



Fine root production and turnover across a complex edaphic gradient of a *Pinus palustris*–*Aristida stricta* savanna ecosystem

J.B. West^{a,b,*}, J.F. Espeleta^{a,c}, L.A. Donovan^a

^aDepartment of Plant Biology, University of Georgia, Athens, GA, USA

^bDepartment of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA

^cLa Selva Biological Station, Organization for Tropical Studies, Puerto Viejo de Sarapiquí, Costa Rica

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Abstract

Fine root dynamics significantly affect plant performance through soil resource capture, and ecosystem function through soil carbon and nitrogen cycling. The responses of fine roots to natural gradients in resource availability, however, are poorly understood. We assessed fine root dynamics across a soil texture gradient in *Pinus palustris* Mill.–*Aristida stricta* Michx. savannas. These savannas are currently the subject of considerable conservation and restoration efforts in the southeastern US. Fine root dynamics were determined for two growing seasons in three soil types with minirhizotrons. The soils were characterized as: shallow, loamy soils; intermediate depth sandy soils; and deep, sandy soils. Although soil moisture was not quantified in this study, increasing drainage capacity and clear shifts to xerophytic vegetation strongly suggest increasing soil moisture limitation from shallow to deep soils. Potential net N mineralization, microbial biomass and annual overstory litterfall were also characterized across the gradient. Consistent with increasing soil moisture limitation, fine root production increased and diameters decreased from shallow to deep sands, as did the amount of deep root production. Litterfall also declined across this gradient. In contrast, fine root turnover rates were highest in the intermediate soils where nitrogen availability was highest. These results suggest that fine root turnover rate may vary independently of annual fine root production and these components may differentially respond to multiple limiting resources.

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1. Introduction

An understanding of the relationships between soil resource availability and fine root dynamics is critical to many fundamental questions in terrestrial ecology. Because fine roots function primarily as resource-capture organs, fine root responses comprise a major component of whole plant response to changes in soil

resource availability (Robinson, 1991; Aerts and Chapin, 2000). In addition, fine root turnover contributes significantly to soil organic matter pools (Gill and Jackson, 2000), making fine root turnover rates potentially important modulators of soil carbon and nitrogen cycling (Gill and Jackson, 2000; Aerts and Chapin, 2000; Silver and Miya, 2001). Although fine root dynamics clearly play substantial roles in these processes, our understanding of this important component of terrestrial ecosystems remains severely limited (Nadelhoffer, 2000), hampering efforts to understand these systems in general (Geider et al.,

* Corresponding author. Tel.: +1-612-625-7271;

fax: +1-612-624-6777.

E-mail address: westx062@umn.edu (J.B. West).

2001), as well as how they may respond to change (Norby and Jackson, 2000).

Primarily due to the limited dataset on fine root dynamics, there remains a lack of consensus on even the direction of response of fine root dynamics to changes in resources. For example whether proportional fine root production increases or decreases with increased nutrient availability is still unclear (Nadelhoffer, 2000), and fine root response to soil moisture availability also remains poorly understood (Joslin et al., 2001). Based on optimal allocation models, fine root production may be expected to increase when soil resource limitation increases (Caldwell and Richards, 1986). This prediction, however, has found mixed support when tested at scales larger than individual plants (Aerts and Chapin, 2000; Nadelhoffer, 2000). The rate of fine root turnover (the proportion of the root pool replaced per year) may generally be expected to increase with increased nutrient availability (Chapin et al., 1993; Ryser, 1996; Aerts and Chapin, 2000; but see Burton et al., 2000). Nutrient-poor habitats may select for decreased nutrient losses, whereas nutrient-rich habitats may select for rapid growth rates (Aerts and Chapin, 2000). These differential adaptive responses may be the result of fundamental biological tradeoffs; such as for leaves the capacity for high photosynthetic rates versus long leaf lifespans (Reich et al., 1992). It is not known whether nutrient-poor habitats also select for decreased nutrient losses in root turnover, or whether there are similar fundamental tradeoffs for roots (Bassirirad, 2000). However, given the potentially significant carbon and nutrient losses in root turnover (Nadelhoffer, 2000), root lifespans should show similar patterns in response to nutrient availability as leaves. Natural gradients often exhibit complex patterns of soil resource availability. For example, nitrogen and water availability may not change predictably across natural edaphic gradients (Wilson et al., 1999), and it is not understood how fine root systems respond to this complexity. Direct observation of changes in fine root dynamics across gradients in soil resource availability promises to considerably improve our understanding of these relationships.

