

Nitrogen Controls on Fine Root Substrate Quality in Temperate Forest Ecosystems

Joseph J. Hendricks,^{1*} John D. Aber,¹ Knute J. Nadelhoffer,²
and Richard D. Hallett¹

¹Complex Systems Research Center, Institute for the Study of Earth, Ocean, and Space, Morse Hall, University of New Hampshire, Durham, New Hampshire 03824; ²The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA

ABSTRACT

Nitrogen controls on fine root substrate quality (that is, nitrogen and carbon-fraction concentrations) were assessed using nitrogen availability gradients in the Harvard Forest chronic nitrogen addition plots, University of Wisconsin Arboretum, Blackhawk Island, Wisconsin, and New England spruce-fir transect. The 27 study sites encompassed within these four areas collectively represented a wide range of nitrogen availability (both quantity and form), soil types, species composition, aboveground net primary production, and climatic regimes. Changes in fine root substrate quality among sites were most frequently and strongly correlated with nitrate availability. For the combined data set, fine root nitrogen concentration increased (adjusted $R^2 = 0.46$, $P < 0.0001$) with increasing site nitrate availability. Fine root “extractive” carbon-fraction concentrations decreased (adjusted $R^2 = 0.32$, $P < 0.0002$), “acid-soluble” compounds increased (adjusted $R^2 = 0.35$, $P < 0.0001$), and the “acid-insoluble” carbon fraction remained relatively high and stable (combined mean of $48.7 \pm 3.1\%$ for all sites) with increasing nitrate avail-

ability. Consequently, the ratio of acid-insoluble C–total N decreased (adjusted $R^2 = 0.40$, $P < 0.0001$) along gradients of increasing nitrate availability. The coefficients of determination for significant linear regressions between site nitrate availability and fine root nitrogen and carbon-fraction concentrations were generally higher for sites within each of the four study areas. Within individual study sites, tissue substrate quality varied between roots in different soil horizons and between roots of different size classes. However, the temporal variation of fine root substrate quality indices within specific horizons was relatively low. The results of this study indicate that fine root substrate quality increases with increasing nitrogen availability and thus supports the substrate quality component of a hypothesized conceptual model of nitrogen controls on fine root dynamics that maintains that fine root production, mortality, substrate quality, and decomposition increase with nitrogen availability in forest ecosystems in a manner that is analogous to foliage.

Key words: fine roots; substrate quality; nitrogen; carbon fractions; temperate forest ecosystems.

INTRODUCTION

Nitrogen has long been recognized as a limiting resource to carbon and nutrient cycling dynamics in

most boreal, temperate, and some tropical forest ecosystems (Chapin and others 1986; Field and Mooney 1986). However, despite substantial research efforts, the patterns and mechanisms of nitrogen control on carbon and nutrient cycles at the ecosystem scale remain unclear. Whereas a generalized theory of nitrogen controls on foliage dynamics has been established (Mooney and Gulmon 1982; Field and Mooney 1986; Reich and others 1997), hypotheses of nitrogen controls on

Received 16 February 1999; accepted 4 August 1999.

Corresponding author's current address: Department of Biology, State University of West Georgia, Carrollton, Georgia 30118, USA

R.D. Hallett's current address: Northeast Research Station, USDA Forest Service, Durham, New Hampshire 03824, USA.

Corresponding author's e-mail: jhendric@westga.edu

important belowground processes, such as fine root dynamics, have not been substantiated (Schoettle and Fahey 1994; Eissenstat and Yanai 1997; Zak and Pregitzer 1998). To gain a more comprehensive and integrated understanding of forest ecosystem structure and function, it is critical to assess the effects of nitrogen availability on fine root processes and, in turn, evaluate the relationships between above- and belowground dynamics.

The theory of nitrogen controls on foliage dynamics has served as a model for assessing fine root dynamics (Vogt and others 1991; Hendricks and others 1993; Schoettle and Fahey 1994; Eissenstat and Yanai 1997). This theory maintains that as nitrogen availability increases, canopy net photosynthesis also increases via higher photosynthetic rates per unit leaf area and/or greater leaf area production (Field and Mooney 1986; Chapin and others 1987; Evans 1989; Reich and others 1991, 1997). As a result, leaf tissues achieve a net positive carbon balance sooner and, for evergreens, have shorter foliage retention times (Reich and others 1991; Schoettle and Fahey 1994). In addition, as nitrogen availability increases, leaves have lower concentrations of defense compounds, such as lignin, astringent phenolics, and terpenes, which, coupled with reduced nutrient retranslocation efficiencies during senescence, results in the deposition of more readily decomposable leaf litter (Mooney and Gulmon 1982; Coley 1988; McNulty and others 1991). The more rapid decomposition and nutrient mineralization of this leaf litter increases further the nitrogen availability of the site, thereby completing a positive feedback for this system.

In a recent review and synthesis, we formulated the hypothesis that fine root production (that is, absolute production rates; the relative allocation of carbon to fine root production is hypothesized to remain constant), mortality, substrate quality, and decomposition increase with nitrogen availability in temperate forest ecosystems in a way that is analogous to foliage (Hendricks and others 1993). We have assessed the effects of nitrogen availability on fine root production and mortality in previous studies (Aber and others 1985; Nadelhoffer and others 1985; Raich and Nadelhoffer 1989; Nadelhoffer and Raich 1992; Hendricks and others 1997). The objective of this study was to assess nitrogen controls on fine root substrate quality defined here as tissue chemical characteristics, such as nutrient concentrations, as well as the form and concentration of carbon compounds that influence decomposition rates (Berg 1986; Lohmus and Ivask 1995).

Fine root decomposition studies that measured both root substrate quality and mass loss rates have

indicated that the initial mass loss, attributed to the removal of "extractive" (that is, more readily decomposable carbon compounds consisting of nonpolar constituents, such as fats, oils, and waxes, and polar constituents, such as nonstructural carbohydrates and polyphenols) and "acid-soluble" (that is, moderately decomposable carbon compounds consisting primarily of cellulose and hemicellulose) carbon fractions, is strongly and positively correlated with tissue nitrogen concentration (Herman and others 1977; Berg 1984; Berg and others 1987; McLaugherty and Berg 1987; Grimm 1988; Aber and others 1990; Lohmus and Ivask 1995). However, the accelerating effect of nitrogen on tissue mass loss decreases with the depletion of extractive and acid-soluble carbon components, and the residual "acid-insoluble" (that is, highly recalcitrant carbon compounds consisting of lignin and other highly reduced compounds, such as suberin, cutin, and tannin protein complexes) carbon fraction becomes a stronger regulator of decomposition. Consequently, the initial ratio of acid-insoluble carbon to nitrogen concentration (acid-insoluble C-total N) has proven to be an integrated index of fine root substrate quality, which is strongly and negatively correlated with mass loss rates (Herman and others 1977; Berg 1984; Berg and others 1987; Grimm 1988; Larsson and Steen 1988; Aber and others 1990; Lohmus and Ivask 1995).

The effects of nitrogen availability on fine root substrate quality have received little research attention in forest ecosystems (Muller and others 1989; Stump and Binkley 1993). Whereas previous studies have revealed that fine root nitrogen concentration is positively correlated with nitrogen availability (Margolis and Waring 1986; Friend and others 1990; Yin and Perry 1991), the effects of nitrogen on fine root carbon-fraction concentrations are poorly understood. To gain an improved understanding of nitrogen controls on fine root substrate quality and potential decomposition dynamics, we assessed fine root nitrogen and carbon-fraction concentrations along nitrogen availability gradients within and among cold-temperate coniferous and deciduous forest ecosystems. We hypothesized based on our proposed conceptual model of fine root-nitrogen interactions that fine root: (a) nitrogen concentrations would increase; (b) carbon-fraction concentrations would vary, and, in particular, acid-insoluble carbon concentrations would decrease; and (c) consequently, acid-insoluble C-total N ratios also would decrease across gradients of increasing nitrogen availability.

