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Research

Predicting fine root lifespan from plant functional traits in temperate trees

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Summary

- Although linkages of leaf and whole-plant traits to leaf lifespan have been rigorously investigated, there is a limited understanding of similar linkages of whole-plant and fine root traits to root lifespan. In comparisons across species, do suites of traits found in leaves also exist for roots, and can these traits be used to predict root lifespan?
- We observed the fine root lifespan of 12 temperate tree species using minirhizotrons in a common garden and compared their median lifespans with fine-root and whole-plant traits. We then determined which set of combined traits would be most useful in predicting patterns of root lifespan.
- Median root lifespan ranged widely among species (95–336 d). Root diameter, calcium content, and tree wood density were positively related to root lifespan, whereas specific root length, nitrogen (N) : carbon (C) ratio, and plant growth rate were negatively related to root lifespan. Root diameter and plant growth rate, together (R^2 = 0.62) or in combination with root N : C ratio (R^2 = 0.76), were useful predictors of root lifespan across the 12 species.
- Our results highlight linkages between fine root lifespan in temperate trees and plant functional traits that may reduce uncertainty in predictions of root lifespan or turnover across species at broader spatial scales.

Introduction

Fine roots play a key role in soil nutrient, water, and carbon (C) cycling. Globally, up to one-third of terrestrial net primary productivity is allocated to fine roots (Jackson *et al.*, 1997) and fine root lifespan specifically controls a dominant flux of C from plants into soils through the turnover of root tissue. Fine root lifespan also exerts an indirect control on nutrient and water uptake by mediating the total amount of roots present as well as the age structure and uptake efficiency of a root population. Still, owing to the difficulty of observing roots directly, quantifying fine root lifespan represents a particular challenge in ecology while, by contrast, global patterns of leaf traits and function have been characterized across biomes and plant functional types (Reich *et al.*, 1992, 1998; Wright *et al.*, 2004). Our inability to describe patterns of root lifespan across species limits both our empirical understanding of terrestrial ecosystems and our ability to model water, nutrient and C fluxes within these systems based on plant functional traits.

Researchers have long sought to link plant traits with suites of functional traits describing plant and ecosystem processes at a range of spatial scales (Reich *et al.*, 1992; Wright *et al.*, 2004; Westoby & Wright, 2006; Swenson & Enquist, 2007). However, few studies have been able to link fine root lifespan in a broad context with species- and root-specific traits. Those that have are primarily limited to reviews that have compared estimates across sites and methodologies (Gill & Jackson, 2000; Peek, 2007; Gu *et al.*, 2011). These reviews, and the few studies that have directly observed root lifespan across species, suggest that relationships may indeed exist between fine root lifespan and other functional traits. Gu *et al.* (2011) reviewed fine root lifespan in temperate trees across eight studies and found that root diameter and root order (related to root diameter) were positively correlated with root lifespan. Withington *et al.* (2006) found that root N : C ratio was negatively correlated with root lifespan in temperate trees but root diameter was not related to lifespan. The lack of a relationship between root diameter and lifespan may be the result of the relatively narrow range in root diameter of the tree species included in the study. Other studies of grassland species have identified these same relationships between root nitrogen (N) concentrations, or N : C ratios, and root lifespan as well as a positive relationship between root lifespan and root tissue density and a negative relationship with root respiration (Ryser, 1996; Schlapfer & Ryser, 1996; Tjoelker *et al.*, 2005). While these studies were conducted with grassland species, sometimes used containers, and did not involve direct root observation, they are largely consistent with observations in leaves. In global data sets of a wide range of species and habitats, respiration and tissue

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density of leaves are often linked to leaf lifespan in addition to traits such as leaf tissue N concentration and leaf thickness (Reich *et al.*, 1992; Wright *et al.*, 2004).