In this study we quantified fine root production and turnover, overstory litter production, and nitrogen availability (potential net N mineralization and microbial biomass N) in replicated stands across a soil

texture gradient of a *Pinus palustris* Mill.–*Aristida stricta* Michx. savanna ecosystem. These savannas exhibit strong soil resource limitation and are dependent on frequent ground fires to maintain their open savanna vegetation structure (Christensen, 1988). The gradient consisted of increasing surface horizon sand content, and a corresponding increasing depth to clay (Bt horizon). Known relationships between soil texture and soil moisture availability (cf. Kabat et al., 1995) indicate that water availability decreased across this gradient. Prior studies of this system report low plant densities and decreased production on sites with sandier soils (Christensen, 1988; Mitchell et al., 1999; Kirkman et al., 2001). The observed changes in oak species dominance have also been partially attributed to differences among species in their ability to tolerate or avoid low soil moisture availability (Vaitkus and McLeod, 1995; Donovan et al., 2000; Espeleta and Donovan, 2002). The patterns in overstory production and clear differences in standing aboveground biomass on our sites (West, pers. obs.) further indicated a strong soil moisture gradient across the texture gradient.

We operationally defined fine roots as those <1 mm in diameter (most roots observed were <0.5 mm), recognizing that functional differences among roots may exist even at the scale of tenths of millimeters (King et al., 2002). We further define turnover as an annual *rate* of loss (units: per year), a definition that has been employed in recent reviews of fine root dynamics (Gill and Jackson, 2000; Norby and Jackson, 2000), and one that is conceptually consistent with its use in ecosystem models (flux/pool size). Our objective was to determine how changes in community-level fine root dynamics across the gradient related to changes in soil texture and N availability.

2. Materials and methods

This study was conducted at the Carolina Sandhills National Wildlife Refuge. The refuge is situated within the Fall-line Sandhill physiographic province, between the Piedmont and the Coastal Plain of the southeastern US near McBee, South Carolina (latitude 34°33'N, longitude 80°13'W) at an elevation of approximately 100 m a.s.l. Mean annual temperature is 15 °C (January: mean 5 °C, July: mean 20 °C) and

mean annual rainfall is 1200 mm, with little seasonality in precipitation. The overall study design consisted of three replicate stands for each of three soil texture types, for a total of nine stands. A 100 m² plot was established within each stand in February 1999 (April 1999 for the mesic stands) in an area dominated by a *P. palustris* overstory and an *A. stricta* herbaceous layer. The soils were distinguished primarily by surface horizon percent sand and depth to silicate clay accumulation (Bt horizon). For this reason the gradient was described as: “deep”, “intermediate” and “shallow” soils. The deep soils had sandy (>90% sand) surface horizons to a depth of >200 cm before significant clay accumulation (a Bt horizon). The intermediate soils consisted of moderately deep (<75 cm depth to Bt), sandy surface horizons. The shallow soils had relatively shallow (<35 cm depth to Bt), loamy sand (50–70% sand) surface horizons (USDA, 1995; West, pers. obs.). This soil texture gradient is often described as a soil moisture gradient (Christensen, 1988; Mitchell et al., 1999; Kirkman et al., 2001). At the refuge this soil texture gradient generally followed a topographic gradient, with the deep (=xeric) soils occurring on ridge tops and the soils becoming shallower and more mesic down slopes. The dominant tree (*P. palustris*) and grass (*A. stricta*) species co-occur across this gradient. Oaks (*Quercus* spp.) are also common, however relative species dominance changes across the gradient such that, among the oaks, *Q. laevis* Walt. is dominant on the deep sands, mixtures that include *Q. laevis*, *Q. incana* Bartr. and *Q. margaretta* Ashe ex Small are found on the intermediate soils, and species such as *Q. marilandica* Muench dominate on the shallowest soils. The stands are regularly burned and were all burned in the spring of 1998.