STUDY AREAS AND SITES

Nitrogen controls on fine root substrate quality were assessed using nitrogen availability gradients in four study areas: Harvard Forest in Petersham, MA, the University of Wisconsin Arboretum near Madison, WI, Blackhawk Island located in the Wisconsin River near Wisconsin Dells, WI, and the New England transect, which extended from western New York to the coast of Maine. The nitrogen gradients within these four areas varied widely in form (that is, natural, experimentally manipulated via fertilization, and induced via atmospheric N deposition) and spatial scale (ecosystem to region). The 27 study sites encompassed within these four areas collectively represent a wide range in nitrogen availability (both quantity and mineral form), soil types, species composition (coniferous and deciduous), aboveground net primary production, and climatic regimens for cold-temperate forest ecosystems. The specific site names follow the nomenclature used in previously published studies and generally were based on the most dominant tree species in the site.

The Harvard Forest chronic nitrogen addition plots were located in a 2.3-ha red pine (*Pinus resinosa*) plantation established in 1926 and an adjacent 2.3-ha mixed-hardwood forest with a mixed land-use history including intensive agriculture and burning (Foster 1992). In 1988, three nitrogen treatment plots (control, low N, and high N, each measuring 30 m × 30 m) were established in each forest. The control, low N, and high N plots have received 0, 50, and 150 kg N ha⁻¹y⁻¹, respectively, via six equal applications of NH₄NO₃ solution during the growing season each year. Fine root samples for this study were collected during the fourth year of nitrogen application. See Magill and others (1997) for additional information concerning the vegetative composition and soils of the Harvard Forest sites.

The University of Wisconsin Arboretum contains an assemblage of natural stands and plantations that are representative of the important forest ecosystems of the region (Sachse 1974). Fine root samples were collected from four coniferous (white pine, red pine, mixed pine, and white spruce) and five deciduous (black oak, red oak, white oak, sugar maple, and paper birch) stands that were located within 2 km of one another. The three oak stands were mature (that is, dominants were greater than 125 years old) forests, whereas the remaining six stands were established in the 1940s on land previously used for agricultural purposes. See Nadelhoffer and others (1983, 1985) for additional information regarding

the vegetative composition and soils of the arboretum sites.

Blackhawk Island supports a wide variety of soil types that form a broad edaphic moisture and nutrient availability gradient. We sampled eight stands (dominants were greater than 100 years old) along the gradient; three coniferous forests (red pine, white pine, and hemlock) and five deciduous forests (white oak, red oak 1, red oak 3, sugar maple 1, and sugar maple 2) sites. See Pastor and others (1982, 1984) for additional information concerning the vegetation and soils of the Blackhawk Island sites.

The New England transect was comprised of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) stands along a regional nitrogen deposition and availability gradient in the northeastern United States (McNulty and others 1991). Fine root samples were collected in four sites along this gradient: Whiteface Mountain, NY, Mt. Mansfield, VT, Mt. Washington, NH, and Mt. Desert Island, ME. In the three western locations, sample plots were established on steeply sloping terrain at approximately 1000-m elevation above sea level in spruce-fir pockets surrounded by American mountain-ash (*Sorbus americana*), paper birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), and striped maple (*Acer pensylvanicum*). In the coastal Maine location, plots were located on level terrain at 15-m elevation in spruce-fir stands separated by yellow birch, striped maple, and Atlantic white cedar (*Chamaecyparis thyoides*). The dominant soil type in each site was a Dysic Lithic Borofolist (Ricker series).

METHODS

Nitrogen Availability Assessments

Net nitrogen mineralization and nitrification were assessed in each site by using the *in situ* buried bag technique (Eno 1960). The New England transect sites were sampled in 1990 by using a series of four monthly incubations during the growing season (May through August). On each sample date, 18 cores (5.4 cm diameter) of the organic soil horizon were collected in each site. Six of the cores were placed in a cooler (5–7°C) for transport to the lab. The remaining 12 cores were placed in polyethylene bags (0.1 mm thickness) and returned intact to their original locations for an approximate monthly incubation period. At the end of the incubation, the 12 cores were retrieved and taken to the lab for processing.

In the lab, each core was sieved to remove mineral particles (greater than or equal to 1 mm), twigs, and roots. Ammonium and nitrate were

extracted from a 10-g (wet weight) subsample in 100 mL of 2 N KCl for 24 h, and the filtered extract was analyzed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ on a Technicon TRAACS 800 autoanalyzer (Tarrytown, NY, USA). A 10-g subsample was dried at 105°C for 48 h to determine soil moisture content. Net nitrogen mineralization was calculated as $\text{NH}_4\text{-N}$ plus $\text{NO}_3\text{-N}$ in the incubated samples minus initial values. Net nitrification was calculated as the difference between initial and final $\text{NO}_3\text{-N}$ values. The bulk density of the organic horizon in each site was determined (5.4-cm-diameter cores dried at 105°C for 48 h) to express mineralization and nitrification values on an area basis. In addition, the contribution of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in atmospheric deposition to nitrogen availability in each location was estimated using a model developed by Ollinger and others (1993).

Annual nitrogen mineralization and nitrification were measured in the other sites in a similar manner as part of associated studies (see Table 1). Fine root collections were conducted during the same year of the nitrogen mineralization assessments, except for the Blackhawk Island sites, which were sampled 10 years after nitrogen availability assessments.

Fine Root Collections

Harvard Forest. Fine root sampling in the Harvard Forest chronic nitrogen addition plots was conducted six times at approximately monthly intervals from mid-April to October 1991. Samples were collected from one 5 × 5-m subplot within the control, low N, and high N treatments of the red pine and mixed-hardwood stands. The basic sample unit was a soil monolith (10 cm wide × 20 cm length, and extending to a mineral soil depth of 10 cm), which reduced plot disturbance. Five monoliths were collected from each treatment plot per sample period in the red pine stand, whereas eight monoliths per sample period were collected in the mixed-hardwood plots due to a larger and more variable root standing biomass.

Individual monoliths were removed from randomly selected 0.71 × 0.71-m cells within each subplot. A 10 × 20-cm wooden template and metal skewer (to probe around the perimeter) were used to locate an area within the cell that was not obstructed by large coarse roots (that is, those greater than 3 cm in diameter) or rocks. Once located, the monolith was excavated (with special effort not to sever transverse coarse roots), bagged, and immediately placed in a cooler for transport. The Harvard Forest monoliths were not divided into organic and mineral horizons before root sorting

because the availability of nitrogen in each horizon could not be clearly distinguished due to the regular large additions of nitrogen in solution.

University of Wisconsin Arboretum. The Arboretum sites were sampled on 25 April, 7 July, 15 September, and 5 December 1981 and 24 April 1982. Collections one through four were conducted in six sites (black oak, red oak, white oak, sugar maple, white pine, and red pine), and the final collection was made in all nine locations. During each collection, seven cores (6 cm diameter) of the 0–20 cm soil horizon (which also corresponds with the nitrogen availability assessment format and reflects the lack of a persistent forest floor on these mull soils) were removed in each site. Root samples from seven cores were later composited to yield one sample per site for each collection date.

Blackhawk Island. The Blackhawk Island sites were sampled 7–10 October 1991. In each location, a plot center point was randomly selected in the vicinity of the nitrogen availability assessment plots. Four 12-m transects were established in the cardinal directions from the center point. Soil cores (5.5 cm diameter) were collected at the center point and at 2-m intervals along each transect to yield 25 cores per site. The division of cores by horizon followed the criteria used by Pastor and others (1984) for the nitrogen availability assessments. Individual cores then were composited to yield five samples per horizon for each site.

New England Transect. Fine root samples were collected during October 1991. In each site, a plot center was established randomly in the vicinity of the nitrogen availability assessment plots. The 15 dominant or codominant individuals of red spruce and balsam fir closest to this point were hand-sampled by excavating three primary structural roots and associated major laterals (that is, those greater than or equal to 5 mm in diameter) to at least the crown radius. Soil mats encompassing minor woody lateral and attached fine roots were bagged and placed in a cooler for transport to the lab. Roots from individual trees were composited to yield five samples per species for each site.

