Journal of Ecology 2006
94, 40–57

Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review

JOSEPH J. HENDRICKS, RONALD L. HENDRICK†, CARLOS A. WILSON‡, ROBERT J. MITCHELL‡, STEPHEN D. PECOT‡ and DALI GUO*‡

Department of Biology, University of West Georgia, Carrollton, GA 30118, USA, †Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA, and ‡Joseph W. Jones Ecological Research Center at Ichauway, Rt. 2, Box 2324, Newton, GA 39870, USA

Summary

1 Elucidation of the patterns and controls of forest net primary production at ecosystem scales has been hindered by a poor understanding of fine root production, due largely to technical limitations.

2 Fine root (≤ 0.5 mm diameter) production was assessed using minirhizotron, soil core, ingrowth core, nitrogen budget and carbon budget techniques in three longleaf pine-wiregrass forest ecosystem types (hydric, mesic and xeric) forming an edaphic resource availability and above-ground productivity gradient.

3 Fine root production estimates differed substantially in magnitude, e.g. values ranged from 0 to 4618 kg ha^{-1} $year^{-1}$ for the soil core and minirhizotron techniques, respectively, in the hydric site.

4 Minirhizotron production estimates in the hydric, mesic and xeric sites were 4618, 1905 and 2295 kg ha^{-1} $year^{-1}$, respectively.

5 Soil core and ingrowth core root production estimates were on average 81 and 54% lower, respectively, than corresponding minirhizotron production estimates, and minirhizotron estimates were negatively related to soil core and ingrowth core estimates across the resource gradient.

6 The N budget method yielded unreliable root production estimates, presumably due to the underestimation of N availability for plant assimilation.

7 C budget estimates of total below-ground C allocation (6773, 5646 and 4647 kg C ha^{-1} $year^{-1}$) were positively related to minirhizotron production estimates, but negatively related to soil core and ingrowth core production estimates.

8 Critical evaluations of the assumptions, potential errors and results for each method suggest that the minirhizotron technique yielded the most reliable root production estimates, and that the negative relationship between minirhizotron and core-based estimates may be attributed to the inherent deficiency of the core techniques in assessing root production when mortality and production occur simultaneously.

9 Minirhizotron root production estimates were positively related to foliage production estimates, supporting the hypothesis of constant proportional allocation of production to foliage, wood and fine roots across resource availability gradients in temperate forests.

10 These results suggest that fine root production is not negatively correlated with soil resource availability and foliage production as is commonly perceived in the ecological community and represented in ecosystem computer models.

Key-words: C budget, fine roots, ingrowth core, longleaf pine, minirhizotron, mortality, N budget, production, soil core, wiregrass

Journal of Ecology (2006) **94**, 40–57
doi: 10.1111/j.1365-2745.2005.01067.x

Correspondence: Joseph J. Hendricks (tel. +1 678 839 4037; fax +1 678 839 6548; e-mail jhendric@westga.edu).
*Present address: Department of Ecology, College of Environmental Sciences, Peking University, Beijing, 100871 China.

Introduction

Carbon allocation and net primary production (NPP) influence the structure and function of forest ecosystems (Zak & Pregitzer 1998; Aber & Melillo 2001). Although it has been well established that availability of water, nitrogen and/or phosphorus generally controls C allocation and NPP (Keyes & Grier 1981; Nadelhoffer *et al*. 1985), the mechanisms regulating soil resource–plant interactions have yet to be clearly defined (Norby & Jackson 2000; Trumbore & Gaudinski 2003). Previous assessments of resource controls on plant dynamics have focused primarily on above-ground processes, while important below-ground processes, such as fine root production and mortality, are less well understood (Norby & Jackson 2000; Aber & Melillo 2001; Fitter 2005). Consequently, assessment and prediction of soil resource controls on the structure and function of forest ecosystems is contingent on an improved understanding of fine root dynamics and the relationship between above- and below-ground production (Zak & Pregitzer 1998; Norby & Jackson 2000; Trumbore & Gaudinski 2003).

Two contrasting hypotheses have evolved regarding soil resource controls on C allocation and NPP (Hendricks *et al*. 1993). One (hereafter referred to as the 'differential allocation' hypothesis) maintains that an increase in total NPP as resource availability increases is accompanied by an increase in the proportion of NPP allocated to foliage and wood, and a decrease in the proportion allocated to fine roots (Gower *et al*. 1992; Albaugh *et al*. 1998; Tateno *et al*. 2004). The second hypothesis (hereafter referred to as the 'constant allocation' hypothesis) also maintains that total NPP increases as resource availability increases, but the proportion of total NPP allocated to foliage, wood and fine roots remains relatively constant (Aber *et al*. 1985; Nadelhoffer *et al*. 1985; Raich & Nadelhoffer 1989).

Both hypotheses propose that there is a relative decrease in fine root standing biomass along gradients of increasing resource availability, but suggest different mechanisms by which this is achieved (Hendricks *et al*. 1993). The differential allocation hypothesis proposes that it is due to a reduction in C allocation to root production while root mortality rates remain constant or decrease (Keyes & Grier 1981; Haynes & Gower 1995). In contrast, the constant allocation hypothesis contends that the decrease is attributed to an increase in mortality rates while the proportion of C allocated to root production remains constant (Nadelhoffer *et al*. 1985; Nadelhoffer & Raich 1992).

Numerous factors may have contributed to the divergence of these hypotheses, including the influence of community type (e.g. response of coniferous vs. deciduous forest), interactions between resources (e.g. nutrients and water) and the potentially overriding impact of climate on C allocation (Gower *et al*. 1992, 1996; Pregitzer *et al*. 1995; Albaugh *et al*. 1998). These two hypotheses may also represent endpoints along a gradient of possible responses (Zak & Pregitzer 1998; Nadelhoffer 2000). However, numerous investigators have hypothesized that the divergence may be primarily caused by the methods used to assess fine root dynamics (Hendricks *et al*. 1993; Nadelhoffer 2000; Norby & Jackson 2000).

Methods for assessing fine root production and mortality are based on potentially tenuous assumptions and are subject to sampling errors (Fahey *et al*. 1999; Lauenroth 2000). The differential allocation hypothesis is based largely on soil core assessments, which assume that fine root production and mortality occur asynchronously (Kurz & Kimmins 1987; Publicover & Vogt 1993). In contrast, the constant allocation hypothesis is supported by elemental budget techniques (i.e. C and N budgets), which assume that C and N pools and fluxes can be measured accurately at ecosystem scales (Nadelhoffer *et al*. 1985; Raich & Nadelhoffer 1989). When soil core and N budget techniques were used simultaneously in 13 forest ecosystems, fine root production and mortality estimates differed significantly between the two approaches, and the discrepancy increased along a gradient of increasing resource availability and above-ground NPP (Aber *et al*. 1985), suggesting that one or both techniques may be inadequate, particularly when soil resource availability is high (Hendrick & Pregitzer 1993; Hendricks *et al*. 1993; Norby & Jackson 2000; King *et al*. 2002).

Minirhizotron techniques allow direct measurement of fine root production and mortality, thus avoiding the major limitation that has hindered the more traditional soil core and budget approaches (Eissenstat & Caldwell 1988; Hendrick & Pregitzer 1992, 1996). Whilst commonly used to assess fine root production and longevity (Vogt *et al*. 1998; Crocker *et al*. 2003), severing roots during tube installation and modifying the rooting environment at the tube–soil interface (Johnson *et al*. 2001; Withington *et al*. 2003) may lead to errors. As no standard method exists for assessing fine root dynamics (Fahey *et al*. 1999; Lauenroth 2000; Norby & Jackson 2000), it has been widely suggested that multiple assessment techniques should be employed as a means of corroborating estimates, or, in the absence of corroboration, of evaluating the shortcomings of each method (Fahey *et al*. 1999; Lauenroth 2000; Nadelhoffer 2000; Hertel & Leuschner 2002). However, we are aware of no study that has comprehensively compared the commonly used fine root production assessment methods.

Longleaf pine-wiregrass (*Pinus palustris* Miller-*Aristida beyrichiana* Trin. and Rupr.) forests are well suited for comparing root assessment methods and the relationship between above- and below-ground NPP. These forests exhibit a wide range of above-ground NPP across an edaphic resource gradient extending from xeric sandhills to the edge of wetlands without any associated change in dominant species (Mitchell *et al*. 1999; Wilson *et al*. 1999, 2002). Fine root dynamics may also be disproportionately critical in these fire-maintained

forests where plants typically allocate a greater proportion of C and nutrients below-ground (Landers *et al*. 1995). The sandy soils, with no persistent organic horizon and minimal mineral horizon development, facilitate more consistent assessment of root dynamics across the gradient than sites that differ in soil depth, horizon development, texture and geology. An improved understanding of the role of fine roots in the structure and function of longleaf pine-wiregrass forests is critical for the development of conservation, silvicultural and restoration strategies for these ecosystems that are valued for both economic (e.g. high-quality wood products and wildlife amenities) and ecological (e.g. nearly two-thirds of the rare, threatened and endangered species of the south-eastern USA reside in these forests) reasons (Landers *et al*. 1995; Kirkman *et al*. 2001).

The primary objective of this study was to gain an improved understanding of the patterns and controls of fine root NPP in longleaf pine-wiregrass forests. In an effort to avoid the major limitations that have hindered previous studies, the most commonly used root production assessment techniques were employed in concert across an edaphic resource and above-ground productivity gradient in association with assessments of other key ecosystem processes. The specific objectives of this study were to: (i) evaluate the fine root production assessment techniques; (ii) assess fine root production rates; and (iii) test competing hypotheses regarding soil resource controls on above- vs. below-ground NPP allocation (i.e. the constant vs. differential allocation hypotheses) in longleaf pine-wiregrass forest ecosystems.

Materials and methods

STUDY SITES

This study was conducted at the Jones Ecological Research Center near Newton, Georgia. The Jones Center is located in the Dougherty Plain Physiographic Region of the Lower Coastal Plain and Flatwoods Section (Mitchell *et al*. 1999). The climate is humid subtropical; mean daily temperatures range from 21–34 °C in summer and 5–17 °C in winter, and the average annual precipitation of 131 cm is evenly distributed throughout the year (Goebel *et al*. 1997).

