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Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests

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Abstract Minirhizotrons were used to observe fine root (≤1 mm) production, mortality, and longevity over 2 years in four sugar-maple-dominated northern hardwood forests located along a latitudinal temperature gradient. The sites also differed in N availability, allowing us to assess the relative influences of soil temperature and N availability in controlling fine root lifespans. Root production and mortality occurred throughout the year, with most production occurring in the early portion of the growing season (by mid-July). Mortality was distributed much more evenly throughout the year. For surface fine roots (0–10 cm deep), significant differences in root longevity existed among the sites, with median root lifespans for root cohorts produced in 1994 ranging from 405 to 540 days. Estimates of fine root turnover, based on the average of annual root production and mortality as a proportion of standing crop, ranged from 0.50 to 0.68 year^{-1} for roots in the upper 30 cm of soil. The patterns across sites in root longevity and turnover did not follow the north to south temperature gradient, but rather corresponded to site differences in N availability, with longer average root lifespans and lower root turnover occurring where N availability was greater. This suggests the possibility that roots are maintained as long as the benefit (nutrients) they provide outweighs the C cost of keeping them alive. Root N concentrations and respiration rates (at a given temperature) were also higher at sites where N availability was greater. It is proposed that greater metabolic activity for roots in nitrogen-rich zones leads to greater carbohydrate allocation to those roots, and that a reduction in root C sink strength when local nutrients are depleted provides a mechanism through which root lifespan is regulated in these forests.

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Introduction

Fine root turnover has a strong influence on belowground allocation of C and nutrients in forest ecosystems (Gholz et al. 1985; Nadelhoffer et al. 1985; Joslin and Henderson 1987; Arthur and Fahey 1992; Hendrick and Pregitzer 1993a). As such, there is a great deal of interest in understanding how soil environmental factors, such as temperature and N availability, affect root lifespan. It has been suggested that higher soil temperatures might decrease root lifespan (Hendrick and Pregitzer 1993b; Self et al. 1995), and root longevity appears to be generally greater in species from cold environments (Eissenstat and Yanai 1997). Within a forest type, improved N availability sometimes leads to decreases in fine root production and biomass (Haynes and Gower 1995), but evidence exists for both increased (Keyes and Grier 1981; Vogt et al. 1986b; Pregitzer et al. 1993) and decreased (Aber et al. 1985; Nadelhoffer et al. 1985; Pregitzer et al. 1995) fine root lifespans in more fertile soils. This contradictory evidence has led to the development of a variety of hypotheses to explain root longevity (Nadelhoffer et al. 1985; Hendricks et al. 1993; Eissenstat and Yanai 1997), but direct observational tests of these hypotheses in mature forest ecosystems are needed.

Hendrick and Pregitzer (1993b) examined fine root longevity in two northern hardwood forests in Michigan and found shorter root lifespans at the more southern site. They speculated that warmer soil temperatures at the southern site might be the cause. This paper reports the results of a study that geographically expands their work to quantify fine root demography at four sites along a latitudinal temperature gradient. Recent work has documented that differences in N availability also exist among the four study sites (Zogg et al. 1996), in a pattern that does not correspond to the temperature gradient. These natural differences in ambient conditions allowed us to assess the relative influences of temperature and N availability on fine root lifespans at the sites, using minirhizotrons to observe fine root production and longevity over two growing seasons. Objectives of the study were: (1) to define seasonal patterns of fine root production and mortality; (2) to determine if differences existed among the four sites in fine root longevity and turnover; (3) to assess whether such differences corresponded to differences among sites in temperature or N availability; and (4) to compare fine root production, mortality and turnover in surface (0–10 cm depth) and subsurface soils (20–30 cm and 40 –50 cm depths).

Materials and methods

Fine root production and longevity were studied in four northern hardwood forests located along a 3° latitudinal transect in Michigan (Table 1). The forests are second-growth northern hardwoods, approximately 85 years of age, dominated by sugar maple (*Acer saccharum* Marsh.), and occurring on sandy, well-drained spodosols (Burton et al. 1991; MacDonald et al. 1991; Randlett et al. 1992). Mean annual air temperature increases by about 3°C from north to south (sites A–D) along the latitudinal gradient, and differences among the sites in N availability, fine root N concentration, and fine root respiration rate have been documented (Burton et al. 1996; Zogg et al. 1996), with significantly higher N availability, fine root N concentrations, and fine root respiration rates occurring at sites B and C (Table 1).

Fine root production and mortality data reported in this paper were collected from three 30×30 m study plots located at each site. In September and October of 1993, five clear polybutyrate minirhizotron tubes (2 m long×5.08 cm inside diameter) were installed at each plot at a 45° angle to the soil surface to a vertical depth of >70 cm. Rectangular image frames (0.9×1.3 cm) were scribed every 0.9 cm along a transect on the exterior surface of each minirhizotron tube prior to installation. Every fifth image frame was scribed with an identifying number. The image frames were oriented upward during tube installation, and tubes were anchored to prevent inadvertent movement or rotation. This enabled the videotaping of the same locations within the soil on all sampling dates. The aboveground portions of the tubes were painted black to prevent light penetration and then repainted white to minimize heat load.

Video images were collected from the minirhizotron tubes at approximately five week intervals from mid-May through early November in 1994, and at 5- to 6-week intervals from mid-April to mid-November in 1995 and late April to early June in 1996. All sites were sampled during each sampling period, with the exception of site A in April, 1995, which was inaccessible due to deep snow cover. Image collection proceeded from south (site D) to north (site A) and typically was completed within 7 days. The sampling periods used to generate the data reported in this paper were: 17–24 May, 19–27 June, 26–30 July, 30 August–5 September, 4–10 October, and 2–7 November 1994; 13–23 April, 15–22 May, 28 June–5 July, 7–12 August, 21–25 September, and 14–20 November 1995; and 22 April–9 May, and 7–18 June 1996. All video images were recorded on Hi-8 mm videotape using a model BTC 1.125 Minirhizotron Research Color Camera (Bartz Technology Co., Santa Barbara, Calif., USA).

