

## NOTE

## Rapid fine root disappearance in a pine woodland: a substantial carbon flux

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**Abstract:** Fine root production and mortality are difficult to estimate accurately, because some fine roots die within days of being produced, and many apparently healthy roots disappear rapidly with no obvious period of senescence. Such root dynamics are difficult to analyze without very fine-scaled temporal observations. To capture the behavior of short-lived and rapidly disappearing roots, we sampled minirhizotron tubes weekly for 11 months in a *Pinus palustris* Mill. woodland. Fine root ( $\leq 2$  mm diameter) length production and length mortality during this period were  $1.57 \pm 0.23$  mm-cm<sup>-2</sup> (mean  $\pm$  SE) and  $1.19 \pm 0.17$  mm-cm<sup>-2</sup>, respectively. Depending on the type of estimate used, rapid disappearance accounted for between 21 and 37% of total fine root mortality. Rapidly disappearing roots had relatively short life-spans, a median of just 10.5 days. Monthly sampling of the same data set underestimated length production by 15%, overestimated median root life-span by 60%, and obscured causes of root loss. If short-lived roots are not accounted for, total net primary productivity in temperate forests may be underestimated by as much as 10%. We propose that belowground herbivory is the leading explanation for this rapid disappearance.

**Résumé :** La production et la mortalité des racines fines sont difficiles à mesurer avec précision parce que certaines racines fines meurent quelques jours après avoir été produites et que plusieurs racines apparemment saines disparaissent rapidement sans aucune période évidente de sénescence. Une telle évolution des racines est difficile à analyser sans avoir recours à des observations à une très fine échelle temporelle. Pour capter le comportement des racines qui ont une courte durée de vie ou qui disparaissent rapidement, nous avons échantillonné des minirhizotrons sur une base hebdomadaire pendant 11 mois dans un boisé de *Pinus palustris* Mill. Pendant cette période, la production et la mortalité linéaires des racines fines ( $\leq 2$  mm de diamètre) ont atteint respectivement  $1,57 \pm 0,23$  (moyenne  $\pm$  erreur type) et  $1,19 \pm 0,17$  mm-cm<sup>-2</sup>. Dépendamment du type d'estimation utilisée, la disparition rapide explique de 21 à 37 % de la mortalité des racines fines. Les racines qui disparaissent rapidement ont une durée de vie relativement courte avec une valeur médiane de seulement 10,5 jours. Un échantillonnage mensuel du même ensemble de données sous-estime la production linéaire de 15 %, surestime la durée de vie médiane de 60 % et ne permet pas d'identifier les causes de la disparition des racines. Si on ne tient pas compte des racines qui ont une courte durée de vie, la production primaire nette dans les forêts tempérées peut être sous-estimée jusqu'à 10 %. Nous croyons que l'activité souterraine des insectes est la principale explication de cette rapide disparition.

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### Introduction

Fine roots have a large impact on the global carbon cycle and are a major carbon source for soil organisms (Vogt et al. 1986; Chapin and Ruess 2001). The dynamics of fine roots, however, have been difficult to measure (Clark et al. 2001; Pacala et al. 2001). There are many fine root fluxes to track, including growth of new tissue, respiration, secretion of or-

ganic molecules from root to soil, retranslocation, and mortality via senescence, disease, and herbivory (Clark et al. 2001). Methods have been devised to measure or indirectly estimate most of these fluxes (Clark et al. 2001; Milchunas and Lauenroth 2001). However, because some fine roots live for just a few days, and many studies of root turnover rely on sample intervals of weeks or months, ecologists have probably underestimated fine root production and mortality (Johnson et al. 2001). Additionally, the importance of rapid root disappearance (i.e., apparently healthy roots that disappear within a week or less) as well as its potential causes (such as rapid tissue decay or root herbivory) are presently unclear.

Rapid turnover of fine roots in situ can be measured using glass or plastic rhizotrons, or cylindrical tubes called minirhizotrons (Lussenhopp et al. 1991; Lussenhopp and Fogel 1993; Smit et al. 2000; Johnson et al. 2001). Until now, however, sampling intervals in rhizotron studies have

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apparently not been sufficiently fine scaled to estimate rapid root fluxes. Typically, rhizotrons are sampled just 4–12 times per year. If some roots are produced and then totally disappear between sampling events, then not only will mortality and production be underestimated, but also the process that causes the rapid disappearance (Johnson et al. 2001).