The longleaf pine-wiregrass forests are maintained using understorey prescribed burning (1- to 5-year intervals; sites used in this study were burned 2 years prior to field sampling). The assessments of soil resource controls on fine root dynamics were conducted using three ecosystem types (hydric, mesic and xeric, based on the difference in soil moisture), which varied in soil characteristics, resource availability, vegetation composition and above-ground NPP (Table 1). The hydric, mesic and xeric sites correspond to ecosystem types 9, 12 and 13, respectively, in a classification system of the Center property (Goebel *et al*. 1997). Three replicate sites per ecosystem type were established. The area of the sites ranged from 0.47 to 1.31 ha (mean = 0.66 ha) such that at least 50 longleaf pine trees were located in each site.

FINE ROOT SPATIAL DISTRIBUTION

Prior to the initiation of production assessments, 10 soil cores (6.5 cm diameter × 1 m deep) were collected

Table 1 Soil characteristics, soil resource availability and above-ground net primary production estimates for the hydric, mesic and xeric sites used in this study. Values represent the mean ± 1 SE

Index	Hydric	Mesic	Xeric
Soil			
Type	Aquic Arenic Paleudults	Grossarenic Paleudult	Typic Quartzipsamment
Landscape position	Upland terraces	Upland terraces	Upland sand ridges
Slope (%)	0	2	3–4
Argillic horizon depth (cm)	≤ 50 cm	150 cm	> 300 cm
Soil moisture capacity (g/cm^3)	0.108	0.082	0.042
Soil resource availability*			
N mineralization (kg N ha^{-1} year^{-1})			
0–10 cm	3.5 (0.4)	6.8 (1.4)	11.8 (0.6)
0–90 cm	5.3 (0.6)	11.4 (2.3)	15.5 (0.8)
Soil Moisture (%, w:w)†	12.4 (1.1)	9.0 (0.9)	4.4 (0.3)
Above-ground NPP (kg ha^{-1} year^{-1})			
Overstory‡			
Longleaf Pine – foliage	2790.5 (281.8)	2833.7 (63.3)	772.8 (135.8)
Longleaf Pine – stem and branches	2166.2 (88.4)	2164.7 (156.3)	648.3 (141.3)
Oaks – foliage	4.1 (–)	5.3 (–)	601.6 (132.6)
Oaks – stem and branches	2.9 (–)	3.1 (–)	467.5 (198.0)
Understory§	3728.0 (452.8)	3056.9 (340.3)	2122.7 (143.1)
Total	8687.0 (117.6)	8058.1 (229.1)	4612.9 (215.8)

*From Wilson *et al*. (2002).
†From Wilson *et al*. (1999).
‡From Mitchell *et al*. (1999).
§From Kirkman *et al*. (2001).

in mid-summer from one site of each ecosystem type using an auger with a plastic tube liner (Giddings Machine Co., Fort Collins, CO, USA). Cores were divided into six horizons (0–10, 10–20, 20–30, 30–40, 40–70 and 70–100 cm). Each horizon was carefully washed through a 0.5 mm mesh sieve to isolate roots, which were sorted by size (< 0.5, 0.5–2.0 or > 2 mm diameter) and vitality (live or dead, assessed visually and manually based on colour, elasticity and resilience). Root samples were oven-dried (70 °C) to a constant mass and weighed.

FINE ROOT NPP

Fine roots were operationally classified as ≤ 0.5 mm in diameter based on the definition proposed by Pregitzer *et al.* (2002) and an assessment of root form and function in longleaf pine forests by Guo *et al.* (2004). Fine root NPP was assessed using the following five methods.

Minirhizotron

Five minirhizotron tubes (185.4 cm long × 5.1 cm diameter cellulose acetate butyrate plastic pipes) were installed in each of the study sites 6 months prior to the initiation of image collections (see Hendrick & Pregitzer 1992, 1993, 1996). Each tube had 180 cells (0.95 cm h × 1.25 cm w) along one side. Images of fine roots in the cells of each tube were collected at 2-month intervals for a year using a colour camera system (Bartz Technology, Santa Barbara, CA, USA) and analysed using ARCOS® software (Graphic Equation, Houston, TX, USA).

Relative rates of production and mortality during a sample interval were calculated by dividing new root length appearance, and previously existing root length disappearance, respectively, by the root length present at the beginning of the interval for the cells in the 0–30 cm stratum of each tube. Absolute production and mortality rates were then calculated by multiplying the relative production and mortality rates by the average root standing biomass measured at the beginning of the interval using soil cores.

The validity of these production and mortality estimates was evaluated using an approach described by Hendrick & Pregitzer (1993). Fine root standing biomass at the beginning of a sample interval (measured using soil cores) was used with the relative estimates of root production and mortality during the sample interval (measured using minirhizotrons) to predict the fine root standing biomass at the end of the sample interval. The predicted fine root standing biomass estimates were then compared with those determined empirically from soil cores.

Soil core

In coordination with minirhizotron image collections, 20 soil cores (each 10 cm diameter × 30 cm deep) were collected on six dates at 2-month intervals from one site of each ecosystem type. Each core was washed through a 0.5 mm mesh sieve, and the isolated roots were sorted into size and vitality classes as previously described. Root biomass and necromass estimates have been expressed on an ash-free, dry mass basis.

Fine root production and mortality were calculated using the maximum-minimum, sequential core and decision matrix approaches (Gower *et al.* 1992; Publicover & Vogt 1993). For each approach, production and mortality were calculated using: (i) only statistically significant differences in root biomass and necromass between sample dates ($P \leq 0.05$ assessed using a repeated measures analysis of variance; Littell *et al.* 1996) to yield conservative estimates (hereafter referred to as estimates derived using 'significant differences'); and (ii) all temporal differences in root biomass and necromass between sample dates, regardless of statistical significance, to yield more liberal estimates (hereafter estimates derived using 'all differences').

Ingrowth core

The ingrowth core method was based on the use of long- and short-term *in situ*, root-free soil cores (Neill 1992). Four months prior to the first collection date, 160 long-term cores were established in each site used for soil core collections, and 20 of these cores were harvested in coordination with the minirhizotron and soil core collections every 2 months. Also, 20 short-term ingrowth cores were established on each collection date and collected on the following date. Ingrowth cores were established by extracting a soil core (10 cm diameter × 35 cm depth), filling the hole with root-free soil tamped to approximate the original bulk density and placing a PVC pin flag in the centre to mark the core location. Following the ingrowth period, cores were collected using a smaller diameter corer (7.6 cm diameter × 30 cm depth) with the PVC pin flag serving as the centre point. Root biomass estimates from the smaller diameter collection cores were adjusted to account for the unsampled area of the larger diameter ingrowth cores.

Long- and short-term ingrowth cores were processed as described for the soil cores. In turn, root production was estimated using four approaches: (i) the sum of mean biomass values from the six sets of short-term cores, denoted as 'Σ short-term cores'; (ii) the mean biomass value from the last set of long-term cores, denoted as 'last long-term core'; (iii) the highest mean biomass value from the various sets of long-term cores, denoted as 'peak long-term core'; and (iv) the mean biomass value from the last set of long-term cores adjusted for root mortality, denoted as 'last long-term core + mortality' (see Neill 1992 for additional explanations).

Nitrogen budget

The N budget estimates the total mass of N allocated to fine roots as the difference between annual N uptake by the vegetation and the annual allocation of this N to non-fine root pools. To assess the N uptake by vegetation,

net N mineralization in the 0–10 cm and 0–90 cm soil horizons was measured as part of associated studies (see Table 1 and Wilson *et al*. 1999, 2002). Atmospheric deposition inputs of N (inorganic and organic; Wilson *et al*. 1999, 2002) were assessed using three deposition collectors located in open fields adjacent to each study site. Nitrogen input via symbiotic N_2-fixation has been assessed in associated studies (Hendricks & Boring 1999; Hiers *et al*. 2003). The loss of N via leaching and gaseous mechanisms was considered to be negligible in these N-poor systems (Nadelhoffer *et al*. 1985; Wilson *et al*. 1999, 2002) (Table 1).

The annual allocation of available N to non-fine root pools was assessed in associated studies (Mitchell *et al*. 1999; Kirkman *et al*. 2001). Nitrogen allocation to overstorey foliage was estimated using litterfall mass and N concentration data (Mitchell *et al*. 1999). Understorey foliar allocation was estimated using clip plot data to assess the net increase in foliage N during the study period (Kirkman *et al*. 2001). Nitrogen allocation to perennial wood and bark was estimated using site-specific allometric production equations and average wood N concentrations (Mitchell *et al*. 1999). In addition, N allocation to below-ground perennial wood and bark (i.e. coarse roots) was assumed to be 13% of above-ground perennial wood and bark production (Nadelhoffer *et al*. 1985).

After calculating the total mass of N allocated to fine roots, mortality rates may be estimated by dividing the annual mass of N allocated to fine roots by the mean fine root N content (assessed by analysing the roots in soil cores for total N using a CHN analyser; Perkin Elmer, Norwalk, CT, USA). In turn, production may be estimated by multiplying the mean fine root standing biomass by the associated fine root mortality rate (Nadelhoffer *et al*. 1985).

Carbon budget

The C budget is based on the assumption that the soil C pool is in an approximately steady state condition (i.e. annual changes in soil C storage are small relative to the C fluxes into and out of the soil; Raich & Nadelhoffer 1989). Based on this assumption, total C allocation to roots may be calculated by subtracting the C added to the soil via above-ground litter from the C removed from the soil via respiration (Raich & Nadelhoffer 1989). While the C budget does not provide an estimate of root production, the estimate of total C allocation to roots may serve as an upper level bound on production estimates derived using other techniques (Nadelhoffer & Raich 1992).

