

# Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods

John D. Aber<sup>1</sup>, Jerry M. Melillo<sup>2</sup>, Knute J. Nadelhoffer<sup>2</sup>, Charles A. McClaugherty<sup>3</sup>, and John Pastor<sup>4</sup>

<sup>1</sup> Department of Forestry, University of Wisconsin-Madison, Madison, WI 53706, USA

<sup>2</sup> Ecosystem Center, Marine Biological Laboratory, Woods Hole, MA 02543, USA

<sup>3</sup> Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

<sup>4</sup> Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830, USA

**Summary.** Two methods of estimating fine root production and turnover are compared for 13 forest ecosystems exhibiting a wide range in form ( $\text{NH}_4^+$  vs.  $\text{NO}_3^-$ ) and quantity of available nitrogen. The two methods are by comparison of seasonal maxima and minima in biomass and by nitrogen budgeting. Both methods give similar results for stands with low rates of nitrification. The budgeting method predicts higher fine root turnover and productivity than the max-min method for systems with significant rates of nitrification.

methods of estimating fine root production and turnover for a range of site and species combinations. The first method is a standard calculation based on sequential changes in fine root biomass. The second uses measured values for nitrogen availability and allocation above ground to solve for apparent allocation below ground by difference (Nadelhoffer et al. 1985).

## Methods

### *Study sites*

We have measured sequential changes in standing crop of fine (<3 mm diam.) root biomass in a total of 13 stands in Wisconsin and Massachusetts (Table 1). These include a very wide range of species composition, soil type, nitrogen availability (both quantity and form) and above ground net primary production. More complete site descriptions may be found in Nadelhoffer et al. (1983), Pastor et al. (1984) and McClaugherty et al. (1982).

### *Fine root sampling*

Root sampling in all stands involved collection of replicate soil cores and hand washing and sorting of roots from the soil matrix.

In the Harvard Forest sites, collections were made at monthly intervals between July 1978 and July 1979, excepting February and March when the soils were frozen. Nine randomly spaced samples 1.9 cm in diameter were collected separately in the forest floor and to a depth of 15 cm in the mineral soil. All roots in each sample were hand sorted by size class and into live and dead categories using a dissecting microscope (see McClaugherty et al. 1982 for more details).

Cores at the Wisconsin sites were collected using a 6.1 cm diam. soil probe. In the Arboretum where forest floors were virtually non-existent, 7 samples were taken from the 0–10 cm level and 4 additional from the 10–20 cm level. A total of five collections were made (25 April, 7 July, 15 September and 5 December 1981, plus 24 April 1982). The Blackhawk Island soils were separated into forest floor/Al and the top 15 cm of mineral soil below this horizon. Four collections were made at roughly two month intervals beginning 2 May 1983. Collected cores were washed over a 0.5 mm screen with the bulk of the live, intact root mass remaining in the screen. Roots were then

The production, turnover and decomposition of fine roots are major processes in the carbon and nutrient dynamics of forest ecosystems (Edwards and Harris 1977; Persson 1978; Keyes and Grier 1981; McClaugherty et al. 1982; Vogt et al. 1982). A clear understanding of fine root dynamics is necessary for addressing important issues at several levels of resolution in biology.

At the physiological level, there is debate over whether the relative allocation of carbon and nitrogen to roots increases or decreases with increasing nitrogen availability. At the plant community level, changes in carbon and nitrogen allocation between roots and aboveground tissues are thought to affect competition between species and thus future community dynamics. At the ecosystem level, allocation patterns determine the array of litter types created by the plants. This in turn largely determines decomposition rates and future nutrient availability, completing an important feedback between plants and soil. At the global level, fine root production represents a large and relatively unknown portion of the production/decomposition carbon balance.