A PC-based, interactive image analysis system (ROOTS, Hendrick and Pregitzer 1992a, 1993a) was used to analyze root images. Videotaped minirhizotron images were projected onto a computer monitor, and the image from each frame was temporarily "captured" on-screen by ROOTS using a TARGA+ videographics card (Truevision, Inc., Indianapolis, Ind., USA). For the first image collection date, the lengths and diameters of all roots were traced to the nearest 0.01 mm; and each root was given an identification number, classified as living or dead (based upon color and consistency in the image), and designated as white or brown. All measurements and classifications were written to a dBASE III+ file (Ashton-Tate, Torrance, Calif., USA) by ROOTS. The tracings were saved in separate disk files. For subsequent image sets, the tracings from the previous date were overlain on the new image, allowing previously existing roots to be identified. These were then retraced and designated as white, brown, dead, or missing. New roots also were traced, given identification numbers, and designated as new. Roots that were missing and did not reappear at subsequent image collection dates were assumed to have died. Complete records were kept for all roots, even after they were classified as dead or missing. By using ROOTS to match tracings with identification numbers, the fates of individual roots or units of root length were followed from initiation until death (Hendrick and Pregitzer 1992a,1992b).

Fine root lifespans at the sites were assessed by studying the survival of contemporaneously produced root cohorts from each site. Cohorts consisted of all roots ≤1 mm in diameter produced

Table 1 Selected characteristics of four northern hardwood forests in Michigan, USA. Overstory data are from the year 1995. Site means for N mineralization, root N concentration, and root respiration followed by a different *letter* are significantly different at the 0.05 level of probability

Characteristic	Site A	Site B	Site C	Site D
Latitude (N)	46°52′	45°33′	44°23′	43°40′
Longitude (W)	88°53′	84°51′	85°50′	86°09′
Mean annual precipitation[a] (mm)	883	893	870	779
Mean annual temperature[b] (°C)	3.8	5.2	6.1	6.8
Total basal area (m^2 ha^{-1})	34	31	32	33
Sugar maple basal area (%)	86	86	83	75
Overstory age	88	82	83	87
Net N mineralization[c] (µg N g $soil^{-1}$)	0.29b	0.46a	0.48a	0.32b
Fine root N concentration[d] (mg g^{-1})	17.4b	18.8a	18.6a	17.4b
Fine root respiration[d] (nmol O_2 g^{-1} s^{-1} at 24°C)	11.0b	13.4a	13.8a	11.6b

[a] For the years 1994–1996, recorded using weighing rain gauges (Model 5-780, Belfort Instrument Co., Baltimore, Md., USA) located in open areas within 5 km of each site

[b] For the years 1994–1996, recorded at 2 m using thermistors which were read every 30 min throughout the year, with averages recorded every 3 h using data loggers (EasyLogger Models 824 and 925, Data Loggers, Inc., Logan, Utah, USA)

[c] Data from Zogg et al. (1996) for the top 10 cm of soil and organic matter occurring beneath the surface litter (O_i) layer. Net N mineralization was determined using the buried bag technique, with bags replaced at 5-week intervals from May through November 1994. Bulk densities of the surface 10 cm, determined at a later date, were similar among sites (G.P. Zogg, unpublished work)

[d] Data from Burton et al. (1996) for roots ≤1 mm in diameter collected from the top 10 cm of soil and organic matter occurring beneath the surface litter (O_i) layer

between any two sampling dates at a site (mean diameter of all roots studied was actually 0.31 mm). At each site, cohorts from three depths were identified and tracked: 0–10 cm, 20–30 cm, and 40–50 cm. Images from all 15 tubes at each site were analyzed for the 20–30 cm and 40–50 cm depths. For the 0–10 cm depth, much higher root densities and constraints on the amount of time and labor available for digitizing images necessitated the use of only nine tubes per site (three from each plot). For each depth increment, the survival of cohorts produced within each sampling interval was determined for each subsequent sampling date, and survival was expressed as a fraction of initial cohort root number still surviving. Fine root survival functions were determined using the life table method of failure-time analysis (Fox 1993), which is appropriate for right-censored data (Lee 1992). The SAS lifetest procedure (SAS Institute 1989) was used to perform these analyses and to determine product-limit survival estimates of mean and median root lifespans. Differences among sites in root survival for each cohort initiation date were tested using the Wilcoxon multiple comparison described by Fox (1993).

Fine root production for each sampling interval was determined by summing the length of all new roots and adding the extension growth of all previously existing roots. Fine root mortality for each sampling interval was determined by summing the lengths of all roots that had died during that interval and adding root length lost by existing roots due to herbivory or dieback. Monthly estimates of fine root production and mortality at the sites were made by assuming production was constant for each day in the time interval between consecutive imaging dates. Estimates of daily production and mortality were then summed for each month. Production and mortality were both expressed as root length per minirhizotron tube area observed (mm cm^{-2}).

Estimates of annual fine root turnover (proportion of standing root biomass replaced annually) were made using: (1) the ratio of annual root length produced to average live root length observed; (2) the ratio of annual root length mortality to average live root length observed; and (3) the average of the above two measures. Differences among sites in annual root turnover were determined using analysis of variance and Tukey's HSD test, using turnover estimates from each of the three plots per site. The inverse of median cohort lifespan (year^{-1}) for the 1994 root cohorts was used as an additional index of differences among the sites in annual root turnover.

Results

For roots in the surface soil (0–10 cm depth), there were significant differences in fine root longevity among the four study sites, with fine root survival over time at sites B and C equal to or greater than that at sites A and D for almost every cohort (Fig. 1, Table 2). This pattern across sites in fine root survival does not correspond to the north to south temperature gradient, but rather reflects site differences in N availability and fine root N concentration (Table 1), with longer average root lifespans occurring where N availability is greater. Median root lifespans for the 1994 surface soil root cohorts were 405, 528, 540, and 475 days for sites A, B, C, and D, respectively. At the 20–30 cm depth, roots from sites B and C also tended to have greater lifespans than roots from sites A and D (Fig. 2, Table 2), but the differences were not statistically significant. For roots deeper in the soil profile (40–50 cm), there was no clear pattern among the sites in ranking of fine root longevity (Fig. 3, Table 2).

Fine root production at all soil depths occurred throughout the growing season, but was greater during the early portion (Fig. 4). Peak monthly production at the individual sites always occurred in either June or July. Of annual fine root production, 42% had occurred by the end of June (1–1.5 months after leaf emergence), with 36% of annual production occurring in May and June alone. Less than 5% of annual root production occurred during the winter months (November–March). Averaged across sites, fine root production in the surface soil (0–10 cm) was 3.5 times greater than at the 20–30 cm depth, and 9.2 times greater than at the 40–50 cm depth. Differences among the depths were most extreme at site A which had 17 times more root production in surface soil than at the 40–50 cm depth.