When the plots were established, three clear butyrate minirhizotron tubes (2 m long × 5.08 cm inside diameter) were installed at a 30° angle to the soil surface to a vertical depth of approximately 65 cm at haphazard locations within each plot (see Hendrick and Pregitzer, 1996 for a more detailed description of minirhizotrons). The tubes were scribed down their lengths with regular 0.9 cm × 1.3 cm rectangles to allow repeated imaging of the same locations. The tubes were imaged using a Hi-8 camcorder and a Bartz Minirhizotron Research camera (Bartz Technology Co., Santa Barbara, CA) on 22 June, 15 July, 19

August, 24 September, 18 December, 1999; 4 February, 18 March, 9 June, 15 July, 28 August, 9 October, 6 December 2000.

The initial imaging date was analyzed using a PC-based image analysis system (ROOTS, Hendrick and Pregitzer, 1992). Using a TARGA videographics card (Truevision Inc., Indianapolis, IN) root numbers, widths and lengths were traced to the nearest 0.01 mm. This analysis allowed the generation of a regression between root number and root length ($y = 4.50x$, $R^2 = 0.86$, $P < 0.01$). Several other studies have shown a tight correlation between root number and root length as observed in minirhizotron images, suggesting that once the relationship is known for a given site the metrics may be used interchangeably (summarized in Crocker et al., 2003). However, it is possible that the relationship between number and length changed over time or between sites in our study. Therefore, root number rather than length was used in all analyses. Roots were counted by first digitally capturing individual images of each frame from each tube. Roots were then identified as “new”, “brown”, or “white” (white, but not new). Although pine roots were often easily identified, we were unable to confidently separate all visible roots even by group. Excavations of roots in nearby sites suggested that the potential to misidentify roots in minirhizotron images was high. We therefore did not attempt to discriminate between species. Mycorrhizal infection was also not recorded. Much of the vegetation in these savannas is likely infected by arbuscular mycorrhizae, which would often not be visible in minirhizotron images. Our primary objective in this study was the quantification of community-level changes in fine root dynamics. Production and death were quantified by simultaneously viewing images from consecutive dates and recording the number of roots that appeared, remained, or disappeared between those dates. Root color or other characteristics were unreliable in determining root death, so root death was quantified solely based on root disappearance. Although this method does not discriminate between causes of death such as herbivory, pathogens and root senescence, it represents roots that are lost and transferred to soil pools. Root numbers were then pooled within each plot by summing the number of roots observed in each of the three tubes and are expressed as the number of roots per plot.

Based on prior observations of root distributions, two soil depth classes were established (0–30 and 30–65 cm). New and cumulative root production and cumulative death were analyzed using a mixed-model repeated-measures analysis (Littell et al., 2000). All statistical analyses were conducted using SAS (SAS Institute, Cary, NC). Fine root turnover was calculated in three ways for the year January–December 2000: (1) total number of roots produced (per year)/maximum standing pool of live roots (Gill and Jackson, 2000), (2) total number of roots produced (per year)/mean standing pool of live roots, and (3) total number of dead roots (per year)/mean standing pool of live roots (Burton et al., 2000). Each of these estimates was analyzed separately in a mixed-model ANOVA (Littell et al., 1996).

Overstorey litter production (oak + pine) was estimated with circular litter traps (diameter = 40 cm). Two litter traps per plot were placed at opposite corners of each plot. The litter captured in the traps from January–December 2000 was pooled for each plot and then dried and weighed. When sampling soils, cores were augured at least 1 m directly behind each minirhizotron tube (three cores per plot) in order to limit disturbance of any roots that may come into contact with the minirhizotron surface. For microbial biomass C and N, soil samples were collected in September 1999 (3.5 cm diameter at 5–10 cm depth). The soils were sieved (2 mm diameter mesh) and were analyzed for microbial carbon and nitrogen content using a fumigation/direct extraction (0.5 M K₂SO₄) technique ($k_C = 0.33$, $k_N = 0.45$; Callaham and Hendrix, 1998). Total persulfate N (Cabrera and Beare, 1993), and total organic carbon were measured in the extract solution before and after fumigation of the soils with chloroform. Potential net nitrogen mineralization rate was estimated using laboratory incubations of soil collected in August 2000 (3.5 cm diameter at 2–10 cm depth). Incubations were 30 days long and at 23 °C in the dark. Pre- and post-incubation extractions were done with a 2 M KCl extract solution. The extractant was filtered and analyzed for NH₄⁺ and NO₃⁻ by con-flow colorimetric analysis (Alpkem RFA300, OI Corporation, College Station, TX). For both microbial biomass and potential N mineralization, soils were collected, placed in sealable plastic bags in an ice-filled cooler, and then transported to the laboratory where they were stored at 3 °C until

the analyses could be performed. All of the soil data were analyzed using mixed-model ANOVA and data were transformed as necessary to meet model assumptions. The three samples taken within a plot were treated as subsamples nested within the plot and the unit of replication for all analyses is the plot (=stand).