Despite the central importance of fine root dynamics at all these levels, neither a clear and consistent pattern of fine root dynamics in communities of perennial plants, nor an understanding of factors controlling those dynamics has emerged. For example, it is still not clear whether fine root turnover rate increases with higher nutrient availability (Grime 1977; Orians and Solbrig 1972; Chapin 1980; Chapin and Van Cleve 1981) or decreases (Thornby 1972a, b; Wareing and Patrick 1975; Keyes and Grier 1981). This is due largely to uncertainties as to how annual fluxes of carbon and nutrients through fine roots are best measured.

The purpose of this paper is to compare two different

**Table 1.** Site descriptions and data for 13 forest stands in Wisconsin and Massachusetts used in this study

Stand	Soil Type <sup>a</sup>	Forest Floor Type	Nitrogen				Biomass				
			Mineralization (kg N/Ha·Yr)	Nitrification (% of Mineralization)	N Availability (kg/Ha·Yr)	N Allocation Above-ground (kg/Ha·Yr)	NPP Above-ground (Mg/Ha·Yr)	Mean fine root Mass (Mg/Ha)	Fine Root Production (Mg/Ha)		
								Budget	Max-Min		
Wisconsin											
U.W. Arboretum											
A	Red Oak	ALF	MULL	125	100	133	68	13.6	2.70	5.5	0.52
B	Black Oak	ALF	MULL	135	100	143	62	11.2	2.70	6.1	1.74
C	White Oak	ALF	MULL	99	100	107	60	11.0	3.41	4.1	1.15
D	White Pine	ALF	MULL	86	71	79	39	8.7	3.72	2.5	0.97
E	Red Pine	ALF	MULL	39	50	47	27	7.1	4.41	2.0	0.69
F	Sugar Maple	ALF	MULL	94	100	102	40	8.6	4.28	5.5	1.10
Blackhawk Island											
G	Red Pine	ENT	DIST <sup>b</sup>	28	82	36	22	4.1	4.02	1.2	2.53
H	White Pine	SPOD	MOR	52	46	60	33	6.4	2.89	1.4	1.62
I	White Oak	ALF	MOR	84	4	92	43	8.4	5.15	3.4	3.05
J	Red Oak 1	ALF	MODER	78	30	86	49	8.1	3.89	2.5	2.35
K	Sugar Maple 2	ALF	MULL	125	100	133	56	9.5	3.23	6.5	1.06
Massachusetts											
Harvard Forest											
L	Red Pine	SPOD	MOR	81	0	89	45	9.8	5.10	4.2	4.1
M	Oak-Maple	SPOD	MOR	93	0	101	54	9.3	6.10	4.0	5.1

<sup>a</sup> ALF = alfisol, ENT = entisol, SPOD = spodosol,

<sup>b</sup> DIST = disturbed

further sorted from attached debris by hand under magnification (see Nadelhoffer et al. 1985 for more details).

Harvard Forest root data were originally presented by McClaugherty et al. (1982). Data for the Wisconsin sites are presented here for the first time.

#### Nitrogen availability

Nitrogen mineralization and nitrification have been measured in all stands using the buried bag in situ incubation technique (Eno 1960; Ellenberg 1977). This method involves monthly collection of 7 to 20 paired samples in each horizon. One of each pair is brought to the laboratory for extraction of nitrate and ammonium (150 ml 1N KCl, 10 g soil, 24–36 h). The second is placed, unsieved in a polyethylene bag and returned, undisturbed, to its original position in the soil for one month. At the end of this incubation period, the soil core is retrieved and extracted for nitrate and ammonium. Change in total nitrate plus ammonium is net mineralization for the incubation period. Change in nitrate alone is net nitrification. Incubations were carried out monthly during the growing season and at 2 to 6 month intervals during the winter. In all cases, the same soil horizons were sampled as above for root production.

