Functional Ecology 2005
19, 81–87

Quantifying root lateral distribution and turnover using pine trees with a distinct stable carbon isotope signature

K. JOHNSEN,† C. MAIER and L. KRESS

USDA Forest Service, Southern Research Station, 3041 Cornwallis Road, PO Box 12254, Research Triangle Park, NC 27709, USA

Summary

1. In order to help assess spatial competition for below-ground resources, we quantified the effects of fertilization on root biomass quantity and lateral root distribution of mid-rotation *Pinus taeda* trees. Open-top chambers exposed trees to ambient or ambient plus 200 μmol mol^{-1} atmospheric CO_2 for 31 months.

2. Tank CO_2 was depleted in atmospheric ^{13}C; foliage of elevated CO_2 trees had $\delta^{13}C$ of −42·9‰, compared with −29·1‰ for ambient CO_2 trees.

3. Roots 1 m from the base of elevated CO_2-grown trees had more negative $\delta^{13}C$ relative to control trees, and this difference was detected, on average, up to 5·8, 3·7 and 3·7 m away from the trees for 0–2, 2–5 and >5 mm root-size classes, respectively. Non-fertilized tree roots extended as far as fertilized trees despite the fact that their above-ground biomass was less than half that of fertilized trees.

4. These results are informative with respect to root sampling intensity and protocol, and the distances required between experimental manipulations to evaluate below-ground processes of independent treatments.

5. Fine-root turnover has usually been estimated to range from weeks to 3 years, representing a major avenue of carbon flux. Using a mixing model we calculated that 0–2 mm roots had a mean residence time of 4·5 years indicating relatively slow fine-root turnover, a result that has major implications in modelling C cycling.

Key-words: ^{13}C, carbon isotopes, carbon sequestration

Functional Ecology (2005) **19**, 81–87

Introduction

Root production and turnover are critical components of a forest's carbon budget. Coarse roots can provide a perennial C sink, and root growth and death provide an important flow of C below ground. Stand-level empirical root studies are fraught with methodological difficulties that make quantification of the flow of C into and out of roots problematic (Vogt 1990; Hendrick & Pregitzer 1992; Publicover & Vogt 1993). Root quantity, size distribution and spatial distribution all affect the ability of trees to exploit and compete with other trees and other vegetation for soil resources (Casper *et al*. 2003). Root turnover rate influences C cycling from vegetation to soil and the atmosphere (Dewar & Cannell 1992; Matamala *et al*. 2003).

Fertilization of Southern Pine stands is increasing rapidly as a management tool; industrial fertilization increased from 16 200 ha in 1988 to 344 250 ha in 1998 (NCSFNC 1999). In a controlled seedling study, using Loblolly Pine (*Pinus taeda* L.), soil nutrient additions decreased overall dry matter partitioning to roots *vs* shoots (Li *et al*. 1991). Larger-scale studies examining below-ground responses of forest stands to fertilization have generally shown a decrease in some component of root production. Haynes & Gower (1995), in a study using a 31-year-old Red Pine (*Pinus resinosa* Ait.), found that fertilization with macro- and micronutrients suppressed growth of roots of all size classes. In contrast, in a study of mid-rotation Loblolly Pine, Albaugh *et al*. (1998) found that 'optimal' fertilization decreased only the fine-root component; the biomass of larger root classes was increased with fertilization, the result of the large overall growth response of these stands to improved nutrition. In an in-depth analysis of the C cycle of the same stands used in the study of Albaugh *et al*. (1998), Maier & Kress (2000) found that despite a 32% overall increase in below-ground biomass, soil CO_2 efflux was not increased in the fertilized stands relative to the control stands. Maier & Kress (2000) and Lai *et al*. (2002) concluded that fertilization, via its increase in net primary productivity, combined with no effect on soil CO_2 evolution, had rapidly shifted their Loblolly Pine stands from overall sources to overall sinks for atmospheric CO_2.

