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COMPARISONS OF STRUCTURE AND LIFE SPAN IN ROOTS AND LEAVES AMONG TEMPERATE TREES

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Abstract. Global data sets provide strong evidence of convergence for leaf structure with leaf longevity such that species having thick leaves, low specific leaf area, low mass-based nitrogen concentrations, and low photosynthetic rates typically exhibit long leaf life span. Leaf longevity and corresponding leaf structure have also been widely linked to plant potential growth rate, plant competition, and nutrient cycling. We hypothesized that selection forces leading to variation in leaf longevity and leaf structure have acted simultaneously and in similar directions on the longevity and structure of the finest root orders. Our four-year study investigated the links between root and leaf life span and root and leaf structure among 11 north-temperate tree species in a common garden in central Poland. Study species included the hardwoods *Acer pseudoplatanus* L., *Acer platanoides* L., *Fagus sylvatica* L., *Quercus robur* L., and *Tilia cordata* Mill.; and the conifers *Abies alba* Mill., *Larix decidua* Mill., *Picea abies* (L.) Karst., *Pinus nigra* Arnold, *Pinus sylvestris* L., and *Pseudotsuga menziesii* (Mirbel) Franco. Leaf life span, estimated by phenological observations and needle cohort measurements, ranged from 0.5 to 8 yr among species. Median fine-root life span, estimated using minirhizotron images of individual roots, ranged from 0.5 to 2.5 yr among species. Root life span was not correlated with leaf life span, but specific root length was significantly correlated with specific leaf area. Root nitrogen : carbon ratio was negatively correlated with root longevity, which corroborates previous research that has suggested a trade-off between organ life span and higher organ N concentrations. Specific traits such as thickened outer tangential walls of the exodermis were better predictors of long-lived roots than tissue density or specific root length, which have been correlated with life span in previous studies. Although theories linking organ structure and function suggest that similar root and leaf traits should be linked to life span and that root and leaf life span should be positively correlated, our results suggest that tissue structure and longevity aboveground (leaves) can contrast markedly with that belowground (roots).

Key words: *conifers; fine roots; hardwoods; leaf life span; minirhizotron; root life span; suites of traits; trait syndromes.*

Introduction

The longevity of plant organs is an important factor in plant growth strategies (Grime 1977, Reich et al. 1992), plant competition (Aerts and Berendse 1989), nutrient cycling (Berendse and Aerts 1987, Aerts et al. 1992), and responses to global carbon change (Reich et al. 1997). Many important ecological factors have been associated with long tissue and organ life span. These include low potential growth rate (Chapin et al. 1993), superior sustained growth in areas with low resource availability (Aerts and Berendse 1989, Schläpfer and Ryser 1996), high shade tolerance (Reich et al. 2003), and long nutrient retention times (Grime 1977, Aerts 1995). Although root systems can represent >50% of total net primary productivity (Caldwell 1987), the majority of the studies providing evidence for growth strategies have focused on leaves (Monk 1966, Williams et al. 1989, Reich et al. 2003).

The collective data on leaves have indicated that plants have trade-offs in terms of energy requirements and physical constraints, such that general patterns have emerged as successful trait syndromes (sensu Reich et al. 2003) or suites of traits (sensu Chapin et al. 1993). For example, plant species with longer leaf life spans also tend to have lower potential growth rates, specific leaf areas (leaf area/dry mass, SLA), leaf nitrogen concentrations, and mass-based photosynthetic rates (Reich et al. 2003, Wright et al. 2004).

Trait syndromes are often related to the main processes associated with resource capture: assimilation (photosynthesis, nutrient uptake), organ structure related to resource collection (SLA and specific root length [SRL]), maintenance (respiration), and turnover (organ

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life span) (Reich et al. 2003). Leaves and the finest lateral roots share attributes that suggest that they might have generally similar trait syndromes: both organs are ephemeral, typically exhibit determinant growth, do not undergo secondary thickening, have the primary function of resource acquisition, and use resources for respiration (Eissenstat and Yanai 1997). Just as thin leaves (high SLA) are less expensive (per unit surface [area] with potential for light interception) for plants to produce, long, thin roots (high SRL) are less expensive to produce per unit surface (length) with potential for nutrient acquisition. Because many of the functions of roots are similar to leaves, roots may have trait syndromes associated with root life span. These traits may or may not parallel leaf trait syndromes.

Though a linkage between root and leaf life span has been proposed (Chapin 1980), leaf and root traits have rarely been investigated together with regard to longevity, though some information is available for grassland species. For example, Ryser and colleagues (Ryser 1996, Schläpfer and Ryser 1996), who examined root and leaf turnover in grass species with respect to their growth rate and nutrient availability, found that slower-growing species had longer-lived leaves and roots when leaf and root turnover were calculated as the ratio of necromass to total component (leaf or root) biomass. Also, studies in Minnesota, USA, at Cedar Creek examined root and leaf life span in >30 grassland species with respect to various traits. Using measurements of root life span based on the ratio of standing fine-root (<2 mm) biomass to fine-root production into ingrowth cores, they found that across the forbs, grasses, and legumes, long root life span was significantly associated with slow root respiration rates, low specific root length, and low nitrogen-to-carbon (N:C) ratios (Tjoelker et al. 2005). They also found long leaf life span associated with slow photosynthetic rates, slow leaf respiration rates, low SLA, and low N:C ratios. Leaf and fine-root N as well as life span were correlated on a rank basis, and the authors felt their data reflected a common leaf and root trait syndrome.

We examined root and leaf traits of 11 woody species selected to represent a wide range in leaf life span. Six of the 11 species were conifers in the *Pinaceae*; the others were hardwoods in diverse families. There have been anecdotal observations that conifer roots are longer-lived than hardwood roots of temperate forest trees (Vogt and Bloomfield 1991). Such observations are also consistent with the findings that roots of more primitive families, such as the *Magnoliaceae* and *Pinaceae*, generally have thicker roots than species in more evolutionarily advanced families, such as the *Aceraceae*, *Fagaceae*, and *Tiliaceae* (e.g., Baylis 1975, Comas and Eissenstat 2004). These observations, combined with the typically evergreen habit of the conifers, suggest that the putative differences in root life spans between hardwoods and conifers may simply reflect more primitive traits of the conifers.

We included the coniferous species *Larix decidua* (deciduous larch) in our study to examine the interaction of the conifer–hardwood relationship and the deciduous–evergreen habit. If larch root characteristics are more similar to the roots of the other conifer species, this would indicate a stronger phylogenetic influence on the roots; however, if they are more similar to the roots of the hardwood species, this would indicate a closer coupling of leaf function with root function.

To test the potential link between root and leaf longevity, we estimated root life span using a mini-rhizotron technique. We first hypothesized that fine-root life span would be positively correlated with leaf life span among diverse tree species that vary widely in leaf life span. Second, given that leaf syndromes appear to be important parts of the ecological strategy of species, we hypothesized that root structural characteristics and root chemistry would be related to root longevity in a manner analogous to that typically found in leaves. Third, we hypothesized that conifer root longevity would be longer than those of hardwood roots based on reviews of limited past research.

Methods

Field site

Our field site was a common garden planting in the Siemianice Experimental Forest in central Poland (51°14.87′ N, 18°06.35′ E; altitude, 150 m). Climate of the region is transitional between maritime and continental, and the mean annual precipitation was 591 mm with approximately half falling from May to August (weather data was recorded 300 m from the field site from 1968 to 1997). Mean temperature was 8.2°C with a mean growing season of ~213 d, calculated as the number of days with a mean temperature ≥5°C (Szymanski and Ceitel 1989, Ceitel and Wawro 1999*a*, *b*).

The site consisted of two adjacent plantings. There were 14 tree species total, nine species per planting, with some species duplicated between plantings (Szymanski 1982). Each planting had three replicate blocks; species were planted in nine monospecific 20 × 20 m plots in each block, for a total of 27 plots per planting. Trees were planted in 1970 and in 1971 as 1- and 2-yr-old seedlings, respectively, at 1 × 1 m spacing, although the spacing has changed somewhat due to some prescribed and self-thinning. Each planting had a fairly uniform topography and soil with very few understory plants present (Withington et al. 2003). The soil in all the plots was nutrient-poor with a plowed A-horizon; soil texture averaged 80% sand and 15% silt. Soils were generally loamy sands and classified as fine-loamy, mixed, Mesic Kanhaplic Haplustalfs and sandy, mixed, Mesic Typic Ustipsamments. However, over the 30 years of the experiment, species modified soil characteristics (Reich et al. 2005), such that species differed in their edaphic environment during the time period of the present study. For this experiment, we sampled all nine species in the

first planting: five deciduous broad-leaved species, *Acer pseudoplatanus* L., *Acer platanoides* L., *Fagus sylvatica* L., *Quercus robur* L., and *Tilia cordata* Mill.; a deciduous conifer, *Larix decidua* Mill.; and three evergreen conifers, *Abies alba* Mill., *Picea abies* (L.) Karst., and *Pseudotsuga menziesii* (Mirbel) Franco. In the second planting we sampled three species: the evergreen conifers *Pinus nigra* Arnold, *Pinus sylvestris* L., and *Picea abies*.