Because roots of co-occurring plants strongly intermix and can be difficult to distinguish at the species level, few studies have examined species-specific differences in root lifespan. Here we observed species-specific fine root lifespan in 12 temperate trees from eight genera of widely diverging phylogeny using mini-rhizotrons in a common garden in central Pennsylvania, USA. Unlike previous studies, this 13-yr-old common garden allowed us to directly contrast roots of different species of widely different root morphology and life history traits and determine relationships between fine root lifespan and plant functional traits. We had three specific objectives in this study. First, we examined whether fine root lifespan in trees is related to root morphological, physiological, and chemical traits. We hypothesized that root N : C ratio, respiration, and specific root length (SRL) would be negatively related to lifespan, whereas root diameter, tissue density, calcium (Ca) content, sugar and carbohydrate concentration would be positively related to fine root lifespan. Additionally, we tested whether root lifespan of trees colonized by arbuscular mycorrhizal (AM) fungi differed from that of ectomycorrhizal (EM) trees – differences in mycorrhizal fungi can strongly impact root morphology and chemistry (Smith & Read, 2008). Secondly, we examined whether fine root lifespan is related to whole-plant traits such as growth rate or wood density, which have been identified as important traits related to other physiological and structural properties of plants (Chave *et al.*, 2009; van Kleunen *et al.*, 2010). We hypothesized that root lifespan would be positively related to wood density and negatively related to plant growth rate. Together, these root and whole-plant traits represent a suite of relatively easy-to-measure, interrelated traits with logical connections to fine root lifespan (Fig. 1, Supporting Information, Notes S1). However, because an appreciable portion of the variation in fine root lifespan is likely to be decoupled from any one trait or group of correlated traits, our third objective was to determine whether qualitative or quantitative estimates of fine root lifespan based on a combined model of whole-plant and fine root traits could further improve our understanding of fine root lifespan. Our third objective will help identify predictors of fine root lifespan and develop indices of root dynamics in the absence of empirical survivorship data. This is particularly important given the difficulty of root measurements and the pressing need to improve descriptions of below-ground processes in ecosystem- and landscape-scale modeling efforts (Ostle *et al.*, 2009; Iversen, 2010).

Materials and Methods

Site description

The common garden site is located in central Pennsylvania, USA (40°42′N 77°57′W) and is a randomized complete block design consisting of 16 tree species in eight replicated blocks. The soil is well drained, moderately fertile Hagerstown silt loam with pH ranging from 6.1 to 6.5. Before 1995, the site was a grass hayfield. Each species plot consisted of six individual trees planted in two rows with a spacing of 3 m within and between rows. Spacing between plots was 5 m. Most individual trees were planted from 1-yr-old nursery seedlings in 1996, except for *Acer negundo* and *Sassafras albidum* which were transplanted from locally collected seedlings. *A. negundo* was planted in 1996 while *S. albidum* was planted in 1998. During the time of the study, most trees were between 12 and 15 yr old.

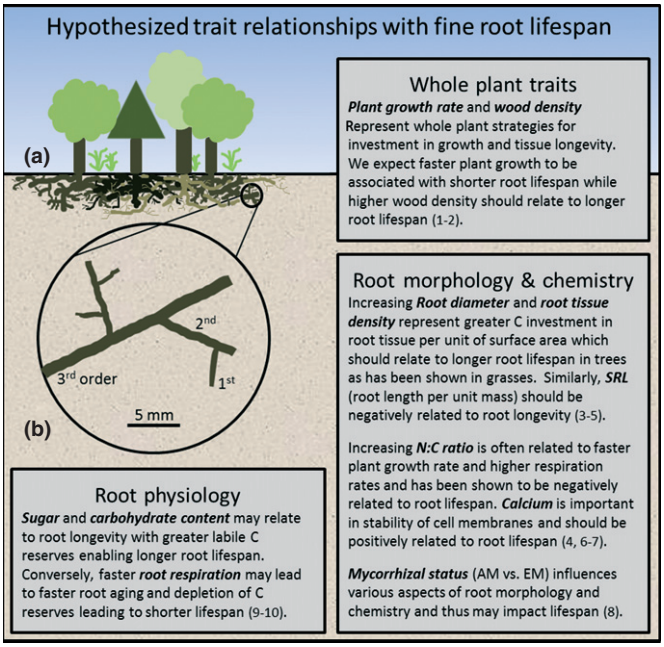

Fig. 1 Hypothesized relationships between measured fine root and whole-plant traits with fine root lifespan (SRL, specific root length; AM, arbuscular mycorrhizal fungi; EM, ectomycorrhizal fungi). The figure also demonstrates the intermixing of roots between species below ground despite relatively well partitioned space between species above ground (a) and a basic diagram of morphometric root ordering scheme used in our root dissections (Fitter, 1982; Pregitzer *et al.*, 2002) highlighting first-, second-, and third-order roots (b). References: 1, Reich *et al.* (1992); 2, Metcalfe (2003); 3, Wells & Eissenstat (2001); 4, Tjoelker *et al.* (2005); 5, McCormack *et al.* (2010); 6, Marschner (2012); 7, Withington *et al.* (2006); 8, Smith & Read (2008); 9, Marshall & Waring (1985); 10, Pregitzer *et al.* (1998).