†Author to whom correspondence should be addressed. E-mail: kjohnsen@fs.fed.us

In this study we again used a long-term field experiment assessing fertilization responses of Loblolly Pine trees grown on a sandy site (Albaugh *et al*. 1998; Maier & Kress 2000). We used an open-top elevated CO_2 study where individual, large trees were grown under ambient or elevated CO_2 for 31 months. Elevated CO_2 was provided with an external CO_2 supply that was substantially depleted in ^{13}C relative to the atmosphere. Thus the strong $^{13}C : {}^{12}C$ label allowed us to partition root biomass from soil cores into a fraction derived from individual trees in the elevated CO_2-supplied chamber and a fraction derived from non-chamber trees within the stand. We tested if fertilization altered root quantity, root size and spatial distribution. In addition, we used the biomass and stable-isotope data to estimate the mean residence time of fine roots.

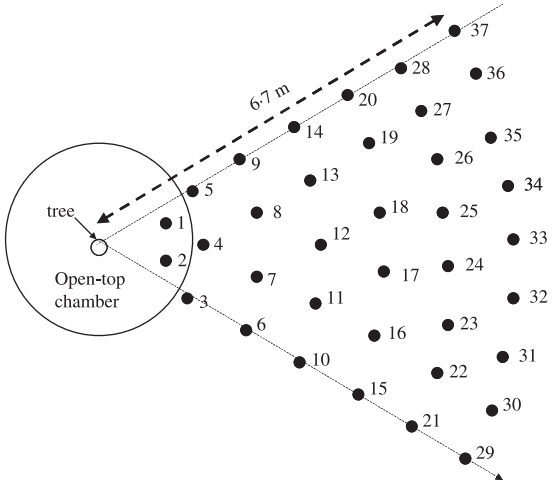

Fig. 1. Sample locations for root biomass and root $\delta^{13}C$ for chamber trees.

Materials and methods

The study was conducted at the South-east Tree Research and Education Site (SETRES), which is located in the Sandhills of Scotland County, North Carolina, USA (34°55′N, 79°30′W). SETRES is located on an infertile, excessively drained site and was hand planted on a 2×3 m spacing in 1985 using a mix of 10 open-pollinated families originating from the North Carolina Piedmont. The full SETRES study is a 2×2 factorial experiment with fertilization and irrigation treatments and four replicate blocks. Fertilization was applied to achieve 'optimum' foliar nutrition. For the optimum nutrition treatment, nitrogen was applied annually in an attempt to achieve a concentration in leaf dry matter of 1·3% N with other macro- and micronutrients in balance; control foliar N concentration was ≈ 0·9%. Fertilization treatment goals have been achieved (Albaugh *et al*. 1998). More details on the site, stand and treatments are given by Albaugh *et al*. (1998, 2004).

Two trees in the control (no fertilization or irrigation) and fertilized-only plots, in three of the four blocks, were selected for the CO_2 experiment; a total of 12 trees were used. Whole-tree, open-top chambers, ≈12 m high and 3 m in diameter, were constructed that enclosed the entire above-ground portion of each tree. Tank CO_2 was bled into the lower quarter of the chamber, and was mixed within the chamber via two plenum fans. CO_2 concentrations were monitored continuously and CO_2 was provided to elevated CO_2 chambers to maintain ambient +200 μmol mol^{-1} CO_2. This design was repeated in three of the four main treatment blocks (12 whole-tree chambers). CO_2 treatments began in August 1996 and continued through February 1999, a total of 31 months. More details on the chamber experiment are given by Maier *et al*. (2002) and Oren *et al*. (2001).

During February 1999 we sampled, at 1 m intervals (using a 15·2 cm diameter soil corer down to 1 m), to a 6·7 m horizontal distance from the base of each tree as shown in Fig. 1. For the six ambient CO_2 trees only core locations (Fig. 1) 1–9 were sampled, while for the six elevated CO_2 trees all 37 core locations were sampled. Cores were stratified to three depths (0–15, 15–50 and 50–100 cm) and carefully passed (dry) through a 3·2 mm mesh screen to remove live pine roots. Roots were then sorted into three size classes (0–2, 2–5 and >5 mm), dried and weighed. For each tree, roots per size class/distance interval were bulked and ground with a Wiley mill with a 20 mesh screen.

To examine the $^{13}C : {}^{12}C$ signature provided by the tank CO_2, 1999 first-flush foliage was collected in February 1999 from the upper, middle and lower thirds of the canopy from each chamber tree. To test if tank CO_2 contaminated trees outside the chambers, mid-canopy foliage was sampled within and adjacent to the root-sampling area (Fig. 1) for each of the elevated CO_2-chamber trees. Foliage from approximately 10 fascicles per sample were ground and analysed for $\delta^{13}C$ as above.