Soil CO_2 evolution was measured every 2 months in each site. On each sample date, CO_2 evolution was measured at 15 randomly selected points during a morning (08.00–09.00) and afternoon (14.00–15.00) phase. For each phase, a PVC chamber (7.6 cm diameter × 10.2 cm height with a rubber septum) was placed 0.5 cm into the ground over each sample point. At 2.5, 5, 7.5, 10, 20, 30 and 40 minutes, a syringe was used to homogenize the atmosphere and remove a 20-mL gas sample from the chamber head space. This was analysed for CO_2 using a GC-14 A (Shimadzu, Columbia, MD, USA) within 7 hours of collection. The CO_2 data were corrected for temperature differences between the soil and the chamber head space. A mean for the phase and day were calculated and used to derive annual CO_2 evolution estimates (Pietikainen *et al*. 1999; Knoepp & Vose 2002). The contribution of above-ground litter to the soil C flux estimates was considered to be negligible as: (i) there was not a persistent organic horizon on the forest floor; (ii) the substrate quality of above-ground litter in these systems is low, resulting in slow biological decomposition rates prior to thermal mineralization (Hendricks *et al*. 2002); (iii) much of the recalcitrant foliar litter was trapped in wiregrass crowns above the soil surface, which further reduces the litter decomposition rates and the potential C input to the soil system (see Hendricks *et al*. 2002); and (iv) much of the C lost during the minimal decomposition that does occur is respired directly to the atmosphere (i.e. not via the soil system) or immobilized in the tissues of the decomposer organisms. Thus, the annual estimate of soil C evolution was considered to be the estimate of the total C allocation to roots during the year.

Results

FINE ROOT SPATIAL AND TEMPORAL DISTRIBUTION

The assessment of fine root depth distribution revealed an exponential pattern in each site (Fig. 1). The exponential constant (k) decreased progressively from the hydric to the xeric site. Despite differences in root depth distributions, a large proportion of the fine roots were contained in the upper 30 cm of the 1 m soil profile (87, 85 and 70% in the hydric, mesic and xeric sites, respectively, Fig. 1). The 20 soil cores collected during the annual assessment yielded root biomass estimates with coefficients of variation averaged across all dates of 47.4 ± 7.5%, 62.2 ± 10.0% and 44.5 ± 9.0%, for hydric, mesic and xeric sites, respectively (Fig. 2).

Temporal patterns of fine root biomass and necromass were similar in the three site types (Fig. 2). The difference between minimum and maximum root biomass values measured during the year increased progressively from the xeric (77%) to the hydric (102%) to the mesic (195%) site. However, the average difference in fine root biomass between successive sample intervals was highest for the xeric site (24%) followed by the mesic (23%) and hydric (13%) sites (Fig. 2). Fine root necromass estimates were consistently lower than corresponding biomass estimates, but necromass temporal patterns were comparable with biomass patterns, with minimum estimates recorded from mid-summer to early fall and maximum estimates recorded from mid-winter to early spring (Fig. 2).

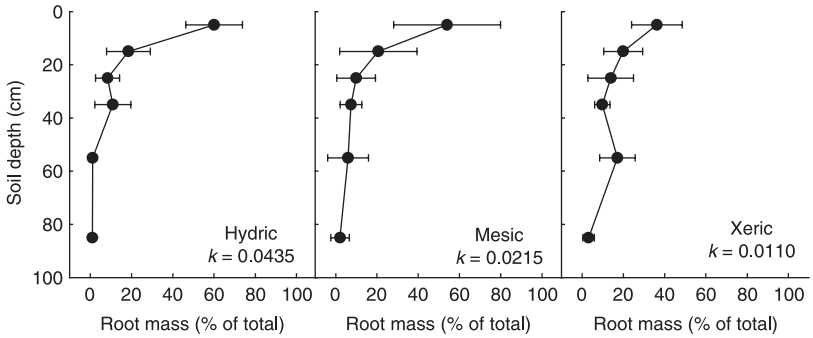

Fig. 1 Fine root standing biomass distribution within the 1 m soil profile of the hydric, mesic and xeric sites. Values represent the mean ± 1 SD. The k-values reported for each site are the decay constants derived using the standard exponential model ($y = e^{-kt}$) to describe the vertical distribution of fine roots.

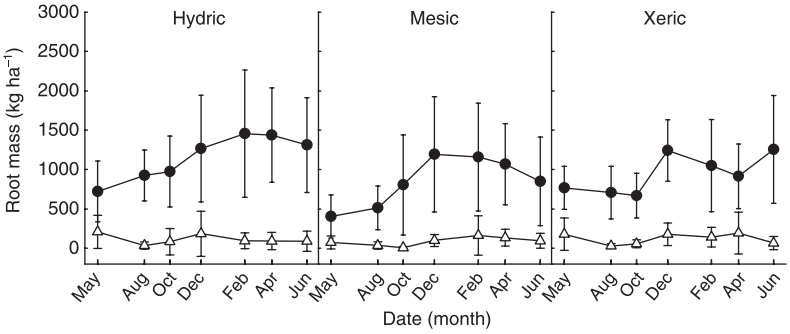

Fig. 2 Fine root biomass and necromass temporal distribution patterns in the hydric, mesic and xeric sites. Values represent the mean ± 1 SD.

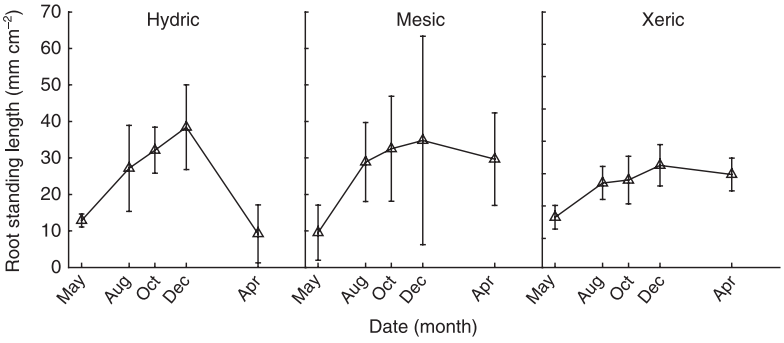

Fig. 3 Minirhizotron fine root standing length temporal patterns for the hydric, mesic and xeric sites. Values represent the mean ± 1 SE.

FINE ROOT NPP

Minirhizotron

Root production and mortality rates 'equilibrated' along the minirhizotron tube surface approximately 8 months after tube installation (Fig. 3). Root standing length increased from the point of tube installation (9–30 November) to the second sample date (5 August). After the second date, however, standing length generally stabilized; the average difference in mean standing length between samples for the hydric, mesic and xeric sites was 38.0 ± 33.0, 11.5 ± 4.0 and 14.3 ± 10.3%, respectively (Fig. 3). The relatively large variation for the hydric sites was attributed to a significant decline in standing length on the last sample date (April 22) following an extended period of standing water and saturated soil conditions (Fig. 3).

The comparison of predicted vs. actual fine root standing biomass at the end of a sample interval also suggested that root dynamics equilibrated following the second date (Table 2). There was a large differential between the actual and predicted final standing biomass values after the first sample interval before equilibration occurred (–198, –418 and –351% for the hydric, mesic and xeric sites, respectively; Table 2). However, the differential for subsequent sample intervals (i.e. after the presumed equilibration) decreased dramatically

Table 2 Validation assessment of minirhizotron fine root production and mortality rate estimates for the hydric, mesic and xeric sites over four sample intervals. See the Methods section for a description of the validation procedure

Site	Sample interval (start–finish)	Initial standing biomass (kg ha^{-1}) (A)	Minirhizotron production estimate (mm cm^{-2} day^{-1}) (B)	Minirhizotron mortality estimate (mm cm^{-2} day^{-1}) (C)	Predicted final standing biomass (kg ha^{-1}) (D) = (A × (B/C))	Actual final standing biomass (kg ha^{-1}) (E)	Predicted vs. actual final standing biomass (% difference) ((E-D)/E) × 100
Hydric	15 May–5 August	721.0	0.405	0.106	2754.9	923.9	−198.2
	5 August–4 October	923.9	0.367	0.280	1211.0	974.3	−24.3
	4 October–4 December	974.3	0.426	0.319	1301.0	1266.1	−2.8
	4 December–22 April	–	–	–	–	–	–*
Mesic	15 May–5 August	404.0	0.435	0.066	2662.9	513.6	−418.4
	5 August–4 October	513.6	0.318	0.251	650.7	804.5	19.1
	4 October–4 December	804.5	0.320	0.282	912.9	1193.8	23.5
	4 December–22 April	1193.8	0.113	0.158	853.8	1067.8	20.0
Xeric	15 May–5 August	766.6	0.262	0.063	3188.2	706.4	−351.4
	5 August–4 October	706.4	0.138	0.135	722.1	668.3	−8.1
	4 October–4 December	668.3	0.259	0.184	940.7	1242.7	24.3
	4 December–22 April	1242.7	0.093	0.097	1191.4	915.2	−30.2

*The validation of minirhizotron production and mortality rate estimates for the hydric sites over the last sample interval could not be conducted due to the prolonged flooding of these sites, which precluded the simultaneous collection of the final soil cores and minirhizotron images.

(13.5 ± 15.2, 20.9 ± 2.3 and 20.9 ± 11.4%, respectively). Following the presumed equilibration, the predicted final standing biomass values were within one standard deviation of the actual values in each site for all sample intervals (Table 2, Fig. 2).

The general agreement between predicted and actual fine root standing biomass estimates following tube equilibration increases confidence in the reliability of the relative production and mortality estimates (Table 2). Consequently, minirhizotron production estimates were annualized based on data from the post-equilibration sample intervals. Annualized production estimates for the hydric, mesic and xeric sites were 74.1 ± 8.0, 76.2 ± 23.8 and 52.0 ± 6.7 mm cm^{-2} year^{-1}, respectively, expressed on a tube surface area basis, and 4618, 1906 and 2295 kg ha^{-1} year^{-1}, respectively, expressed on a ground surface area basis (Table 3).

Table 3 Fine root production estimates (kg ha^{-1} year^{-1}) via the minirhizotron, soil core and ingrowth core calculation approaches in the hydric, mesic and xeric sites

Method	Hydric	Mesic	Xeric
Minirhizotron	4618.3	1905.5	2295.2
Soil core			
Significant differences			
Maximum-minimum	734.0	790.0	587.1
Sequential core	0.0	290.9	574.4
Decision matrix*	0.0	290.9	694.8
All differences			
Maximum-minimum	734.0	790.0	587.1
Sequential core	734.0	790.0	914.5
Decision matrix	885.7	910.6	941.6
Ingrowth core			
Σ short-term	1068.6	1409.0	2015.0
Last long-term	703.7	916.0	1106.2
Peak long-term	703.7	916.0	1106.2
Last long-term + mortality†	703.7	994.8	1694.2

*For soil core decision matrix calculations – significant difference only:
If Δ biomass > 0 and Δ necromass > 0 then production = Δ biomass + Δ necromass
If Δ biomass > 0 and Δ necromass < 0 (or Δ necromass was NS) then production = Δ biomass
If Δ biomass < 0 (or Δ biomass was NS) and Δ necromass > 0 then production = Δ biomass + Δ necromass
If Δ biomass < 0 (or Δ biomass was NS) and Δ necromass < 0 (or Δ necromass was NS) then production = 0
†For ingrowth core last long-term + mortality calculations:
If short-term > Δ long-term, then mortality = short-term – Δ long-term
If short-term < Δ long-term, then mortality = 0

Soil core

Soil core production estimates varied substantially based on the calculation method and the type of mass increment used (Table 3). When 'all differences' in standing biomass increments were considered, the decision matrix method yielded higher production estimates (range of 885.7–941.6 kg ha^{-1} year^{-1} for the hydric and xeric sites, respectively) than the sequential core and maximum-minimum approaches. However, when only the 'significant differences' in standing biomass were considered, the maximum-minimum approach yielded the highest estimates in two (i.e. hydric and mesic) of the three study sites, and the sequential core and decision matrix approaches yielded production estimates of 0 kg ha^{-1} year^{-1} in the hydric site (Table 3).