Fine Root Processing and Analyses

All samples were stored at 2°C for no more than 48 h before sorting fine root tissues. Harvard Forest, Blackhawk Island, and New England transect samples were hand-sorted to obtain fine root tissues that were defined as living, primary ramifications including mycorrhizal tips that did not have external suberization or bark development (generally corresponding to diameters of less than or equal to 0.5 mm and less than or equal to 1 mm for

Table 1. Nitrogen Availability Indices and Corresponding Fine Root Nitrogen and Carbon-Fraction Concentrations for the 27 Study Sites

Site	Horizon (cm)	Mineralization (kg N ha ⁻¹ y ⁻¹)	Nitrification (kg N ha ⁻¹ y ⁻¹)	Nitrogen (%)	Extractives (%)	Acid Solubles (%)	Acid Insolubles (%)	Acid Insoluble C-total N
Harvard Forest ^a								
Red pine								
Control	Organic-10	75	22.3	1.39 (0.24)	21.8 (1.9)	30.9 (1.9)	47.3 (1.9)	35.2 (6.4)
Low N	Organic-10	160.1	66	1.91 (0.27)	22.2 (1.4)	30.6 (2.1)	47.2 (2.2)	25.2 (3.1)
High N	Organic-10	255.4	128.7	2.32 (0.23)	21.6 (1.4)	30.9 (2.1)	47.6 (1.9)	20.8 (2.1)
Hardwood								
Control	Organic-10	74.9	1.8	1.21 (0.14)	19.9 (2.7)	30.1 (2.7)	50.0 (2.3)	41.9 (5.4)
Low N	Organic-10	105.3	27	1.34 (0.19)	18.6 (2.0)	29.1 (2.3)	52.3 (2.4)	39.7 (6.3)
High N	Organic-10	300	76.8	1.37 (0.13)	15.9 (2.7)	31.4 (3.1)	50.9 (2.1)	37.3 (4.3)
U.W. Arboretum ^b								
Red pine (RP)	0-20	39	20	1.23 (0.10)	13.1 (2.1)	39.9 (1.4)	47.0 (2.7)	38.4 (2.1)
White spruce (WS)	0-20	58	52	1.92	12.9	40.2	47.0	24.5
Mixed pine (MP)	0-20	61	53	1.83	11.8	35.5	52.7	28.9
White pine (WP)	0-20	81	58	2.00 (0.22)	13.9 (2.0)	39.8 (1.6)	45.8 (2.5)	23.2 (2.2)
Paper birch (PB)	0-20	84	36	1.66	11.3	45.9	42.8	25.8
Sugar maple (SM)	0-20	94	94	1.43 (0.15)	10.5 (1.4)	40.8 (3.3)	49.2 (2.9)	34.2 (4.1)
White oak (WO)	0-20	99	99	1.89 (0.25)	11.3 (1.0)	42.5 (2.2)	46.3 (2.5)	24.9 (3.3)
Red oak (RO)	0-20	125	125	1.59 (0.34)	13.7 (2.0)	43.9 (2.1)	43.2 (1.9)	28.2 (6.0)
Black oak (BO)	0-20	135	135	1.92 (0.25)	9.8 (1.3)	44.1 (2.2)	45.9 (1.3)	24.2 (3.2)
Blackhawk Island ^c								
Hemlock (HEM)	0-4.7	29	6	1.66 (0.11)	15.9 (1.7)	32.4 (1.6)	51.7 (2.2)	31.3 (1.4)
Red pine (RP)	0-10	26	22	1.34 (0.09)	20.8 (1.7)	35.1 (1.4)	44.2 (1.0)	33.1 (2.1)
White pine (WP)	0-2.7	39	19	1.57 (0.10)	19.8 (0.9)	34.8 (0.4)	45.5 (0.8)	29.1 (1.7)
White oak (WO)	0-3.2	67	3	1.10 (0.13)	17.1 (1.0)	31.0 (1.6)	51.9 (1.3)	47.8 (7.6)
	3.2-13.2	25	1	1.09 (0.23)	19.9 (0.3)	34.7 (0.2)	45.3 (0.5)	42.7 (9.6)
Red oak 1 (RO1)	0-2.7	53	19	1.44 (0.08)	16.2 (1.6)	31.7 (1.0)	52.1 (2.5)	36.4 (2.8)
	2.7-12.7	33	1	0.89 (0.03)	20.1 (1.6)	31.4 (0.3)	48.5 (1.3)	54.4 (3.3)
Red oak 3 (RO3)	0-3.4	60	60	1.69 (0.04)	17.2 (0.9)	33.5 (1.5)	49.3 (1.8)	29.2 (0.8)
	3.4-13.4	34	34	1.29 (0.00)	17.9 (2.1)	35.5 (0.3)	46.6 (1.8)	36.0 (1.4)
Sugar maple 1 (SM1)	0-2.8	78	78	2.34 (0.13)	13.8 (1.4)	39.2 (1.4)	47.0 (1.0)	20.2 (1.2)
	2.8-12.8	28	28	1.78 (0.08)	15.1 (0.8)	38.1 (0.8)	46.8 (1.8)	26.3 (1.6)
Sugar maple 2 (SM2)	0-3.3	84	84	1.70 (0.05)	12.0 (1.1)	36.6 (0.5)	51.4 (1.0)	30.4 (1.3)
	3.3-13.3	49	49	1.66 (0.59)	14.2 (0.8)	34.5 (0.1)	51.3 (0.6)	32.9 (1.3)
New England transect ^d								
Whiteface Mtn., NY								
Balsam fir	0-Bedrock	30.6	9.2	1.50 (0.09)	21.2 (1.8)	29.8 (1.5)	49.0 (1.2)	32.8 (2.5)
Red spruce	0-Bedrock	30.6	9.2	1.43 (0.10)	22.9 (0.5)	28.3 (0.7)	48.8 (0.3)	34.3 (2.4)
Mt. Mansfield, VT								
Balsam fir	0-Bedrock	64.8	9.3	1.65 (0.06)	20.0 (1.5)	28.0 (0.8)	52.0 (2.0)	31.6 (2.1)
Red spruce	0-Bedrock	64.8	9.3	1.47 (0.15)	23.3 (0.8)	27.6 (0.6)	49.0 (0.9)	31.9 (4.7)
Mt. Washington, NH								
Balsam fir	0-Bedrock	54.4	5.8	1.41 (0.09)	17.9 (0.6)	29.4 (0.9)	52.7 (1.3)	37.4 (2.6)
Red spruce	0-Bedrock	54.4	5.8	1.19 (0.05)	21.3 (0.8)	26.8 (0.9)	51.9 (0.5)	43.5 (2.1)
Mt. Desert Island, ME								
Balsam fir	0-Bedrock	27.4	3.5	1.26 (0.06)	19.6 (0.8)	26.7 (1.0)	54.0 (1.0)	42.9 (2.5)
Red spruce	0-Bedrock	27.4	3.5	1.08 (0.04)	19.8 (1.5)	26.5 (0.8)	53.6 (1.0)	49.8 (2.6)

Harvard Forest and University of Wisconsin Arboretum data points represent the averages across sample dates due to low temporal variation (see Results and Discussion).

^aHarvard Forest nitrogen availability indices include the annual fertilizer additions. See Magill and others (1997) for details regarding nitrogen availability assessments and results.

^bSee Nadelhoffer and others (1985) for details regarding nitrogen availability assessments and results.

^cSee Pastor and others (1984) for details regarding nitrogen availability assessments and results.