Our objectives were to characterize fine root demography in a pine woodland and to determine the impact of sampling interval on accuracy of estimating fine root production and mortality. We predicted that a significant proportion of fine root biomass disappears rapidly and hypothesize that such rapid disappearance, combined with short life-spans of disappearing roots, leads to a significant underestimate of fine root carbon flux as sampling intervals increase.

## Materials and methods

### Experimental design

Research was conducted at the Joseph W. Jones Ecological Research Center in southwestern Georgia, U.S.A. (31°N, 84°W). Climate is humid subtropical with mean annual precipitation of 132 cm. Soils are Orangeburg series sands over karst limestone bedrock, and the plant community is a 60- to 70-year-old *Pinus palustris* Mill. (longleaf pine) and *Aristida stricta* Michx. (wiregrass) woodland. To investigate overstory density impacts on roots, soil environments, and pine regeneration, six 2.5-ha plots were established: three in areas unharvested (basal area 14.8–18.4 m<sup>2</sup>/ha) and three in areas partially harvested 8 months prior to root measurements (basal area 11.2–15.4 m<sup>2</sup>/ha).

Six 3 × 3 m quadrats, spaced at least 10 m apart, were located within each plot (36 quadrats total) using stratified random placement to ensure quadrats were placed across the full range of local tree basal area (measured within a 15-m radius). So that most roots observed were from a single species (i.e., *P. palustris*), all understory vegetation rooted in each quadrat was removed by hand weeding and applications of 4% glyphosphate solution monthly during the growing season.

In January 1998, a single cellulose acetate butyrate minirhizotron tube (5 cm inside diameter × 80 cm length) was installed at a 45° angle to the soil surface and to a minimum vertical depth of 40 cm in each quadrat. To minimize light leakage and thermal transfer from above- to below-ground, the aboveground portions of tubes were painted (first black, then white) and tightly capped with an insulated foam cap. Tubes were then anchored to metal stakes with wire and hose clamps to minimize rotation and environment-related heaving.

### Root measurements

Minirhizotron sampling was conducted at fairly constant 7-day intervals (mean sampling interval 6.7 days) between July 2, 1998, and May 26, 1999. Images were collected in the field via Hi-8 camcorder (July 1998 – February 1999) or direct digital capture (February – May 1999) using a camera system and software developed by Bartz Technology Company (Santa Barbara, Calif.). A ratcheting index handle mounted on the camera system allowed the camera to return to the same locations in each tube over time. Marks scribed onto the tubes at a 1-cm interval further aided in relocation

of the same images when tubes were sampled. Each tube included 40 images from the soil surface to a depth of approximately 40 cm (accounting for the 45° angle of the tube). Vertical and horizontal dimensions of each sample image were 1.4 × 1.8 cm, respectively; the resolution of the digitized images was 480 × 640 pixels.

ARCOS root tracing software (Graphic Equations Inc., Houston, Tex.) was used to measure the width and length of each fine root at each sample date. Individual fine roots (0.1–2.0 mm diameter, and exclusive of fungal rhizomorphs) were counted if they were partially or wholly within a 430 × 590 pixel reference frame within the sample image. This reference frame allowed us to account for minor shifts in camera position between sampling dates. If an individual root within a reference image formed a branch, the branch was counted as a new individual root. Roots were considered dead on the first date that they either disappeared entirely and permanently from the frame, or appeared to be dead, due to change in color (to gray or black) with subsequent decomposition.