Samples were analysed for a $^{13}C : {}^{12}C$ ratio using the Duke University Phytotron SIRA Seriea II isotope ratio mass spectrometer (Micromass, Manchester, UK) operated in automatic trapping mode after combustion (Micro-Dumas combustion) of samples in an elemental analyser (NA1500 Series 1, Carla Erba Instrumentation, Milan, Italy). The reference CO_2 was standardized against standard Pee Dee belemnite (PDB). A system check of the combustion and mass spectrometer measurement was achieved interspersed (every 10 samples) with two working standards of cellulose with a $\delta^{13}C$ of $-24{\cdot}1 \pm 0{\cdot}03$ and $-23{\cdot}6 \pm 0{\cdot}06$‰. The accuracy of $\delta^{13}C$ with this analysis procedure is ± 0·1‰.

STATISTICAL ANALYSES

Chamber tree foliar $\delta^{13}C$ was analysed by canopy position using ANOVA with a split-plot design, with fertilization treatments as the main-plots and CO_2 treatments as subplots. For all analyses of root biomass, CO_2 treatment and interactions with CO_2 treatment were not statistically significant sources of variation, nor

were there any trends of potential biological importance. Thus all further analyses presented are for fertilization treatments alone. Mean root and foliage $\delta^{13}C$ values of control trees were used to represent background values to assess the distribution of the ^{13}C : ^{12}C signal from the elevated CO_2-chamber trees.

Root and foliar $\delta^{13}C$ was analysed as a function of the distance away from the base of the elevated CO_2-chamber trees. The intersection of each curve with the lower 95% confidence interval of root $\delta^{13}C$ values from trees grown under ambient atmospheric CO_2 was considered the mean distance in which chamber tree roots were detected. Root biomass, by size class and for all three size classes combined, was analysed by ANOVA using a randomized complete block design using fertilization treatment as a class variable; means of all subplots (cores) per chamber tree were used for these analyses. Because of heterogeneity of variance, root biomass values were log-transformed.

ESTIMATING NET REPLACEMENT OF FINE ROOTS

The above data were used to estimate net fine-root (<2 mm) replacement at 1 m from elevated CO_2-chamber trees during the study period. We applied a mixing model to partition roots produced by chamber and non-chamber trees, and to chamber tree roots produced before and after CO_2 treatments commenced.

On average, a core 1 m from a chamber tree would have had nine trees with overlapping root systems, the chamber tree and eight non-chamber neighbour tree ranging from 2 to 4·5 m away. The absolute contribution of any given tree to the biomass at the 1 m core location was assumed to be Δ:

$$\Delta = f(x) - y \qquad \text{eqn 1}$$

where $f(x)$ is the linear equation describing $\delta^{13}C$ at a distance (x) from the tree, and y is the average root $\delta^{13}C$ of ambient CO_2 trees. The fractional contribution (Z) of the chamber tree to root biomass at the 1 m core was estimated as:

$$Z = \Delta_{CTi}/(\Delta_{CT} + \Sigma\Delta_{ij}) \qquad \text{eqn 2}$$

where CT = elevated CO_2 chamber tree; and i represents elevated CO_2-chamber trees 1–6, and j represents neighbour trees 1–8 each at distance x_{ij} from the core location.

The mean foliar (upper canopy) and root $\delta^{13}C$ (mean of all root classes) of ambient CO_2 trees was –28·6 and –27·1, respectively, a difference of –1·5. Although the physiological basis for this difference is not known, we applied this difference to the mean foliar (upper canopy) $\delta^{13}C$ of elevated CO_2 (–41·0), assume roots formed purely from elevated CO_2-derived C had a $\delta^{13}C$ of –41·0 – (–1·5) = –39·5. For the case where fine-root biomass is assumed to be at equilibrium (no change in total fine-root biomass over time), root $\delta^{13}C$ at 1 m from the chamber tree is A:

$$A = \overbrace{\{(1-Z)\times(-27.1)\}}^{a} + \overbrace{\{Z\times[R(-39.5)}^{b} + \overbrace{(1-R)(-27.1)]\}}^{c} \qquad \text{eqn 3}$$

where R is the fraction of the final fine-root biomass replaced during the study period. Section a of equation 3 represents roots produced by non-chamber trees, section b represents roots produced by the chamber trees under elevated CO_2, and section c represents roots produced by the chamber tree prior to exposure to elevated CO_2.