^dNew England transect nitrogen availability values include estimates of total nitrogen deposition obtained using the model developed by Ollinger and others (1993).

deciduous and coniferous species, respectively; McClaugherty and others 1982; Persson 1990). In contrast to these cores that contained organic horizons, the University of Wisconsin Arboretum cores were collected from mull type soils with no persistent organic horizon and, consequently, processed by gently washing soil particles through a 0.5-mm mesh screen (Nadelhoffer and others 1985). Residual live roots then were sorted by size as fine (less than 0.5 mm diameter) and small (0.5–3.0 mm diameter) tissues (Nadelhoffer and others 1985). Root vitality for all samples was assessed visually and manually based on color, elasticity, and resiliency. Sorted root samples then were washed with tap water for approximately 15–20 s by using a 18-mesh sieve, paper towel dried to remove excess moisture, and stored in a freezer for chemical composition assessments.

Before chemical composition analyses, each sample was oven-dried (70°C) to a constant mass, weighed, ground using a Wig-L-Bug Model 6 Amalgamator (Reflex Analytical Corporation, Ridge-wood, NJ, USA), and subsampled for ash determination (500°C for 5 h) to express all indices on an ash-free, dry mass basis (Jones 1984). Root carbon-fraction concentrations including extractives (removed using a two-stage extraction in dichloromethane and boiling water, respectively), acid-soluble structural components (removed using a two-stage digestion in 72% and 2.5% sulfuric acid, respectively), and acid-insoluble structural components (the residual of the two-stage sulfuric acid digestion minus ash mass) were assessed using the forest products serial digestion technique (Ryan and others 1990). Root nitrogen concentrations were determined with a Perkin-Elmer (Norwalk, CT, USA) Model 240B CHN Analyzer for the Harvard Forest, Blackhawk Island, and New England transect samples, and a modified Kjeldahl digest followed by a colorimetric nitrogen analysis by using a Technicon TRAACS 800 autoanalyzer for the arboretum samples.

Statistical Analyses

Simple linear regressions were used to assess relationships between root substrate quality indices and site soil characteristics including nitrogen availability indices. Also, ANOVA techniques were used to determine if root chemistry differed significantly ($P < 0.05$) between soil horizons in the Blackhawk Island sites and between sample dates in the Harvard Forest sites (Statistix 1996). If differences existed, Tukey's HSD (Honest Significant Difference) multiple range test was performed to determine which means differed significantly ($P = 0.05$).

RESULTS AND DISCUSSION

The negative correlation between fine root acid-insoluble C–total N and tissue decomposition rates primarily have been assessed using the buried litter-bag technique (Berg 1986; Dormaar and Willms 1993). Fine root acid-insoluble C–total N control on tissue mass loss rates in these studies may have been modified by the use of initially live roots or roots of variable developmental stages in the assessments, disturbance of the root rhizosphere before the decomposition assessments, and/or the impedance of root contact with the soil matrix during the assessments (McClaugherty and others 1982; Berg 1986; Fahey and others 1988; Vogt and others 1991; Fahey and Arthur 1994). However, whereas the actual rates may have been modified, it is assumed that the basic pattern of root acid-insoluble C–total N control on root mass loss observed in these studies is representative of naturally senescent and decomposing roots and, as such, allow for comparisons among species and ecosystems (Berg 1984; Dormaar and Willms 1993).

Controls on Fine Root Substrate Quality

With the notable exception of the acid-insoluble component, fine root nitrogen and carbon-fraction concentrations varied across the nitrogen availability gradients in the Harvard Forest, University of Wisconsin Arboretum, Blackhawk Island, and New England transect study areas (Table 1). The change in fine root substrate quality indices among sites frequently were correlated with nitrogen availability indices, including annual rates of mineralization and nitrification, as well as nitrogen deposition indices for the New England transect sites. However, annual nitrification rate was the nitrogen availability index that yielded the greatest number of significant linear relationships with fine root substrate quality indices, and the highest coefficients of determination (R^2) for these relationships (Figure 1). Furthermore, nitrate availability proved to be the most strongly correlated variable with fine root substrate quality indices when compared with a broader suite of soil properties (including bulk density, texture, pH, and base cation content) by using the Blackhawk Island data set (results not shown). It is important to note that the higher coefficients of determination for the relationships between fine root substrate quality and site nitrate availability (as opposed to other nitrogen availability indices) may be an artifact of the buried bag technique, which excludes roots and thus provides more substrate (NH_4) for nitrification (Eno 1960). However, it is interesting that these results are

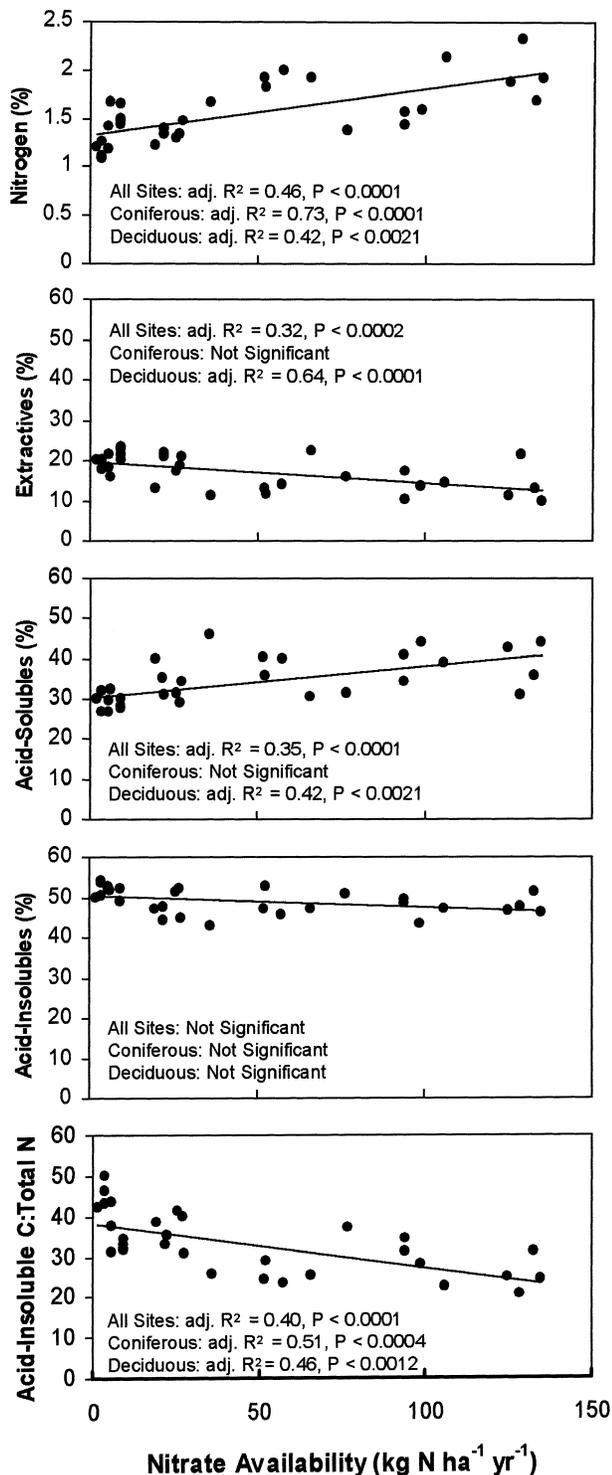


Figure 1. Fine root nitrogen and carbon-fraction concentrations versus site nitrate availability for the combined data set. Harvard Forest and University of Wisconsin Arboretum data points represent the averages across sample dates due to low temporal variation (see Results and Discussion). The regression line in each panel was derived using data from all sites.

consistent with the findings of Aber and others (1985) that indicated that fine root standing biomass, production, and mortality rates were most strongly correlated with nitrate availability in the same Harvard Forest (control plots only), University of Wisconsin, and Blackhawk Island ecosystems used in this study. Collectively, these results suggest that the form of available nitrogen may be more important than the total amount mineralized in regulating fine root dynamics.

Substrate Quality Patterns among Ecosystems

Linear regression analyses using annual nitrification rate as the independent variable for the combined data set (that is, including all sites within the four study areas) revealed that fine root nitrogen concentration increased with nitrate availability (Figure 1), consistent with the findings of other studies (Margolis and Waring 1986; Muller and others 1989; Friend and others 1990; Yin and Perry 1991). Fine root extractive concentrations decreased whereas the acid-soluble fraction increased with increasing nitrate availability (Figure 1).