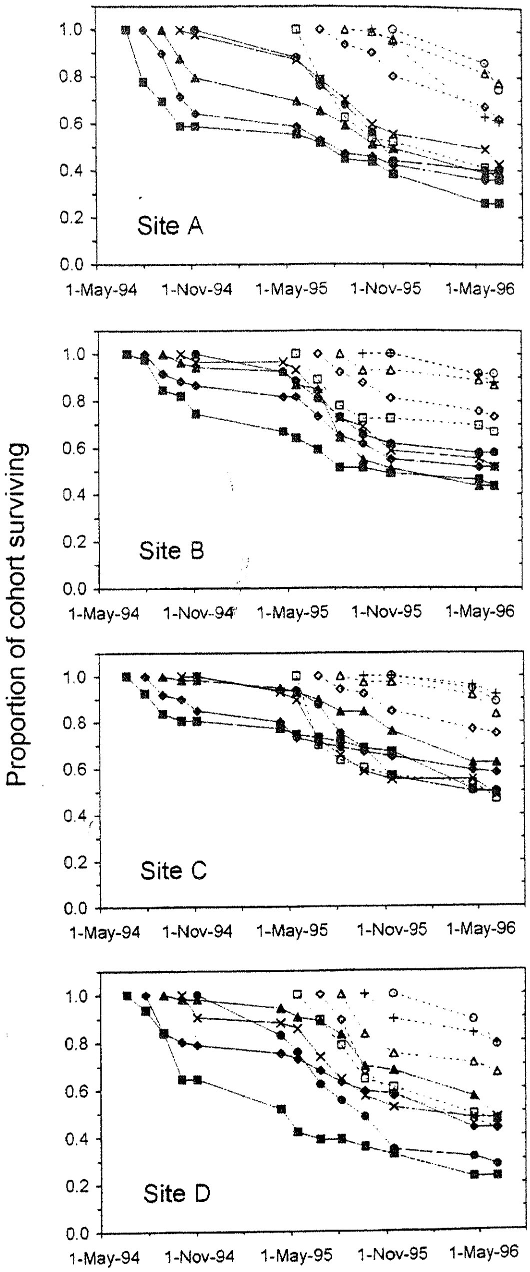

Fig. 1 Survival curves for cohorts of surface soil (0–10 cm deep) fine roots from four Michigan northern hardwood forests. Cohort sizes ranged from 16 to 100 roots (47±25, mean±SD)

Table 2 Proportion of roots surviving at 1 year for 1994 and spring 1995 root cohorts. Survival percentages for cohorts from the 0–10 cm depth followed by different *letters* are significantly different at the 0.05 level of probability (Wilcoxon multiple comparison of survival rate)

Date first observed	Proportion surviving at 1 year			
	Site A	Site B	Site C	Site D
Surface soil (0–10 cm) cohorts				
19–27 June 1994	0.52b	0.59ab	0.73a	0.39b
26–30 July 1994	0.47b	0.65ab	0.69a	0.63ab
30 August–5 September 1994	0.55c	0.62bc	0.85a	0.70b
4–10 October 1994	0.58	0.69	0.59	0.57
2–7 November 1994	0.44b	0.62a	0.56a	0.34b
15–22 May 1995	0.42c	0.69a	0.56ab	0.49bc
28 June–5 July 1995	0.70a	0.73a	0.75a	0.42b
All cohorts, June 1994–July 1995	0.54b	0.67a	0.71a	0.54b
Subsurface soil (20–30 cm) cohorts				
19–27 June 1994	0.53	0.60	0.77	0.57
26–30 July 1994	0.62	0.51	0.61	0.60
30 August–5 September 1994	0.38	0.67	0.55	0.41
4–10 October 1994	0.27	0.80	0.60	0.58
2–7 November 1994	ND[a]	ND	ND	0.32
15–22 May 1995	ND	0.36	ND	0.47
28 June–5 July 1995	0.76	0.64	0.48	ND
All cohorts, June 1994–July 1995	0.54	0.60	0.61	0.52
Subsurface soil (40–50 cm) cohorts				
19–27 June 1994	ND	0.36	0.66	0.42
26–30 July 1994	ND	0.41	0.51	0.91
30 August–5 September 1994	0.75	0.91	1.00	ND
4–10 October 1994	ND	ND	ND	0.50
2–7 November 1994	ND	ND	0.73	ND
15–22 May 1995	ND	ND	ND	0.90
28 June–5 July 1995	1.00	1.00	0.94	ND
All cohorts, June 1994–July 1995	0.88	0.67	0.68	0.60

[a] Not determined due to no new roots or a cohort size of fewer than 10 roots

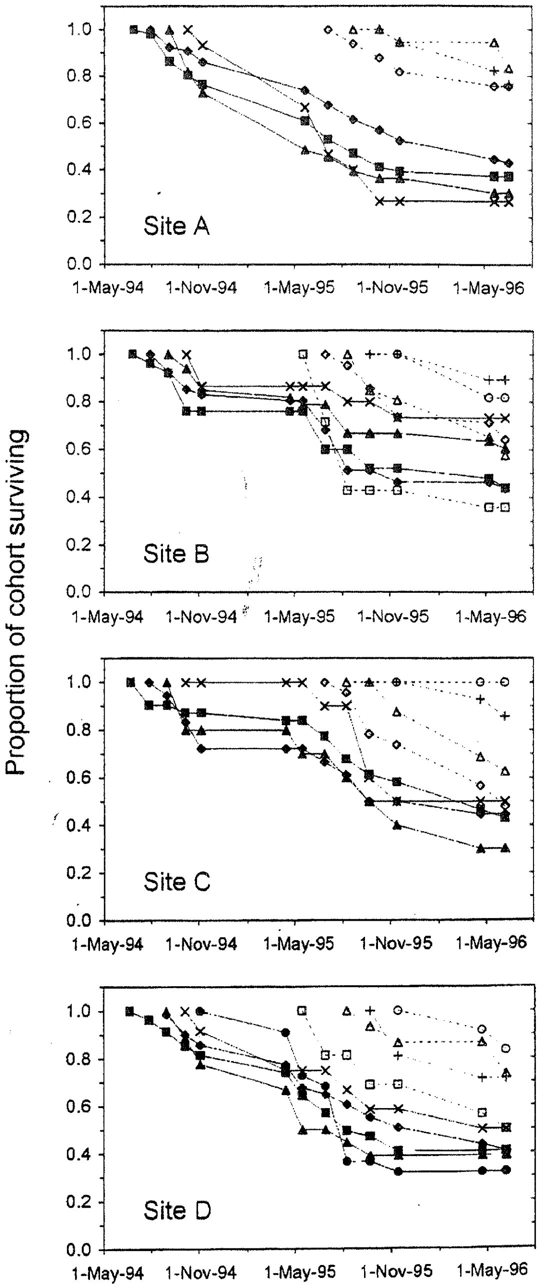

Fig. 2 Survival curves for cohorts of subsurface soil (20–30 cm deep) fine roots from four Michigan northern hardwood forests. Cohort sizes ranged from 1 to 71 roots (18±16, mean±SD). Only cohorts with a minimum of 10 roots are shown