Using root core data from previous years (unpublished), fine-root biomass increased a maximum of 20% during the period the trees were in the chambers. Assuming that fine-root biomass increased by 20% over the study period, then root $\delta^{13}C$ at 1 m from the chamber tree is B:

$$B = 0{\cdot}8\times\{[(1-Z)(-27{\cdot}1)] + Z\times[R(-39{\cdot}5) + (1-R)(-27{\cdot}1)]\} + 0{\cdot}2\times\{[(1-Z)(-27{\cdot}1)] + Z(-39{\cdot}5)\} \qquad \text{eqn 4}$$

The mean estimated $\delta^{13}C$ of fine roots and the estimates of Z were used to solve equations 3 and 4. A and B were plotted as a function of R.

Results

Foliage collected from the elevated CO_2-chamber trees was significantly depleted in ^{13}C relative to ambient CO_2-chamber tree foliage at all three canopy positions (Table 1) Elevated CO_2 provided to the chamber trees did not contaminate neighbouring trees, as no spatial trend in foliar $\delta^{13}C$ was evident among trees (Fig. 2).

There was no interpretable pattern in $\delta^{13}C$ with regard to root depth. Thus the mean values per distance interval per tree were used to assess the lateral distribution of $\delta^{13}C$. Figure 3 shows that, for all root-size classes, $\delta^{13}C$ values were generally most negative (but had highest variation) near the base of the chamber trees and became more positive (and less variable) with distance from the chamber trees, reaching values equal to those observed from roots in the ambient CO_2 plots. Note that the data in Fig. 3 have non-homogeneous variance; however, data transformations did not

Table 1. Mean $\delta^{13}C$ (‰) of foliage from ambient and elevated CO_2-chamber trees. Both fertilizer treatments were used

	Canopy position		
CO_2 treatment	Lower	Middle	Upper
Ambient	–29·4 (0·9)	–29·2 (0·7)	–28·6 (0·7)
Elevated	–43·5 (0·3)	–43·1 (0·7)	–41·0 (0·6)

Values based on six trees per CO_2 treatment; SD in parentheses.

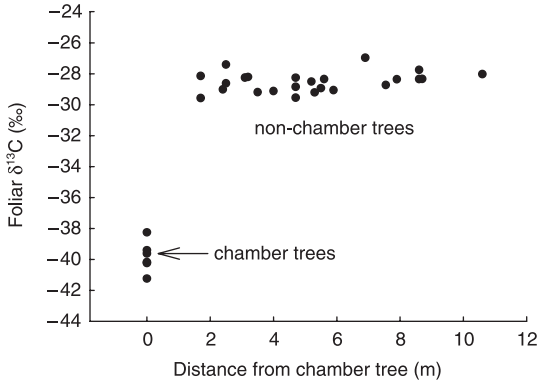

Fig. 2. Foliar $\delta^{13}C$ of chamber trees and neighbour trees as a function of distance from the chamber tree.

improve homogeneity and so non-transformed data were used.

The ^{13}C signal was observed further from the chamber in fine-root (<2 mm) biomass than for the two larger size classes. Using the curves shown in Fig. 3, 0–2 mm size-class roots, on average, extended (= lower 95% CI of roots from ambient plots) for 5·8 m, while 2–5 and >5 mm roots extended ≈3·7 m, each from the chamber tree. There were no differences between fertilized and non-fertilized trees in the fitted equations for each root-size class. Although not always statistically significant, fertilized plots generally had less fine-root (<2 mm) biomass and more coarse root (>2 mm) biomass than non-fertilized plots (Fig. 4); combining all root sizes, fertilized plots had ≈100% more total root biomass than non-fertilized plots (1914 *vs* 969 g m^2, $P = 0{\cdot}0276$).

Using the single curve shown in Fig. 3(a), we estimated (equation 2) that at 1 m from the elevated CO_2 trees, 19% of the fine roots (<2 mm) came from the chamber tree and 81% came from neighbouring trees in the stand. Using a $Z = 0{\cdot}19$ (equations 3 and 4), Fig. 5 shows $\delta^{13}C$ as a function of R for both the steady-state and increasing scenarios. Using the observed mean value of $\delta^{13}C$ at 1 m, R (equations 3 and 4) was estimated to be 0·66 under the steady-state scenario and 0·57 under the increased root biomass scenario.