The relative ranking of root production estimates along the site gradient also differed among methods (Table 3). Maximum-minimum estimates followed the sequence xeric < hydric < mesic, whereas the sequential core and decision matrix approaches indicated that root production increased progressively from the hydric to the xeric site (Table 3).

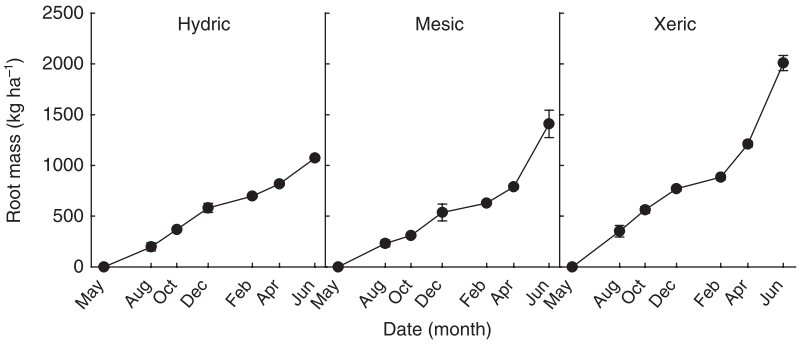

Fig. 4 Short-term ingrowth core fine root biomass estimates summed progressively across sample intervals to yield annual production estimates for the hydric, mesic and xeric sites. Values represent means ± 1 SD.

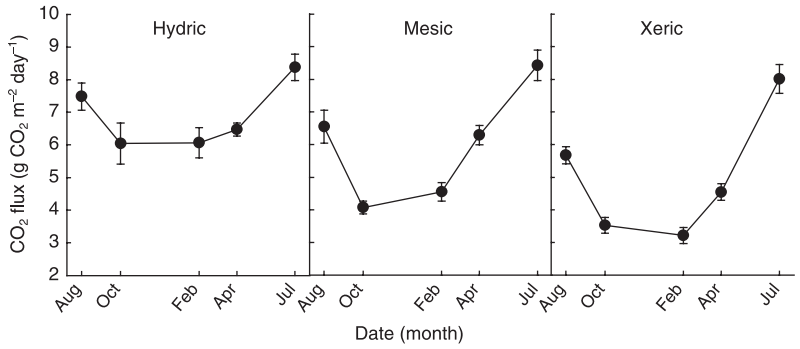

Fig. 5 Daily integrated soil CO_2 flux (± 1 SE) for the hydric, mesic and xeric sites during the annual assessment.

Ingrowth core

Root production estimates using ingrowth core data also differed substantially within sites based on the calculation method employed (Table 3). The sequential collection of short-term cores indicated that fine root production occurred during each sample interval (Fig. 4), and the sum of short-term cores method consistently yielded the highest root production estimates of the four ingrowth core methods used in each site (range of 1068.6–2015.0 kg ha^{-1} year^{-1} for the hydric and xeric sites, respectively). The last long-term and peak long-term production estimates were identical for each site, and these estimates were consistently the lowest based on ingrowth core data (range of 703.7–1106.2 kg ha^{-1} year^{-1} for the hydric and xeric sites, respectively). Accounting for root mortality in the final set of long-term cores increased the last long-term + mortality production estimates by 0, 8 and 53% relative to the last long-term estimates in the hydric, mesic and xeric sites, respectively (Table 3).

While there was some disparity among production estimates within sites, there was general agreement among the ingrowth core methods regarding productivity patterns among the sites (Table 3). The ingrowth core methods indicated that fine root productivity followed the site sequence hydric < mesic < xeric (Table 3).

Nitrogen budget

The N budget method consistently yielded unreliable root production and mortality estimates (Table 4). Prior to accounting for N allocation to fine roots, estimates of N allocation to non-fine root tissues exceeded estimates of N availability by 85 and 46% in the hydric and mesic sites, respectively, and the surplus in the xeric site was only 0.9 kg N ha^{-1} year^{-1} (Table 4). While N allocation to overstorey wood, bark and litter were measured using standard techniques, N allocation to the understorey foliage pool may have been overestimated as (i) some of the N in legume tissues may have been derived from the atmosphere rather than the soil via N_2-fixation, and (ii) N retranslocation from understorey foliage was not assessed in this study. However, eliminating the understorey foliar litter component from the budget still resulted in a net negative amount of N available for fine root production in the mesic and hydric sites, and the excess in the xeric site (5.3 kg N ha^{-1} year^{-1}) was comparable with the mean standing stock of N in fine roots (5.1 ± 1.3 kg N ha^{-1}) (Table 4).

Carbon budget

While the temporal pattern of soil CO_2 flux was similar for the three site types, soil CO_2 respiration rates were consistently higher ($P = 0.0194$) in the hydric sites (Fig. 5). Annualized estimates of soil CO_2 evolution for

Table 4 Nitrogen budget estimates (kg ha^{-1} year^{-1}) for the hydric, mesic and xeric sites. Estimates represent the mean ± 1 SE

Budget component	Hydric	Mesic	Xeric
N uptake (N_u)			
N mineralization (0–90 cm)	5.3 (0.6)	11.4 (2.3)	15.5 (0.8)
N deposition	9.5 (0.2)	8.8 (0.9)	7.7 (0.6)
Total N_u	14.8	20.2	23.2
Allocation to non-fine root tissues			
Wood and bark (N_{wb})			
Above-ground			
Longleaf Pine	5.2 (0.2)	7.7 (0.3)	4.0 (0.1)
Oaks	–	–	1.7 (0.2)
Below-ground			
Longleaf Pine	0.7	1.0	0.5
Oaks	–	–	0.2
Total N_{wb}	5.9	8.7	6.4
Above-ground Litter (N_{al})			
Overstory			
Longleaf Pine	12.8 (1.5)	11.9 (1.1)	5.6 (1.7)
Oaks	–	–	5.9 (1.4)
Understory			
Wiregrass – biomass	1.0 (0.9)	0.9 (0.9)	0.2 (0.3)
Wiregrass – necromass	1.6 (1.0)	1.3 (0.9)	0.6 (0.4)
Other graminoides	0.5 (0.4)	0.5 (0.4)	0.6 (0.5)
Ferns	0.7 (0.9)	0.8 (0.6)	–
Legumes	0.3 (0.2)	1.0 (0.4)	0.5 (0.3)
Other forbs	0.7 (0.2)	0.7 (0.2)	0.7 (0.3)
Woody species	0.9 (1.3)	1.2 (1.1)	0.6 (0.6)
Non-wiregrass necromass	3.0 (1.6)	2.5 (0.8)	1.2 (0.3)
Total N_{al}	21.5	20.8	15.9
Total $N_{wb} + N_{al}$	27.4	29.5	22.3
Allocation to fine roots (N_{fr})			
$N_{fr} = N_u - (N_{wb} + N_{al})$	–12.6	–9.3	0.9

the hydric, mesic and xeric sites were 24.8 ± 2.0, 20.7 ± 1.8 and 17.0 ± 1.0 Mg CO_2 ha^{-1} year^{-1}, respectively. Annual CO_2 flux rates were positively related to foliar production and minirhizotron root production estimates. In contrast, with the sole exception of the maximum-minimum estimates, the CO_2 flux rates were negatively related to fine root production estimates based on the soil core and ingrowth core techniques.

FINE ROOT VS. FOLIAGE PRODUCTION

Estimates of the relative allocation of production to fine roots expressed as a percentage of foliage production differed among the root assessment techniques (Fig. 6). The soil core and ingrowth core relative fine root production estimates consistently increased from the hydric to the xeric sites. In contrast, the minirhizotron

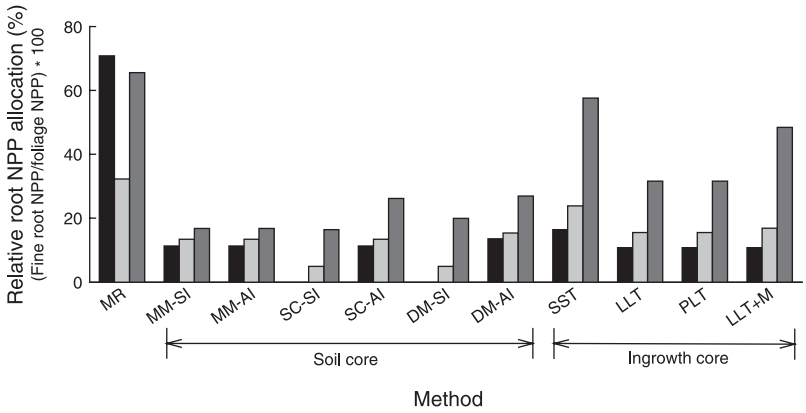

Fig. 6 Minirhizotron, soil core and ingrowth core fine root production estimates expressed as a percentage of foliage production across the hydric, mesic and xeric sites. (MR = minirhizotron, MM-SI = maximum-minimum significant increments, SC-SI = sequential core significant increments, SC-AI = sequential core all increments, DM-SI = decision matrix significant increments, DM-AI = decision matrix all increments, SST = sum of short-term cores, LLT = last long-term core, PLT = peak long-term core, and LLT + M = last long-term core plus mortality). Values represent means of each method.