In contrast, the acid-insoluble fraction, which accounted for almost one-half of the fine root biomass (combined mean of $48.7 \pm 3.1\%$), remained relatively stable among forest ecosystems exhibiting a wide range of nitrate availability ($1\text{--}135 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), soil types, species composition, aboveground net primary production, and climate conditions (Figure 1). Muller and others (1989) also reported that fine root acid-insoluble concentrations were high and relatively stable (mean value of 49.5% with a coefficient of variation of 12%) among beech, mixed mesophytic, hickory, and oak forest types in Kentucky that exhibited nitrogen mineralization potentials ranging from 25 to $115 \text{ mg N kg}^{-1} \text{ soil}$ after a 7-day anaerobic incubation at 40°C . As a result of the relatively stable fine root acid-insoluble fraction and increasing nitrogen concentrations, root acid-insoluble C–total N decreased with increasing nitrogen availability among ecosystems in this and the Muller and others (1989) study (Figure 1).

The coefficients of determination for the linear relationships between nitrate availability and fine root substrate quality indices among sites were generally higher for individual study areas. Fine root nitrogen concentration was the substrate quality index that was most frequently and strongly correlated with nitrate availability. The relationship between root nitrogen and site nitrate availability was particularly strong for the New England Transect red spruce (adjusted $R^2 = 0.97$, $P < 0.0090$)

and University of Wisconsin Arboretum coniferous (adjusted $R^2 = 0.98$, $P < 0.0070$) data sets. Root nitrogen increased with nitrate availability along each of the other gradients as well, yet some of the relationships were not statistically significant due presumably to small sample sizes. In contrast, fine root acid-insoluble concentrations were rarely correlated with nitrate availability, or any other nitrogen availability index, among ecosystems. The relationship between fine root acid-insoluble concentration and nitrate availability was significant for only the New England transect red spruce and combined (that is, red spruce and balsam fir) data sets, and the slopes of the functions (-0.9 and -0.8 , respectively) were close to zero.

Substrate Quality Patterns within Ecosystems

Comparisons of fine roots between soil horizons revealed that root substrate quality also changed significantly with nitrogen availability within ecosystems. Fine root nitrogen concentrations in the Blackhawk Island ecosystems were higher in the humus or A1 horizons (statistically significant for all stands except white oak and sugar maple 2), which exhibited higher nitrogen mineralization and nitrification rates than corresponding subsurface horizons (Figure 2). This is consistent with the results of other assessments of root chemistry by soil horizons, as well as microsite enrichments in forest ecosystems and split-pot studies using forest species, which have indicated that the nitrogen of individual fine roots is derived primarily from the local rooting zone (Vogt and others 1987; Friend and others 1990; Gebauer and Schulze 1991; Hendricks and others 1997; Pregitzer and others 1998). In contrast, root carbon-fraction concentrations were relatively similar between soil horizons, although the differences were often statistically significant (Figure 2). As a result, fine root acid-insoluble C–total N ratios were generally lower in the surface soil horizons.

Whereas root substrate quality varied between horizons in the Blackhawk Island ecosystems, sequential collections in the Harvard Forest and University of Wisconsin ecosystems indicated that temporal variation in root substrate quality within a particular horizon is small (Figure 3). Fine root nitrogen concentrations did not differ significantly among collection dates in the red pine and mixed-hardwood control, low N, and high N sites in the Harvard Forest consistent with the findings of other studies conducted in forest ecosystems (Nambiar 1987; Goldfarb and others 1990; Yin and others 1991). Some of the fine root carbon fractions did differ significantly between sample dates, but the

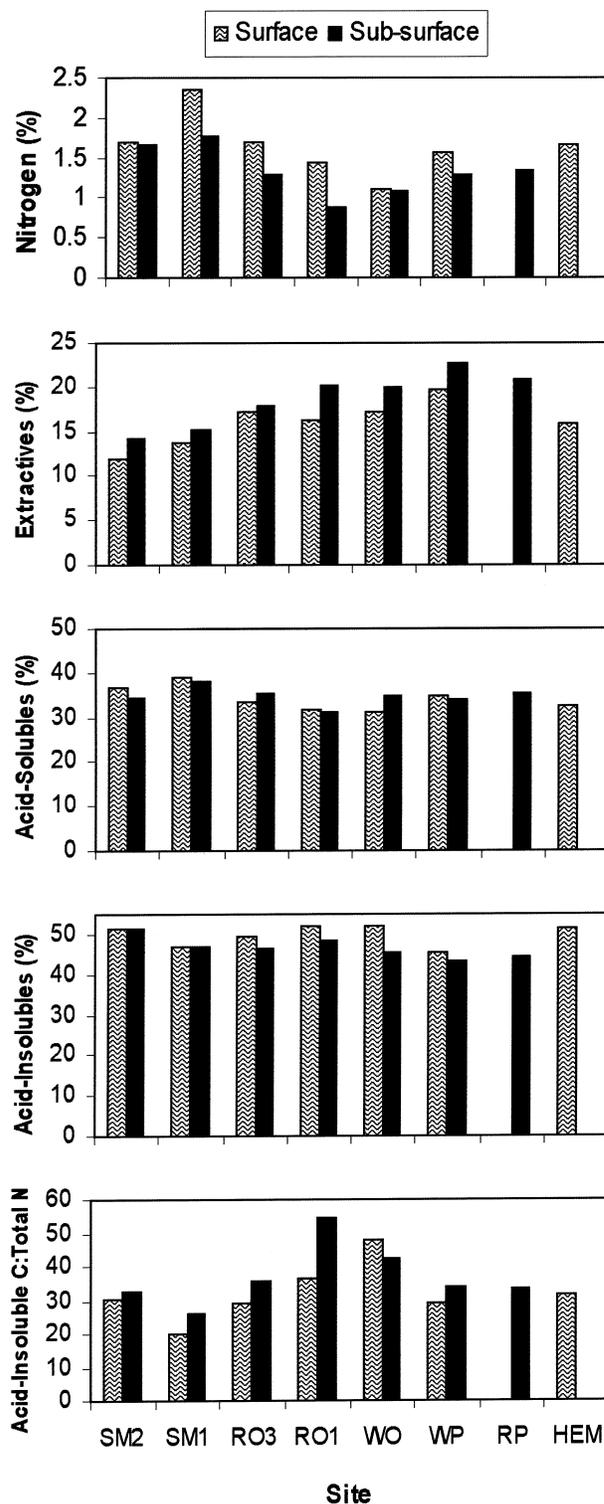


Figure 2. Fine root nitrogen and carbon-fraction concentrations by soil horizon for the Blackhawk Island sites. See Table 1 for site abbreviation codes.

changes in concentration were relatively small. For example, fine root acid-insoluble concentration decreased significantly during the growing season in the control and high N treatments of both the red