To assess potential differences between the plantings, we analyzed *Picea abies* in both plantings using percentage of clay (soil texture) in the plots as a covariate. We used a general linear model to test differences in five measured variables of *Picea abies* both above- and belowground. Trees in 1999 were significantly taller ($F_{1,5} = 8.07$, $P = 0.05$) with greater dbh ($F_{1,5} = 11.05$, $P = 0.03$) in the first planting than the second. When significantly different, aboveground measurements of *Picea abies* were kept separate by planting for analyses. Variables associated with the finest root orders of *Picea abies* (e.g., diameter, production, life span) were not significantly different between plantings (all $P > 0.27$).

Given that the two plantings were adjacent in a flat area, the only likely differences between the plantings would be in the soil characteristics. Therefore, we looked for correlations between soil texture and root characteristics. Percentage of clay varied from 1.2% to 13.5% with all but one plot having <9% clay. At the plot level, there were no significant correlations of percentage of clay with root N:C ratio, SRL, root tissue density, or diameter (data not shown). Clay did not explain a significant amount of the variation in median root life span across species. We were satisfied that soil texture was not a significant source of variation in our study. All root-related measurements on the six plots of *Picea abies* were combined for analyses, and we included the *Pinus* spp. in the analyses with no adjustments for their location in the second planting.

Root life span estimates

Owing to a previous study at this field site that found acrylic minirhizotron tubes provided root standing biomass estimates more consistent with those estimated by soil cores than cellulose acetate butyrate tubes (Withington et al. 2003), only acrylic tubes were used in this study. The minirhizotron tubes had an inside diameter of 5.1 cm, a wall thickness of 3.2 mm, and a length of 60 cm. Tubes were sealed with a rubber stopper and wrapped in black electrical tape to keep light and rain from entering the tubes; no other covers were used because the tubes were shaded most of the time. In November 1998, the tubes were installed randomly in the plots at an angle of 30° from vertical and at least 3 m from the plot borders with the top 10 cm of the tube above the soil surface. Three tubes were installed per plot, three plots per species. We used only two *Abies alba* plots (six tubes total) because the third was overgrown with a different tree species.

Minirhizotron images were collected using a minirhizotron camera and associated image capture software (Bartz Technology, Santa Barbara, California, USA) starting in May 1999, six months after tube installation. Problems associated with installation disturbance on subsequent root dynamics (Joslin and Wolfe 1999) were considered in the data analysis. Images were collected from May through December 1999 at 2–4 week intervals. Because the 1999 data indicated very long-lived roots, sampling intervals were lengthened in 2000–2002 to monthly intervals from April through November.

Images of the windows in the tubes were viewed as a time sequence. Roots observed on the first sampling date were not used, as their birth dates were unknown. The date a root was first observed and the date of disappearance were recorded. If the observation of a root became obscured because another root grew in front of it or if a root was still alive at the end of the data collection period, then that root was recorded as statistically censored (i.e., time to root death was greater than the observation time; Allison 1995). Root birth and root death were estimated as the day midway between successive imaging dates. Individual root life span was calculated as the number of days from root birth to root death.

Determining the vitality of roots from external appearance alone is difficult. Our first step was to correlate appearance of roots in the minirhizotron windows to root vitality using a modified version of the vital stain procedure of Comas et al. (2000). Although the vital staining correlated well with root function in grape roots for Comas et al. (2000), for our species, external appearance alone was not enough to evaluate root vitality. Roots with a dark-brown to black coloration were not consistently dead or dying. For >95% of the roots, we relied on the date of disappearance as the date of death; no outward signs of loss of cortical tissue and hyphal mantle deterioration were evident before such disappearances. Thus, root life span and root persistence were essentially synonymous in this study.

Often, root life span (the inverse of root turnover) is estimated by methods that can estimate only root production and root standing crop (Gill and Jackson 2000). Minirhizotron production data were used to estimate mean root life span as an alternative to median life span based on survivorship analysis. Minirhizotron root production (number of roots born) was converted to root length using a subset of images distributed across the study period, including each year and representing each season. From this subset of images, root length was determined for each species using the program WinRHIZO Tron (Regent Instruments, Quebec, Canada) and correlated with total number of roots (for all 11 species, no r^2 was <0.88).

We calculated the amount of time for cumulative root length mortality to equal cumulative root length produc-

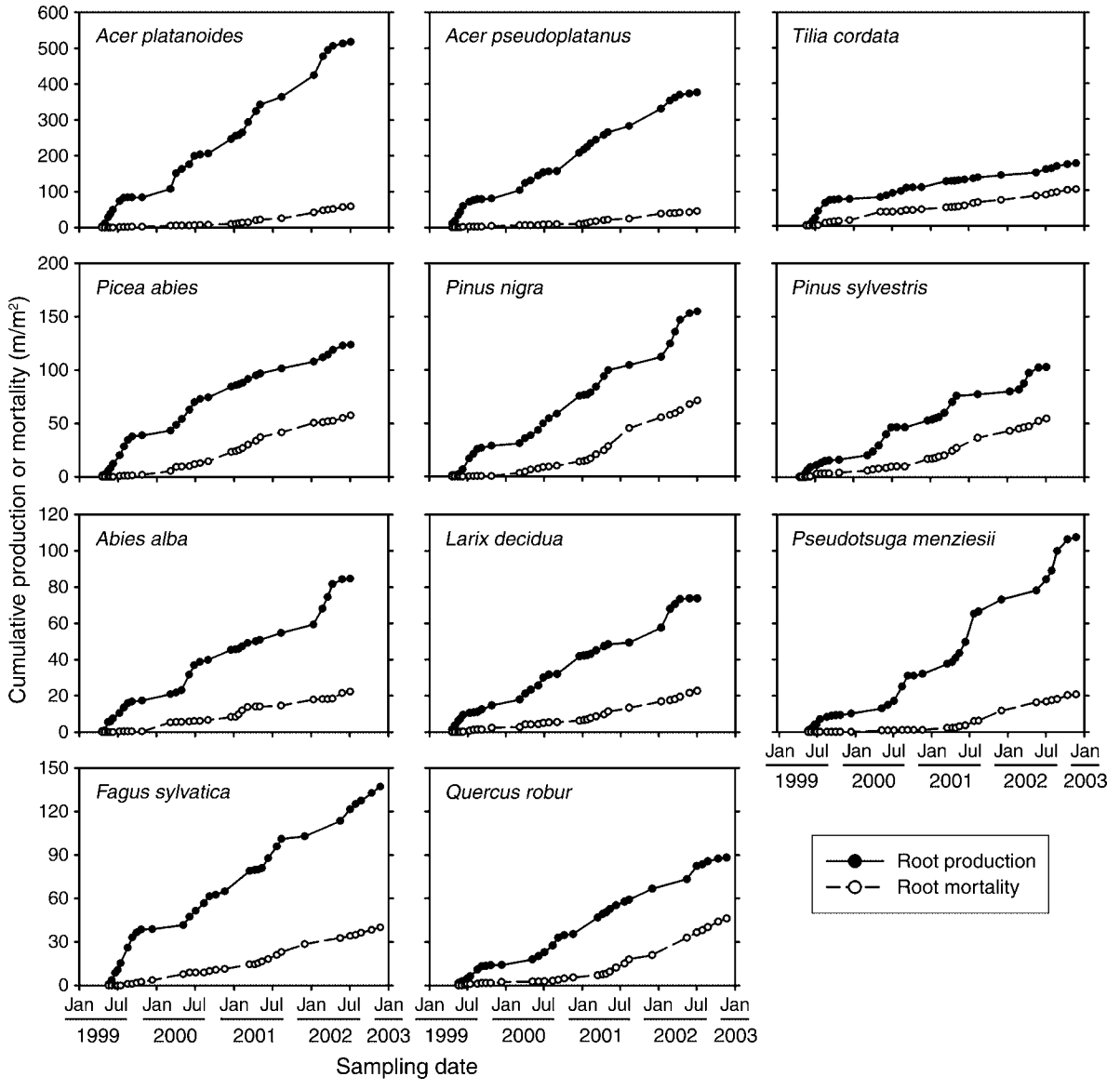

FIG. 1. Cumulative production and cumulative mortality of fine roots (first- and second-order roots only) against minirhizotron tubes from May 1999 to November 2002, averaged across plots (two, three, or six plots per species). The mean difference between production and mortality can be found in Table 3. Note the difference in the *y*-axis scales. Our field site was a common garden planting in the Siemianice Experimental Forest in central Poland.

tion after minirhizotrons had been installed for 1.5 yr (Fig. 1). We then calculated the harmonic mean of five intervals to get an estimate of root life span for each species (LS_{PMR}, Tables 1 and 2). A second estimate of mean fine-root life span was calculated as the ratio of the maximum standing root crop to the annual root length production (SC:Prod) from the last two years of the study.

Survivorship curves and root life span estimates (LS_{25R}, LS_{50R}) for each species were calculated using the BASELINE statement of PROC PHREG in SAS version 8.02 (SAS Institute, Cary, North Carolina, USA). Pearson product-moment correlations were used to test for correlations between tissue life span and characteristics such as N:C ratio and SRL. Root and leaf life spans were log-transformed before data analyses. Cox proportional hazards models were used to test for differences within each species for the influence of diameter, soil depth, and time to pigmentation on root life span (Cox 1972, Allison 1995, Wells and Eissenstat 2001).

Root order and root pigmentation

We were interested in comparing only first- and second-order roots of each species, but root order is frequently difficult to determine definitively in minirhizotron windows because the total root is not visible.

TABLE 1. Definitions and descriptions of abbreviations used in the manuscript.