Fine root length production for week  $x$  was estimated as new root production between week  $x - 1$  and week  $x$ , plus length growth of existing roots during the same period. Rapid disappearance for week  $x$  was estimated conservatively (i.e., resulting in a low value) as all roots present in week  $x - 2$  that increased in length by week  $x - 1$ , and were then missing in week  $x$ . We also used a more liberal estimate of rapid disappearance (resulting in a larger estimate) by relaxing the requirement that roots grow between weeks  $x - 2$  and  $x - 1$ . However, a root that declined in length from week  $x - 2$  to week  $x - 1$  and then disappeared in week  $x$ , was never classified as a rapidly disappearing root. All root losses that did not fall into the rapid disappearance category were counted as “senescence” mortality. The beginning phases of root senescence are difficult to detect, because individual cells within a root die before a loss of root length occurs (Comas et al. 2000); however, once a root is completely dead, its vital status can be determined fairly accurately (Wang et al. 1995).

Fine root lengths (production and mortality) were ultimately converted to per-tube estimates (mm root-cm soil<sup>-2</sup>) based on the area (1.25 × 1.66 cm inside reference frame) per image and number (40) of images per tube. Because minirhizotron tubes were widely spaced and stratified across a range of nearby overstory tree densities, we considered each tube an individual experimental unit. The influences of the harvest treatments and environmental variables on root demography are considered in Jones et al. (2003).

### Statistical analyses

We compared production and mortality measurements from the weekly sampling regime to those calculated using the same data set but with 2-week, 1-month, 2-month, and 3-month sampling regimes. Differences between pairs of sampling regimes were compared using bootstrap simulations of 20 000 iterations each (Efron and Tibshirani 1993). The distribution of the 20 000 differences in each test was inspected to determine the probability that the difference in growth or mortality estimates between regime pairs was zero. A Bonferroni correction was used to maintain accurate experiment-wide type I error over the 15 pairwise compari-

sons of sample regime. Product-limit estimates of median life-span for each of the sampling regimes were produced using the LIFETEST procedure in the Statistical Analysis System (SAS Institute Inc., Cary, N.C.).

Rapid disappearance as a percentage of total mortality was compared across root size and soil depth categories using  $\chi^2$  tests. Because of the nature of the minirhizotron method and our sampling protocol, we were unable to make distinctions concerning root order (i.e., primary, secondary, tertiary branching), a factor that can affect root life-span.

## Results

A total of 931 individual fine roots were encountered in the minirhizotron images. From these roots, we estimated that fine root length production and total length mortality were  $1.57 \pm 0.23 \text{ mm}\cdot\text{cm}^{-2}$  and  $1.19 \pm 0.17 \text{ mm}\cdot\text{cm}^{-2}$ , respectively, over the course of the study.

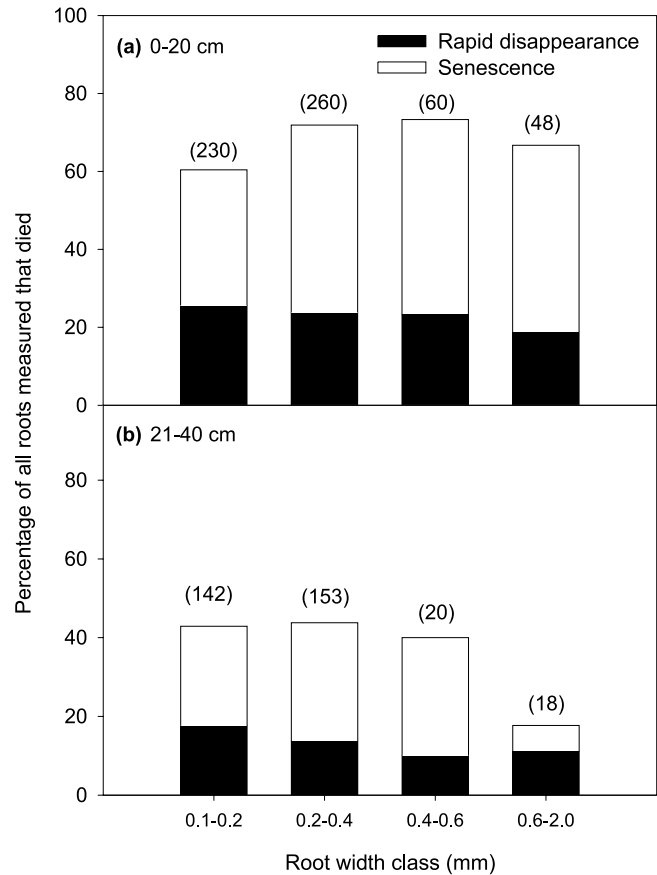
Rapid root disappearance was a large flux and was widespread among fine roots of different sizes and soil depths (Fig. 1). Our conservative estimate was 24% of the total root length mortality, and our more liberal one was 37%. The number of roots that underwent rapid disappearance (i.e., irrespective of their length) was 21% of the total number observed. Within each depth class (0–20 and 21–40 cm), rapid disappearance occurred at similar rates across four (0.1–0.2, 0.2–0.4, 0.4–0.6, and >0.6 mm) fine root diameter classes ( $\chi^2$ ,  $df = 2$ ;  $p > 0.43$ ; largest two classes combined for this analysis). We, therefore, combined diameter classes and found that rapid disappearance was more common in the 0–20 cm than in the 21–40 cm soil depth ( $\chi^2$ ,  $df = 1$ ;  $p = 0.001$ ).