Plant traits

The 12 species used in this study exhibited a wide range of life histories and fine root traits (Tables 1, S1) and included three congeneric contrasts (three *Acer*, two *Pinus*, and two *Quercus* species). Trunk diameter at breast height (DBH) at 10 yr of age was used as an integrative measure of whole-plant growth over 10 yr. These site-specific measurements of plant growth were qualitatively compared with more widely available estimates reported in *Silvics of North America* (Burns & Honkala, 1990a,b) and were similar.

Stem wood density was measured in July 2011. For each species plot, one live branch between 5 and 10 cm in diameter was collected. To minimize differences in wood density resulting from microclimate variability, lower branches (shaded) were collected from the interior portion of the plot whenever possible.

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Table 1 Fine root and whole-plant traits of 12 temperate tree species measured in a common garden in central Pennsylvania, USA

Species	SRL[a] ($m\ g^{-1}$)	RTD[a] ($g\ cm^{-3}$)	N : C ratio[1]	Resp.[b] (nmol $O_2\ g^{-1}\ s^{-1}$)	Ca content[1] ($mg\ g^{-1}$)	Sugars[a] ($mg\ g^{-1}$)	TNC[a] ($mg\ g^{-1}$)	Wood density ($kg\ m^{-3}$)	DBH at 10 yr (cm)
Acer negundo	44.5 (2.7)	0.55 (0.01)	0.053 (0.002)	5.3 (1.0)	6.92 (0.60)	7.9 (2.0)	12.6 (4.5)	597 (15)	13.8 (1.0)
Acer rubrum	46.2 (2.2)	0.43 (0.05)	0.043 (0.002)	5.1 (1.6)	5.72 (0.51)	18.1 (5.9)	19.8 (7.1)	639 (34)	10.4 (0.4)
Acer saccharum	45.1 (2.9)	0.57 (0.04)	0.041 (0.003)	4.1 (0.3)	7.35 (0.84)	17.5 (2.2)	29.4 (7.5)	786 (17)	10.4 (0.4)
Carya glabra	91.0 (5.2)	0.58 (0.10)	0.061 (0.013)	5.6 (3.3)	12.63 (4.30)	18.6 (7.3)	25.7 (4.4)	903 (36)	6.4 (0.5)
Juglans nigra	20.2 (3.1)	0.83 (0.01)	0.059 (0.001)	10.6 (3.1)	11.61 (0.69)	75.0 (1.1)	78.1 (4.8)	706 (21)	12.8 (0.7)
Liriodendron tulipifera	8.9 (1.3)	0.32 (0.04)	0.054 (0.002)	9.1 (2.4)	3.86 (0.70)	35.8 (0.3)	51.3 (7.1)	577 (38)	15.9 (0.6)
Pinus strobus	33.4 (12.7)	0.67 (0.04)	0.039 (0.003)	3.9 (0.8)	8.27 (0.58)	27.0 (9.2)	32.7 (14.0)	510 (25)	10.2 (0.6)
Pinus virginiana	33.1 (1.8)	0.74 (0.05)	0.048 (0.011)	6.7 (0.8)	12.65 (2.75)	38.2 (15.6)	48.2 (8.9)	610 (46)	15.1 (0.4)
Populous tremuloides	65.2 (2.1)	0.67 (0.04)	0.034 (0.007)	5.9 (0.4)	9.61 (1.85)	24.2 (1.0)	43.2 (10.4)	543 (13)	20.7 (1.3)
Quercus alba	70.4 (16.6)	0.66 (0.05)	0.042 (0.005)	4.1 (0.7)	9.01 (0.90)	32.6 (12.4)	32.3 (8.4)	923 (26)	10.0 (1.3)
Quercus rubra	64.2 (4.7)	0.75 (0.09)	0.047 (0.003)	3.6 (0.7)	7.80 (1.20)	19.6 (1.8)	19.6 (8.3)	793 (31)	12.5 (0.7)
Sassafras albidum	13.8 (0.9)	0.34 (0.06)	0.063 (0.006)	6.0 (0.4)	5.92 (1.08)	26.6 (2.4)	31.7 (4.3)	663 (21)	9.3 (0.9)

Traits reported (mean ± SE) are specific root length (SRL), root tissue density (RTD), N : C ratio, root respiration (Resp.), calcium content, sugar concentration (sugars; expressed as glucose equivalents g^{-1} root), total nonstructural carbohydrate concentration (TNC; expressed as glucose equivalents g^{-1} root), stem wood density (wood density) and trunk diameter at breast height (DBH) at 10 yr.