Abbreviation	Description
Dia-T_R	total root diameter (mm)
Dia-P_R	diameter of plant tissue only, fungal mantles excluded (mm)
LS_L	mean leaf life span (yr)
LS_{25R}	first quartile estimate of root life span (yr)
LS_{50R}	second quartile (median) estimate of root life span (yr)
LS_{SCR}	mean estimated root life span (maximum standing crop/annual root production) (yr)
LS_{PMR}	root life span estimated from the amount of time required for cumulative root mortality to equal cumulative root production (yr)
N/C_R	ratio of root nitrogen to root carbon (mass/mass)
$\%N_L$	leaf percentage nitrogen (mass/mass)
$Prod_L$	leaf production ($kg \cdot ha^{-1} \cdot yr^{-1}$)
$Prod_R$	root production against the minirhizotron tubes ($m \cdot m^{-2} \cdot yr^{-1}$)
RLD	root length density, total amount of root length of all root orders per unit soil volume (length/soil volume, cm/cm^3)
RLD_{1+2}	root length density of first- and second-order roots (percentage of RLD)
SC	root standing crop (cm/m^2)
SLA	specific leaf area (area/unit mass, cm^2/g)
SRL	specific root length (length/unit mass, cm/g)
TissDen	root tissue density (mass/volume, g/cm^3)

Root diameter is more easily measured, so we looked for a correlation between diameter and root order that would allow us to analyze only the finest root orders. We looked at the distributions of root diameters from first- and second-order scanned roots, separated into groups at 0.1-mm intervals using specialized software (WinRhizo, Regent Instruments). We compared these to the distribution of minirhizotron root diameters, which were determined by direct measurement on a computer screen using the image from the date a root was first observed (Appendix A). By comparing the two distributions, we were able to select a maximum root diameter for each species that would allow us to use roots of each species that were first order and possibly second order but unlikely to be third order or higher (Table 2). Unless otherwise noted, all results are for the finest two orders of roots.

Besides life span, time to root pigmentation was also determined. The transition of roots from white to pigmented usually indicates a reduction in root metabolic activity (Comas et al. 2000, Bouma et al. 2001). Roots generally changed color only once before dying. The date when at least 50% of a root's length was pigmented was noted. The relationship between time to pigmentation and median root life span among the species was tested with a general linear model. The influence of the time to pigmentation on root mortality within each species was tested with a Cox proportional hazards model (Cox 1972, Allison 1995, Wells and Eissenstat 2001).

Root morphology, anatomy, and nitrogen concentrations

Root diameter, tissue density, SRL, and nitrogen concentration are important traits hypothesized to be

TABLE 2. Fine-root (smallest two orders) and leaf life span estimates plus the diameter cutoffs for the fine roots.

Species	Max diam. (mm)	LS_{50R} (yr)	LS_{PMR} (yr)	LS_{SCR} (yr)	LS_L (yr)
Acpl	0.35	1.62 (0.73, 3.01)	2.33	1.80	0.46
Acps	0.35	2.47 (0.65, undef.)	2.24	1.69	0.46
Fasy	0.30	0.57 (0.33, 1.38)	1.14	0.55	0.45
Quro	0.30	0.98 (0.45, 1.49)	1.47	0.69	0.47
Tico	0.35	0.64 (0.49, 1.10)	1.58	1.87	0.43
Abal	0.40	1.13 (0.45, 1.93)	1.47	2.00	8.22
Lade	0.40	1.10 (0.54, 2.50)	1.98	1.48	0.51
Piab	0.40	0.70 (0.42, 1.10)	1.44	0.97	8.77
Pini	0.30	0.77 (0.48, 1.46)	1.43	0.83	3.84
Pisy	0.40	0.67 (0.44, 1.11)	0.71	1.18	2.44
Psme	0.45	1.62 (0.64, undef.)	1.41	3.27	5.48

Notes: Because most roots could not be observed in their entirety, a diameter cutoff for each species was determined for the roots observed against the tubes (Max diam.). This ensured that we included all of the first-order roots with some small second-order roots, but no third-order roots. Median fine-root life span (LS_{50R}) is shown with first and third quartiles as indicators of variability and is based on roots born between May 1999 and November 2001 and followed through November 2002. Root life span was also estimated as the harmonic mean of the number of days between two equal values of cumulative production and cumulative mortality (LS_{PMR}) from minirhizotron data. A third estimate of root life span was estimated as the ratio of the maximum standing crop against the minirhizotron tubes in 2002 to the mean root production in 2001 and 2002 (LS_{SCR}). Mean leaf life span (LS_L) is based on leaf-fall data over 11 mo for deciduous species and based on needle cohorts present for evergreen species. Species abbreviations are the first two letters of the genus and species. The abbreviation "undef." means the value is too large to be defined, >900 d. Our field site was a common garden planting in the Siemianice Experimental Forest in central Poland.

correlated with root life span of the finest root orders. Because the fungal ectomycorrhizal mantle appreciably affects root diameter, we also made anatomical sections of roots to distinguish plant root diameter from the entire mycorrhizal root diameter. Nonmycorrhizal white roots were examined separately from the mycorrhizal, pigmented roots.

Soil cores (4.8 cm diameter) from previously undisturbed soil were randomly collected in July 1999 in each plot to a depth of 15 cm. Roots were cleaned from the soil cores by hand in plastic tubs and sorted into three root order groups: (a) first, (b) second, and (c) third and fourth. For our purposes, first-order roots are all external links with no daughter roots; second-order roots have only first-order daughter roots, and so on up the hierarchy. Additional soil cores were collected in July 2001 in each plot at two depths: 0–15 cm and 16–30 cm. These roots were cleaned and sorted into three groups: the combined orders (a) 1 and 2, (b) 3 and 4, and (c) 5 and higher. All roots were scanned on a desktop scanner using WinRHIZO software at 400 dots per inch (DPI; Regent Instruments) to obtain diameter distributions for roots of known order. After scanning, root samples were dried for 48 h at 50°C and weighed. Root length density (L_v, length/soil volume) was calculated for each root order class, and total L_v represents the sum of the three classes. Specific root length, which is inversely proportional to the square of root diameter, assuming cylindrical geometry (SRL = [length/volume] × [volume/mass]), was calculated as the ratio of the root length in the sample to the dry mass. Dried roots were pulverized using a SPEX mixer/mill (SPEX Industries, Metuchen, New Jersey, USA), and 15-mg subsamples were ashed in a muffle furnace at 500°C for 6 h so that dry mass could be expressed on an ash-free basis.

In June 2001, roots were excavated in each plot at two locations to a depth of 15 cm. Roots were gently washed by hand and then preserved in 60% ethanol for later anatomical observations by light microscopy. Cross sections were made by hand under a dissecting scope. A minimum of 36 roots of each species was selected, and sections were made 1 mm behind the root cap for each root. The finest root orders were pooled. Sections were stained with 0.05% toluidine blue (in acetate buffer pH 4.5) to color the cell walls. We measured 25–30 cross sections from different roots for total diameter and ectomycorrhizal mantle thickness (where present).

Root tissue density was calculated as the ratio of the ash-free dry mass of the sample to root volume. Root volume was estimated using root diameter and root length and assuming cylindrical geometry. Using the values for mantle thickness, we calculated the mean diameter of the scanned roots without the hyphal mantle for the nine ectomycorrhizal species (all but the *Acer* spp.). We then used these diameter estimates to calculate a second estimate of SRL that excluded fungal mantles, assuming tissue densities of the mantle and plant root as well as percentage of ash masses were the same.

Because minirhizotron observations indicated that the white roots of ectomycorrhizal species lived a long time, we also looked for specific anatomical differences between mycorrhizal and white roots. Nonectomycorrhizal roots were collected in the top 10 cm at three random locations in the plots using hand trowels. None could be found for the *Pinus* species. These difficult-to-find roots were generally white to beige with root hairs and exhibited longer lengths (>2 cm) than ectomycorrhizal (ECM) roots. Seven to 12 nonmycorrhizal roots of each species were hand-sectioned at the beginning of the maturation zone and stained for suberin and lignin with 0.05% phloroglucinol followed by two drops of 36% HCl (Jensen 1962). The presence or absence of a thickened hypodermal layer (exodermis) in the sections was noted.

Nitrogen concentration in roots was estimated in relatively young roots of known maximum age from ingrowth tubes. In May 2001, five ingrowth tubes were installed per plot (11 species, three plots each). Ingrowth tubes were made from plastic screen (1.5 × 1.5 mm holes) rolled to make tubes 3 cm in diameter and 25 cm long. The organic layer, if present, was pulled back from an area between two trees ~1 m apart. The tubes were installed horizontally in the mineral soil just under the organic layer. Prior to installation, mineral soil, sifted to remove roots and large organic debris, was added to each ingrowth tube. Ingrowth tubes were excavated after 90 d. Cores were pooled per plot and roots extracted. Roots were immediately hand-washed and sorted into two classes: (a) root orders 1 and 2 (finest two orders) and (b) orders 3 and 4. No roots of higher order were present. The roots were dried at 50°C for 36–48 h. We determined carbon and nitrogen concentrations of the samples for each plot using an elemental analyzer (model EA1108; Fisons Instruments, Pt. Pleasant, New Jersey, USA).

