 6 m depth in Paragominas forest soils is derived from root/rhizosphere processes that return CO_2 to the atmosphere within 1–2 years. While the hypothetical model of fine root dynamics that we have proposed here can reproduce the observations of both fine root turnover time and the age of C in root tissues, it requires that a major portion of the C moving through root pools must be stabilized for a decade in soil organic matter before it is decomposed to also explain pore space CO_2 isotope signatures. At these very low levels of CO_2 production ($24 \text{ g C m}^{-2} \text{ yr}^{-1}$), other fluxes may also play a potential role – for example additional C inputs may be derived from decomposition of dissolved organic C transported downward from the surface, and production of roots >2 mm diameter may be important.

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