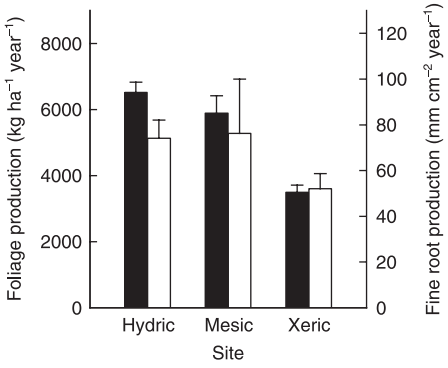

Fig. 7 Minirhizotron fine root production estimates on a tube surface area basis vs. foliage production in the hydric, mesic and xeric study sites. Values represent means ± 1 SD.

relative fine root production estimates expressed on a ground surface area basis were higher and more uniform at the extremes of the edaphic gradient (Fig. 6). A comparison of annualized minirhizotron root production estimates, expressed on a tube surface area basis, and corresponding foliar production estimates revealed a relatively uniform allocation pattern and, thus, a positive relationship between fine root and foliar production across the resource gradient (Fig. 7).

Discussion

The minirhizotron, soil core, ingrowth core, N budget and C budget techniques yielded conflicting results that may be selectively interpreted as support for both the constant and differential allocation hypotheses (Table 3, Figs 6 and 7). While the potential for these techniques to produce divergent results has been widely recognized, all continue to be used due to a lack of consensus regarding the most appropriate means of assessing root production (Fahey *et al*. 1999; Lauenroth 2000; Hertel & Leuschner 2002). Consequently, evaluations of resource controls on fine root production continue to be confounded by methodology (Norby & Jackson 2000; Fitter 2005). The results of this study may be particularly valuable for several reasons. First, this study employed a wide range of methods commonly used to assess root production. Secondly, these techniques were used across sites that differed in resource availability and above-ground productivity, enabling an evaluation of the assumptions and potential errors of each approach. Finally, the root assessments were conducted in association with assessments of resource availability and above-ground NPP necessary to evaluate root production in an ecosystem context. Thus, these data may be used to evaluate the key assumptions and errors of each technique and, hence, the reliability of the production estimates.

METHOD ASSUMPTIONS AND POTENTIAL ERRORS

Minirhizotron

Disturbance of roots and the rooting environment during minirhizotron tube installation may alter root dynamics at the tube–soil interface (Joslin & Wolfe 1999; Johnson *et al*. 2001). Consequently, root dynamics along the tube surface are generally allowed to 'equilibrate' prior to image collections. In this study, root dynamics were assumed to have equilibrated after 8 months based on the stabilization of fine root standing length (Fig. 3). This is shorter than the 1–2 years generally reported for other systems (Burke & Raynal 1994; Joslin & Wolfe 1999; Wells *et al*. 2002). Joslin & Wolfe (1999) noted that the equilibration phase in a mixed hardwood forest in Tennessee was similar in duration to the disturbance-induced stimulation of nitrification that can promote root proliferation (Eissenstat & Caldwell 1988; Pregitzer *et al*. 1993). Disturbance-induced increases in nitrification in this study were probably low due to the lack of a surface organic horizon, low soil organic matter concentrations and low N mineralization rates (Table 1). It is noteworthy that the equilibration period reported here is comparable with that reported by Price & Hendrick (1998) for a sweetgum (*Liquidambar styraciflua* L.) plantation growing in a similar soil type and climate in Georgia, USA.

Following equilibration, it is assumed that root dynamics at the tube–soil interface are representative of those in the bulk soil. Hendrick & Pregitzer (1993) indicated that the relative root production and mortality rates at the tube surface were representative of bulk soil rates based on an independent validation procedure. Using this procedure, the average differences between the actual and predicted fine root standing biomass estimates following tube equilibration were relatively low in the hydric, mesic and xeric sites (13.5, 20.9 and 20.9%, respectively), and fell within the range of values (8.1–34.4%) reported by Hendrick & Pregitzer (1993) for two sugar maple (*Acer saccharum* Marsh.) forests in Michigan, suggesting that the minirhizotron relative production and mortality estimates were representative of those in the bulk soil (Table 2). Consequently, minirhizotron production and mortality rates were coupled with initial standing biomass estimates for the corresponding intervals to provide root production estimates on a ground surface area basis. The annualized fine root production estimates for the hydric, mesic and xeric sites were 4618, 1906 and 2295 kg ha^{-1} year^{-1}, respectively, corresponding to 71, 32 and 66% of foliage production (Tables 3 and 5, Fig. 6).

The minirhizotron production patterns reported here contradict the patterns recently reported by West *et al*. (2004) using minirhizotrons in South Carolina longleaf pine-wiregrass forests. However, there are several key differences in the approaches of these studies. For example, the index of root production

Journal of Ecology, **94**, 40–57

Table 5 Comparison of foliage and fine root net primary production (NPP; kg ha^{-1} year^{-1}) estimates for temperate forest ecosystems[A]. Fine root production estimates are categorized by assessment technique, and absolute fine root production estimates are followed in parentheses by relative fine root production estimates expressed as a percentage of the corresponding foliage production estimate for the site or treatment

		Fine root NPP (% of Foliage NPP)								
		Soil core								
Species	Foliage NPP	Maximum–minimum	Sequential core	Decision matrix	Ingrowth core	Nitrogen budget	Mini-rhizotron	Fine root size (mm)	Site or treatment	Reference[I]
Coniferous										
Pinus palustris	6523	734 (11)[D]	734 (11)[D]	886 (14)[D]	1069 (16)[G]		4618 (71)	< 0.5	Hydric	This
	5896	790 (13)[D]	790 (13)[D]	911 (16)[D]	1409 (24)[G]		1906 (32)		Mesic	study
	3497	587 (17)[D]	915 (26)[D]	942 (27)[D]	2015 (58)[G]		2295 (66)		Xeric	
Abies amabilis	1770		6500 (367)					< 2	23 year-old	1, 2
	1280		12900 (1008)						180 year-old	
Pinus elliottii	3825	5250 (137)		3620 (95)[E]				< 1	27 year-old	3, 4
Pinus resinosa	1485	2155 (145)		2330 (157)				< 1	Unfertilized	5
	1745	1440 (83)		1790 (103)					Fertilized	
Pinus taeda	2700			2000 (74)				< 2	Control	6
	3400			1700 (50)					Irrigated (I)	
	5600			1100 (20)					Fertilized (F)	
	6900			1200 (17)					I and F	
Pseudotsuga menziessii	2000	5600 (280)						< 2	Low Productivity	7
	3200	1400 (44)							High Productivity	
Pseudotsuga menziessii	2002[B]			6500 (325)				< 1	Dry	8, 9
	1652[B]			6300 (381)					Moderate	
	2149[B]			4800 (223)					Wet	
Pseudotsuga menziessii	1940			3640 (188)				< 2	Control	10
	2400			1460 (61)					Fertilization	
	1760			1590 (90)					Wood Chip (WC)	
	2050			1380 (67)					Irrigation (I)	
	2260			950 (42)					WC and I	
Pseudotsuga menziessii	1950[C]				1726 (89)			NS[H]	20 year-old	11
	3350[C]				1205 (36)				40 year-old	
	1450[C]				3878 (267)				Old-growth	
Coniferous/Deciduous										
Pinus resinosa	5300	4100 (77)				4200 (79)		< 3		12, 13
Quercus rubra	4400	5100 (116)				4000 (91)				
Picea glauca	2680					1600 (60)		< 3		13, 14
Pinus resinosa	2520	690 (27)				1980 (79)				
Pinus strobus	2870	970 (34)				2570 (90)				
Pinus resinosa-strobus	3120					2620 (84)				

Journal of Ecology, **94**, 40–57

Table 5 *Continued*

	Fine root NPP (% of Foliage NPP)								
		Soil core							
Species	Foliage NPP	Maximum–minimum	Sequential core	Decision matrix	Ingrowth core	Nitrogen budget	Mini-rhizotron	Fine root size (mm)	Site or treatment	Reference[I]
Acer saccharum	2870	1100 (38)				4020 (140)				
Betula papyrifera	2840					3240 (114)				
Quercus alba	3610	1150 (32)				4130 (114)				
Quercus rubra	4170	520 (13)				5240 (126)				
Quercus velutina	4130	1740 (42)				5910 (143)				
Pinus resinosa	2430	2530 (104)				1200 (49)		< 3		13, 15
Pinus strobus	3100	1620 (52)				1400 (45)				
Acer saccharum	3800	1060 (28)				6500 (171)				
Quercus alba	3000	3050 (102)				3400 (113)				
Quercus rubra	3570	2350 (66)				2500 (70)				
Picea abies	2400			5208 (217)				< 1		16
Fagus sylvatica	3400			3108 (91)						
Deciduous										
Acer saccharum	4068						7302 (180)	< 2	Northern site	17
	4225						8081 (191)		Southern site	
Acer–Nyssa	5360				5970 (111)			NS[H]		18, 19
Fagus–Quercus	303	915 (302)		1360 (449)[E]	147 (49)			< 2		20
Quercus alba	3310			566 (17)[F]				< 1		21
	3310			728 (22)[F]	519 (16)[F]			< 2		
N. hardwood forest	2590[B]	2312 (89)		2004 (77)[E]				< 3		22

[A]The data in this table were derived from studies that used a fine root classification of ≤ 3 mm in diameter and were conducted in relatively 'mature' temperate forest ecosystems with no recent history of stand-altering disturbance.
[B]Values derived from estimates reported in Nadelhoffer & Raich (1992).
[C]Values derived from a figure in the cited paper.
[D]Soil core production estimates based on 'all differences' between sample intervals. See Table 3 for corresponding soil core production estimates based on 'significant differences' between sample intervals.
[E]Estimate derived using a decision matrix calculation including a decomposition component to account for necromass loss during sample intervals.
[F]Estimates reported on a 14-month basis were converted to a 12-month basis using a conversion factor of 0.857.
[G]Ingrowth core estimates based on the 'Σ short-term' cores calculation approach. See Table 3 for additional ingrowth core production estimates.
[H]NS = not specified; root size class was not specified, but was assumed to be ≤ 3 mm since these roots had recently colonized the ingrowth cores.
[I]References: 1 = Vogt *et al*. (1982); 2 = Vogt *et al*. (1983); 3 = Gholz *et al*. (1985); 4 = Gholz *et al*. (1986); 5 = Haynes & Gower (1995), 6 = Albaugh *et al*. (1998), 7 = Keyes & Grier (1981), 8 = Santantonio (1982); 9 = Santantonio & Hermann (1985); 10 = Gower *et al*. (1992), 11 = Klopatek 2002, 12 = McClaugherty *et al*. (1982); 13 = Aber *et al*. (1985), 14 = Nadelhoffer *et al*. (1985), 15 = Nadelhoffer & Raich (1992), 16 = Van Praag *et al*. (1988); 17 = Hendrick & Pregitzer (1993), 18 = Gomez & Day (1982); 19 = Symbula & Day (1988); 20 = Hertel & Leuschner (2002), 21 = Joslin & Henderson (1987); 22 = Burke & Raynal (1994).

varied between studies (West *et al*. 2004 used cumulative root number estimates), and the tube equilibration period differed (2–4 months for West *et al*. 2004 despite a distinct disequilibrium between root production and mortality rates).