Mortality was more evenly distributed over the growing season than production (Fig. 5), and peak mortality rates did not occur at the same time of year at all sites. Unlike root production, significant mortality did occur during the winter. Root mortality for the November–March period was typically greater than that for any single growing season month and accounted for 20% of annual root mortality. Root production exceeded mortality during the 2 years of study, indicating that the minirhizotron tubes had not yet fully equilibrated with the surrounding soil following disturbance associated with installation. As the soil adjacent to the tubes is recolonized by roots, it is expected that annual production and mortality will eventually come into an approximate equilibrium. The ratio of production to mortality declined from 2.0 in year 1 of the study to 1.4 in year 2, as the equilibration process proceeded.

Estimates of fine root turnover derived from the production and mortality data indicate that the proportion of fine root biomass that dies and is replaced each year at sites B and C is less than or equal to that at sites A and D for the 0–10 cm and 20–30 cm depths (Table 3). This is in agreement with the longer root lifespans that occur at sites B and C (Table 2). Since a majority of roots occur in the surface soil, combined turnover across all depth increments was also lower at sites B and C than at sites A and D.

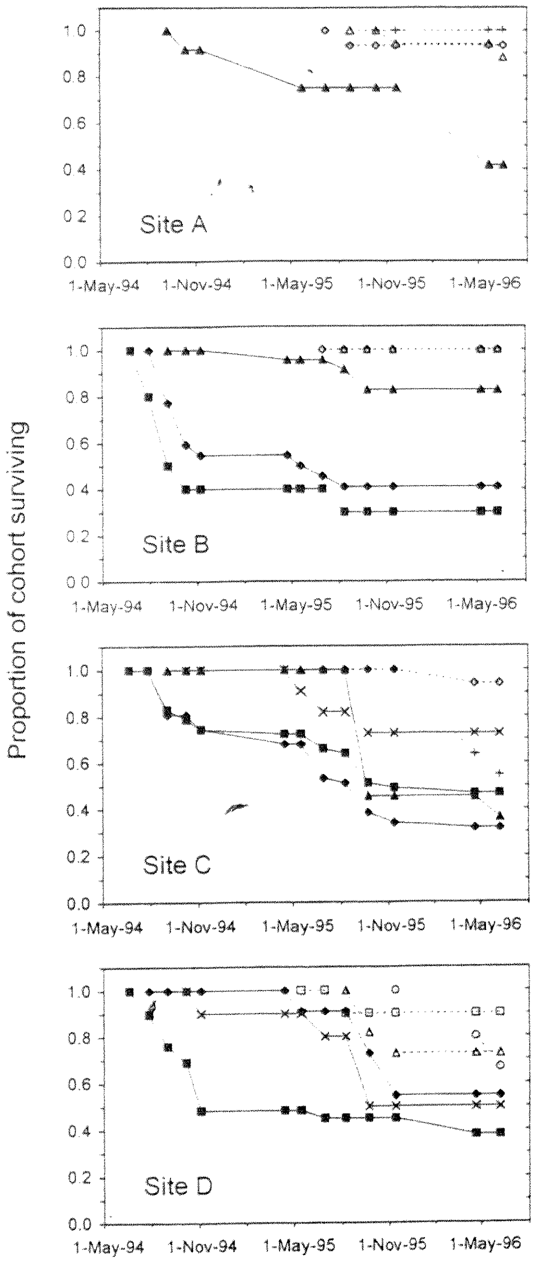

Fig. 3 Survival curves for cohorts of subsurface soil (40–50 cm deep) fine roots from four Michigan northern hardwood forests. Cohort sizes ranged from 0 to 47 roots (8±10, mean±SD). Only cohorts with a minimum of 10 roots are shown

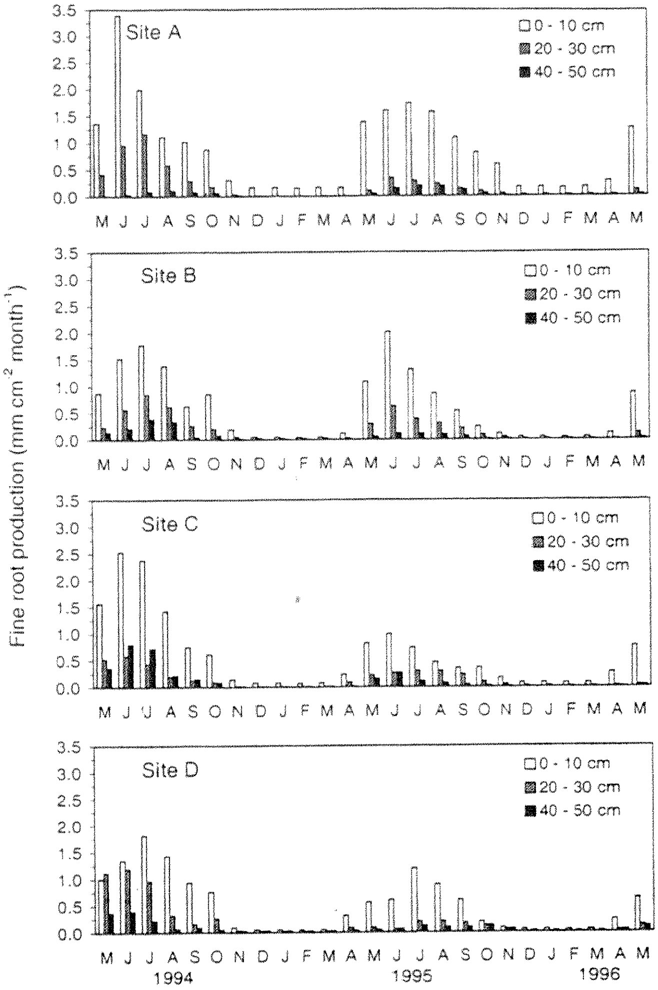

Fig. 4 Monthly fine root production rates for the period May 1994 to May 1996 for four Michigan northern hardwood forests