[a]Refers to first-order roots only.

[b]Respiration measurements were made on fresh, field collected roots. Data reported are for intact branches of first- and second-order roots.

Owing to the smaller stature of *S. albidum*, two plots did not contain branches of adequate size, but recently dead individuals were available within the plot and were used as a substitute. These recently dead trees were harvested for stem wood that was used for density calculations. The density values determined for recently dead samples were not significantly different from live branch samples ($P = 0.81$). Determination of wood density was based on a modified protocol commonly used by the wood products industry (ASTM, 2008). Briefly, for each branch sample, the bark was removed and three small blocks (*c.* 1–2 cm^3) were cut. Blocks were dried at 105°C to a constant weight (24–36 h) and their final weight was recorded. Each block was then coated in a thin layer of wax and the volume was determined by water displacement using a graduated cylinder. The density was calculated as mass/volume. The calculated density for each group of three blocks was averaged into a single value for each branch and plot.

Root traits

Root traits analyzed included characteristics of root morphology, root physiology and root chemistry. Root traits were assessed in three of the eight blocks. All traits were assessed on a root order basis following the morphometric ordering classification (Fig. 1) (Fitter, 1982; Pregitzer *et al.*, 2002).

Root harvests took place between 26 May and 27 June 2009 and covered each species' plot across three blocks ($n = 3$). Bulk root samples were collected randomly with a shovel and hand trowel from the upper layers of soil (0–15 cm depth). Each sample was inspected to ensure that it contained sufficient quantities of intact branches (including first- through fifth-order roots) for all later analyses and the soil volume excavated to collect samples varied from *c.* 2000 to 6000 cm^3. Once collected, the samples were placed in a cooler and transported immediately to the laboratory where they were dissected to order within a few hours of harvest. During dissection, care was taken to use only live, fibrous (nonpioneering; *sensu* Zadworny & Eissenstat (2011) fine roots. Furthermore, to maintain consistency between species and sample dates, roots that were clearly still actively growing were not used. A subset of the dissected roots was taken for respiration measurements (see later) and the remaining sample was scanned on an Epson Perfection 4490 desktop scanner (resolution of 400 dpi, document type set to 'film mode') and analyzed with WinRhizo software (Regent Instruments, Quebec City, Quebec, Canada) for diameter and length. These roots were then oven-dried at 70°C for *c.* 24 h, weighed and stored for later analysis. From this information, SRL was calculated by dividing the total length for a given scan by the total DW (dry weight) of the sample ($m\ g^{-1}$). An estimate of root tissue density was also calculated by dividing the total volume of the roots (assuming cylindrical geometry) by the total weight.

Immediately following dissection, a subset of roots was placed in MES buffer and then used to determine respiration using Clark-type oxygen electrodes (Hansatech Oxygraph, King's Lynn, UK). The respiration chambers were kept at a constant temperature of 19°C during all measurements. These roots were then oven-dried at 70°C for *c.* 24 h and weighed.

Dried root samples were used for carbohydrate and elemental analysis. Nonstructural carbohydrates were determined colorometrically using a modified Nelson procedure (Nelson, 1944; Smogyi, 1952). For each sample, roots were ground and replicate 5 mg samples were placed into test tubes with 1 ml of dH_2O. Samples were then boiled for 10 min and cooled to room temperature. Once cool, 100 µl of 0.5 M sodium acetate was added to one tube (tube A) while 100 µl of 0.5 M sodium acetate containing five units of amyloglucosidase and 2.5 units of α-amylase was added to the second (tube B). Following a 24 h incubation period, reducing sugar concentration was determined from tube A, and total nonstructural carbohydrate content (sugar + starch) was determined from tube B (expressed as glucose equivalents).

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For all elemental analyses, dried root samples were ground and *c.* 5 mg was used for C and N analysis and 10 mg for Ca analysis. Carbon and N concentrations were determined using a Fisons EA 1108 CNS-O Analyzer (Fisons Instruments, Mt. Pleasant, NJ, USA). For determination of Ca concentrations, samples were dry ashed at 500°C and suspended in 10 ml of 1 N HCl matrix. Samples were then analyzed by the Agricultural Analytical Services Lab (Pennsylvania State University, University Park, Pennsylvania, USA) using Inductively coupled plasma mass spectrometry (ICP-MS).