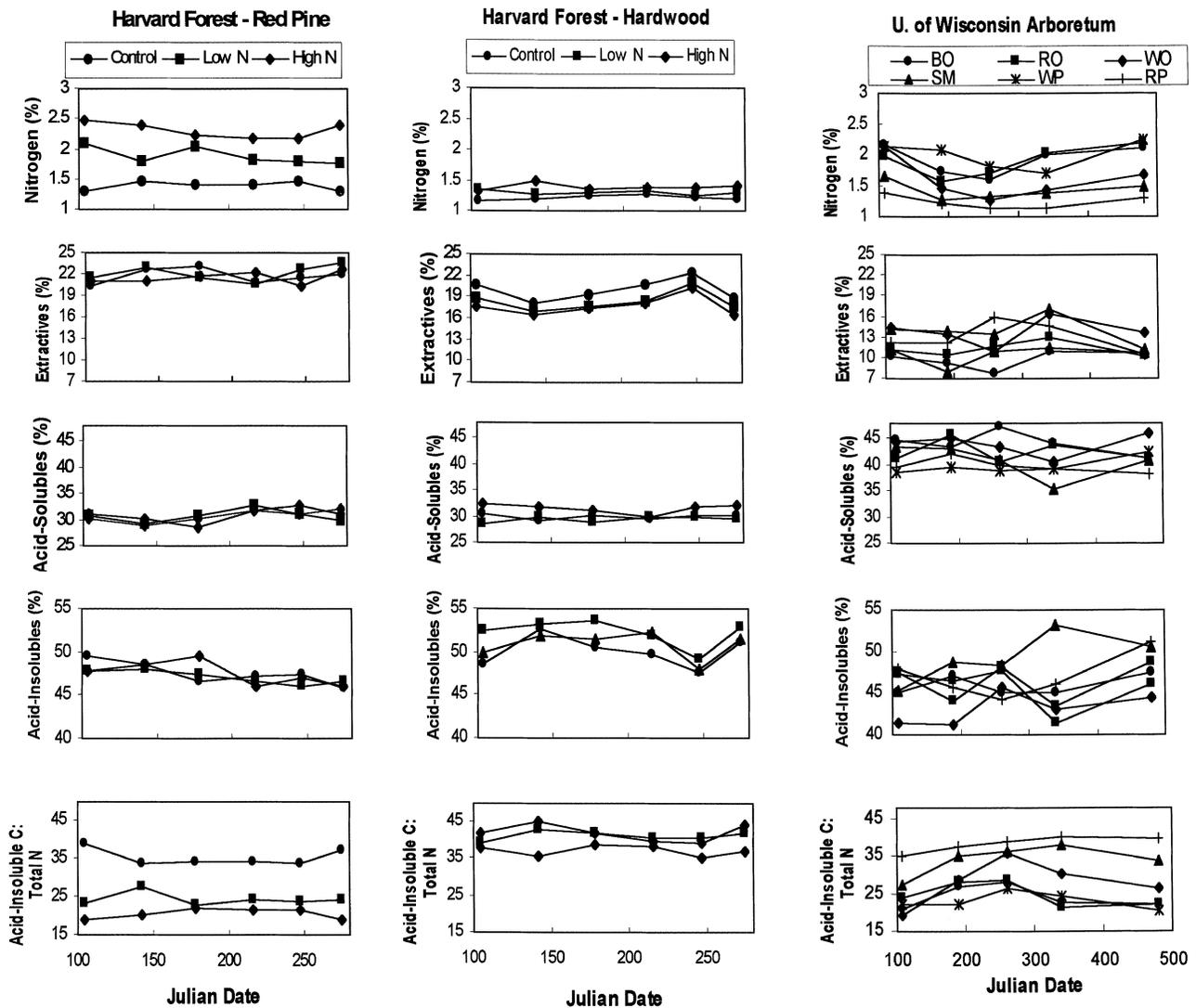


Figure 3. Fine root nitrogen and carbon-fraction concentration temporal patterns for the Harvard Forest and University of Wisconsin Arboretum sites.

pine and mixed-hardwood forests. However, the differences between the seasonal maximum and minimum values never exceeded 10% of the maximum value. These temporal patterns were corroborated by the trends observed for the six University of Wisconsin Arboretum ecosystems. The statistical significance of the arboretum patterns could not be assessed because roots were composited to one sample per date for each ecosystem. The relatively low temporal variation in fine root substrate quality within ecosystems suggests that the differences in fine root collection dates for the 27 sites used in this study had little influence on the relationships between nitrate availability and fine root substrate quality indices among ecosystems.

A comparison of fine (less than 0.5 mm diameter) and small (0.5–3.0 mm diameter) roots collected at the same place and time in the University of Wisconsin

Arboretum ecosystems indicated that root substrate quality varies by size class. Fine roots consistently had higher nitrogen and acid-insoluble concentrations and lower extractive and acid-soluble fractions compared with small roots (Figure 4). Although the statistical significance of the differences could not be assessed, the nitrogen and acid-insoluble fraction patterns are consistent with other reports (Helmisaari 1991; Vogt and others 1991; Yin and Perry 1991; Pregitzer and others 1998). Differences in root substrate quality between size classes may largely explain why the acid-insoluble concentrations reported here (combined mean of 48.7%) are at the high end of the reported range (16%–59%); most studies used larger fine root classification criteria than were used in this study (McClougherty and others 1982, 1984; Marshall 1986; Fahey and others 1988; Muller and

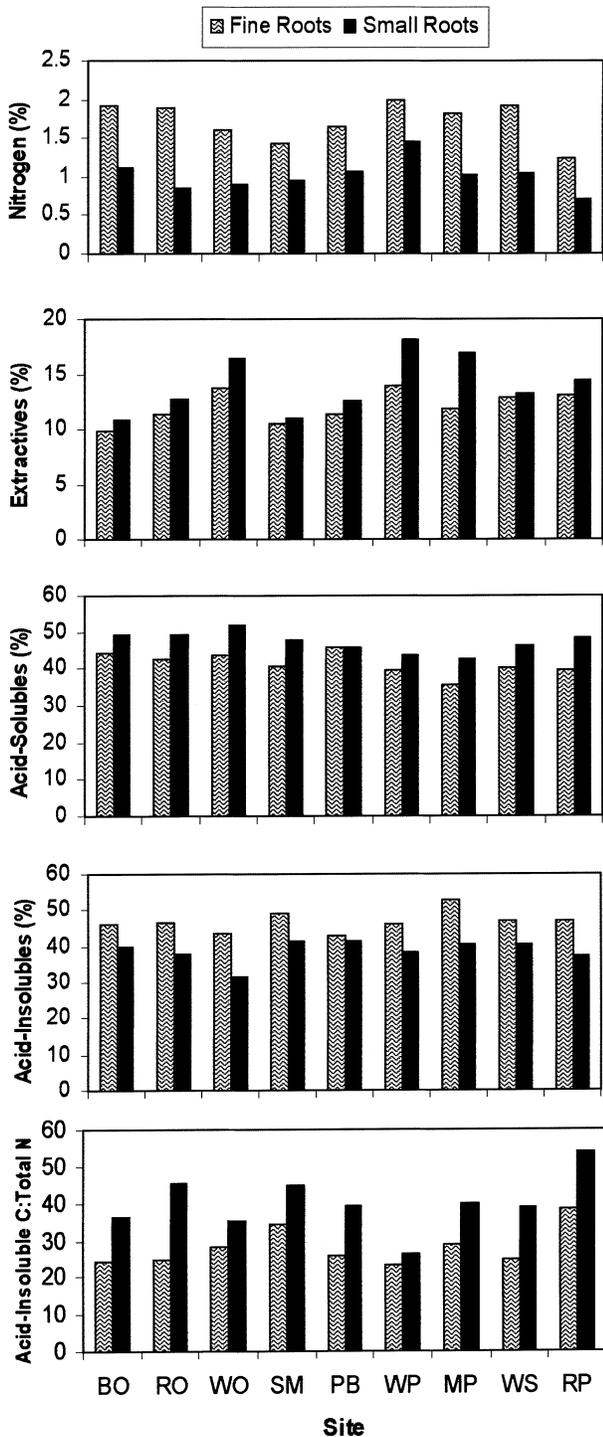


Figure 4. Comparison of fine (less than 0.5-mm diameter) and small (0.5–3.0 mm diameter) root nitrogen and carbon-fraction concentrations for the University of Wisconsin Arboretum sites. See Table 1 for site abbreviation codes.

others 1989; Vogt and others 1991; Stump and Binkley 1993). While there is not a standard size class or operational definition of a fine root, the classification criteria used in this study were based

on distinct morphological characteristics presumed to be associated with roots that function in water and nutrient uptake, do not increase in diameter via secondary cambial growth, and are relatively ephemeral (see Persson 1990; Vogt and others 1991). Other studies that used similar fine root classification criteria to those used in this study have reported comparable root acid-insoluble concentrations for coniferous and deciduous species (Muller and others 1989; Vogt and others 1991).