Discussion

The use of open-top chambers, providing elevated CO_2 to individual trees in a plantation, provided a rare opportunity to examine the lateral root distribution and turnover of individual trees in a stand. This analysis hinged on the tank CO_2 providing a strong $^{13}C : {}^{12}C$ signature, and this was achieved as chamber tree foliage $\delta^{13}C$ was ≈ 12‰ more negative than ambient CO_2 trees. Another important consideration is that the chambers appeared to act as excellent chimneys, propelling the depleted ^{13}C CO_2 into the atmosphere, as trees external to the chambers were not contaminated.

All crowns were contained within the 1·52 m radius of the chambers and yet, on average, the ^{13}C signature

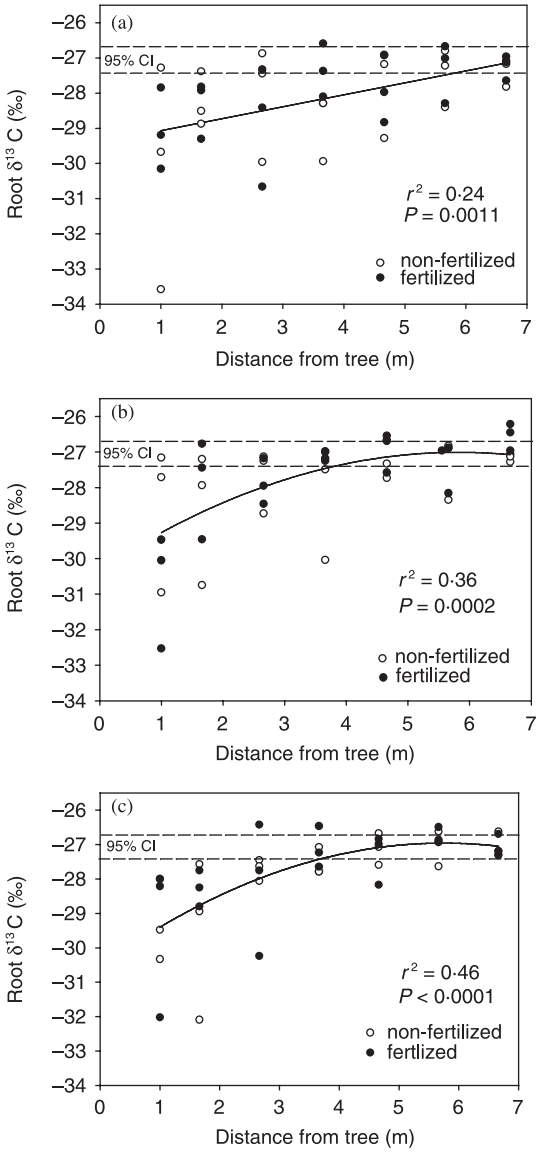

Fig. 3. Root $\delta^{13}C$ as a function of distance from the elevated CO_2-chamber trees for (a) 0–2; (b) 2–5; (c) >5 mm root-size classes. Horizontal lines represent upper and lower 95% confidence intervals for samples from ambient CO_2 plots.

was apparent up to 5·3, 3·7 and 3·7 m away from the trees for 0–2, 2–5 and >5 mm root-size classes, respectively. Variation around the fitted curves indicated chamber-tree roots were found even further from the base of the tree.

It is clear that detecting the ^{13}C signal of the smallest roots (0–2 mm) was more likely than for the larger root-size classes; new fine roots formed during the study were comprised of C with the tank gas ^{13}C signature, while larger (older) roots would have had only a fraction of their C gained during that period. The apparent differential extent of the ^{13}C signal between the finer (0–2 mm) roots and the coarser roots (>2 mm) may be due to dilution alone. In addition, we assumed that ^{13}C would be retained within individual trees; this assumption may not be totally correct. Carbon might be transferred among individual trees