Soil core

Soil core estimates of fine root production are dependent on accurate periodic assessments of root standing biomass. Random errors in biomass estimates may be confounded by repeated sampling, thus yielding overestimates (Lauenroth 2000; Nadelhoffer 2000). However, the techniques used in this study yielded unrealistically low estimates (Tables 3 and 5). Maximum-minimum, sequential core and decision matrix production estimates based on significant differences in standing biomass between intervals (i) were on average 81% lower than corresponding minirhizotron estimates (Table 3), and (ii) constituted only 4, 8 and 18% of corresponding foliage production, respectively, which is substantially lower than the average calculated from other soil core studies in temperate forests (138 ± 174%, range = 13–1008%, n = 43; Table 5).

While the low production estimates may be attributed to variation in root biomass and necromass estimates that precluded statistically significant differences, the estimates of production based on all differences were still, on average, 68% lower than minirhizotron estimates and comparable with those based on significant differences (Table 3). Thus, the low soil core estimates appeared to be associated with the basic assumptions of the techniques.

The maximum-minimum approach is based on the assumption that root production and mortality occur in two asynchronous phases during the year (Lauenroth 2000). This assumption appeared to be violated in our study based on the simultaneous assessment of production and mortality along minirhizotron tubes (Table 2), and the consistent root production in the sequential short-term ingrowth cores throughout the year (Fig. 4). Longleaf pine-wiregrass forests generally exhibit continuous C fixation activity throughout the year due to the dominance of species utilizing both the C_3 (longleaf pine) and C_4 (wiregrass) photosynthetic pathways, relatively mild winters, and even distribution of annual precipitation (Mitchell *et al*. 1999; Kirkman *et al*. 2001). The finding that fine root production and mortality were not temporally isolated is consistent with reports for several other temperate forest ecosystems (King *et al*. 2002; Carter *et al*. 2004; West *et al*. 2004), and the potential for the maximum-minimum approach to underestimate fine root production has been widely recognized (Fahey *et al*. 1999; Lauenroth 2000; Hertel & Leuschner 2002).

While the sequential core approach may be used in sites with multiple phases of root production during an annual cycle, this approach still assumes that root production and mortality occur asynchronously (Lauenroth 2000). As noted previously, this assumption appeared to be violated in our study sites, suggesting that the sequential core approach also underestimated fine root production. Numerous studies employing both the sequential core and minirhizotron techniques have indicated that the core approach yielded lower production estimates (Hendrick & Pregitzer 1993; Hansson *et al*. 1995; Rytter 1999; King *et al*. 2002). Notably, Rytter (1999) reported that sequential core estimates were 65–70% lower than corresponding minirhizotron estimates in a basket willow (*Salix viminalis* L.) plantation, which is comparable with the average differential reported in this study. Also, King *et al*. (2002) noted that the mortality of fine roots measured using minirhizotrons went undetected by the sequential core assessments conducted by Albaugh *et al*. (1998) in the same loblolly pine (*P. taeda* L.) ecosystems.

The shortcomings of the maximum-minimum and sequential core approaches have been theoretically addressed by the decision matrix approach that calculates production based on both biomass and necromass temporal fluctuations (Gower *et al*. 1992; Publicover & Vogt 1993). The most significant limitation of this approach is accurately quantifying root necromass accrual. Necromass estimates are typically highly variable due to the difficulty of distinguishing and separating root litter from associated soil organic matter (Vogt *et al*. 1998; Lauenroth 2000). Also, the potentially rapid disappearance of root necromass due to consumption and/or decomposition may lead to underestimates (Hendrick & Pregitzer 1992, 1993; Stevens *et al*. 2002). Consistent with these limitations, the decision matrix production estimates were equal or comparable with the sequential core estimates (Table 3). While the decision matrix approach has been modified to account for root decomposition (i.e. the compartment flow approach; Makela & Vanninen 2000), this approach is currently suspect due to the poor understanding of the rates and controls of root decomposition *in situ* (Fahey *et al*. 1999; Nadelhoffer 2000).

Ingrowth core

The ingrowth core approach is based on the assumption that root and soil disturbance during core installation does not alter root dynamics during the ingrowth period (Lauenroth 2000). Numerous researchers have speculated that this approach will yield overestimates due to (i) severing roots during the core installation, resulting in the proliferation of adventitious roots, (ii) altered chemical (i.e. water and nutrient availability) and physical (i.e. bulk density) properties of the soil, and (iii) reduced root competition in the medium (Vogt *et al*. 1998; Fahey *et al*. 1999; Lauenroth 2000). Consistent with this hypothesis, the sum of short-term ingrowth core production estimates (which accumulate more disturbance effects than longer-term cores) were greater than the corresponding long-term estimates (Table 3). However, while long-term cores may cause less disturbance, root

production estimates may be confounded by concurrent production and mortality leading to underestimates (Steele *et al*. 1997; Lauenroth 2000).

Root production based on the ingrowth core approach appeared to be conservative (Table 3). Consistent with other studies, the ingrowth core estimates were comparable with the soil core estimates (Table 3) (Neill 1992; Steele *et al*. 1997; Makkonen & Helmisaari 1999). Also, consistent with Steele *et al*. (1997), ingrowth core production estimates were on average 54% lower than minirhizotron estimates. In addition, the average of the ingrowth core production estimates in the hydric, mesic and xeric sites constituted only 12, 18 and 42% of corresponding foliage production, respectively, which is substantially lower than the average calculated from other ingrowth core studies in temperate forests (95 ± 91%, range = 16–267%, $n = 6$; Table 5). Although the 'last long-term + mortality' calculation theoretically accounts for root mortality in the long-term cores, estimates based on this algorithm were identical to those based on 'last long-term' and 'peak long-term' methods in the hydric sites that had the highest mortality rates based on minirhizotron analyses (Table 3). Hansson *et al*. (1995) also concluded that the ingrowth core approach underestimated root production in a semi-arid shrubland despite using a combination of long-term and short-term cores to correct for mortality during sample intervals.

Nitrogen budget

The N budgeting approach assumes that major fluxes of available N into, within and out of ecosystems are measured accurately (Nadelhoffer *et al*. 1985); errors associated with the measurement of each process may cumulatively render the root production estimates unreliable. In this study, the N budget method consistently yielded unreliable estimates (Table 4). Prior to accounting for N allocation to fine roots, estimates of N allocation to non-fine root tissues exceeded the measured amount of N available for uptake in two of the three sites (Table 4). As N allocation to the predominant non-fine root tissues was measured using reliable standard techniques (Mitchell *et al*. 1999; Kirkman *et al*. 2001), the assessments of this study apparently failed to account for important sources of available N. Ruess *et al*. (1996) also indicated that the N budget method failed to account for large amounts of N acquired by plants in relatively N-poor taiga forests of the Alaskan interior. These results emphasize the need to obtain more accurate estimates of N availability via processes such as organic N assimilation, N_2-fixation, N retranslocation and gross N mineralization in order to use the N budget method in N-poor systems (Ruess *et al*. 1996; Hendricks & Boring 1999; Schimel & Bennett 2004).

Carbon budget

The C budget estimates total below-ground C allocation as the difference between C loss from the soil via respiration and C addition to the soil via above-ground litterfall based on the assumption that the soil C pool is in a steady state condition (Raich & Nadelhoffer 1989). The equivalence of soil organic matter concentrations at the beginning and end of this annual assessment suggests that this assumption was valid (Aber & Melillo 2001). While it may be argued that 1 year is not long enough to allow a change in the C concentration of the relatively large soil pool to be measured (McDowell *et al*. 2001), changes in the C storage of the soils were probably small due to (i) the low organic matter concentrations, (ii) the mature status of the hydric, mesic and xeric study sites (i.e. longleaf pine mean ages of 56, 73 and 51 years, respectively), and (iii) the absence of experimental resource manipulations that may stimulate abrupt changes in C flow dynamics (Gower *et al*. 1996; McDowell *et al*. 2001). Furthermore, Giardina & Ryan (2002) recently indicated that errors in C budget estimates due to changes in soil C are small, even for young and recently disturbed forests.

While the steady state assumption appeared reasonable for these sites, the C balance estimates of total below-ground C allocation were probably conservative due to the use of a closed chamber system to measure soil respiration (Fig. 5) (Nay *et al*. 1994; Knoepp & Vose 2002). Knoepp & Vose (2002) reported that a similar closed chamber system yielded soil CO_2 flux estimates that were on average 35% lower than those obtained using an open chamber system in forests. However, Knoepp & Vose (2002) also indicated that the closed and open chamber estimates were positively correlated ($R^2 = 0.86$), suggesting that the closed chamber estimates allow for valid comparisons of soil CO_2 flux and below-ground C allocation among sites. The annualized soil C flux estimates in our sites (6773, 5646 and 4648 kg C ha^{-1} year^{-1} for the hydric, mesic and xeric sites, respectively) were within the range reported for other temperate forests (e.g. 2300–11 000 kg C ha^{-1} year^{-1}; Raich & Nadelhoffer 1989; Gower *et al*. 1996; McDowell *et al*. 2001). Furthermore, the significant ($P = 0.0194$) increase in soil CO_2 flux across the resource gradient and the positive relationship between soil CO_2 flux and foliage production are consistent with the patterns observed across a global above-ground production gradient (Raich & Nadelhoffer 1989).