Evaluation of the Nitrogen–Fine Root Conceptual Model

As hypothesized, fine root acid-insoluble C–total N decreased across gradients of increasing nitrogen availability within and among a wide variety of cold-temperate coniferous and deciduous forest ecosystems. Whereas these results provide additional support for the substrate quality component of our model of nitrogen controls on fine root dynamics, the mechanism of fine root acid-insoluble C–total N change across nitrogen gradients differed from the hypothesized model. Although fine root nitrogen concentration was positively correlated with nitrogen availability consistent with the proposed model, root acid-insoluble concentrations did not decrease across nitrogen gradients as hypothesized. The stable pattern of fine root carbon allocation to acid-insoluble compounds, which are assumed to function as structural defense compounds, differs from the patterns demonstrated for nonstructural defense compounds, such as astringent phenolics, which decrease with increases in site nitrogen availability and fine root nitrogen concentration (Muller and others 1989).

The observed fine root acid-insoluble carbon fraction pattern also differs from foliage patterns of carbon allocation to acid-insoluble compounds, which is negatively correlated with site nitrogen availability (Mooney and Gulmon 1982; McNulty and others 1991; Scott and Binkley 1997). Scott and Binkley (1997) assembled data from forest ecosystems exhibiting a wide range in soil, vegetation, and climatic regimes and determined that net mineralization rates were negatively correlated with foliage acid-insoluble C–total N ($R^2 = 0.74, P < 0.01$) due primarily to decreases in foliage acid-insoluble carbon concentrations ($R^2 = 0.63, P < 0.01$); foliage nitrogen concentrations were not correlated with nitrogen mineralization among sites. The Scott and Binkley (1997) data set included the University of Wisconsin Arboretum and Blackhawk Island sites used in this study. Also, the negative correlation between nitrogen availability and foliage acid-insoluble C–total N is consistent with the findings

reported by McNulty and others (1991) for red spruce foliage across the New England transect. In addition to these assessments among sites, numerous site-specific studies have revealed significant negative relationships between available nitrogen and foliage acid-insoluble carbon fraction concentrations (Gower and Son 1992; Stump and Binkley 1993). However, despite the differences in the mechanism of change between fine root and foliage tissues, the acid-insoluble C–total N ratio of both tissue types decreases with increasing nitrogen availability.

A potential shortcoming of this study is that live roots were used for the assessment of tissue substrate quality whereas foliage studies generally have used freshly senescent tissues. The retranslocation of materials during senescence may change root litter acid-insoluble C–total N patterns across nitrogen availability gradients and, consequently, the positive correlation between fine root and foliage litter substrate quality. However, the root acid-insoluble fraction is comprised of highly recalcitrant, structurally bound compounds, which are unlikely to be transformed during senescence. Also, nitrogen retranslocation during root senescence generally is considered to be insignificant (Nambiar 1987; Dubach and Russelle 1994; but see Meier and others 1985; Goldfarb and others 1990). Whereas this assertion is more questionable and warrants further investigation, the occurrence of nitrogen retranslocation actually may magnify rather than reduce the differences in root acid-insoluble C–total N across nitrogen availability gradients if root retranslocation efficiencies increase in more infertile sites analogous to foliage. Thus, this suggests that fine root necromass acid-insoluble C–total N, and, consequently, potential decomposition rate will increase with increasing nitrogen availability in temperate forest ecosystems as occurs for foliage (Berg 1986; Melillo and others 1989; Stump and Binkley 1993).

Few studies have directly compared fine root and foliage decomposition within and among species in forest ecosystems (McClougherty and others 1984). However, Grimm (1988) conducted a fine root decomposition study, and White and others (1988) conducted a foliage decomposition study by using six common species in the same locations of early successional forests in the southern Appalachian Mountains of North Carolina, but the initiation date of the two studies differed by 1 year. Comparison of results revealed a positive correlation between fine root and foliage acid-insoluble C–total N ratios (adjusted $R^2 = 0.86$, $P < 0.0046$), a negative correlation between the initial acid-insoluble C–total N

and mass loss for both tissue types, and a strong positive correlation between the fine root and foliage decay constants among species (adjusted $R^2 = 0.93$, $P < 0.0014$). The positive correlation between fine root and foliage substrate quality and decomposition rates among species provides additional support for the substrate quality and decomposition components of our hypothesized model of nitrogen controls on fine root carbon and nutrient cycling dynamics (Hendricks and others 1993).

CONCLUSION

The results of this study indicate that fine root substrate quality increases with nitrogen availability and thus supports the substrate quality component of our hypothesized model of nitrogen controls on fine root dynamics in forest ecosystems. Before concluding, however, that fine root decomposition rates increase in more fertile sites analogous to foliage, additional questions regarding the processes regulating the transfer of roots to the soil organic matter pool must be addressed. Our conclusion is based on the assumption that fine root acid-insoluble C–total N is a primary regulator of root carbon and nutrient transfers to the soil organic matter pool as supported by the findings of root litterbag decomposition studies. This assumption should be substantiated by additional studies that more rigorously assess the patterns and controls of fine root herbivory, nutrient retranslocation during senescence, and root necromass disappearance via microbial decomposition and faunal consumption. In turn, this improved understanding of the rates and mechanisms controlling the fates of fine roots will facilitate a more comprehensive evaluation of the hypothesized conceptual model of nitrogen controls on fine root dynamics and provide valuable insight into the role of fine roots in the structure and function of forest ecosystems.

ACKNOWLEDGMENTS

We thank Joyce Andersen, Bill Berger, Kate Bolster, Rich Boone, Jessica Burton, John Canning, Mary Alice Cheney, Lionel Chute, Alice Cialella, Bill Currie, Diego Fernandez Fransisco de Velasco, David Dwyer, Jenn Ellis, Hansi Hals, Wendy Harris, Kim Jackowski, Thea Jaster, Jason Kaye, Bill Korohmas, Shawn Landry, Jill Listowich, Tim Longway, Alison Magill, Mary Martin, Steve McNulty, Jeff Meriam, Sarah Millham, Eric Miller, Jim Muckenhoupt, Steve Newman, Scott Ollinger, Lisa Peters-Forcier, Joyce Peterson, Precilla Petitti, Gloria Quigley, Amy Simoneau, Maggie Soulia, Karen Vellekamp, Mara Veverbrants, Lynn Waller, Susanna Walter, Wendy War-

ren, and Christina Wilson for help in collecting, processing, and analyzing samples. Drs. Kurt S. Pregitzer, Barrett N. Rock, Lawrence O. Safford, and C. Tattersall Smith, Jr. as well as anonymous reviewers provided incisive and helpful criticism on earlier versions of this article. Support for this project was provided by the National Aeronautics and Space Administration (graduate training grant) and the National Science Foundation (NSF-BSR-9009190, NSF-BSR-94408794, and the Harvard Forest Long-Term Ecological Research (LTER) grants).