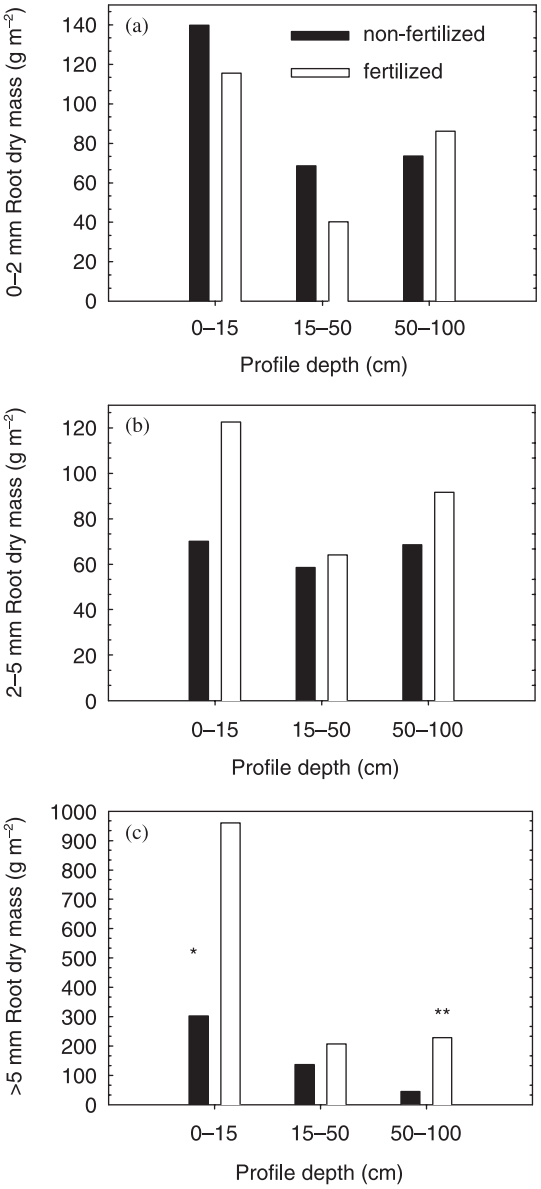

Fig. 4. Root biomass, by root size class and depth, for unfertilized and fertilized Loblolly Pine trees. Treatment means were different at *, $P = 0{\cdot}0591$; **, $P = 0{\cdot}0157$. All other treatment comparisons, within a size class/depth combination were not significantly different ($P > 0{\cdot}16$).

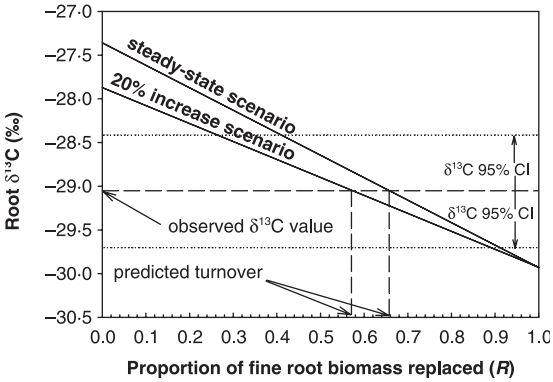

Fig. 5. Predicted (solid lines) relationship between root $\delta^{13}C$ and proportion of fine-root biomass replaced (R) for two scenarios: steady-state and 20% fine root-mass increase. Estimated mean fine-root $\delta^{13}C$ (Fig. 3) at 1 m from elevated CO_2-chamber trees was used to predict the proportion of fine-root biomass under the two scenarios over the 31 month study period. 95% confidence intervals for predicted mean fine-root $\delta^{13}C$ (Fig. 3) at 1 m are also shown.

by root grafts (Schultz & Woods 1967); however, in our experiences excavating Loblolly Pine root systems at SETRES and elsewhere, we have rarely observed root grafting (personal observation). Carbon may also be transferred among trees by mycorrhizal transfer, but this appears to be a minor phenomenon (Robinson & Fitter 1999). Therefore it is likely that the ^{13}C signal resided only within the root systems of chamber trees. The non-homogeneous variation in root $\delta^{13}C$ is also instructive. The high variation in $\delta^{13}C$ that diminishes with distance from the chamber trees reflects the non-uniform distribution of their root systems.