Rapidly disappearing roots tended to have very short life-spans, often disappearing within the first few weeks after production. Median life-span of all rapidly disappearing roots for which a birth date was known (i.e., excluding roots of unknown age observed on the first sample date) was 10.5 days ( $CI_{95\%} = 7.0$  to  $14.0$ ,  $n = 180$ ). In contrast, more than 50% of nonrapidly disappearing roots survived past the end of our 48-week sample period (which precluded estimates of median life-span).

Fine root dynamics displayed significant seasonal patterns (Fig. 2). Mean weekly rates of fine root production ( $df = 3$ ,  $48$ ,  $p < 0.0001$ ), mortality ( $df = 3$ ,  $48$ ,  $p = 0.05$ ), senescence ( $df = 3$ ,  $47$ ,  $p = 0.03$ ), and disappearance ( $df = 3$ ,  $47$ ,  $p = 0.01$ ) all varied significantly between seasons. Post-hoc analysis of these patterns using Tukey's test ( $p < 0.05$ ) showed that fine root production was highest in the summer of 1998. Rapid disappearance of fine roots was significantly greater in summer than in winter. Both fine root senescence and total root mortality (combining senescence and rapid disappearance) were significantly greater in spring than in winter.

As sampling interval increased, rapidly disappearing short-lived roots were missed, causing estimates of production and mortality to decline significantly ( $p < 0.001$  for all pairwise comparisons of production or mortality) (Fig. 3). Estimates of median fine root life-span increased from 87.5 (weekly interval) to 139 days (monthly interval) to 271 days (2-month interval). No estimate of median life-span could be produced from the seasonal (3-month interval) data set, be-

**Fig. 1.** Percentage of all *P. palustris* fine roots measured that died via senescence and rapid disappearance for various root diameter classes in the 0–20 cm (a) and 21–40 cm (b) soil depths. Percentages are derived from conservative estimates of rapid disappearance. Values in parentheses above bars are numbers of roots in each class.



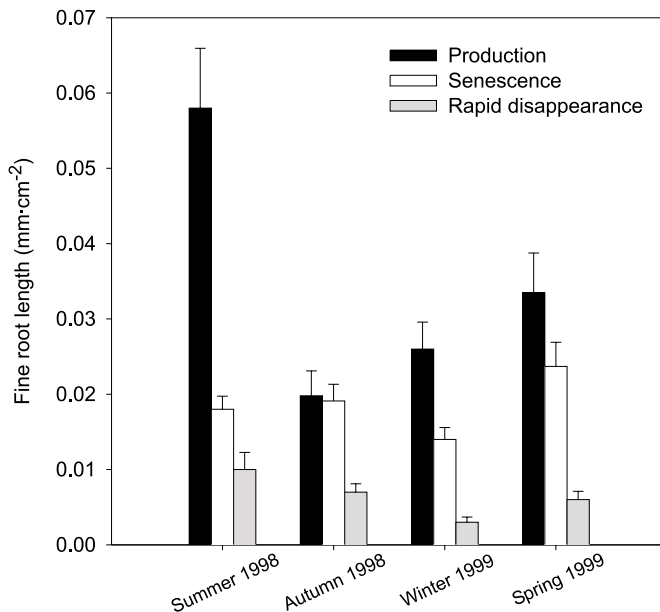
cause fewer than 50% of the roots died during the study period.