REFERENCES

- Aber JD, Melillo JM, Nadelhoffer KJ, McClaugherty CA, Pastor J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* 66:317–321.
- Aber JD, Melillo JM, McClaugherty CA. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can J Bot* 68:2201–2208.
- Berg B. 1984. Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. *Soil Biol Biochem* 16:609–617.
- Berg B. 1986. Nutrient release from litter and humus in coniferous forest soils—a mini-review. *Scand J For Res* 1:350–369.
- Berg B, Muller M, Wesen B. 1987. Decomposition of red clover (*Trifolium pratense*) roots. *Soil Biol Biochem* 19:589–593.
- Chapin FS III, Vitousek PM, Van Cleve K. 1986. The nature of nutrient limitation in plant communities. *Am Nat* 127:48–58.
- Chapin FS, Bloom AJ, Field CB, Waring RH. 1987. Plant response to multiple environmental factors. *BioScience* 37:49–57.
- Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74:531–536.
- Dormaar JF, Willms WD. 1993. Decomposition of blue grama and rough fescue roots in prairie soils. *J Range Manage* 46:207–213.
- Dubach M, Russelle MP. 1994. Forage legume roots and nodules and their role in nitrogen transfer. *Agron J* 86:259–266.
- Eissenstat DM, Yanai RD. 1997. The ecology of root lifespan. *Adv Ecol Res* 27:1–60.
- Eno CF. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Sci Soc Am Proc* 24:277–299.
- Evans JR. 1989. Photosynthesis and nitrogen relationship in leaves of C₃ plants. *Oecologia* 78:9–19.
- Fahey TJ, Arthur MA. 1994. Further studies of root decomposition following harvest of a northern hardwoods forest. *For Sci* 40:618–629.
- Fahey TJ, Hughes JW, Mou P, Arthur MA. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *For Sci* 34:744–768.
- Field C, Mooney HA. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givinish T, editor. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press. p. 25–55
- Foster DR. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J Ecol* 80:753–772.
- Friend AL, Eide MR, Hinckley TM. 1990. Nitrogen stress alters root proliferation in Douglas-fir seedlings. *Can J For Res* 20:1524–1529.
- Gebauer G, Schulze ED. 1991. Carbon and nitrogen isotope ratios in different compartments of a healthy and declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. *Oecologia* 87:198–207.
- Goldfarb D, Hendrick R, Pregitzer K. 1990. Seasonal nitrogen and carbon concentrations in white, brown, and woody fine roots of sugar maple (*Acer saccharum* Marsh). *Plant Soil* 126:144–148.
- Gower ST, Son Y. 1992. Differences in soil and leaf litterfall nitrogen dynamics of five forest plantations. *Soil Sci Soc Am J* 56:1959–1966.
- Grimm ACH. 1988. Fine and coarse root decomposition in early successional forest stands of the southern Appalachians [MS thesis]. Atlanta, GA: Emory University.
- Helmisaari HS. 1991. Variation in nutrient concentrations of *Pinus sylvestris* roots. In: McMichael BL, Persson H. editors. *Plant roots and their environment*. Elsevier Scientific Publishers, Amsterdam. p 204–212.
- Hendricks JJ, Nadelhoffer KJ, Aber JD. 1993. Assessing the role of fine roots in carbon and nutrient cycling. *Trends Ecol Evol* 8:174–178.
- Hendricks JJ, Nadelhoffer KJ, Aber JD. 1997. A ¹⁵N tracer technique for assessing fine root production and mortality. *Oecologia* 112:300–304.
- Herman WA, McGill WB, Dormaar JF. 1977. Effects of initial chemical composition on decomposition of roots of three grass species. *Can J Soil Sci* 57:205–215.
- Jones JB Jr. 1984. *A laboratory guide of exercises for conducting soil tests and plant analyses*. Athens, GA: Benton Laboratories, Inc.
- Larsson K, Steen E. 1988. Changes in mass and chemical composition of grass roots during decomposition. *Grass Forage Sci* 43:173–177.
- Lohmus K, Ivask M. 1995. Decomposition and nitrogen dynamics of fine roots of Norway spruce (*Picea abies* (L.) Karst) at different sites. *Plant Soil* 168–169:89–94.
- Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. *Ecol Appl* 7:402–415.
- Margolis HA, Waring RH. 1986. Carbon and nitrogen allocation patterns of Douglas-fir seedlings fertilized with nitrogen in autumn. I. Overwinter metabolism. *Can J For Res* 16:897–902.
- Marshall JD. 1986. Drought and shade interact to cause fine root mortality in Douglas-fir seedlings. *Plant Soil* 91:51–60.
- McClougherty C, Berg B. 1987. Cellulose, lignin, and nitrogen concentrations as rate regulating factors in late stages of forest litter decomposition. *Pedobiologia* 30:101–112.
- McClougherty CA, Aber JD, Melillo JM. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63:1481–1490.
- McClougherty CA, Aber JD, Melillo JM. 1984. Decomposition dynamics of fine roots in forested ecosystems. *Oikos* 42:378–386.
- McNulty SG, Aber JD, Boone RD. 1991. Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. *Biogeochemistry* 14:13–29.
- Meier CE, Grier CC, Cole DW. 1985. Below- and above-ground N and P use by *Abies amabilis* stands. *Ecology* 66:1928–1942.

- Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B, Nadelhoffer KJ. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant Soil* 115:189–198.
- Mooney HA, Gulmon SL. 1982. Constraints on leaf structure and function in relation to herbivory. *BioScience* 32:198–206.
- Muller RN, Kalisz PJ, Luken JO. 1989. Fine root production of astringent phenolics. *Oecologia* 79:563–565.
- Nadelhoffer KJ, Raich JW. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* 73:1139–1147.
- Nadelhoffer KJ, Aber JD, Melillo JM. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (USA). *Can J For Res* 13:12–21.
- Nadelhoffer KJ, Aber JD, Melillo JM. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66:1377–1390.
- Nambiar EKS. 1987. Do nutrients retranslocate from fine roots? *Can J For Res* 17:913–918.
- Ollinger SV, Aber JD, Lovett GM, Millham SE, Lathrop RG, Ellis JE. 1993. A spatial model of atmospheric deposition for the northeastern US. *Ecol Appl* 3:459–472.
- Pastor J, Aber JD, McClaugherty CA, Melillo JM. 1982. Geology, soils, and vegetation of Blackhawk Island, Wisconsin. *Am Midland Nat* 108:266–277.
- Pastor J, Aber JD, McClaugherty CA, Melillo JM. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65:256–268.
- Persson H. 1990. Methods of studying root dynamics in relation to nutrient cycling. In Harrison AF, Ineson P, Heal OW, editors. *Nutrient cycling in terrestrial ecosystems, field methods, applications, and interpretation*. London: Elsevier Applied Science Publishers. p 198–217.
- Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. 1998. Variations in sugar maple root respiration with root diameter and soil depth. *Tree Physiol* 18:665–670.
- Raich JW, Nadelhoffer KJ. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology* 70:1346–1354.
- Reich PB, Uhl C, Walters MB, Ellsworth DS. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86:16–24.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proc Nat Acad Sci USA* 94:13730–13734.
- Ryan MG, Melillo JM, Ricca A. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Can J For Res* 20:166–171.
- Sachse ND. 1974. A thousand ages: the history of the University of Wisconsin Arboretum. Madison, WI: University of Wisconsin Press.
- Schoettle AW, Fahey TJ. 1994. Foliage and fine root longevity of pines. *Ecol Bull* 43:136–153.
- Scott NA, Binkley D. 1997. Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia* 111:151–159.
- Statistix. 1996. Version 3.5. Statistix Analytical Software, St. Paul, MN.
- Stump LM, Binkley D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Can J For Res* 23:492–502.
- Vogt KA, Dahlgren R, Ugolini F, Zabowski D, Moore EE, Zasoski R. 1987. Above- and belowground: I. Concentrations of Al, Fe, Ca, Mg, K, Mn, Cu, Zn, and P for *Abies amabilis* and *Tsuga mertensiana*. *Biogeochemistry* 4:277–294.
- Vogt KA, Vogt DJ, Bloomfield J. 1991. Input of organic matter to the soil by tree roots. In: McMichael BL, Persson H, editors. *Plant roots and their environment*. Elsevier Science Publishers, Amsterdam. p 171–190.
- White DL, Haines BL, Boring LR. 1988. Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. *Can J For Res* 18:54–63.
- Yin X, Perry JA. 1991. Factors affecting nitrogen concentration of fine roots in forest communities: regression analysis of literature data. *For Sci* 37:374–382.
- Yin XW, Perry JA, Dixon RK. 1991. Temporal changes in nutrient concentrations and contents of fine roots in a *Quercus* forest. *For Ecol Manage* 44:175–184.
- Zak DR, Pregitzer KS. 1998. Integration of ecophysiological and biogeochemical approaches to ecosystem dynamics. In: Pace ML, Groffman PM, editors. *Successes, limitations, and frontiers in ecology*. New York: Springer. p 372–403.