Leaf and tree biometric data

Foliar life span of deciduous species was determined using a combination of phenological observations (spring leaf unfolding) and data on leaf shedding obtained from litter traps. Needle longevity for evergreen conifers (*Abies alba*, *Picea abies*, *Pinus nigra*, *Pinus sylvestris*, and *Pseudotsuga menziesii*) was assessed by counting annual needle cohorts. Measurements were made in mid-July 2002. None of the species exhibit multiple flushes at the experimental site. Mean needle longevity per branch was assessed by counting the number of annual cohorts that retained a majority (>50%) of their needles. Thus, our data are representative of mean needle life span (Reich et al. 1996). Because shading induces greater needle longevity lower in the crown (Reich et al. 1994), we evaluated needle longevity for three randomly selected upper and three lower branches per plot and used the mean values from all plots and crown position for these analyses.

TABLE 3. Root morphological characteristics (mean, with SE in parentheses) determined from mixed-age, first- and second-order (finest orders) roots observed in minirhizotron tubes or collected from soil cores.

Species	SRL (m/g)	TissDen (g/cm^3)	Dia-T_R (mm)	$Prod_R$ (m·m^{-2}·yr^{-1})	RLD (cm/cm^3)	RLD_{1+2} (%)	N:C (mass/mass)
Hardwoods							
Acpl	52.1 (5.2)	0.143 (0.01)	0.41 (0.02)	129.2 (17.1)	9.91 (1.22)	56.8	0.024 (0.001)
Acps	49.1 (2.6)	0.133 (0.01)	0.46 (0.06)	92.7 (11.0)	11.78 (1.20)	51.0	0.031 (0.002)
Fasy	90.7 (13)	0.173 (0.03)	0.36 (0.03)	34.3 (2.9)	7.88 (0.93)	52.9	0.044 (0.007)
Quro	68.1 (9.8)	0.133 (0.01)	0.46 (0.04)	22.0 (3.5)	8.64 (1.00)	59.8	0.036 (0.003)
Tico	45.8 (7.3)	0.214 (0.07)	0.43 (0.03)	42.0 (9.6)	7.02 (1.14)	48.8	0.047 (0.004)
Mean	61.1[a] (4.7)	0.159 (0.02)	0.42[b] (0.02)	64.0 (20.3)	9.05[a] (0.83)	53.8 (2.0)	0.036 (0.004)
Conifers							
Abal	26.0 (4.2)	0.153 (0.01)	0.62 (0.05)	21.1 (3.3)	5.92 (0.39)	49.4	0.041 (0.008)
Lade	40.9 (2.7)	0.155 (0.01)	0.53 (0.01)	18.4 (2.1)	7.14 (0.61)	66.0	0.051 (0.009)
Piab	33.4 (2.5)	0.196 (0.02)	0.54 (0.03)	30.1 (3.8)	6.14 (0.75)	58.8	0.053 (0.004)
Pini	39.9 (8.4)	0.287 (0.04)	0.45 (0.05)	38.7 (5.5)	6.81 (1.74)	66.7	0.035 (0.003)
Pisy	24.7 (2.3)	0.248 (0.04)	0.58 (0.05)	25.7 (3.4)	3.47 (0.80)	68.1	0.050 (0.007)
Psme	27.2 (3.7)	0.188 (0.01)	0.57 (0.05)	26.9 (6.9)	6.02 (1.80)	56.1	0.034 (0.010)
Mean	32.0[b] (2.9)	0.204 (0.02)	0.55[a] (0.02)	27.0 (3.0)	5.91[b] (0.53)	60.9 (3.0)	0.044 (0.003)

Notes: Specific root length (SRL) was corrected for mean hyphal mantle thickness. Root tissue density was calculated as the ratio of root mass to root volume assuming a cylindrical geometry (TissDen). Total diameter was the mean of scanned roots from soil cores (Dia-T_R). Root production is the length produced per year per unit viewing area of minirhizotron surface ($Prod_R$). Root length density was calculated from intact-soil core data for all roots present (RLD) and for only first- and second-order roots (RLD_{1+2}). Nitrogen : carbon ratio was determined for young (<90 d), first- and second-order roots collected in August 2000 (N:C). Species abbreviations are the first two letters of the genus and species names. Different superscript letters indicate that hardwood and conifer mean values are significantly different at $P < 0.05$.

The projected leaf area was determined using an image analysis system and the WinFOLIA Pro for broadleaved species and WinSEEDLE Software for conifers (Regent Instruments). Specific leaf area (defined as the projected leaf area divided by leaf dry mass) was calculated for the current-year leaves used for determination of foliar life span.

Foliar nitrogen concentration was measured on dried (65°C for 48 h) tissue ground in a mill (Kikro-Feinmühle Culatti, IKA Labortechnik, Staufen, Germany). Tissue samples were digested by the micro-Kjeldahl method and processed using a BÜCHI Distillation Unit B-322 (BÜCHI Analytical, Flawil, Switzerland). Data are means of equally weighted composite samples of mature current-year foliage obtained from the individual branches (four per plot, two plots per species).

Total foliar and other nonfoliar miscellaneous litterfall (woody litter, debris, seeds, etc.) were collected monthly from 31 May 1996 through 30 April 1997 using 0.38-m^2 litter traps. To the bottom of each trap under coniferous species, 1-mm mesh plastic window screen was attached. Eight litter traps per plot were placed directly on the forest floor. Litter was oven-dried at 65°C, and estimates of the annual production of litter biomass were calculated.

RESULTS

Defining first- and second-order roots

To compare roots with similar putative functions among 11 species, we needed to compare roots of the same order. Order is relatively easy to determine with excavated roots but is problematic in minirhizotron images with only portions of roots visible. Mean fine-root diameters from intact cores were similar among the species and ranged from 0.36 mm in *F. sylvatica* to 0.62 mm in *Abies alba* (Table 3). Mean root diameters from excavated first- and second-order roots were moderately larger than the root diameters collected from the minirhizotron images (Table 3, Appendix A). This was due to the greater amount of second-order roots in the scanned samples compared to the minirhizotron samples. The scanned samples had distinct bimodal distributions reflecting the two root orders; the first peak in the scanned-root distribution (the first-order roots) matches the peak in the minirhizotron root diameter distribution for each species (Appendix A). We selected maximum diameters to use as a cut-off for selecting first-order roots in the minirhizotron images by looking at the two diameter distributions simultaneously and choosing a diameter that gave ~75–80% of the first-order roots and only a small percentage of the second-order roots (Table 2, Appendix A). These cut-offs were used to select only first-order roots of each species observed in the minirhizotron windows for subsequent data analysis.

Correlation of root life span with leaf life span

Mean leaf life spans of the deciduous hardwood species were ~0.45 yr and had a range of only 20 d. *Larix decidua*, a deciduous conifer, had only a slightly longer mean leaf life span at 0.51 yr. Leaf life span of the five evergreen conifers had a much larger range in leaf life span, from 2.44 yr for *Pinus sylvestris* to 8.77 yr for *Picea abies* (Table 2).

The median life span of the fine roots (LS_{50R}) was not correlated with leaf life span, either across all species ($P = 0.73$) or within the hardwood ($P = 0.32$, data not shown) or conifer groups ($P = 0.93$; Table 4, Fig. 2).

TABLE 4. Pearson product-moment correlation coefficients for leaf life span (LS_L), percentage of nitrogen ($\%N_L$), specific leaf area (SLA), and leaf production ($Prod_L$) with all root and leaf characteristics for all 11 species and for just the six conifer species.

Root and leaf traits	Coefficient, by leaf trait			
	LS_L	$\%N_L$	SLA	$Prod_L$
All species ($n = 11$)				
LS_{25R}	−0.161	−0.006	0.167	0.014
LS_{50R}	−0.119	0.258	0.169	−0.117
LS_{SCR}	0.008	0.153	0.113	−0.256
LS_{PMR}	−0.373	0.432	−0.373	−0.094
N/C_R	0.233	−0.134	−0.330	−0.278
SRL	**−0.769**	**0.655**	**0.771**	0.496
TissDens	0.447	**−0.741**	−0.559	0.218
Dia-T_R	**0.725**	−0.487	**−0.758**	**−0.707**
Dia-P_R	*0.586*	−0.228	−0.486	**−0.675**
$Prod_R$	−0.388	0.189	0.513	**0.630**
LS_L		**−0.738**	**−0.863**	−0.508
$\%N_L$			**0.826**	0.103
SLA				0.417
Pinaceae ($n = 6$)				
LS_{25R}	−0.301	0.250	0.615	−0.314
LS_{50R}	−0.047	0.557	0.684	−0.706
LS_{SCR}	−0.132	0.387	0.664	−0.521
LS_{PMR}	−0.191	0.547	0.609	−0.654
N/C_R	−0.340	0.212	0.191	−0.010
SRL	−0.482	0.029	0.192	0.075
TissDens	0.127	**−0.913**	**−0.814**	**0.964**
Dia-T_R	0.233	0.504	0.313	−0.568
Dia-P_R	0.318	0.567	0.368	−0.705
$Prod_R$	0.508	**−0.907**	*−0.762*	0.696
LS_L		−0.398	−0.548	−0.019
$\%N_L$			*0.797*	**−0.874**
SLA				−0.736

Notes: All comparisons are on a log–log basis. See Table 1 for descriptions of abbreviations. Coefficients in italic type are significant at $\alpha = 0.10$. Coefficients in boldface type are significant at $\alpha = 0.05$.