In a review on the lateral distribution of tree roots, Stone & Kalisz (1991) reported a tremendous range in radial root elongation among different tree species grown under a range of conditions; radial roots extending up to 50 m, with some pine species with reported values over 20 m. In this mid-rotation Loblolly Pine stand, most roots of individual trees roots were found within a radial distance approximately 3·7 times as far as the extension of their crowns.

The lateral root distribution of trees from the two fertilizer treatments were very similar, although the above-ground biomass of non-fertilized trees was less than half that of fertilized trees (Albaugh *et al.* 1998; Maier *et al.* 2002). Thus much smaller non-fertilized trees extended their root as far as much larger fertilized trees, in agreement with the well documented decrease in fine-root biomass resulting from fertilization on this site (a trend in this study, statistically significant in Albaugh *et al.* 1998; and Maier & Kress 2000). Non-fertilized trees have acclimated to exploit resources from a much larger volume of soil than do fertilized trees, by both growing more fine-root biomass per unit ground area and extending that biomass as far into the stand as the much larger fertilized trees.

Understanding spatial variation in root distribution is useful for many reasons. First, in understanding and modelling competition dynamics among and within species, quantifying a plant's below-ground zone of influence (Casper *et al.* 2003) is requisite. Root-distribution data are useful in planning studies where above-ground treatments (such as girdling; Högberg *et al.* 2001) are imposed in a stand and below-ground processes are measured. The data also provide insight into spatial sampling requirements for root and soil CO_2 efflux sampling, so that varying root densities, and respiration, occurring within a stand are fully characterized.

We estimated a range in net root replacement during the experimental period, ranging from 0·66 for the steady-state scenario to 0·57 for the increasing root biomass scenario. The interpretation of 'net root replacement' is not unambiguous. Our experiment lasted

31 months, far longer than many reported fine-root life spans (see below). Thus many cohorts of short-lived roots may have been produced, died and even decomposed during the experimental period; C consumed by these processes would have been ignored in these analyses. Although we do not know the specific turnover dynamics of the fine-root biomass that we calculated was produced during the study period, our calculations do indicate that ≈50% of the fine-root biomass of the chamber trees at the beginning of the experiment was still there at the end of the 31 months. Assuming an increasing root biomass, this indicates a mean residence time of 4·5 years (31 months experiment duration/0·57 = 54·4 months = 4·5 years). This estimate of fine-root life span is long relative to many reported previously. The data of Hendrick & Pregitzer (1992), further interpreted by Atkinson (1992), showed that fine roots of *Acer saccharum* lived ≈ 0·5 years. Although studying a much more limited period, Black *et al*. (1998) reported a great range among four species in the amount of root mortality over a 63 day period; 40% of *Prunus avium* fine roots died within 14 days of initiation. Edwards & Harris (1977) and Matamala & Schlesinger (2000), both utilizing biomass and necromass data, estimated that Loblolly Pine fine roots live ≈1 and 3 years, respectively. However, by using the $\delta^{13}C$ signature provided by free-air carbon enrichment, Matamala *et al*. (2003) estimated that Loblolly Pine roots had a mean residence time of 4·2 and 5·7 years for <1 mm and 1–2 mm size classes, respectively, values that bracket our estimate.

Thus there is increasing evidence that fine-root turnover is less frequent than previously accepted. Jackson *et al*. (1997) estimated that, globally, 33% of annual net primary productivity is portioned into fine roots. However, their analysis assumed that fine roots lived an average of 1 year. When modelling C cycling, assuming that less frequent fine-root turnover (as estimated in our study) decreases annual fine-root production alters the partitioning of gross primary productivity and reduces the flux of C from fine roots to soil and the atmosphere (Dewar & Cannell 1992; Matamala *et al*. 2003). Given their high biomass (Albaugh *et al*. 2004; Samuelson *et al*. 2004) and slow decay rates (Ludovici *et al*. 2002), tap roots and large roots are probably much more important in contributing to below-ground forest C sequestration.

Acknowledgements

We appreciate the hard work by Pete Anderson collecting and sorting root cores. Thanks to Mary Topa and Dan Richter for reviewing an earlier draft of the paper.

References

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W. & King, J.S. (1998) Leaf area and above- and below-ground growth responses of loblolly pine to nutrient and water additions. *Forest Science* **44**, 1–12.

Albaugh, T.A., Allen, H.L., Dougherty, P.M. & Johnsen, K.H. (2004) Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *Forest Ecology and Management* **192**, 3–19.