Discussion

Fine root production, mortality and turnover

The finding that root production was continuous over the entire growing season, with a majority of production occurring in the spring and early summer (by mid-July), is consistent with numerous previous observations for sugar maple (Morrow 1950) and northern hardwood forests (Fahey and Hughes 1994; Burke and Raynal 1994; Hendrick and Pregitzer 1996, 1997). Hendrick and Pregitzer (1996) reported circumstantial evidence that episodic deep (50–100 cm) root production was related to periods of high water demand. Sites C and D experienced strong soil moisture deficits during the 1995 growing season (Burton et al. 1998), but no increase in root production was observed during these drought periods at the deepest depth used in this study (40–50 cm). Instead, a decrease in root production occurred at sites C and D at all depths during the 1995 growing season (Fig. 4), in agreement with previous reports of reduced root initiation and elongation in dry soils (Morrow 1950; Teskey and Hinckley 1981; Kuhns et al. 1985). This does not preclude the possibility that dry conditions resulted in enhanced root production at depths deeper than 50 cm, as observed by Hendrick and Pregitzer (1996). Fine root mortality was continuous throughout the year and more evenly distributed over time than production, similar to previous reports for sites C and D (Hendrick and Pregitzer 1996).

Estimates of fine root turnover calculated using the annual rate of production were greater than those calculated using the annual rate of mortality (Table 3). This is

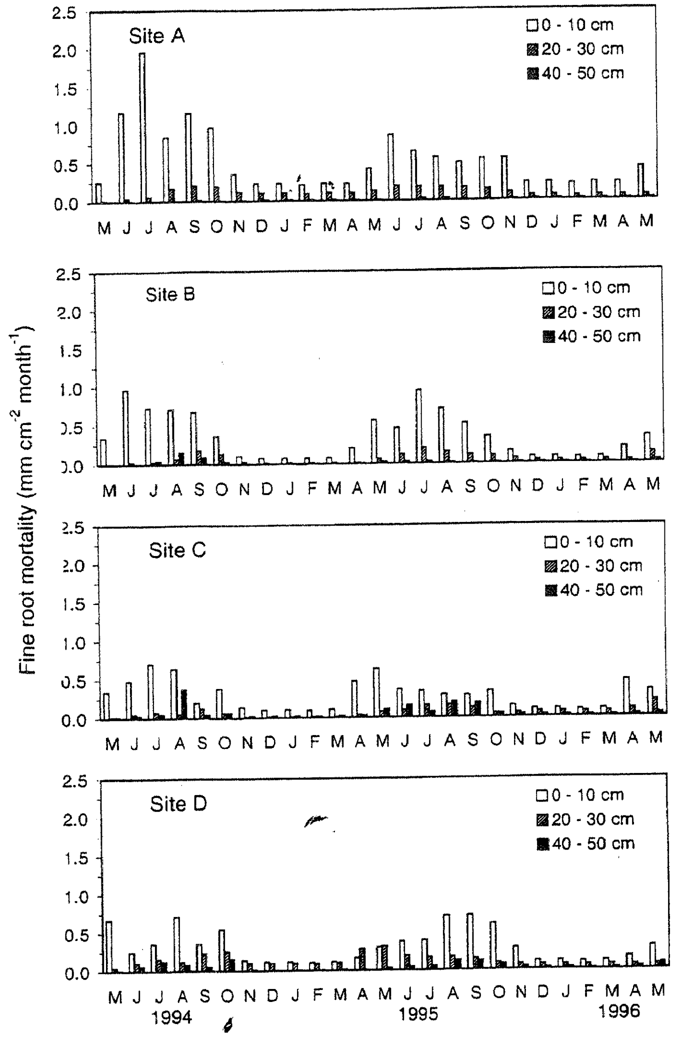

Fig. 5 Monthly fine root mortality rates for the period May 1994 to May 1996 for four Michigan northern hardwood forests

Table 3 Estimates of fine root turnover for four Michigan northern hardwood forests. Site means followed by different *letters* are significantly different at the 0.05 level of probability

Basis of estimate	Fine root turnover (year^{-1}) for Site A	Site B	Site C	Site D
Surface soil (0–10 cm) cohorts				
Annual length production[a]	0.81ab	0.76ab	0.72b	0.82a
Annual length mortality[a]	0.52	0.42	0.36	0.52
Average of production and mortality[a]	0.66a	0.59ab	0.54b	0.67a
Median root lifespan[a]	0.90a	0.69b	0.68b	0.77ab
Subsurface soil (20–30 cm) cohorts				
Annual length production	0.88	0.76	0.77	0.76
Annual length mortality	0.48a	0.25b	0.39ab	0.50a
Average of production y and mortalit	0.68	0.50	0.58	0.63
Subsurface soil (40–50 cm) cohorts				
Annual length production	1.06	0.81	0.89	0.85
Annual length mortality	0.20	0.25	0.48	0.50
Average of production and mortality	0.63	0.53	0.68	0.68
All depth increments combined				
Annual length production	0.83	0.76	0.75	0.80
Annual length mortality	0.50a	0.36b	0.37ab	0.50a
Average of production and mortality	0.66a	0.56b	0.56b	0.65ab

[a] Turnover estimates from production and mortality data were derived by dividing annual root length production (or mortality) by the average total root length observed. For surface soil roots, turnover estimates from median root lifespans were calculated as the inverse of median root lifespan for all 1994 root cohorts at a site

thought to be a consequence of the minirhizotron tubes not having fully equilibrated following installation (Joslin and Wolfe 1999). Eventually, as the tubes reach equilibrium, annual rates of production and mortality should become approximately equal. For this to occur, measured rates of production for the sites must decrease, or rates of mortality must increase, or both. In any of these possible scenarios, the standing crop of root length visible on the tube surface will increase during the time equilibrium is being approached. Thus the observed ratios of annual root length production to total live root length are likely to have overestimated turnover, while the ratios of root length mortality to total live root length underestimated turnover.