Conifers exhibited a similar range in LS_{50R} (0.67–1.62 yr) as that of hardwoods (0.57–2.47 yr; Table 2). Leaf life span was longer for the conifers (0.51–8.77 yr) than for the hardwoods (0.43–0.47 yr; Table 2).

Because many studies investigating root turnover use methods that assume steady-state conditions in order to correlate root production with root life span, we examined our data for similar relationships. Root production was much greater in the first year when the roots were exploring disturbed soil near the tubes (Fig. 1). Root production and mortality were roughly equal for most species by the end of the second year as indicated by fairly constant standing crop (Appendix B). Root life span based on the differences in time for equivalent values of cumulative fine-root length production and mortality (LS_{PMR}) was correlated with median-root life span ($r = 0.67$, $P = 0.025$). Fine-root length production and mortality was generally longer than the median life spans (Table 2). For *Tilia cordata* (0.64–1.58 yr) and for *Picea abies* (0.70–1.44 yr), LS_{PMR} was more than twice as long as median life span. Root life span based on root production and standing crop (LS_{SCR}) was not correlated with median fine-root life span ($r = 0.10$, $P = 0.767$) nor was it correlated with any other root or leaf characteristics (Table 5). Standing-crop-based estimates of root life span were generally longer than LS_{50R} (Table 2). The range of root life spans for the cohort-based estimates and the standing-crop-based estimates were similar for the hardwoods, but whereas LS_{50R} had *Acer pseudoplatanus* roots living the longest by far, the LS_{SCR} estimate indicated that *T. cordata* roots lived longest. For the conifers, the estimated values by the approaches were similar.

Correlation of leaf life span with leaf characteristics

We examined leaf traits that previously have been correlated with leaf life span across a wide range of species. In our study, leaf N concentration was generally higher in the deciduous species than in the evergreens (Table 6, Fig. 3). Leaf N was inversely correlated with leaf life span across all 11 species ($P = 0.01$) and was also positively correlated with specific leaf area ($P = 0.01$; Table 4). Specific leaf area was also higher for the deciduous species compared with the evergreens and inversely correlated with leaf life span across all species ($P = 0.002$). There was considerable overlap in yearly leaf biomass production (Table 6).

Correlation of root life span with root characteristics

Across species.—We used the ratio of nitrogen to carbon (N:C) to represent the nitrogen concentration of the fine roots, which avoided problems of soil contamination associated with dry mass estimates. Mathematically, this places the emphasis on the differences in N (in contrast to C:N ratio), and N:C ratio is more analogous to leaf N concentration. Overall, there was a tendency for longer-lived roots to have lower N:C ratios. For the finest roots, the N:C ratio was negatively correlated with LS_{50R} across all 11 species ($P = 0.02$; Fig. 3, Table 5). Although LS_{PMR} was correlated with LS_{50R}, LS_{PMR} only tended toward negative correlation with N:C ratio ($P = 0.09$).

In contrast to general plant growth strategies, new root production tended to be positively correlated with LS_{50R} ($P = 0.08$; Table 5). The *Acer* species had a large effect on the correlation. *Acer platanoides*, for example, exhibited root growth of >100 $m \cdot m^{-2} \cdot yr^{-1}$, yet had one of the longest median fine-root life spans. If the two *Acer*s were omitted, there was little evidence of a relationship between median root life span and root production ($P = 0.12$).

Contrary to expectation, we found that denser root tissue tended to be associated with shorter LS_{50R} ($P = 0.06$), and SRL was not correlated with LS_{50R} ($P = 0.59$; Table 5). Mean fine-root diameters calculated with or without hyphal mantles were not correlated with root life span, perhaps because fine-root diameters were quite variable within a species (Appendix A).

Within a species.—There was large variation in patterns of root survivorship among the species (Fig. 4). We examined three characteristics of individual roots observed in the minirhizotron windows: diameter, depth

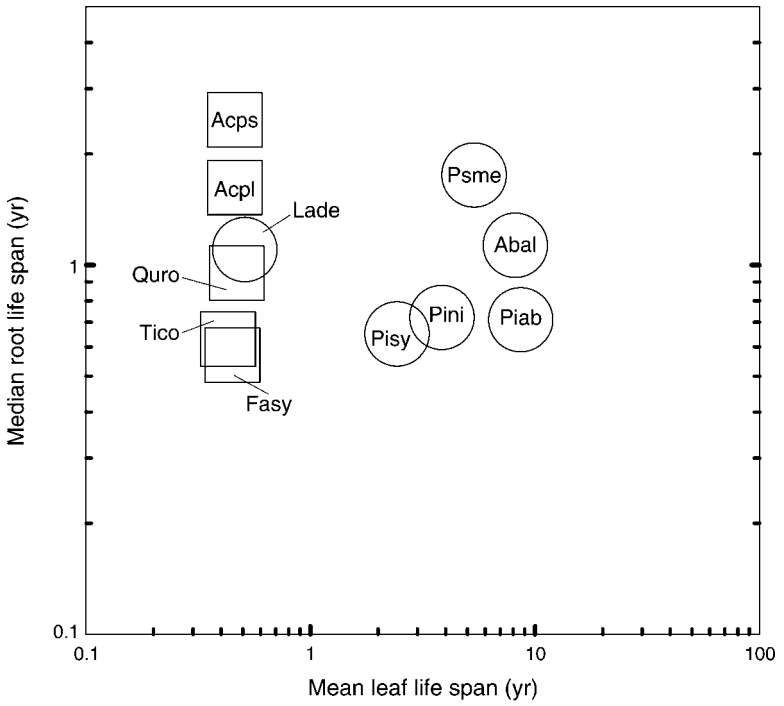

FIG. 2. Relationship of fine-root life span to leaf life span (note log scales). Hardwoods are denoted by squares, and conifers by circles. Species abbreviations are the first two letters of the genus and species. *Picea abies* is plotted as the mean of the two sites for leaf life span.

in soil, and time to pigmentation. Fine-root life span was significantly associated with root depth in soil in seven species (Appendix C); deeper roots lived longer than shallower roots. In four species, larger diameter roots had less risk of death than thinner roots (Appendix C).

The longer a root remained white, the lower was its risk of mortality in the next sampling interval and the longer its life span (Appendix C). In essence, white roots had a lower risk of future mortality than did pigmented roots. This difference was 1.3% ($P = 0.0003$) for *Acer*

TABLE 5. Pearson product-moment correlation coefficients among root characteristics across all 11 species and among the six conifer species.

Root traits	Coefficient, by root trait								
	LS_{50R}	LS_{SCR}	LS_{PMR}	N/C_R	SRL	TissDens	Dia-T_R	Dia-P_R	$Prod_R$
All species ($n = 11$)									
LS_{25R}	**0.845**	0.346	**0.675**	**−0.698**	−0.204	−0.323	0.110	0.348	**0.654**
LS_{50R}		0.101	**0.667**	**−0.704**	−0.103	**−0.619**	0.156	0.446	0.406
LS_{SCR}			0.342	0.101	−0.368	0.032	0.222	0.391	0.156
LS_{PMR}				*−0.542*	0.283	**−0.605**	−0.245	0.019	0.104
N/C_R					−0.238	0.380	0.328	0.067	**−0.652**
SRL						−0.393	**−0.912**	**−0.835**	−0.243
TissDens							0.124	−0.167	0.264
Dia-T_R								**0.906**	−0.040
Dia-P_R									−0.064
Pinaceae ($n = 6$)									
LS_{25R}	**0.857**	−0.246	0.397	−0.563	0.111	−0.245	−0.035	0.075	−0.204
LS_{50R}		0.253	0.486	−0.531	−0.142	−0.606	0.355	0.508	−0.432
LS_{SCR}			0.359	0.303	−0.261	**−0.834**	0.682	*0.755*	*−0.763*
LS_{PMR}				−0.130	0.670	−0.567	−0.244	−0.064	−0.561
N/C_R					0.065	−0.246	0.225	0.067	−0.598
SRL						0.092	**−0.814**	*−0.752*	0.267
TissDens							−0.636	−0.719	0.793
Dia-T_R								**0.971**	−0.305
Dia-P_R									−0.326

Notes: All comparisons are on a log–log basis. See Table 1 for descriptions of abbreviations. Coefficients in italic type are significant at $\alpha = 0.10$. Coefficients in boldface type are significant at $\alpha = 0.05$.

TABLE 6. Leaf morphology (specific leaf area, SLA), production ($Prod_L$), and chemistry (percentage of nitrogen, %N); values are means, with SE in parentheses.

Species	SLA (cm^2/g)	$Prod_L$ ($kg \cdot ha^{-1} \cdot yr^{-1}$)	$\%N_L$ (mass/mass)
Acer platanoides	272 (8)	2953	1.62
Acer pseudoplatanus	213 (35)	3827	2.20
Fagus sylvatica	287 (5)	3305	2.18
Quercus robur	172 (1)	2225	1.86
Tilia cordata	309 (31)	2957	1.87
Mean	251[a] (25)	3053[a] (261)	1.95[a] (0.11)
Abies alba	58.5 (4)	908	1.72
Larix decidua	103 (5)	1183	1.81
Picea abies	54.4 (9)	1770	1.20
Pinus nigra	38.6 (0.4)	3047	1.08
Pinus sylvestris	44.8 (0.3)	3165	1.18
Pseudotsuga menziesii	74.1 (2)	1400	1.32
Mean	62.2[b] (9.6)	1912[b] (394)	1.39[b] (0.12)

Notes: Values for *Picea abies* are the means of the two plantings. Different superscript letters indicate hardwood and conifer mean values are significantly different at $P < 0.05$.

platanoides, 0.5% ($P = 0.041$) for *Acer pseudoplatanus*, 0.6% ($P = 0.003$) for *F. sylvatica*, and 0.3% ($P = 0.001$) for *Q. robur*. The risk of root mortality for *L. decidua* decreased 2.5% ($P = 0.05$); *Picea abies*' risk decreased 0.2% ($P = 0.02$); *Pinus nigra*'s risk decreased 0.6% ($P = 0.001$); and *Pinus sylvestris*' risk decreased 0.5% ($P = 0.008$).