Nitrogen mineralization data can be combined with other measurements, allowing a calculation of nitrogen availability to plants as:

$$N_a = N_m + N_p - N_l \quad (1)$$

where  $N_a$  is nitrogen availability,  $N_m$  is measured mineralization,  $N_p$  is precipitation input (measured at approximate-

ly  $8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) and  $N_l$  is leaching loss below the rooting zone (negligible in all stands except the Arboretum white pine stand). See Nadelhoffer et al. (1983, 1985), Pastor et al. (1984), Aber et al. (1983) for more detailed descriptions of methods. Mineralization data for the Harvard Forest and Arboretum sites are as presented by Aber et al. (1983) and Nadelhoffer et al. (1985). Blackhawk Island data are higher than reported by Pastor et al. (1984) due to inclusion of mineral soil rates.

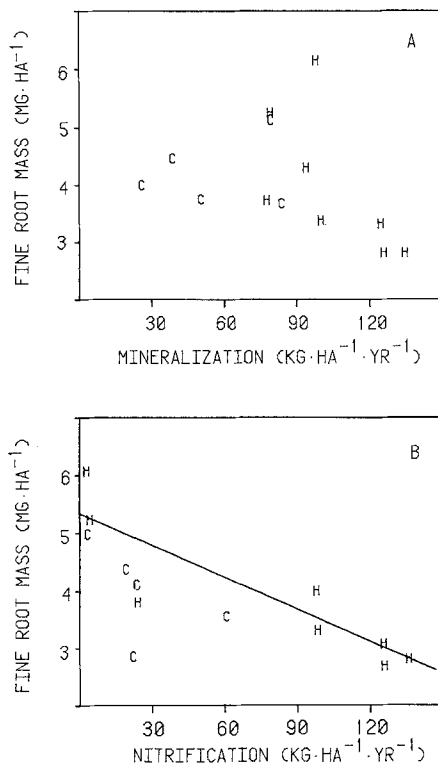
#### Calculating fine root production

Annual fine root production is estimated here in two ways. The first is by subtracting minimum measured biomass for any sampling data during the year from the maximum (max-min method, McClaugherty et al. 1982). The second method (budgetary method) assumes that all available nitrogen is taken up by plants and allocated to three pools: above ground litter (leaves, fruits, etc.), woody tissues (both above ground stems and branches plus woody roots), and fine roots. This gives the equation:

$$N_a = N_u = N_{al} + N_{wb} + N_{fr} \quad (2)$$

where  $N_a$  is availability as before,  $N_u$  is nitrogen uptake,  $N_{al}$  is allocation to above ground litter,  $N_{wb}$  is allocation to woody tissues and  $N_{fr}$  is allocation to fine roots. Rearranging this equation gives a calculated allocation of nitrogen to fine roots as:

$$N_{fr} = N_a - N_w - N_{al} \quad (3)$$



**Fig. 1A, B.** Mean annual fine root biomass as a function of: **A** Annual  $N$  mineralization, and **B** Annual nitrification. Line in **B** is for hardwood sites only ( $y = 5.33 - 0.0185x$ ,  $R^2 = 0.78$ ,  $P < 0.05$ )

Net primary production in fine roots is then:

$$NPP_{fr} = N_{fr} / N_{conc} \quad (4)$$

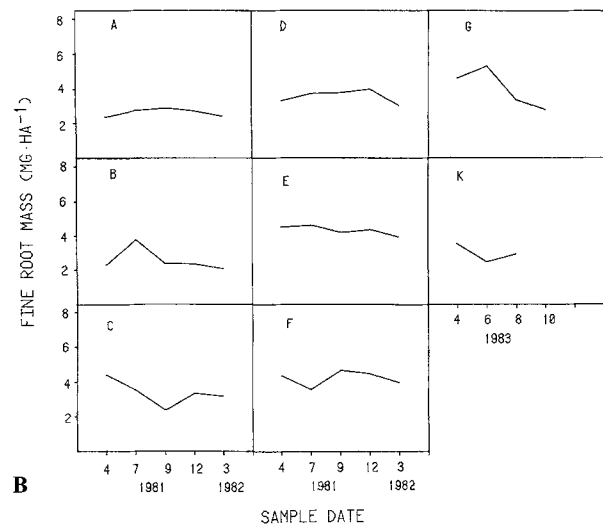
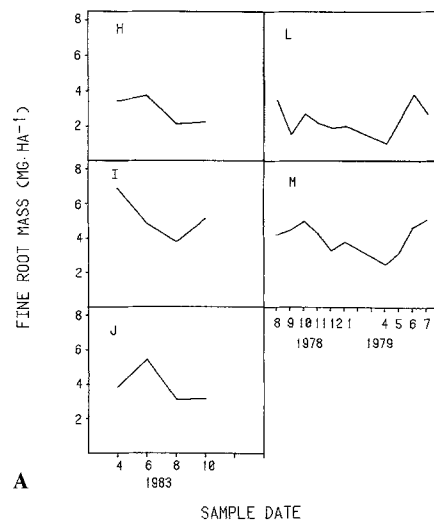
where  $NPP_{fr}$  is production of fine roots,  $N_{fr}$  is total allocation of nitrogen to fine roots as above and  $N_{conc}$  is measured nitrogen concentration in fine roots. Data for each stand are summarized in Table 1 (see Nadelhoffer et al. (1985), Pastor et al. (1984) and Aber et al. (1983) for sources of data).

## Results and discussion

Annual net  $N$  mineralization ranged from 28 to 135  $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  in this set of stands (Table 1). Nitrification varied between 0 and 100% of mineralization. There is no correlation between  $N$  mineralization and the percentage of this nitrified for this set of stands.

### Mean fine root biomass and seasonal dynamics

Mean annual fine root biomass is not related to  $N$  mineralization (Fig. 1A). However, it is significantly ( $R^2 = 0.78$ ,  $P < 0.05$ ) and negatively correlated with nitrification for the deciduous stands (Fig. 1B). The relationship is not significant for the conifer stands because of a single substantial outlier. These results suggest that the form of nitrogen may be more important than the total amount mineralized in determining the mass of fine roots maintained in forest ecosystems. It further suggests that the greater mobility of nitrate versus ammonium in soils may reduce the amount of root mass or surface area required for effective uptake of all available  $N$  in the nitrate form.

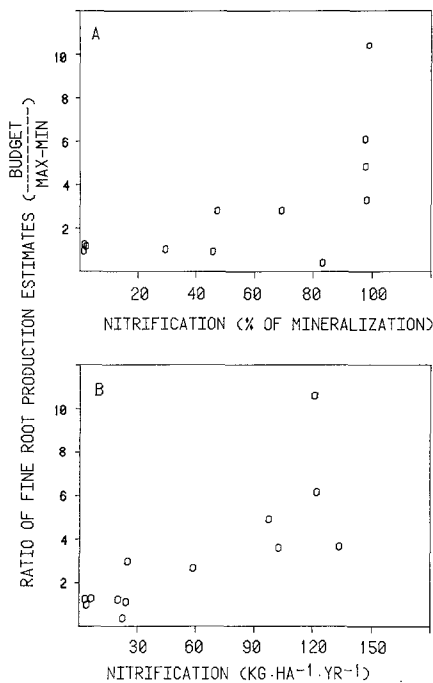


**Fig. 2A, B.** Seasonal changes in fine root biomass for **A** 5 stands with ammonium-dominated nitrogen cycles, and **B** 8 stands with nitrate-dominated cycles. Letters in upper left corner refer to stand designations in Table 1

Differences in seasonal dynamics in fine root biomass are also apparent between stands in which ammonium is the dominant form of available  $N$  (Fig. 2A) and those where nitrate predominates (Fig. 2B). Seasonal fluctuations are larger in the ammonium dominated sites.