## Discussion

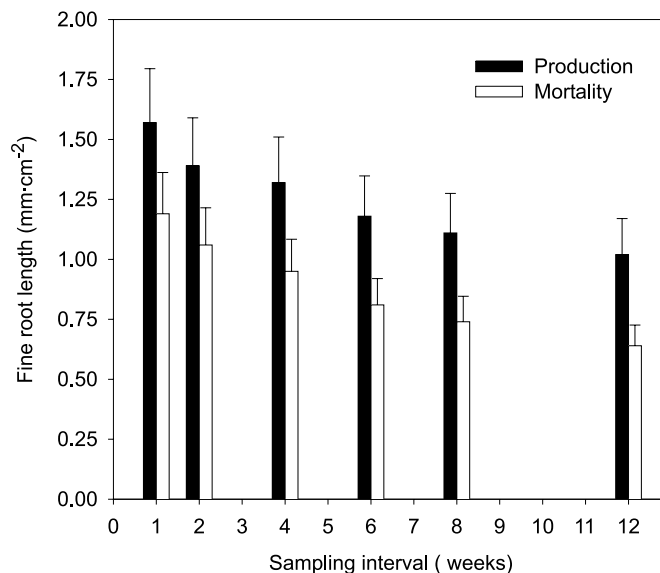
Our production and total mortality estimates were low but within the range reported for pine and temperate deciduous forests (Hendrick and Pregitzer 1993; Joslin et al. 2000). The low estimates probably reflect low tree density and strong water and nutrient limitations on plant growth at our study site (Mitchell et al. 1999).

Averaged over time, fine root mortality is approximately equivalent to fine root production, and thus can be used to estimate belowground net primary productivity (NPP). In the 11 months of this study, mortality and production were indeed nearly equivalent (Fig. 3). Thus, our estimates of rapid fine root disappearance (21–37% of total mortality, depending on estimation procedure used) show that a relatively large proportion of belowground NPP disappears without undergoing an obvious decomposition period. Given the short life-spans of these disappearing roots, most would not be captured by longer sampling intervals; the decline in production and mortality measures we observed as sampling interval increased attests to the quantitative impacts of missing

**Fig. 2.** Seasonal changes in fine root production, senescence, and rapid disappearance for *P. palustris* fine roots during an 11-month period. Bars show weekly means, and error bars are SEs ( $n = 36$  minirhizotron tubes). Post-hoc significance of seasonal patterns (from Tukey's test) are detailed in the text.



**Fig. 3.** Estimates of length production and total length mortality (senescence plus rapid disappearance) for *P. palustris* fine roots during an 11-month period, derived from sampling the same data set using different time intervals between samples. Bars are means, and error bars are SEs ( $n = 36$  minirhizotron tubes).



these rapidly disappearing roots and supports our hypothesis that longer sampling intervals significantly underestimate fine root carbon flux.

Indirect evidence suggests that much of the rapid disappearance we observed may result from root herbivory. Large densities or biomass of belowground herbivores have been reported for natural and agricultural ecosystems (Brown and

Gange 1990; Hunter 2001; but see Ausmus et al. 1978), and strong impacts of belowground herbivores have been demonstrated for a number of processes including plant establishment, aboveground plant growth, production of chemical defenses in both roots and shoots, and a wide range of interactions between plants, soil microfauna and soil macrofauna (Cantor and Whitham 1989; Freckman and Virginia 1989; Brown and Gange 1990; Wardle and Barker 1997; Denton et al. 1999; Hunter 2001). Root feeding by whitefringed beetle larvae (*Graphognathus* spp.) and white grubs (*Phyllophaga* spp.) has been implicated in large-scale mortality of loblolly pine seedlings elsewhere in Georgia (Mitchell et al. 1991). While no direct censuses of root-feeding insects were conducted over the course of our study, the most important herbivores in our study system are probably nematodes (Ruehle 1961), mites (Esher et al. 1992), and beetle larvae in the genera *Anomala*, *Cotalpa*, *Dichelonyx*, *Diploaxis*, *Graphognathus*, *Phyllophaga*, and *Serica* (USDA 1985).