For the minirhizotron tubes used in this study, root turnover rates calculated using the average of production and mortality would appear to provide the best estimates of annual fine root turnover. The range of turnover rates from this method, 0.50–0.68 year^{-1} for the various sites and depths (Table 3), is well within the range reported in the literature for a wide variety of deciduous forest types: 0.33 year^{-1} for birch-aspen, 0.94 year^{-1} for balsam poplar, and 0.75 year^{-1} for alder-balsam poplar in Alaska (Ruess et al. 1996); 0.21 year^{-1} for white oak in Missouri (Joslin and Henderson 1987); 0.67–0.89 year^{-1} for a mixed deciduous forest in Massachusetts (McClaugherty et al. 1982); 0.6 year^{-1} in a Belgian beech forest (Van Praag et al. 1988); and 0.19–0.64 year^{-1} (maximum-minimum method) and 0.64–2.26 year^{-1} (N budget method) for oak and maple forests in Wisconsin (Aber et al. 1985). Most of these turnover rates were calculated from root production values derived using either the difference in maximum and minimum live root biomass measured during the year (maximum-minimum method, McClaugherty et al. 1982) or the N budget method of Aber et al. (1985). Both of these methods are subject to errors associated with their inherent assumptions. For example, the maximum-minimum method assumes that root production and mortality do not occur simultaneously during the growing season (Aber et al. 1985). Making this assumption would lead to underestimation of root production and turnover in stands such as our study sites, in which root production and mortality are concurrent throughout the year. The N budget method makes a variety of assumptions, including accurate measurement of N mineralization using the buried bag technique and the forest stand taking up all N made available through mineralization and atmospheric inputs (Aber et al. 1985). Failure of these and other assumptions associated with the technique could result in either under- or overestimation of fine root production and annual turnover. Root turnover estimates made using minirhizotrons avoid these problems, but are subject to a variety of possible errors, including the previously mentioned disturbance associated with tube installation, and the assumption that fine root dynamics along the soil-tube interface are the same as those in bulk soil.

In our study, equilibration following tube installation appears to be proceeding more rapidly at sites A and D than at sites B and C. In the upper 10 cm of soil, ratios of fine-root production to mortality were 1.6, 1.8, 2.0, and 1.6 at sites A, B, C, and D, respectively, over the 2-year study period. Although the tubes were not fully equilibrated during the experiment, we believe that the pattern we observed among sites in annual root turnover is real. The same pattern occurred across sites whether annual rates of mortality, annual rates of production, or median root lifespans of contemporaneous cohorts were used as the basis for estimating annual turnover (Table 3), and the pattern among sites in root lifespan was similar in both years (Fig. 1, Table 2), despite the fact that the ratio of production to mortality was much closer to equilibrium in year two. This suggests that the longer root lifespans and lower annual turnover at sites B and C are real rather than being artifacts of site differences in rates of tube equilibration following disturbance. It is more likely that slower equilibration at sites B and C is actually a consequence of the longer root lifespans observed at those sites; i.e., where roots live longer, it takes more time after recolonization for the initial flush of root production to die, thus mortality lags further behind production at those sites.

Overall, we feel minirhizotrons provide a powerful tool for assessing root longevity and turnover, and our turnover estimates compare well with published values for other sugar maple-dominated forests. Burke and Raynal (1994) estimated fine root (<3 mm) turnover of 0.8 to 1.2 year^{-1} for northern hardwoods at Huntington Forest in New York, using production estimates derived from three different techniques: the maximum-minimum method, a phenology-based examination of changes in live and dead root biomass (Vogt et al. 1986a), and the litterfall ratio method of Nadelhoffer and Raich (1992). The fine root (<1 mm) production estimates of Fahey and Hughes (1994) can be used to estimate turnover rates of 0.54–0.66 year^{-1} for a northern hardwood stand in New Hampshire (production estimated using ingrowth cores and *in situ* screens). For sugar maple stands in Wisconsin, Aber et al. (1985) estimated fine root (<3 mm) turnover rates of 1.29–2.01 year^{-1} using the N budget method and 0.26–0.33 year^{-1} using the maximim-minimum method. Hendrick and Pregitzer (1993a) previously used minirhizotrons to study fine root dynamics at two of the northern hardwood sites used in this study. Their data from 1989 can be used to estimate fine root (<2 mm) turnover rates for their northern and southern sites (sites C and D in this report) of 0.83 and 0.79 year^{-1} using the ratio of root length production to average total root length observed during the year, and 0.76 and 0.66 year^{-1} comparing the average of root length production and mortality to total root length observed. These values are only slightly greater than determined for the same sites in this study (*c.* 11%), and the relative ranking of the sites remains the same, indicating that the results of minirhizotron studies are quite repeatable.

Median root lifespans (days to 50% mortality) of the individual cohorts examined in this study ranged from as little as 74 days to greater than 500 days (Figs. 1,2,3), but most cohorts, including all surface soil (0–10 cm) cohorts, had median root lifespans greater than 300 days. These values for surface fine roots are somewhat greater than those previously reported for sugar maple forests (Hendrick and Pregitzer 1992a, 1993b; Fahey and Hughes 1994). The inverse of median root lifespans from the 1994 surface soil root cohorts was used to estimate an index of root turnover for the sites (Table 3). Annual fine root turnover rates so derived were similar to those based on the ratio of root length production to total root length observed, but lower than those based on root length mortality or the average of root length production and mortality (Table 3). However, the values did correctly assess relative differences among the sites in fine root turnover (Table 3), with greater turnover occurring at sites A and D, where N availability was lower and median root lifespans were shorter.

Turnover estimates based on median root lifespan will only be accurate if the rate of mortality remains relatively constant until all roots have died. In our study, this was not the case. For example, the average mortality rate across all sites in surface soil fine roots declined from 0.17% day^{-1} during the first growing season of a root cohorts existence to 0.12% day^{-1} during the second growing season. This would cause the inverse of median root lifespan to overestimate turnover. Hendrick and Pregitzer (1992a) observed a similar decline in mortality rate as root cohorts were followed over time. This decline over time in fine root mortality rate may be related to differences in architectural position within the root system of apparently similar fine roots. In sugar maple, root diameters <0.5 mm can exist for as many as six root orders (Pregitzer et al. 1997). These orders include many short lateral roots which serve as the absorbing structure but also include longer lateral connecting roots that likely function in transport of water and nutrients. These roots are all <0.5 mm, but may have very different lifespans. Root cohorts observed along our minirhizotron tube surfaces likely contained both types of "fine roots", especially in 1994 when the soil-tube interface was being recolonized. This could explain why the cohorts exhibited higher mortality rates early in their existence than at later times when they may have been comprised primarily of longer-lived connecting roots.