All fine roots are white when they are born. Most fine roots in this study became pigmented very quickly, within ~14 d after first appearance in the minirhizotron windows. In the six conifer species, 60–90% of the roots were brown in <2 wk. For hardwoods, the amounts were similar, with 70–88% of the fine roots becoming pigmented in <14 d.

Mycorrhizas and root anatomy

Except for a few white roots in teh ECM species, all fine roots observed in cross section were mycorrhizal, consistent with observations of roots in the minirhizotron windows. The two *Acer* species were predominantly colonized with arbuscular mycorrhizal fungi. Although *Acer* has been listed as also potentially forming ectomycorrhiza (Smith and Read 1997), trypan-blue staining of roots from the site found no evidence of ectomycorrhizal infection (B. Kieliszewska-Rokicka, *personal communication*), and none of the *Acer* roots visible in the minirhizotron windows exhibited ECM morphotypes. The other nine species were predominantly colonized with ECM fungi and frequently exhibited multiple morphotypes in close proximity. Mean mantle thickness for the ectomycorrhizal species ranged from 0.03 to 0.10 mm, with the thickest mantles appearing on the conifer species; however, in terms of thickness relative to the length of the root diameter, the largest mantles were observed on *F. sylvatica* (Table 7).

The first-order roots of both *Acer*s had a pronounced exodermis (Appendix D). Wall thickening (~20 μm thick) was only on the outer tangential walls of the exodermis (the cell layer just interior to the epidermis). Passage cells, which do not have thickened walls, were also observed in the exodermis in some sections. These would allow water, nutrients, and arbuscular mycorrhizal hyphae to enter the root cortex.

A small percentage (<2%) of the finest order roots collected for *Abies alba*, *L. decidua*, *Pseudotsuga menziesii*, *Picea abies*, *F. sylvestris*, *Q. robur*, and *T. cordata* were white; these roots had root hairs and were >2 cm long (Table 7). We examined 5–10 white, nonectomycorrhizal roots of each of the ectomycorrhizal species to note how they differed from roots with distinct mantles. A very similar, thickened exodermis was noted in the nonectomycorrhizal white roots of *L. decidua*, *Picea abies*, *Pseudotsuga menziesii*, *F. sylvestris*, *Q. robur*, and *T. cordata*. The exodermis of these six species was not as thick as that of the *Acer* species, but it was present in all root sections (Table 7, Appendix D).

Conifers vs. hardwoods

The mean root diameters of the five hardwood species with mantles, if present, were ~23% thinner than the conifer roots ($P = 0.002$; Table 3). The mean root diameters of the hardwoods excluding mantles were only marginally thinner than the conifers ($P = 0.066$).

Specific root length was significantly longer in the hardwood roots than in the conifer roots ($P = 0.01$; Table 3). Because tissue density is often negatively correlated with SRL, we predicted a similar relationship between the hardwoods and conifers for root tissue density. Root tissue density was insignificantly greater in the conifers than in the hardwoods and was not correlated with SRL ($P = 0.29$; Table 5).

Total root length density (L_v), including roots of all orders, was 53% greater in the hardwood plots than in the conifer plots ($P = 0.01$), but L_v of the finest order roots was not significantly (21%) greater in the hardwood plots than the conifer plots ($P = 0.86$; Table 3). All species had 50–61% of the total root length composed of first- and second-order roots. The mean percentage of the finest order roots in the conifers (61%) was 13% greater than that in the hardwoods ($P = 0.10$), reflecting

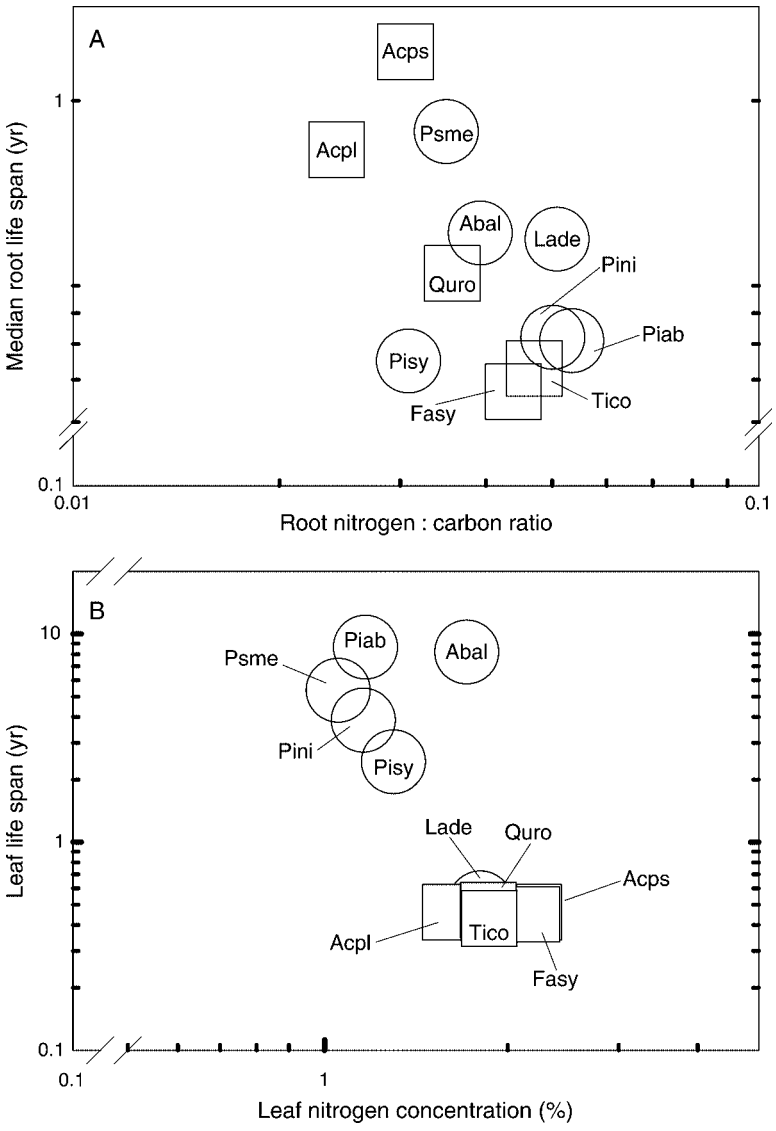

FIG. 3. The relationships between (A) longevity in roots and nitrogen : carbon ratio and (B) longevity in leaves and nitrogen concentration. Traits are on a log–log scale. Hardwoods are denoted by squares, and conifers by circles. Species abbreviations are the first two letters of the genus and species.

the differences in root architecture between the two groups (Table 3), with the hardwood species having many more orders of branching.

The range in N:C ratios was greater in the hardwood fine roots than in the conifer roots, and the overall mean value was not significantly different between the hardwood and conifer species (Table 3). Root life span was negatively correlated with N:C ratios of the hardwood species ($P < 0.0001$) but was not correlated with the N:C ratios of the conifer species ($P < 0.10$).

Root growth rate was determined by fine-root length production in the minirhizotrons. Hardwood roots tended to grow faster than conifer roots. Although variability was high, estimated root length production was ~50% greater for the hardwoods than for the conifers ($P = 0.08$).

The relationships among leaf N concentrations, SLA, and leaf production were similar to previous reports in the literature. Leaf N concentrations were significantly greater in the hardwoods than in the conifers ($P = 0.01$). Also, the SLA of the deciduous hardwood leaves was significantly greater than that of conifer leaves ($P < 0.0001$; Tables 4 and 6). Mean leaf production was significantly greater in the hardwoods than in the conifers ($P = 0.047$).