### Fine root production

Estimates for fine root production by the two methods used are generally very similar for stands in which less than 50% of mineralized ammonium is nitrified (Fig. 3A). As nitrification increases above this level, the estimate based on the nitrogen budget becomes increasingly larger than the max-min estimate. The one exception to this is the red pine stand on Blackhawk Island where the max-min estimate is more than twice the budgetary value. This stand is on the sandiest soil and root measurements were made in a year of significant summer drought. The max-min estimate is based on a large decline in root mass during the period. Perhaps this decline represents an atypical seasonal fluctuation (cf. Santantonio 1980).



**Fig. 3A, B.** Ratios of fine root production estimates by the two methods used. The ratio is production as estimated by the budget method divided by production as estimated by the max-min method. The ratios are plotted against: **A** the percentage of annual mineralization nitrified in the same year, and **B** total nitrification in  $\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$

Plotted as a function of absolute nitrification ( $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ), the ratio of the two production estimates is uniformly near 1.0 only at zero nitrification. It increases roughly linearly with increasing nitrification.

#### Comparison of the two methods

The close agreement between the two root production estimation methods in stands with low nitrification suggests that each is a valid method for stands in which ammonium is the predominant form of nitrogen taken up. This agreement is even more interesting considering the different methods and investigators involved. It suggests a lack of systematic bias between the different sampling schemes employed.

In nitrate dominated stands, the question arises as to which of the two methods is more accurate. The budgetary approach assumes that  $N$  mineralization is measured accurately, that all available  $N$  is taken up, that  $N$  allocation above ground is also measured accurately and that the difference between these two is allocated to fine roots and mycorrhizae. The accuracy of the mineralization method has been supported by comparisons of seasonal changes in ammonium and nitrate inside and outside the bags (Nadelhoffer et al. 1984), analyses of  $\text{CO}_2$  and  $\text{O}_2$  contents within the bags and comparisons of measured mineralization with uptake by herbaceous crops (Westerman and Crothers 1981) and by the ability to balance calculated  $N$  availability against directly measured uptake (Aber et al. 1983). Errors associated with collection and analysis of litter are very small (Pastor et al. 1984; Nadelhoffer et al. 1983). Errors associated with  $N$  allocation to perennial tis-

ues cannot be computed directly but this flux is never more than 20% of total uptake so even large fractional errors would not significantly alter estimates of allocation to fine roots.

The max-min method assumes only that fine root production and mortality are asynchronous; that fine root production occurs in pulses of one to several months duration and that mortality does not occur during this period. While field data from root regrowth into root free cores supports a strong seasonality in root production on ammonium sites (eg. McClaugherty et al. 1982), no field data of this type exist for nitrate forest sites.

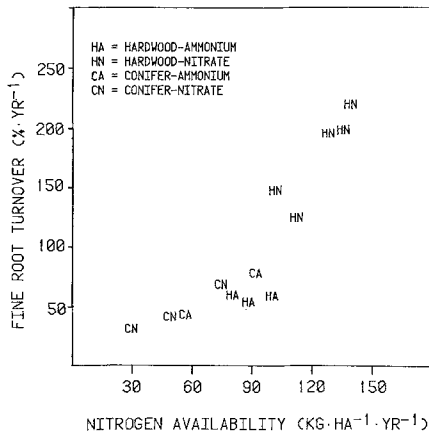
Some evidence against the max-min method can be obtained by calculating approximate  $N$  budgets for stands in which fine root production has been estimated by the max-min method. For example, Keyes and Grier (1981) compare rich and poor sites of Douglas-fir, as determined by the rate of above ground production. They found that fine root biomass changed little over the growing season in the rich site and thus calculated very low fine root production. This led to the conclusion that total net primary production in the two stands was similar, but that a larger fraction was allocated below ground on the poor site. A problem here is that fine roots are relatively rich in nitrogen as compared with senescent leaves or wood. A larger allocation of production to fine roots, along with their higher nitrogen concentration, leads to calculations of higher total nutrient requirement on the poorer site. This seems unlikely in a forest type where nitrogen is generally a limiting nutrient. It is at least as likely that fine root production was underestimated by the max-min method in the richest site.