Atkinson, D. (1992) How long is the life span of a root? *Trends in Ecology and Evolution* **7**, 173–174.

Black, K.E., Harbon, C.G., Franklin, M., Atkinson, D. & Hooker, J.E. (1998) Differences in root longevity of some tree species. *Tree Physiology* **18**, 259–264.

Casper, B.B., Schenk, H.J. & Jackson, R.B. (2003) Defining a plant's belowground zone of influence. *Ecology* **84**, 2313–2321.

Dewar, R.C. & Cannell, M.G.R. (1992) Carbon sequestration in the trees, products and soils of forest plantations: an analysis using UK examples. *Tree Physiology* **11**, 49–71.

Edwards, N.T. & Harris, W.F. (1977) Carbon cycling in a mixed deciduous forest floor. *Ecology* **69**, 870–873.

Haynes, B.E. & Gower, S.T. (1995) Below ground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* **15**, 317–325.

Hendrick, R.L. & Pregitzer, K.S. (1992) The demography of fine roots in a northern hardwood forest. *Ecology* **73**, 1094–1104.

Högberg, P., Nordgren, A., Buchmann, N. *et al.* (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**, 789–792.

Jackson, R.B., Mooney, H.A. & Schulze, E.-D. (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* **94**, 7362–7366.

Lai, C.-T., Katul, G., Butnor, J. *et al.* (2002) Modelling the limits on the response of net carbon exchange to fertilization in a south-eastern pine forest. *Plant, Cell & Environment* **25**, 1095–1119.

Li, B., Allen, H.L. & McKeand, S.E. (1991) Nitrogen and family effects on biomass allocation of loblolly pine seedlings. *Forest Science* **37**, 271–283.

Ludovici, K.H., Zarnoch, S.J. & Richter, D.D. (2002) Modeling *in-situ* pine root decomposition using data from a 60-year chronosequence. *Canadian Journal of For Research* **32**, 1675–1684.

Maier, C. & Kress, L.W. (2000) Forest floor CO_2 evolution in 11-year old loblolly pine (*Pinus taeda* L.) stand under high and low moisture and nutrient availability. *Canadian Journal of Forest Research* **30**, 347–359.

Maier, C.A., Johnsen, K.H., Butnor, J., Kress, L. & Anderson, P. (2002) Effects of nutrients and CO_2 amendments on branch growth, phenology and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees. *Tree Physiology* **22**, 1093–1106.

Matamala, R. & Schlesinger, W.H. (2000) Effects of elevated atmospheric CO_2 on fine root production and activity in an intact temperate forest ecosystem. *Global Change Biology* **6**, 967–979.

Matamala, R., Gonzàlez-Meler, M.A., Jasdtrow, J.D., Norby, R.J. & Schlesinger, W.H. (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* **302**, 1385–1387.

NCSFNC (1999) *North Carolina State Forest Nutrition Cooperative, Twenty-Eighth Annual Report*. Department of Forestry, North Carolina State University, Raleigh, NC, USA.

Oren, R., Ellsworth, D.S., Johnsen, K.H. *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in CO_2-enriched atmosphere. *Nature* **411**, 469–472.

Publicover, D.A. & Vogt, K.A. (1993) A comparison of methods for estimating forest fine root production with respect to sources of error. *Canadian Journal of Forest Research* **23**, 1179–1186.

Robinson, D. & Fitter, A.H. (1999) The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *Journal of Experimental Botany* **50**, 9–13.

Samuelson, L., Johnsen, K.H., Stokes, T. & Cooksey, T. (2004) Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to six years of intensive management. *Forest Ecology and Management* **192**, 59–70.

Schultz, R.P. & Woods, F.W. (1967) The frequency and implication of intraspecific root-grafting in loblolly pine. *Forest Science* **13**, 226–239.

Stone, E.L. & Kalisz, P.J. (1991) On the maximum extent of tree roots. *Forest Ecology and Management* **46**, 59–102.

Vogt, K.A. (1990) Tree root turnover and senescence. *Plant Roots: The Hidden Half* (eds Y. Waisel, A. Eshel & U. Kafkafi), pp. 287–306. Marcel Decker, New York, USA.

Received 16 December 2003; revised 29 June 2004; accepted 3 September 2004