3. Results

Cumulative fine root production increased with increasing sandy horizon depth (Fig. 1A and B). Overall, shallow (<30 cm) root production was greater than deep (30–65 cm) production and death. Also, deep fine root production was significantly higher in the “deep” soil relative to the “intermediate” and “shallow” soils (Fig. 1B). New root production was observed year-round, with distinct increases evident during the warmer months (Fig. 1A). Seasonality in root production deeper in the soil profile was evident

Table 1
Repeated-measures analysis of cumulative root production and death^a

	nDF	dDF	F
Cumulative production			
Time	11	132	20.53 ^{***}
Gradient	2	12	8.53 ^{**}
Time × gradient	22	132	3.83 ^{***}
Depth	1	12	6.15 [*]
Time × depth	11	132	0.77
Gradient × depth	2	12	0.54
Time × gradient × depth	22	132	0.95
Cumulative death			
Time	11	132	8.93 ^{***}
Gradient	2	12	5.10 [*]
Time × gradient	22	132	2.19 ^{**}
Depth	1	12	4.78 [*]
Time × depth	11	132	1.67
Gradient × depth	2	12	0.21
Time × gradient × depth	22	132	0.79

^a The gradient effect compares the shallow, intermediate, and deep sands, and depth compares 0–30 to >30–65 cm. Data were analyzed in a mixed-model repeated-measures ANOVA. The Toeplitz covariance structure was selected from several common covariance structures based on Akaike’s information criterion.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

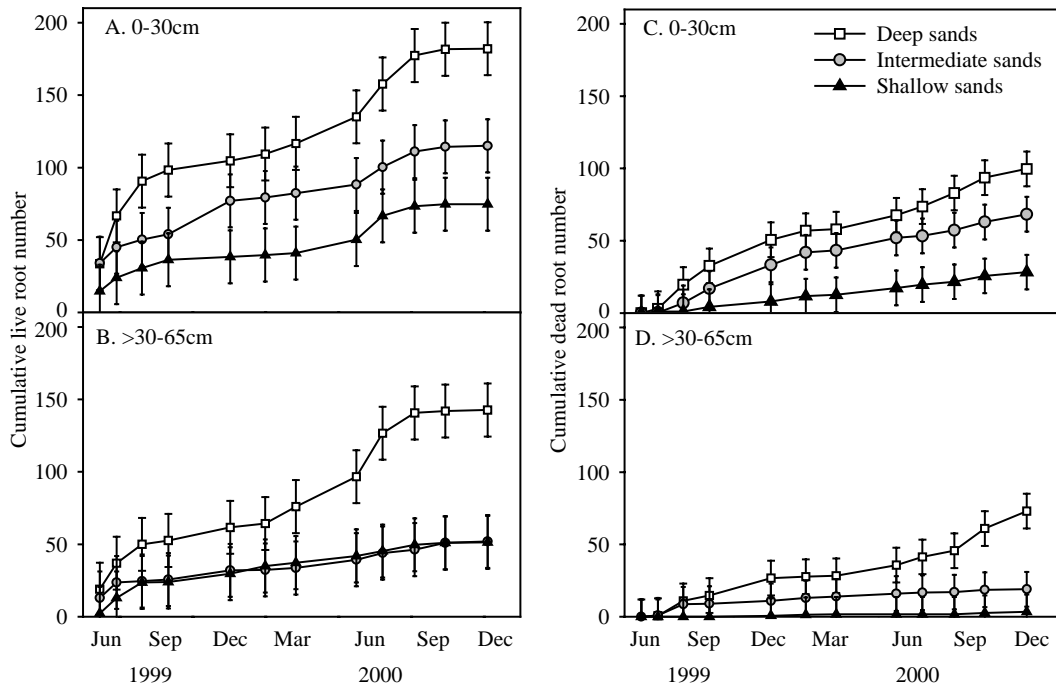


Fig. 1. Mean cumulative number of fine roots (number of roots per plot ± 1 S.E., see Section 2 for details) that were produced (A and B) and died (C and D) from June 1999 to December 2000. Statistical analysis is presented in Table 1.

only for the deepest soils (Fig. 1B; Table 1). Root death exhibited a similar pattern as production (Fig. 1C and D). Root death occurred throughout the year as well, but did not exhibit a clear seasonal pattern. In addition to the differences in fine root production across the gradient, there was a clear shift in fine root diameter distributions with roots becoming thinner from shallow to deep soils (Fig. 2).