If the rapid disappearance we observed was indeed the result of herbivory, the role of belowground herbivores may be even greater than our data suggest. The trend in Fig. 3 suggests that larger estimates of production and mortality might have occurred if we had sampled more often than weekly. Furthermore, some herbivores may clip roots outside of the minirhizotron field of view (FOV), causing roots in the FOV to die and disappear slowly, and thus not be counted in our estimates of rapid disappearance. Finally, nematodes and aphids may destroy individual root cells and increase leakage of organic compounds without causing sudden loss of the entire root (Denton et al. 1999).

Our estimates of rapid root disappearance may have been biased, either upward or downward, by the artificial surface created by the minirhizotron tubes. However, two potential biases associated with the minirhizotron method (Johnson et al. 2001) were minimal in our study. The first bias, a tendency to miss roots within the top few centimetres of soil, probably had minimal impact, because fine roots in our study system are not concentrated within a litter layer; this is more a problem for northern conifer forests. Waiting 6 months after installation before sampling minimized the second potential bias: the effects of soil disturbance during tube installation. A small bias due to disturbance may have occurred, because fine root standing crop increased during the first 3 months of the study and stabilized thereafter (Jones et al. 2003). However, patterns in root mortality were similar across all seasons, and delayed colonization did not appear to influence rates of rapid disappearance; while rapid disappearance appeared to account for the greatest percentage of overall root mortality in the summer of 1998, disappearance rates were not significantly higher than in autumn 1998 or spring 1999 (Fig. 2).

One can question if such disappearances result from herbivory, because we made no direct observations of roots being eaten. Instead, we had to assume that rapid disappearance (within 7 days) was herbivory and not senescence followed by rapid decay. We checked this assumption by measuring decay time for 57 roots where the date of senescence was clearly identifiable. Mean and minimum times between first date of senescence and date of total disappearance were 41 and 20 days, respectively. The range of decay times (20–127 days) was similar across diameter

classes (0.1–0.2, 0.2–0.4, 0.4–0.6, and >0.6 mm); however, the mean decay time for the widest root class (>0.6 mm, 62 days) was significantly higher than for roots from either of the two most narrow classes (0.1–0.2, 32 days; 0.2–0.4, 37 days; Tukey's post-hoc analysis,  $p = 0.03$ ). These values are much longer than 7 days, confirming our assumption. Even longer decay periods have been recorded in other North American forests (McLaugherty et al. 1982; Santantonio and Grace 1987; Fahey et al. 1988; Fahey and Arthur 1994), and thus, it may be relatively easy to estimate herbivory in more than just our study system.

The short life-span of rapidly disappearing roots is consistent with the hypothesis that young roots are less well defended against herbivory (Eissenstat and Yanai 1997). Whether caused by herbivores or not, however, the presence of many roots with short life-spans supports our hypothesis that extending the sampling interval in minirhizotron studies results in underestimates of belowground productivity. A recent simulation study makes the same argument (Johnson et al. 2001). If we are correct, then existing models of ecosystem- and global-level carbon cycling should add 10% to net primary productivity estimates. This figure is based on the assumptions that fine root growth is 20% greater than previously thought (which is approximated by the lowest disappearance estimate in our study), and that 50% of total fixed carbon is allocated belowground (Vogt et al. 1986; Waring and Running 1998). The global-level magnitude of this increase is large, about 0.3 Pg C·year<sup>-1</sup> for forests in the lower 48 United States alone, assuming a forest cover of  $2.47 \times 10^8$  ha and a mean NPP of about 10 000 kg C·ha<sup>-1</sup>·year<sup>-1</sup> (Waring and Running 1998). By comparison, total net carbon sequestration in the same region has been estimated between 0.3 and 0.6 Pg C·year<sup>-1</sup> (Pacala et al. 2001). A second, more qualitative change in ecosystem models may be needed to account for a large, and heretofore underestimated, flow of root carbon to herbivores. This flow influences the structure and function of the entire soil community, including microbes and mycorrhizal fungi, which control rates of organic matter decomposition and nutrient mineralization.

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