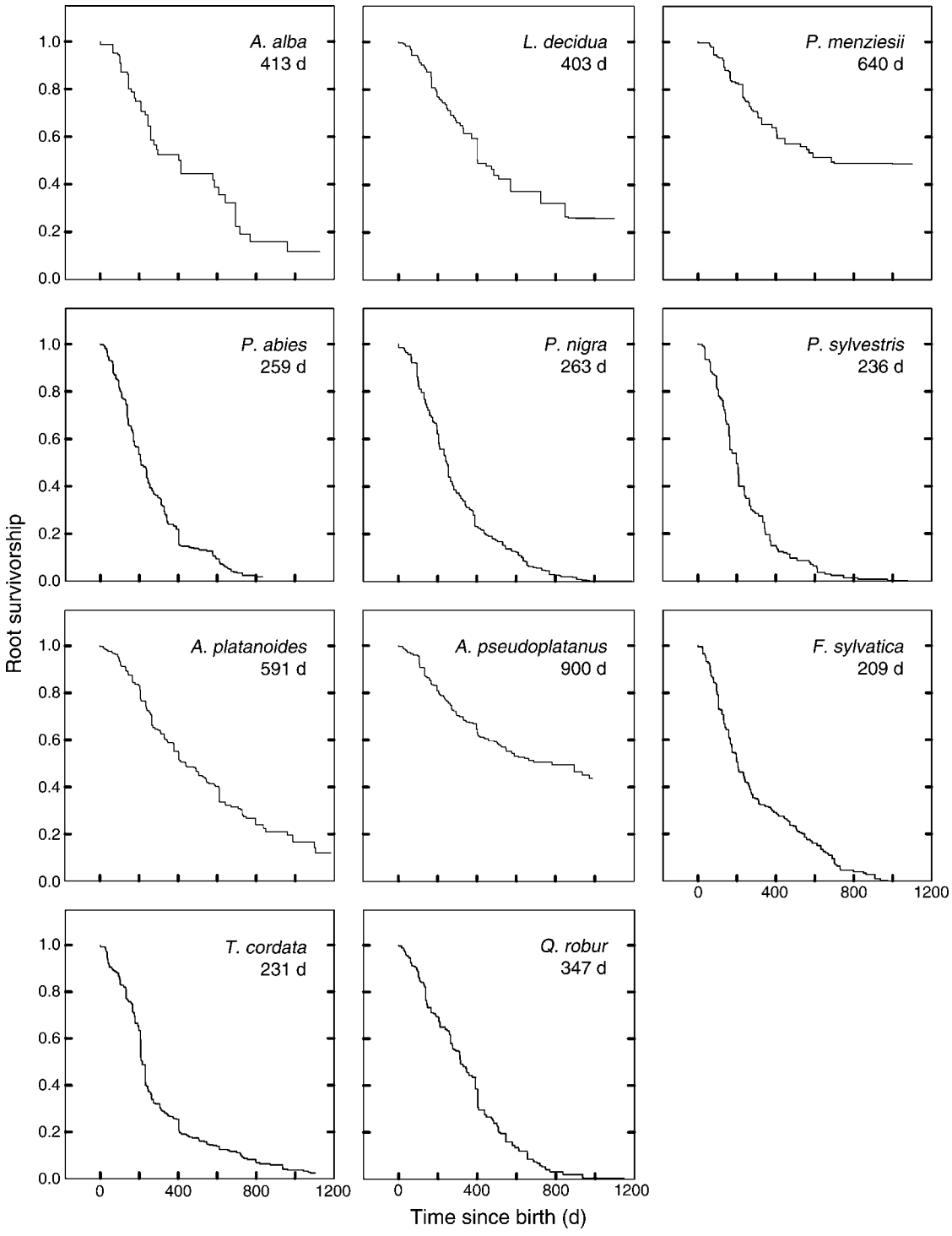

FIG. 4. Root survivorship curves from minirhizotron data for each species. Root birth and death are estimated as halfway between successive sampling dates from when a root was not present to the date it first appeared. Cox proportional hazards models were run with depth in soil, diameter, and pigmentation held constant. Median root survivorship is noted for each species.

TABLE 7. Anatomical characteristics observed and measured on mixed-age, first-order roots.

Species	XS-area (mm^2)	Mantle (%)	Epidermis	Root hairs	Exodermis
Acer platanoides	0.135	···	myc +	myc ++	++
Acer pseudoplatanus	0.164	···	myc +	myc ++	++
Fagus sylvatica	0.080	14.0	myc 0, wh +	myc 0, wh ++	myc 0, wh ++
Quercus robur	0.119	9.4	myc 0, wh +	myc 0, wh +	myc 0, wh +
Tilia cordata	0.126	5.1	myc 0, wh +	myc 0, wh ++	myc 0, wh ++
Abies alba	0.273	4.1	myc 0, wh +	myc 0, wh ++	myc 0, wh 0
Larix decidua	0.159	6.3	myc 0, wh +	myc 0, wh ++	myc 0, wh ++
Picea abies	0.166	6.3	myc 0, wh +	myc 0, wh +	myc 0, wh ++
Pinus nigra	0.108	9.4	myc 0	myc 0	0
Pinus sylvestris	0.181	9.2	myc 0	myc 0	0
Pseudotsuga menziesii	0.212	4.3	myc 0, wh +	myc 0, wh ++	myc 0, wh ++

Notes: Characteristics are as follows: mean cross-sectional area of the plant part of the mycorrhizal root (XS-area); mean percentage of the root diameter contributed by ectomycorrhizal mantle (Mantle); whether or not the epidermis (hardwoods) or the outermost layer of cortex (conifers) was largely intact (white roots, wh; mycorrhizal roots, myc; mostly intact [>90%], +; some degradation [<90%], 0); presence of root hairs (many [>16 hairs on circumference], ++; some [~10–14 hairs on circumference], +; none, 0); and presence of exodermis in white root samples (always, ++; not in every cross section, +; never, 0). An exodermis was never observed in ectomycorrhizal roots.

Relationships among root traits and leaf traits of all 11 species

Across all 11 species, SLA was inversely correlated with total root diameter ($P = 0.002$) and marginally correlated with root diameter excluding the mantle ($P = 0.07$). This relationship was mainly driven by the phylogenetic differences between the *Pinaceae* and the other tree families. Trees in the pine family tended to have leaves with lower SLA and coarser roots than those of hardwoods, which corresponds to the *Pinaceae* being an evolutionarily more primitive plant family than the hardwood families examined. Within the *Pinaceae*, there was no significant correlation between SLA and root diameter (Table 4, $r < 0.37$). Specific leaf area was positively correlated with SRL across all 11 species ($P = 0.01$; Table 4), an indication that trees that produced roots with high length:mass ratios also produced leaves with high surface area:mass ratios.

Specific root length was inversely correlated with root diameter, excluding the hyphal mantle ($P = 0.004$) and with total root diameter ($P = 0.001$; Table 5). Therefore, thinner roots had more length per unit mass. Root tissue density, a component of SRL like root diameter, was not correlated with SRL for our species.

DISCUSSION

Our study is the first of its kind, to our knowledge, to use minirhizotrons to assess such a relatively large number of tree species growing in replicated, monoculture plots. Even so, we were unable to demonstrate a correlation between fine-root and leaf life span (Fig. 2, Table 4). The different methods of estimating root life span (median, residence time based on cumulative production and cumulative mortality, residence time based on standing crop) gave similar results. The species with the longest-lived leaves (*Picea abies*) did not have the longest-lived fine roots, nor did the species with the shortest-lived leaves (the deciduous species) have the shortest-lived roots. There was also no correlation of root life span with leaf life span among the six *Pinaceae* species, although they had a large range in both leaf and root life span. Similarly, Ruess et al. (2003) found *Picea mariana* to have long-lived leaves but short-lived fine roots (~0.3 yr).

Numerous studies across a wide range of species and from a wide range of habitats have revealed a tight linkage of leaf structure with leaf life span (e.g., Reich 1993, Reich et al. 1997). In our study, shorter leaf life span was significantly correlated with high leaf N concentration and with high SLA; leaf N concentration was positively correlated with SLA (Table 4), findings that are consistent with previous results linking thin leaves with a higher maximum photosynthetic rate (indicated by leaf N concentration).

There are reasons why roots may not have trait syndromes that are similar to leaves. A root system represents numerous levels of branching that is rarely characterized with respect to its diverse functions; likely only the finest root orders are similar to leaves in terms of resource acquisition and being ephemeral (Wells and Eissenstat 2001, Pregitzer et al. 2002). Even so, the finest root orders are not discrete entities like leaves but represent the terminal ends of a network. Also, leaf function is not directly dependent on symbionts, while root carbon expenditure, resource acquisition, and perhaps defense may be strongly influenced by mycorrhizal fungi and other rhizospheric organisms. Roots also have characteristics without parallels in leaves that correlate with longevity; long-lived roots on the same root system tend to be deeper in the soil and are of higher order (Wells and Eissenstat 2001, Gill et al. 2002).

For most species, we suspect that the best estimator of root life span was median life span (LS_{50R}) based on data compiled from the fates of individual roots: no assumptions about steady-state birth and mortality rates were required, and the median tends to be the best estimator of central tendency in highly skewed distributions (e.g., survivorship). Root life span based on standing crop (LS_{SCR}) is a common way to estimate root life span when

sequential coring or ingrowth cores are used. Most of the study species achieved a fairly consistent standing crop soon after the first year (Appendix B), but LS_{SCR} calculates a mean residence time and therefore, compared to the median values, was inflated by the few, very long-lived roots of each species. Lack of steady-state conditions in which production does not equal mortality also can cause this approach to provide inaccurate estimates of life span (e.g., *Tilia cordata* and *Pseudotsuga menziesii*). Relationships among traits that were significant for the median life span were not significant for LS_{SCR}. Root life span based on cumulative production and mortality, LS_{PMR}, also provided a mean value for root life span (residence time); the values were still longer than our median estimates but were correlated with them. Life span estimates based on LS_{PMR} were potentially more accurate than the median estimate for species with long root life spans where many of the roots were censored, and roots produced early in the study perhaps did not exhibit "typical" life spans. Life span estimates based on productivity (i.e., LS_{SCR}, LS_{PMR}) are more analogous to our leaf life span measurements than the median calculated from many individual roots; however, leaf life span does not exhibit the same kind of temporal variation in production and mortality in our study species as does root life span. Thus, the different sampling efforts between root and leaves reflect the variation and predictability in their birth and death cycles.