It should be noted that a higher annual root turnover rate at a site, i.e., a greater proportion of the root system dying and being replaced, does not necessarily mean that a greater amount of C is being allocated annually to root production. The amount of C allocated to root production will depend on both the percentage of the root biomass that is replaced annually (turnover) and the total biomass of the root standing crop. For our sites, fine root biomass at the low N availability sites (sites A and D) is equal to or greater than that at the sites with higher N availability (A.J. Burton, unpublished work). Thus, for our sites, it appears that greater annual turnover rates do coincide with greater annual belowground C allocation for root production.

Relationship of fine root longevity to N availability and root respiration rate

Hendrick and Pregitzer (1993a) previously examined fine root longevity at two of the study sites used in this research and found differences between sites C and D that were similar to those observed in the current study. They suggested that more rapid fine root death at the southern site (site D) might be associated with warmer soil temperatures at the site. The current data set, which includes two additional, progressively cooler sites, suggests that temperature is not the primary cause of differences among the four sites in root lifespan. Rather, differences among sites in root lifespan appear to be related to variation in N availability. At the site level, root turnover rates were negatively correlated with N mineralization rates for surface roots (r=–0.92, P=0.08) and for all depth increments combined (r=–0.95, P=0.05). Median root lifespans for surface root cohorts were also related to N mineralization (r=0.94, P=0.07).

The finding that fine root turnover is lower where N availability is higher suggests that roots may be maintained as long as the benefit (nutrients) they provide outweighs the C cost of keeping them alive. Eissenstat and Yanai (1997) used simulation modeling and cost-benefit analysis to calculate root lifespans that maximized root efficiency in terms of nutrient acquired per unit C expended for root construction and maintenance. Their analyses suggested that roots located in nutrient-rich patches should live longer. This agrees with the results of the nutrient patch studies conducted by Pregitzer et al. (1993) and Fahey and Hughes (1994) in temperate hardwood forests and appears to be consistent with the finding of longer root lifespans in soils with higher N availability for the four northern hardwood forests in our study.

Previous studies at the four sites have consistently measured higher root N concentrations and respiration rates (at a given temperature) at sites B and C than at sites A and D (Table 1; Burton et al. 1996, 1998; Zogg et al. 1996), indicating that metabolic activity per unit root mass is greater where N availability is greater. Faster depletion of the cytosolic sugar pool in metabolically more active roots has been shown to result in increased carbohydrate allocation to the roots (Minchin et al. 1994), suggesting the possibility that the C sink strength of roots may play a role in regulating their lifespan. Under such a mechanism, root activity would remain high until local nutrients were depleted. At that time, root activity would decline, lowering sink strength relative to other portions of the root system, ultimately leading to cessation of C supply and root death. If time to nutrient depletion is greater in nutrient-rich soil, it could lead to greater root lifespans, such as those observed in the surface soils of the high N availability sites (sites B and C).

The pattern among sites in surface root longevity was not apparent for cohorts from the 40–50 cm soil depth. For these deeper roots, longevity patterns among sites varied considerably among cohort initiation times, but overall annual turnover rates were similar to those of roots closer to the soil surface (Table 3). The N mineralization data for the sites (Table 1) were measured for the top 10 cm of soil, and have not been determined for the 40–50 cm soil depth. But it is very likely that N availability at 40–50 cm is much lower than at 0–10 cm, and that rates of N uptake by these deeper roots are lower than for surface roots. Using the same cost-benefit analogy as for surface roots, similar root turnover rates for surface soil and 40–50 cm deep roots would suggest that the deep roots should have lower maintenance cost per unit time (Eissenstat and Yanai 1997). Measurements made in 1996 at the sites indicate that roots at the 40–50 cm depth do indeed have much lower respiration rates than those closer to the soil surface (Pregitzer et al. 1998). It also is possible that water uptake is a more important function for deeper fine roots than is nutrient acquisition. In that case, the benefit the roots provide would need to be assessed differently than for surface roots when attempting to predict longevity.

Moisture availability has been shown, in some cases, to affect root longevity (Pregitzer et al. 1993) and mortality (Deans 1979; Espeleta and Eissenstat 1998). Soil moisture was plentiful at all of our sites during 1994 (Burton et al. 1998), thus the differences among sites in root longevity were not related to soil moisture availability. During the middle of the 1995 growing season, there were periods of severe soil moisture deficit at sites C and D (Burton et al. 1998), but there is no evidence of enhanced or episodic root mortality at those sites during that time (Figs. 1,2,3). During the same dry periods in 1995, fine root respiration rates decreased significantly (Burton et al. 1998). These findings are in agreement with the cost-benefit approach of Eissenstat and Yanai (1997) to assessing root longevity, as their analyses suggest that shedding roots in dry soil would not be necessary if sufficient reductions in maintenance respiration also occurred.

The cost-benefit analogy and carbon sink-strength mechanism appear to be consistent with the pattern in root longevity observed at the four northern hardwood sites examined in this study, but there remains a great deal of controversy regarding the effects of N availability on root longevity. Estimates of fine root turnover derived from root biomass and nutrient budgets have suggested both increased (Keyes and Grier 1981; Vogt et al.

1986b) and decreased (Aber et al. 1985; Nadelhoffer et al. 1985) fine root lifespans in more fertile soils. In direct observational studies utilizing a single species or forest type, root lifespans have been shown to be both positively (Keyes and Grier 1981; Pregitzer et al. 1993) and negatively (Pregitzer et al. 1995, 2000) related to N availability. These findings have led to the generation of several competing hypotheses regarding the effect of N availability on root longevity and the mechanisms by which N availability might control root longevity (Raich and Nadelhoffer 1989; Hendricks et al. 1993; Eissenstat and Yanai 1997).