Consistent with aboveground biomass differences observed between the sites (pers. obs.), overstory litter production decreased with increasing soil depth (Table 2). The measures of nitrogen availability, however, were highest for the intermediate soils. Potential net N mineralization exhibited a peak in the middle of the soil depth gradient, as did microbial biomass N, although the differences were not statistically significant for microbial biomass N (Table 2).

Contrary to the patterns observed for fine root production and death, the rate of fine root turnover was also highest in the intermediate soils for the three turnover calculations (Fig. 3). Although the measures of turnover agreed qualitatively, there were important

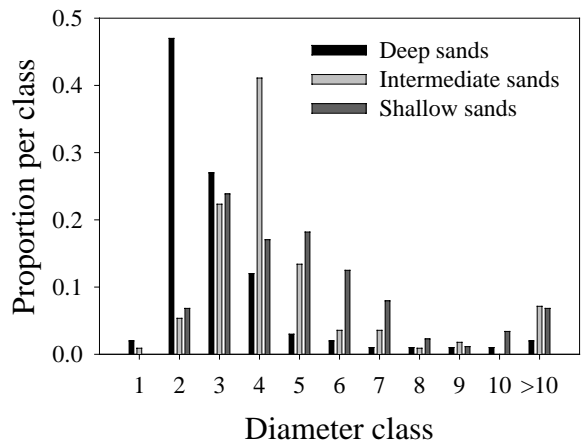


Fig. 2. Fine root diameter distributions across the soil texture gradient from June 1999. Diameter classes represent ranges of fine root diameters (e.g. 1: 0 to <0.1 mm, 2: 0.1 to <0.2 mm, 3: 0.2 to <0.3 mm, etc.). Proportion is the number of roots in each diameter class divided by the total number of roots observed for each of the three gradient positions.

Table 2
Overstorey litterfall and soil characteristics across the soil texture gradient^a

Variable	Deep	Intermediate	Shallow	F-ratio
Overstorey litterfall (g m^{-2})	2.05 (5.12)	11.71 (6.27)	21.15 (5.12)	$F_{2,5} = 6.29^*$
Microbial C (5–10 cm; $\mu\text{g C per g soil}$)	84.68 (26.40)	92.03 (26.40)	122.28 (26.40)	$F_{2,6} = 0.30$
Microbial N (5–10 cm; $\mu\text{g N per g soil}$)	16.51 (3.20)	24.89 (3.20)	19.39 (3.20)	$F_{2,6} = 1.66$
Potential net N mineralization (2–10 cm; $\mu\text{g N per Kg soil}$)	10.38 (38.0)	95.24 (38.00)	60.79 (38.00)	$F_{2,6} = 12.05^{**}$

^a Means are least-squares means (± 1 S.E.) from mixed-model analyses of variance (ANOVA). Three subsamples per site were taken for soils, and each site had two litter traps for litterfall. The results of the ANOVAs are presented as F-ratios.

* $P < 0.05$.

** $P < 0.01$.

quantitative differences between them. For example, the estimates based on root death were notably lower than those based on root production. Turnover decreased significantly with depth for all analyses, and there was no significant interaction between depth and location on the gradient for any measure of turnover (Table 3).