Are root characteristics or chemistry correlated with fine-root life span?

Root nitrogen:carbon ratio was the only root characteristic significantly correlated with fine-root life span in our woody species. A study with herbaceous plants also found significant correlations of N concentration with root life span (Tjoelker et al. 2005). Because N is more directly correlated to root metabolic activity and palatability, it is likely more directly linked to root longevity than characteristics such as SRL and root production. Studies along fertility gradients (Roy and Singh 1994, Tateno and Chapin 1997, Partel and Wilson 2001) indicate N availability can influence SRL, root production, and root longevity. However, in our plots mean soil N (as ammonium and nitrate) was not correlated with either root N:C ratios or root longevity (data not shown), suggesting our results reflect genetic differences in N allocation for root absorptive capacity and defense and not plastic responses to N availability.

The means to deter herbivory are often in opposition to the means to take up resources efficiently. For example, thin leaves and roots can have higher maximum photosynthetic or nutrient absorption rates by allocating more N to those tissues, but this is at the risk of greater susceptibility to herbivory. For leaves, the relationship between N concentration and herbivore palatability has been documented (e.g., Fox and Macauley 1977, Cooke et al. 1984). For roots, the relationship is not well-studied, but there are data to suggest that the relationship should be the same. Within *Acer saccharum* root systems (Wells 1999, Eissenstat et al. 2000), the finest order roots had the highest N concentrations and shortest life spans. Application of fungicide and insecticide to the root zone significantly increased their life spans, suggesting herbivory or parasitism was an important determinant of root life span.

Specific root length is a measure of how biomass is distributed to produce absorptive surface, similar conceptually to specific leaf area. It has been hypothesized that SRL is linked with root nutrient uptake efficiency and life span (Eissenstat 1992, Eissenstat et al. 2000). However, even when we corrected for the presence of mycorrhizal hyphal mantles on the nine ECM species, our results did not reveal a relationship between SRL and root life span (Table 5). Species with similar SRL values often had very different root life spans (e.g., *Picea abies* and *Pseudotsuga menziesii*). Tjoelker et al. (2005) also found no relationship between SRL and root life span.

When we examined other root traits within each species that could influence root life span, root depth and rate of pigmentation were the most closely associated with risk of root mortality (Appendix C). Compared to roots in the surface soil layers, roots deeper in the soil tend to have lower N concentrations (Kimmins and Hawkes 1978, Pregitzer et al. 1998). Deeper roots also tend to experience less variable temperatures, less variable moisture, and possibly fewer herbivores, all of which could result in the longer root life spans we observed.

Faster rates of pigmentation were associated with decreased root longevity within each species (Appendix C). Pigmentation is often an indication of tannin accumulation for defense as well as decreased physiological activity (Comas et al. 2000). If pigmentation in our system was an indication of decreased physiological activity associated with aging, then roots that pigmented faster might also have shorter life spans. However, we also noted in the stained root cross sections that mycorrhizal roots contained more phenolic compounds. If pigmentation was an indication of mycorrhizal fungal infection (e.g., roots without exodermis), then the shorter life spans might have been the result of the mycorrhizal presence or the lack of an exodermis.

Within the root system of a plant, diameter has often been an important correlate of root life span (Gill et al. 2002, Wells et al. 2002, Anderson et al. 2003); however, it was not an important characteristic in our study. This was most likely due to the limited range of root diameters we included for each species to be certain we included only the finest root orders (see *Methods*, Appendix A).

Do the roots of conifers live longer than the roots of hardwoods?

Matamala et al. (*Liquidambar styraciflua* vs. *Pinus taeda*, 2003) and Vogt and Bloomfield (1991) have suggested hardwood species might have shorter root life

spans than those of conifers. However, in our study, we found the two groups had similar root life spans, regardless of how root life span was estimated. We also measured many traits that were similar between the two groups (e.g., diameter, production), suggesting that fine roots of different species have similar functions to match the similar traits.

There has been some previous indication that hardwood roots have smaller diameters than conifer roots (Comas and Eissenstat 2004). While evolutionarily primitive hardwood families, like the *Magnoliaceae*, tend to have thicker roots (Baylis 1975), our hardwood species were all from more advanced families (*Aceraceae*, *Fagaceae*, and *Tiliaceae*) and would be predicted to have thin diameters. Even so, we found substantial overlap in the root diameter values of the hardwoods and conifers. Not finding hardwood root diameters to be significantly thinner than conifer root diameters may be due to the inclusion of only first- and second-order roots in our study with a very narrow range in root diameters for each species (e.g., 0.20–0.35 mm). Alternatively, averaging all the root diameters to one value per species for the correlation matrix might have obscured potential relationships.

Although diameters were not significantly different between the hardwoods and conifers, hardwood roots had significantly longer SRL than the conifers. With higher SLA, greater leaf N concentration, and higher SRL in hardwoods than conifers, it was unexpected to find hardwood roots had significantly lower (−27%) N:C ratios. This observation was possibly due to the N content of the chitin in the larger ECM fungal masses associated with the conifer roots (Markkola et al. 1995).

Leaf biomass production was positively correlated with root length production (Table 4). Production was generally higher in the five hardwood species both above and below ground (Tables 3 and 6), reflecting their faster growth habit compared to the conifers. Even so, there was overlap of root and leaf production between the two groups (Tables 3 and 6). For example, the two *Pinus* species had high leaf production compared with the other four conifers, values more similar to the hardwoods.

Acer *and* Larix.—The extremely long median root life spans of *Acer platanoides* and *A. pseudoplatanus* in our study were unexpected based on their high rate of root production and short leaf life span. Our observation of a very thick, pronounced exodermis may explain their long-lived roots. The exodermis can decrease the rate of ion uptake in the root, but it can provide a protective layer against herbivory and desiccation even after the epidermis has broken down and sloughed off (Kamula et al. 1994, Eissenstat and Achor 1999).

We observed a distinct exodermis in the fine roots of both *Acer* species. Brundrett and Kendrick (1988) reported a similar type of exodermis in *Acer saccharum*. White, nonectomycorrhizal roots with exodermis were also observed in many of the conifers as well as *F. sylvatica*, *Q. robur*, and *T. cordata* (Table 7). These kinds of roots have been reported before for *Pseudotsuga menziesii* (Bogar and Smith 1965). However, we could find no report of the roots of other species in the *Pinaceae* having an exodermis. The exodermis found in the white, nonectomycorrhizal roots, though thinner than the exodermis of the *Acer* species, helps explain our finding that roots that remained white longer tended to have longer root life spans (Appendix C). The exodermis in these species should provide similar protection and increased root longevity as previously suggested in *Acer*.

Larix decidua is an interesting case since it is a deciduous conifer. Aboveground, *L. decidua* is a fast-growing species with high SLA, high leaf nitrogen concentration, and short leaf life span (Tables 2 and 6). Like the leaves, *L. decidua* roots had low root tissue density and had the highest SRL among the *Pinaceae* species. In these aspects, it was more like the deciduous hardwoods in the study, as our hypothesis on parallel root and leaf traits predicted. However, *L. decidua* root production was the slowest of the studied species, its N:C ratio and mean root diameter were large, and its roots lived for a long time (Tables 2 and 3), making *L. decidua* roots similar to other *Pinaceae* roots. *Larix* is a good example of how plants, especially trees, can have very different characteristics above and below ground.

Conclusions

We could not support the hypothesis that fine-root life span and leaf life span are linked. Some species (e.g., *Acer pseudoplatanus*) had short-lived leaves (0.5 yr) but very long-lived fine roots (2.5 yr), while other species (e.g., *Picea abies*) had very long-lived leaves (8.8 yr) but short-lived fine roots (0.7 yr). The roots of the *Acer* species with their thick exodermis were apparently built to survive a long time, their life span controlled to a great extent by their anatomy instead of their physiology. Of the rest of the root traits we measured, only root nitrogen : carbon ratio was inversely correlated with fine-root life span. Even though roots and leaves are on the same individual, they can be under very different environmental pressures, which may cause them to be uncoupled. Because of mycorrhizas, root exudates, and the nature of nutrient cycling, root structure may not be as tightly linked to root life span as leaf structure is linked with leaf life span.

Root life span research lags behind leaf life span research, not due to the lack of important questions, but due to the extensive labor required to characterize root longevity, the need for special technical equipment, and the lack of suitable field sites. Within these limitations, various studies have found relationships among root traits and life span in grasses, forbs, lianas, and trees, but many of these looked at only one or two species or made comparisons among roots on the same individuals. With more research comparing roots of many species, including careful attention to the measurement of root life span, we hope that the interrelationship among root

traits and root life span will eventually be as well understood as those of leaves.

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APPENDIX A

A figure showing percentage of first- and second-order root tips in 10 μm diameter classes (*Ecological Archives* M076-014-A1).

APPENDIX B

A figure showing root standing crop against minirhizotron tubes from May 1999 to November 2002 (*Ecological Archives* M076-014-A2).

APPENDIX C

A table showing the effects of diameter, soil depth, and number of days until a white root turned brown (pigmentation) on the risk of fine-root mortality calculated using Cox proportional hazard regression (*Ecological Archives* M076-014-A3).

APPENDIX D

Cross sections of first-order *Acer pseudoplatanus* and *Picea abies* roots showing presence of endodermis (*Ecological Archives* M076-014-A4).