CONSTANT VS. DIFFERENTIAL ALLOCATION HYPOTHESES

Critical evaluations of the assumptions, potential errors and results of the root assessment methods suggest that the minirhizotron technique yielded the most reliable fine root production estimates. The general agreement between predicted and actual fine root standing biomass estimates following tube equilibration serves as an independent validation that the relative production and mortality estimates were representative of those in the bulk soil (Table 2). The reliability of the minirhizotron estimates is further supported by the positive

relationship between the root production and annual CO_2 flux estimates (Table 3, Fig. 5). Furthermore, comparisons of the minirhizotron production estimates and the annualized soil CO_2 flux rates indicate that approximately 25% of the C allocated below ground is bound in structural components, which is remarkably consistent with the few other estimates derived using the C budget approach. Based on a series of studies conducted by Ewel *et al*. (1987), Gholz & Cropper (1991) and Gholz *et al*. (1991), we calculated that 22% of the C allocated below ground was structurally bound in mature slash pine (*P. elliottii* Engelm. var *elliottii*) ecosystems of north central Florida. Also, our results are comparable with the findings of Raich & Nadelhoffer (1989) using a productivity gradient comprised of 89 sites worldwide, which indicated that approximately one-third of the C allocated to fine roots was bound in structural components.

Fine root production estimates based on the minirhizotron technique were positively related to foliage production, thereby supporting the constant allocation hypothesis regarding soil resource controls on C allocation and NPP in forests (Figs 6 and 7). Although the constant allocation hypothesis has been recently supported elsewhere (Hendricks *et al*. 2000; Nadelhoffer 2000; Espeleta & Donovan 2002; Carter *et al*. 2004), the results of this study are relatively unique in that: (i) root production estimates were based on a technique (minirhizotron) that is not inherently associated with either the constant or differential allocation hypotheses; (ii) these estimates were independently validated and corroborated by C budget estimates; (iii) the assessments were conducted in mature ecosystems that formed a natural resource availability and above-ground productivity gradient; and (iv) the relatively constant proportional allocation of production to fine roots was assessed in a coniferous ecosystem that has typically been associated with the differential allocation hypothesis (Zak & Pregitzer 1998).

It is noteworthy that the NPP allocation patterns based on the minirhizotron approach were diametrically opposed to those based on the soil core and ingrowth core methods despite employing the techniques in concert (Fig. 6). We argue that the core approaches yielded underestimates of root production, and that the magnitude of the error increased as the production and mortality rates increased from the xeric to the hydric sites, resulting in a negative relationship between fine root and foliage production (Fig. 6). While the tenuous assumptions and potential errors of the coring methods have been recognized for over two decades (Singh *et al*. 1984; Kurz & Kimmins 1987), these more conventional techniques, which have been used to generate the majority of fine root production estimates (Table 5, Lauenroth 2000), have promulgated a suspect view of resource controls on root production that is commonly accepted in the ecological community (Smith & Smith 2001; Molles 2005) and represented in computer models of ecosystem dynamics (Gower *et al*. 1992; Woodward & Osborne 2000). Furthermore, these techniques continue to be used in root production assessments (Persson & Ahlstrom 2002; Tateno *et al*. 2004), probably yielding inaccurate and misleading results.

IMPLICATIONS FOR ECOSYSTEM CARBON AND NUTRIENT CYCLING ASSESSMENTS

While it is clear that accurate measurement of fine root production at the ecosystem scale may be compromised by tenuous assumptions and sampling errors, this critical evaluation suggests that the minirhizotron technique yielded the most reliable fine root production estimates. The minirhizotron root production estimates were positively related with foliage production across the edaphic resource gradient, thereby supporting the constant allocation hypothesis regarding soil resource controls on C allocation and NPP in forests. The finding that fine root production was on average 56% of foliage production was low relative to the overall average derived from other temperate forests (126 ± 144%, range = 13–1008%, $n = 67$; Table 5), and probably conservative as: (i) only roots ≤ 0.5 mm in diameter were assessed; (ii) production below the 30 cm soil depth was not measured; (iii) root biomass estimates used to derive the ground surface area estimates were probably conservative due to the use of a conventional sorting approach that probably under-represented first- and perhaps second-order roots (Guo *et al*. 2004); and (iv) C allocation to mycorrhizal fungi was not assessed in this study. Future studies of fine root dynamics could be improved by: (i) employing the minirhizotron technique in concert with other techniques that independently measure fine root production and mortality (e.g. isotope tracer techniques; Hendricks *et al*. 1997; Tierney & Fahey 2002; Trumbore & Gaudinski 2003) to corroborate results; (ii) investigating root dynamics from a root order perspective to more adequately represent the fine root pool (Pregitzer *et al*. 2002; Guo *et al*. 2004); and (iii) including assessments of C allocation to mycorrhizal fungal symbionts (Wallander *et al*. 2001; Fitter 2005). These more comprehensive and rigorous investigations may provide valuable insight into the patterns and controls of below-ground C allocation and net primary production and, hence, the structure and function of forest ecosystems.

Acknowledgements

Many people have supported this project, and it is with deep appreciation that we acknowledge their contributions. Durwin Carter, Mary Cobb, Kurt Fudge, Sean Kelley, Kirk Kolbie, John McGuire, Maureen Mulligan, Stacy Odom, Preston Parker, Hayes Swinney, Chris Thompson, David Walton and Ali Wick assisted in the execution of this study. Dr E. Barry Moser provided valuable statistical consultation services. Drs David M. Eissenstat and Roger W. Ruess provided incisive and

helpful criticisms on previous drafts of this manuscript. Support for this project was provided by the US Department of Agriculture (Grant 00-35101-9283) and the Robert W. Woodruff Foundation.

References

Aber, J.D. & Melillo, J.M. (2001) *Terrestrial Ecosystems*. Saunders College Publishers, Philadelphia, Pennsylvania.

Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A. & Pastor, J. (1985) Fine root turnover in forest ecosystems in relation to quantity and form of N availability: a comparison of two methods. *Oecologia*, **66**, 317–321.

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W. & King, J.S. (1998) Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *Forest Science*, **44**, 317–328.

Burke, M.K. & Raynal, D.J. (1994) Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil*, **162**, 135–146.

Carter, D.C., Hendricks, J.J., Mitchell, R.J. & Pecot, S.D. (2004) Fine root carbon allocation and fates in longleaf pine forests. *Forest Science*, **50**, 177–187.

Crocker, T.L., Hendrick, R.L., Ruess, R.W., Pregitzer, K.S., Burton, A.J., Allen, M.F. *et al.* (2003) Substituting root numbers for length: improving the use of minirhizotrons to study fine root dynamics. *Applied Soil Ecology*, **23**, 127–135.

Eissenstat, D.M. & Caldwell, M.M. (1988) Seasonal timing of root growth in favorable microsites. *Ecology*, **69**, 870–873.

Espeleta, J.F. & Donovan, L.A. (2002) Fine root demography and morphology in response to soil resource availability among xeric and mesic sandhill tree species. *Functional Ecology*, **16**, 113–121.

Ewel, K.C., Cropper,W.P. Jr & Gholz, H.L. (1987) Soil CO_2 evolution in Florida slash pine plantations. I. Importance of root respiration. *Canadian Journal of Forest Research*, **17**, 330–333.

Fahey, T.J., Bledsoe, C.S., Day, F.P., Ruess, R.W. & Smucker, A.M. (1999) Fine root production and demography. *Standard Soil Methods for Long-Term Ecological Research* (eds G.P. Robertson, C.S. Bledsoe, D. Coleman & P. Sollins), pp. 437–455. Oxford University Press, New York.

Fitter, A.H. (2005) Darkness visible: reflections on underground ecology. *Journal of Ecology*, **93**, 231–243.

Gholz, H.L. & Cropper,W.P. Jr (1991) Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. *Canadian Journal of Forest Research*, **21**, 1742–1747.

Gholz, H.L., Fisher, R.F. & Pritchett, W.L. (1985) Nutrient dynamics in slash pine plantation ecosystems. *Ecology*, **66**, 647–659.

Gholz, H.L., Hendry, L.C. & Cropper,W.P. Jr (1986) Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliottii*) in north Florida. *Canadian Journal of Forest Research*, **16**, 529–538.

Gholz, H.L., Vogel, S.A., Cropper,W.P., Jr, McKelvey, K., Ewel, K.C., Teskey, R.O. *et al.* (1991) Dynamics of canopy structure and light interception in *Pinus elliottii* stands of north Florida. *Ecological Monographs*, **61**, 33–51.

Giardina, C.P. & Ryan, M.G. (2002) Total belowground carbon allocation in a fast-growing *Eucalyptus* plantation estimated using a carbon balance approach. *Ecosystems*, **5**, 487–499.

Goebel, P.C., Palik, B.J., Kirkman, L.K. & West, L. (1997) *Field Guide: Landscape Ecosystem Types of Ichauway*. Technical Report Number 97–1. Joseph W. Jones Ecological Research Center at Ichauway, Newton, Georgia.

Gomez, M.M. & Day, F.P. Jr (1982) Litter nutrient content and production in the Great Dismal Swamp. *American Journal of Botany*, **69**, 1314–1321.

Gower, S.T., Pongracic, S. & Landsberg, J.J. (1996) A global trend in belowground carbon allocation: can we use the relationship at smaller scales? *Ecology*, **77**, 1750–1755.

Gower, S.T., Vogt, K.A. & Grier, C.C. (1992) Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. *Ecological Monographs*, **62**, 43–65.

Guo, D., Mitchell, R.J. & Hendricks, J.J. (2004) Fine root branch orders respond differently to carbon source-sink manipulations in a longleaf pine forest. *Oecologia*, **140**, 450–457.

Hansson, A.C., Aiferi, Z. & Andren, O. (1995) Fine-root production and mortality in degraded vegetation in Horqin sandy rangeland in inner Mongolia, China. *Arid Soil Research and Rehabilitation*, **9**, 1–13.

Haynes, B.E. & Gower, S.T. (1995) Belowground 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.

Hendrick, R.L. & Pregitzer, K.S. (1993) The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Canadian Journal of Forest Research*, **23**, 2507–2520.

Hendrick, R.L. & Pregitzer, K.S. (1996) Applications of minirhizotrons to understand root function in forests and other natural ecosystems. *Plant and Soil*, **185**, 293–304.

Hendricks, J.J., Aber, J.D., Nadelhoffer, K.J. & Hallett, R.D. (2000) N controls on fine root substrate quality in temperate forest ecosystems. *Ecosystems*, **3**, 57–69.

Hendricks, J.J. & Boring, L.R. (1999) N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management*, **113**, 167–177.