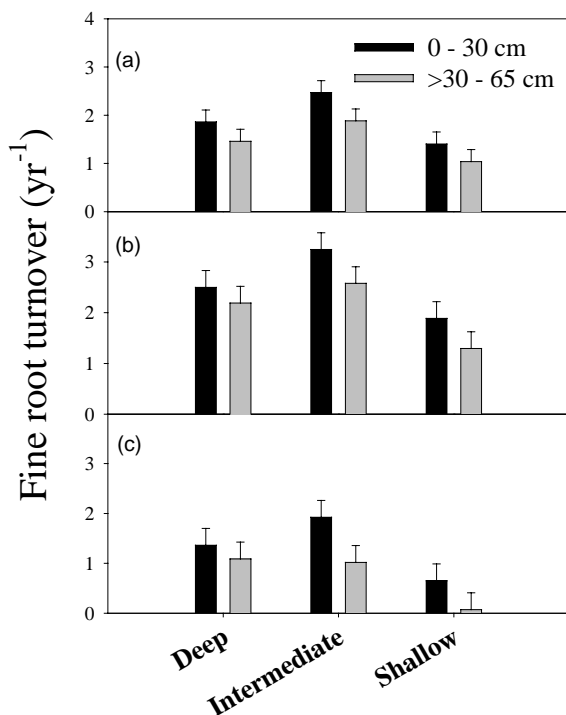


Fig. 3. Mean fine root turnover (± 1 S.E.) based on (a) annual production/maximum standing crop (Gill and Jackson, 2000), (b) annual production/mean standing crop, and (c) annual death/mean standing crop (Burton et al., 2000). Statistical analysis is presented in Table 3.

4. Discussion

Consistent with increasing water limitation as soils became sandier and deeper, fine root production increased across the soil texture gradient, as did the amount of deep root production. Rates of turnover, on the other hand, were not proportional to production and exhibited a peak in the middle of the soil texture gradient, coincident with higher rates of N mineralization. Our fine root production results are consistent with optimal allocation models of soil moisture limitation (Caldwell and Richards, 1986). Under increased water limitation, greater root production provides greater access to the limiting resource (Abrams, 1990). We also observed decreases in fine root diameter across the gradient. Since thinner roots may be more efficient at

Table 3
Mixed-model ANOVA of fine root turnover^a

Fine root turnover	nDF	dDF	F
Production/max			
Gradient	2	12	7.43 ^{**}
Depth	1	12	4.97 [*]
Gradient \times depth	2	12	0.11
Production/mean			
Gradient	2	12	8.08 ^{**}
Depth	1	12	3.78 ⁺
Gradient \times depth	2	12	0.16
Death/mean			
Gradient	2	12	5.97 [*]
Depth	1	12	4.54 [*]
Gradient \times depth	2	12	0.43

^a The gradient effect compares the shallow, intermediate, and deep sands, and depth compares 0–30 to >30–65 cm.

⁺ $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

absorbing water (Eissenstat et al., 2000), this further suggests a central role of water availability in controlling fine root characteristics and production. Although it was not possible to distinguish within-species changes (e.g. for *P. palustris* or *A. stricta*) from changes in species composition (e.g. among *Quercus* spp.) across the gradient, both may have contributed to the observed changes. At the stand scale, therefore, increased sandy horizon depth, from shallow more loamy sands to very deep sandy soils, resulted in fine root responses that likely improved plant access to increasingly limiting soil moisture availability.

As in other reports for pine forests and savannas in the southeastern US (Saterson and Vitousek, 1984; King et al., 2002; Jones et al., 2003; West et al., 2003), root production and death were observed all year. Year-round root production has also been documented in several northern, deciduous forests (e.g. Hendrick and Pregitzer, 1992), resulting presumably from stored C reserves. Since this ecosystem contains evergreen and deciduous species, and we were unable to obtain species-specific information, the contribution of each to winter root production is not known. However, clear increases in root production during the warmer months of the year were observed. This increase may be linked to spring leaf out of the winter deciduous species in addition to warming air and soil temperatures, since the dominant evergreen species maintain relatively constant annual production rates (West et al., 2003; Espeleta, 2002). Root death did not exhibit clear seasonal trends and was relatively constant through time. The lack of a seasonal pattern of root death suggests that controls on root death differ substantially from those on root production (Eissenstat and Yanai, 1997). Since gradual root senescence followed by death and slow decomposition was rarely observed in this study, losses to herbivory might have been important, however we were not able to determine the causes of root death in this study.

In contrast to the patterns observed for root production and death, rates of fine root turnover did not follow the soil texture gradient. The highest turnover rates occurred at the mid-point of the gradient, where our estimates of nitrogen availability were also highest. This observation suggests that nitrogen availability may have exerted a more important control on turnover rate than did soil moisture availability. These findings are consistent with predictions from nutrient

use efficiency theory (Nadelhoffer et al., 1985; Aerts and Chapin, 2000), as well as observations made on leaf turnover (Aerts, 1990; Reich et al., 1992). That is, plants may limit nitrogen losses by decreasing tissue turnover in low nitrogen environments. In this system the greatest amounts of root production were observed where water was likely most limiting, but death did not increase proportionately across the gradient. The most dynamic root systems were observed at the middle of the gradient where N availability was highest. The lowest turnover rates, however, were not observed where N availability was lowest, suggesting that additional factors other than N and water may control turnover when N availability is low. In systems where nutrient and water limitation are positively correlated, fine root production and turnover rates may also covary. However, as was observed in this system, gradients in resource limitation may be complex and plant root systems may therefore show dynamic responses to those gradients.