Some of the contradictory evidence regarding N effects on root lifespan may be a consequence of some experiments studying a single tree species (or forest type) across a range of N availabilities, whereas other studies examined a variety of different tree species, each adapted to sites of different fertility. It is possible that average root lifespan in species adapted to nutrient-poor environments is longer than that in species adapted to nutrient-rich environments, as hypothesized by Nadelhoffer et al. (1985), Eissenstat (1992), and Grime (1994), while increased soil N availability for a given tree species or within a forest type often leads to longer root lifespans as observed in this study and by Pregitzer et al. (1993), Fahey and Hughes (1994), and Keyes and Grier (1981). Figure 6 depicts such a hypothetical situation. Under such a scenario, we suggest that the between-species effects of N availability on root longevity would reflect genetic adaptation of each species to the range of site conditions where it normally occurs. If this were true, one would expect lower average root activity (respiration) in roots of species adapted to N-poor sites. This would create a low C cost, permitting long root lifespans despite low nutrient gain per unit time (Eissenstat and Yanai 1997). Such a cross-species relationship between root longevity and root respiration would be analagous to that reported across species and biomes for leaves, with species that have greater leaf lifespans having lower inherent N concentration and dark respiration rates (Reich et al. 1997, 1998a,1998b).

The hypothetical within-species effect of higher N availability leading to longer root lifespan (species 1, 3, 4, and 6 in Fig. 6) would represent a plastic response to variation in soil resource availability within the range of N availabilities to which the species was adapted. This would allow optimization of above- and belowground resource acquisition, within the genetic constraints of the species. For sugar maple forests, we have found that increasing N availability results in greater root lifespans, and we have depicted this to be the most common within-species response to increasing N availability in Fig. 6. Such a within-species effect of N availability on root longevity is consistent with the results reported by Pregitzer et al. (1993), Fahey and Hughes (1994), and Keyes and Grier (1981). However, experiments with young *Populus* trees (Pregitzer et al. 1995, 2000) and with *Picea abies* (Majdi and Kangas 1997) have found root longevity was decreased by higher N availability. Clearly, the possibility exists that the within-species response of root longevity to increasing N availability may be specific to the species involved, with increases, decreases and no change in root longevity all being potential effects (Fig. 6). It should be noted that differences across forest types in root longevity are usually greater than those occurring within a species. For example, in a study of nine forest ecosystems, Nadelhoffer et al. (1985) estimated that a 3.5-fold increase in net N mineralization resulted in a 5-fold increase in root turnover. This compares to our findings within a single species (sugar maple) that a 50% increase in net N mineralization caused a corresponding decrease in root turnover of only 20 to 30%. The relative slopes of the lines in Fig. 6 are intended to illustrate the possibility that differences in N availability may have a much greater effect on differences in root lifespans across species than within species.

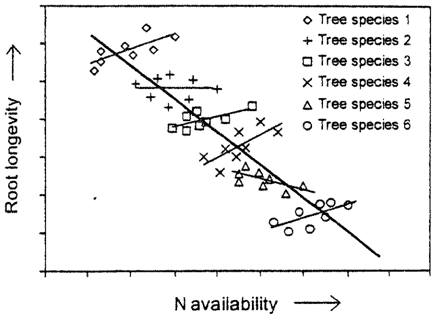

Fig. 6 Hypothetical relationships between fine root longevity and N availability within forest types along N availability gradients (*thin lines*) and across forest types adapted to different ranges in N availability (*bold line*). Across species, root lifespan decreases with increasing N availability. Within species, root lifespan generally increases with increasing N availability, although decreases and no change are also possible responses

A possible explanation for the finding of Majdi and Kangas (1997) that N fertilization decreased root lifespan is that it represents a transient response to a sudden, large change in N availability. Heavy N additions to forests can lead to a reduction in total root biomass (Vogt et al. 1990; Haynes and Gower 1995). For this new "equilibrium" root biomass to be achieved, root production must decrease (Vogt et al. 1990; Gower et al. 1992), and/or average root lifespan must temporarily shorten. Until carbon allocation in the forest has equilibrated with the altered N availability and a quasi steady-state root biomass is achieved, root lifespans may differ from those that will exist after the stand has adjusted to the improved N availability. The finding by Majdi and Kangas (1997) that root lifespans were shorter for *P. abies* that received fertilizer N additions (100 kg N ha^{-1} year^{-1}) may represent such a transient response. Would natural stands of *P. abies* growing on sites of differing nutrient availability also have shorter root lifespans where N availability was greater? Would low, uniform rates of N addition of 10–20 kg N ha^{-1} year^{-1} produce the same results? The answers to such questions are important if we are to be confident in predictions of how current levels of atmospheric N deposition might alter belowground forest C allocation.

For sugar maple-dominated northern hardwood forests, we have found that root lifespan is greater at sites where N availability is higher. This relationship may also hold true within other forest types, provided that the stands were mature forests, with root biomass that was relatively steady over time and in equilibrium with N availability. Heavily fertilized forests or young, fast-growing forests in the early, exploitative stages of stand development might behave quite differently. To understand such effects and to assess the possibility that the effects of N availability on root longevity across species or forest types might differ from those within species (Fig. 6), additional direct observational experiments of root longevity need to be made. Such experiments should include both studies within forest types along natural N availability gradients, and studies across forest types adapted to sites of differing N availability. Coupling these experiments with measurements of root respiration would allow assessment of the roles root C cost and C-sink strength play in determining root lifespan across and within forest types. Experiments in which N availability is artificially altered could also prove useful. Ideally, some of these would be conducted in stands that had received low to moderate N additions continuously for many years, thereby avoiding the potential confounding influence on root longevity that could result from changes in root biomass following heavy N additions. Studying root longevity in small fertilized patches within the root system (*sensu* Pregitzer et al. 1993) could provide an additional means of avoiding or assessing this potential problem.

It is possible that no single theory can explain the effects of N availability on root longevity across all species. Trees such as aspen and sugar maple differ greatly in their aboveground strategies for resource acquisition, so one must question whether it is reasonable to expect them to respond similarly belowground. In this study, sugar maple roots lived longer at sites where N availability was greater. This is consistent with a cost-benefit approach for determining root lifespan (Eissenstat 1992; Eissenstat and Yanai 1997), in which roots are maintained longer in more fertile soils that can supply the roots with nutrients over a longer period of time. We have also measured greater root respiration rates and N concentrations for sugar maple at sites where N availability is higher. We propose that greater metabolic activity for roots in nitrogen-rich soil leads to greater carbohydrate allocation to those roots, and that a reduction in root C sink strength when local nutrients are depleted may provide a mechanism through which root lifespan is regulated in these forests.

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