Hendricks, J.J., Nadelhoffer, K.J. & Aber, J.D. (1993) Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology and Evolution*, **8**, 174–178.

Hendricks, J.J., Nadelhoffer, K.J. & Aber, J.D. (1997) A ^{15}N tracer technique for assessing fine root production and mortality. *Oecologia*, **112**, 300–304.

Hendricks, J.J., Wilson, C.A. & Boring, L.R. (2002) Foliar litter position and decomposition in a fire-maintained longleaf pine-wiregrass ecosystem. *Canadian Journal of Forest Research*, **32**, 928–941.

Hertel, D. & Leuschner, C. (2002) A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. *Plant and Soil*, **239**, 237–251.

Hiers, J.K., Mitchell, R.J., Boring, L.R., Hendricks, J.J. & Wyatt, R. (2003) Legumes native to longleaf pine savannas exhibit capacity for high N_2-fixation rates and negligible impacts due to timing of fire. *New Phytologist*, **157**, 327–338.

Johnson, M.G., Tingey, D.T., Phillips, D.L. & Storm, M.J. (2001) Advancing fine root research with minirhizotrons. *Environmental and Experimental Botany*, **45**, 263–289.

Joslin, J.D. & Henderson, G.S. (1987) Organic matter and nutrients associated with fine root turnover in a white oak stand. *Forest Science*, **33**, 330–346.

Joslin, J.D. & Wolfe, M.H. (1999) Disturbances during minirhizotron installation can affect root observation data. *Soil Science Society of America Journal*, **63**, 218–221.

Keyes, M.R. & Grier, C.C. (1981) Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research*, **11**, 599–605.

King, J.S., Albaugh, T.J., Allen, H.L., Buford, M., Strain, B.R. & Dougherty, P. (2002) Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytologist*, **154**, 389–398.

Kirkman, L.K., Mitchell, R.J., Helton, R.C. & Drew, M.B. (2001) Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany*, **88**, 2119–2128.

Klopatek, J.M. (2002) Belowground carbon pools and processes in different age stands of Douglas-fir. *Tree Physiology*, **22**, 197–204.

Knoepp, J.D. & Vose, J.M. (2002) *Quantitative Comparison of In Situ Soil CO_2 Flux Measurement Methods*. USDA Forest Service Research Paper SRS-28. USDA Forest Service, Asheville, North Carolina.

Kurz, W.A. & Kimmins, J.P. (1987) Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach. *Canadian Journal of Forest Research*, **17**, 909–912.

Landers, J.L., Van Lear, D.H. & Boyer, W.D. (1995) The longleaf pine forests of the southeast: requiem or renaissance? *Journal of Forestry*, **93**, 39–44.

Lauenroth, W.K. (2000) Methods of estimating belowground net primary production. *Methods in Ecosystem Science* (eds O.E. Sala, R.B. Jackson, H.A. Mooney & R.W. Howarth), pp. 58–71. Springer-Verlag, New York.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS® System for Mixed Models*. SAS Institute, Cary, North Carolina.

Makela, A. & Vanninen, P. (2000) Estimation of fine root mortality and growth from simple measurements: a method based on system dynamics. *Trees*, **14**, 316–323.

Makkonen, K. & Helmisaari, H.S. (1999) Assessing fine-root biomass and production in a Scots pine stand – comparison of soil core and root ingrowth core methods. *Plant and Soil*, **210**, 43–50.

McClaugherty, C.A., Aber, J.D. & Melillo, J.M. (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology*, **63**, 1481–1490.

McDowell, N.G., Balster, N.J. & Marshall, J.D. (2001) Belowground carbon allocation of Rocky Mountain Douglas-fir. *Canadian Journal of Forest Research*, **31**, 1425–1436.

Mitchell, R.J., Kirkman, L.K., Pecot, S.D., Wilson, C.A., Palik, B.J. & Boring, L.R. (1999) Patterns and controls of ecosystem function in longleaf pine–wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research*, **29**, 743–751.

Molles, M.C. Jr (2005) *Ecology: Concepts and Applications*, 3rd edn. McGraw-Hill, Boston, Massachusetts.

Nadelhoffer, K.J. (2000) The potential effects of N deposition on fine-root production in forest ecosystems. *New Phytologist*, **147**, 131–139.

Nadelhoffer, K.J., Aber, J.D. & Melillo, J.M. (1985) Fine roots, net primary production, and soil N availability: a new hypothesis. *Ecology*, **66**, 1377–1390.

Nadelhoffer, K.J. & Raich, J.W. (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology*, **73**, 1139–1147.

Nay, S.M., Mattson, K.G. & Bormann, B.T. (1994) Biases of chamber methods for measuring soil CO_2 efflux demonstrated with a laboratory apparatus. *Ecology*, **75**, 2460–2463.

Neill, C. (1992) Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology*, **73**, 1918–1921.

Norby, R.J. & Jackson, R.B. (2000) Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist*, **147**, 3–12.

Persson, H. & Ahlstrom, K. (2002) Fine-root response to nitrogen supply in nitrogen manipulated Norway spruce catchment areas. *Forest Ecology and Management*, **168**, 29–41.

Pietikainen, J., Vaijarvi, E., Ilvesniemi, H., Fritze, H. & Westman, C.J. (1999) Carbon storage of microbes and roots and the flux of CO_2 across a moisture gradient. *Canadian Journal of Forest Research*, **29**, 1197–1203.

Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W. & Hendrick, R.L. (2002) Fine root architecture of nine North American trees. *Ecological Monographs*, **72**, 293–309.

Pregitzer, K.S., Hendrick, R.L. & Fogel, R. (1993) The demography of fine roots in response to patches of water and nitrogen. *New Phytologist*, **125**, 575–580.

Pregitzer, K.S., Zak, D.R., Curtis, P.S., Kubiske, M.E., Teeri, J.A. & Vogel, C.S. (1995) Atmospheric CO_2, soil N and turnover of fine roots. *New Phytologist*, **129**, 579–585.

Price, J.S. & Hendrick, R.L. (1998) Fine root length production, mortality and standing root crop dynamics in an intensively managed sweetgum (*Liquidambar styraciflua* L.) coppice. *Plant and Soil*, **205**, 193–201.

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.

Raich, J.W. & Nadelhoffer, K.J. (1989) Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, **70**, 1346–1354.

Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F. *et al.* (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs*, **73**, 643–662.

Rytter, R.M. (1999) Fine-root production and turnover in a willow plantation estimated by different calculation methods. *Scandinavian Journal of Forest Research*, **14**, 526–537.

Santantonio, D. (1982) *Production and turnover of fine roots of mature Douglas-fir in relation to site*. PhD thesis. Oregon State University, Corvallis, Oregon.

Santantonio, D. & Hermann, R.K. (1985) Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. *Annales Des Sciences Forestieres*, **42**, 113–142.

Schimel, J.P. & Bennett, J. (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, **85**, 591–602.

Singh, J.S., Lauenroth, W.K., Hunt, H.W. & Swift, D.M. (1984) Bias and random errors in estimators of net root production: a simulation approach. *Ecology*, **65**, 1760–1764.

Smith, R.L. & Smith, T.M. (2001) *Ecology and Field Biology*, 6th edn. Benjamin Cummings, San Francisco, California.

Steele, S.J., Gower, S.T., Vogel, J.G. & Norman, J.M. (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiology*, **17**, 577–587.

Stevens, G.N., Mitchell, R.J. & Jones, R.H. (2002) Rapid fine root disappearance in a pine woodland: a substantial carbon flux. *Canadian Journal of Forest Research*, **32**, 2225–2230.

Symbula, M. & Day, F.P. (1988) Evaluation of two methods for estimating belowground production in a freshwater swamp forest. *American Midland Naturalist*, **120**, 405–415.

Tateno, R., Hishi, T. & Takeda, H. (2004) Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. *Forest Ecology and Management*, **193**, 297–306.

Tierney, G.L. & Fahey, T.J. (2002) Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest Research*, **32**, 1692–1697.

Trumbore, S.E. & Gaudinski, J.B. (2003) The secret lives of roots. *Science*, **302**, 1344–1345.

Van Praag, H.J., Sougnez-Remy, S., Weissen, F. & Carletti, G. (1988) Root turnover in a beech and a spruce stand of the Belgian Ardennes. *Plant and Soil*, **105**, 87–103.

Vogt, K.A., Grier, C.C., Meier, G.E. & Edmonds, R.L. (1982)

Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology*, **63**, 370–380.

Vogt, K.A., Grier, C.C., Meier, C.E. & Keyes, M.R. (1983) Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. *Ecological Monographs*, **53**, 139–157.

Vogt, K.A., Vogt, D.J. & Bloomfield, J. (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil*, **200**, 71–89.

Wallander, H., Nilsson, L.O., Hagerberg, D. & Baath, E. (2001) Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytologist*, **151**, 753–760.

Wells, C.E., Glenn, D.M. & Eissenstat, D.M. (2002) Changes in the risk of fine-root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). *American Journal of Botany*, **89**, 79–87.

West, J.B., Espeleta, J.F. & Donovan, L.A. (2004) Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris-Aristida stricta* savanna ecosystem. *Forest Ecology and Management*, **189**, 397–406.

Wilson, C.A., Mitchell, R.J., Boring, L.R. & Hendricks, J.J. (2002) Soil N dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biology and Biochemistry*, **34**, 679–689.

Wilson, C.A., Mitchell, R.J., Hendricks, J.J. & Boring, L.R. (1999) Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas: II. N dynamics. *Canadian Journal of Forest Research*, **29**, 752–760.

Withington, J.M., Elkin, A.D., Bulaj, B., Olesinski, J., Tracy, K.N., Bouma, T.J. *et al.* (2003) The impact of material used for minirhizotron tubes for root research. *New Phytologist*, **160**, 533–544.

Woodward, F.I. & Osborne, C.P. (2000) The representation of root processes in models addressing the responses of vegetation to global change. *New Phytologist*, **147**, 223–232.

Zak, D.R. & Pregitzer, K.S. (1998) Integration of ecophysiological and biogeochemical approaches to ecosystem dynamics. *Successes, Limitations, and Frontiers in Ecosystem Science* (eds P.M. Groffman & M.L. Pace), pp. 372–403. Springer-Verlag, New York.

Received 11 May 2005
revision accepted 23 August 2005
Handling Editor: Michael Hutchings