The three most common equations used to estimate fine root turnover (Burton et al., 2000; Gill and Jackson, 2000) resulted in notable quantitative differences in their estimates of turnover in this study. Lack of equilibration between roots and soil following the disturbance necessary for minirhizotron installation may have caused inflated estimates of annual production, and therefore production-based estimates of turnover in our study (Joslin and Wolfe, 1999). Differences among sites in rate of equilibration may also result in underestimates of standing crop, also potentially inflating our estimates of turnover. However, following an initial flush, production stabilized quickly in this study, suggesting relatively rapid post-disturbance equilibration. The estimates based on root death, on the other hand, may underestimate turnover rates, because of the lag between new root production and death. Over time the two estimates may come to equal each other, as production and death equilibrate (Burton et al., 2000), suggesting that the true values are between those based on production and those based on death. We currently lack the data to quantitatively reconcile these estimates of turnover for this system. Given the qualitative agreement between our turnover calculations, the clear seasonal patterns in production, as well as the stability of our production and death results however, we conclude that the relative differences among stands are real and are not an artifact of the calculations. Our results

support the theoretical predictions of nutrient use efficiency theory (Aerts and Chapin, 2000). However, the opposite trend has also been found (e.g. Burton et al., 2000), and there remains considerable uncertainty about a general fine root response to nitrogen availability (Nadelhoffer, 2000). More work is clearly needed to understand the controls on fine root production and turnover.

All three calculations of fine root turnover resulted in estimates that are considerably higher than previous reports for this system (0.39 per year; Saterson and Vitousek, 1984; but see King et al., 2002). Although Saterson and Vitousek (1984) pointed out that these rates represent minimum values because they are based on “max–min” estimates from sequential soil coring. The rates we report here are also higher than those observed in single-species rhizotrons for the dominant, individual species in this system (West et al., 2003; Espeleta, 2002). Differences in methodology used to observe roots may contribute to these differences. The advantages and disadvantages of the existing methods are discussed in detail elsewhere (Smit et al., 2000), but direct observation methods likely provide the best estimate of population-based parameters such as turnover. An additional interpretation is that roots growing in mixed-species soils may exhibit greater rates of turnover than single species alone (Partel and Wilson, 2002), although data are not currently available to test this hypothesis.

The turnover rates reported here are also substantially higher than most of those reported in the literature, although a small number of studies from tropical grasslands report turnover rates similar to ours (Gill and Jackson, 2000). More importantly, however, the range of variation observed across a gradient in soil texture within this ecosystem (~ 1.5 per year) was greater than the range described by Gill and Jackson (2000) from high latitude to tropical forests. Although there may be global trends in fine root turnover associated with large climatic gradients, our results show large within-ecosystem variation that is associated with relatively small-scale gradients in soil resource availability.

Our understanding of belowground dynamics remains a critical gap in our understanding of terrestrial ecosystems and significantly limits our ability to estimate such things as global productivity (Geider et al., 2001), or the responses of ecosystems to global

change (Norby and Jackson, 2000). However, estimating fine root turnover remains a difficult and time-intensive endeavor. Our results demonstrate that considerable variation in turnover may exist within any biome described by climatic factors such as mean annual temperature (cf. Gill et al., 2002), and that turnover may not change in proportion to biomass. Research that improves our understanding of how fine root production and turnover respond to complex patterns of soil resource availability will considerably improve our understanding of belowground dynamics.

5. Conclusion

The greatest amounts of fine root production and death were observed in the deepest, sandiest soils where overstory productivity was lowest and water was probably most limiting. Fine root turnover across the gradient, however, was highest where nitrogen availability was highest, peaking in the middle of the texture gradient. These results emphasize the potential independence of fine root turnover rates and total fine root production, and suggest that multiple limiting resources may differentially affect these important components of the fine root systems of plants.

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