A second problem with the max-min technique is its sensitivity to selection of number of size classes of roots and number of soil horizons used. Each spatial or morphological subdivision of the root compartment which yields a significant difference in fine root biomass between any 2 sampling periods can be used to increase the calculation of fine root production (see McClaugherty et al. 1982). It is unclear how much of this subdivision is justified or significant and how much results in double counting of production or accumulation of statistical error. As an example, a concurrent loss of mass in larger (0.5 to 3.0 mm diam) fine roots and gain in smaller (<0.5 mm) fine roots may result from allocation of stored carbohydrate in the larger to root production in the smaller. Thus the change in mass may be counted twice.

Pending confirmation of continuous fine root production in forests with substantial available nitrate, we suggest that the  $N$  budgeting technique is a more accurate method for predicting fine root  $N$  and mass dynamics over the entire range of possible soil  $N$  conditions. Both methods appear to be adequate for sites with ammonium economies. There thus appears to be a distinct difference in the pattern and timing of fine root production in nitrate versus ammonium dominated forest ecosystems.

#### Fine root turnover

We have used mean standing crop and fine root production as estimated by the nitrogen budgeting method (Table 1) to calculate estimated fine root turnover rate (Fig. 4). There is an exponential increase in estimated fine root turnover rate with increasing  $N$  availability in nitrate stands ( $R^2 = 0.99$ ,  $P < 0.01$ ). In contrast, turnover rates in ammonium



**Fig. 4.** Fine root turnover (production divided by standing crop) as a function of nitrogen availability. The four symbols denote the four possible combinations of hardwood or conifer sites with nitrate- or ammonium-dominated  $N$  cycles. Four significant regressions can be extracted from these data. 1) For all nitrate sites ( $y = 0.377 - 0.0064x + 0.000141x^2$ ,  $R^2 = 0.99$ ,  $P < 0.01$ ), 2) For all hardwood sites ( $y = -1.95 + 0.0298x$ ,  $R^2 = 0.93$ ,  $P < 0.01$ ), 3) For all conifer sites ( $y = 0.0006 + 0.0088x$ ,  $R^2 = 0.96$ ,  $P < 0.01$ ), and 4) For all 13 sites combined ( $y = 0.789 - 0.0191x + 0.000211x^2$ ,  $R^2 = 0.95$ ,  $P < 0.01$ )

stands is not significantly related to availability. All turnover values are between 48 and 82%·yr<sup>-1</sup>.

This relationship can also be viewed as a conifer-hardwood distinction. Both of these two groups show linear increases in fine root turnover rate with increasing  $N$  availability, regardless of form of availability. The slopes of the two relationships are very different (Fig. 4, Hardwood  $R^2 = 0.93$ ,  $P < 0.01$ ; Conifer  $R^2 = 0.96$ ,  $P < 0.01$ ).

For all data combined, a significant quadratic relationship is obtained with increasing fine root turnover at higher  $N$  availability values, regardless of form of  $N$  available ( $R^2 = 0.95$ ,  $P < 0.01$ ). Taken together, these analyses suggest that fine root turnover increases continuously with increasing  $N$  availability but that the form of this relationship may be further refined by adding the physiognomy of the dominant species or the form of nitrogen available.

## Conclusions

The following patterns in fine root biomass, production and turnover appear related to the quantity and form of nitrogen availability:

- 1) Mean total fine root mass declines with increasing nitrification, at least in deciduous stands,
- 2) seasonal changes in root mass are greater in ammonium dominated stands,
- 3) both methods used to calculate fine root production give similar results for ammonium sites, with the  $N$  budgeting method giving increasingly higher estimates as nitrification increases,
- 4) using the  $N$  budgeting method, which we feel is the most appropriate for the wide range of sites discussed, apparent fine root turnover rate increases exponentially with increasing  $N$  availability. Turnover may be further affected by the form of  $N$  available or by whether the stand is dominated by coniferous or deciduous species.

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