Mycorrhizal status, association with AM or ectomycorrhizal (EM) fungi, of each tree species was determined visually and compared with published resources (Smith & Read, 2008; Brundrett, 2009). Assessments were made repeatedly during the experiment using bulk roots collected from the common garden.

Minirhizotrons

Clear acrylic minirhizotron tubes were installed in 2005, with each one inserted 30 cm from the base of an individual tree at an angle of 30º from the vertical. Tubes were 45 cm long and had an inner diameter of 2.9 cm. Electrical tape was wrapped around the portion of each tube that remained above ground to prevent light penetration and this was then covered with an aluminum can that was spray-painted white to minimize solar heating of the tube. Two tubes were installed in each species plot across all eight blocks for a total of 16 tubes per species and 192 tubes in total. Following tube installation, the tube–soil interface was allowed to equilibrate for nearly 2 yr before imaging began. Beginning in May 2007, images were collected at 2–4 wk intervals from approx. April to December each year for 4 yr. Images were collected using a Bartz 1.125'' digital camera with I-CAP version 4.01 software (Bartz Technology Corp., Carpinteria, CA, USA). During 2007 each tube was imaged only on the upper surface, and images were collected on both the upper and lower tube surfaces from 2008 to 2010. Following collection, images were analyzed for root birth, death, diameter, color, and length as well as rooting depth using Rootfly 1.8.35 (Wells and Birchfield, Clemson University, SC, USA). Root death was indicated when a root fractured or shriveled to approximately half the original diameter. While it is possible that some roots may have been functionally dead before they were classified as dead in our analysis (potentially inflating our observed root lifespan estimates), we expect this occurrence to have been minimal as a result of relatively active decomposition rates under the warm, mesic conditions of the common garden site. A total of 4056 roots were tracked across > 200 000 images (*c.* 17 000 images per species).

Before statistical analysis, some roots were removed from the experiment to ensure that roots analyzed were of a known species and root order. In this study we were primarily interested in assessing the lifespan of the portion of the root system that was most active in nutrient and water uptake and had not undergone secondary growth. We therefore limited our analysis to diameter-based estimates of first- and second-order roots for each species and excluded those roots that fell outside the diameter range of the lowest two orders for a given species. This portion of the root system also accounts for a large proportion of the annual C input into the soil through biomass turnover. Diameter ranges were determined from the root scans described in the previous section (Table 1). By excluding roots outside of a known species diameter range, we were also able to control for some encroachment of roots of different species from neighboring plots. The number of roots removed from analysis for a given species generally ranged from 14 to 30%. However, because of the smaller stature of *S. albidum*, a greater number of roots observed in these plots were likely from neighboring species. Fortunately, the distinctive coarse root structure and size of *S. albidum* enabled us to confidently isolate these roots from other species and we removed a total of 56% of the roots observed in these plots.

Statistical analysis

All fine root and whole-plant traits tested in this study were identified *a priori* as traits likely to be correlated with fine root lifespan (Notes S1). Survivorship summary statistics for each species were calculated using Kaplan–Meier survival analysis (Kaplan & Meier, 1958). Kaplan–Meier survival analysis was also used to test for differences in fine root survivorship related to mycorrhizal status. Cox proportional hazards test (Cox, 1972) was used to identify whole-plant traits and fine root traits that had a significant effect on fine root lifespan. Least-squares linear regression was used to compare correlations among traits. Each species was treated as an independent replicate for regression analysis ($N = 12$). Blocking was established at initiation of the common garden. However, there was no significant effect of block on fine root lifespan of individual species ($P > 0.20$). Following identification of trait relationships, we determined the best model for predicting fine root lifespan based on fine root and whole-plant traits. This was done by selecting candidate variables and using stepwise regression to select the best combined model or models according to Akaike's Information Criterion adjusted for small sample size (AICc). Results were considered statistically significant at $P \leq 0.05$. Statistical analyses were conducted in SAS JMP 9.02 (SAS Institute, Cary, NC, USA).

Results

Measured traits and fine root lifespan

Root lifespan was longest in *Quercus alba* (336 d) and shortest in *Populus tremuloides* (95 d), consistent with their differences in life history (Table 2, Supporting Information, Fig. S1). The coefficient of variation in observed lifespan within a genus was typically as big as, or bigger than, it was across all 12 species (Table S2). Root traits other than lifespan were generally similar within a genus but varied greatly across the 12 species (Table 1). Specific root length ranged from 8.9 m g^{-1} in *Liriodendron tulipifera* and 13.8 m g^{-1} in *S. albidum* to 70.4 m g^{-1} in *Q. alba* and 91.0 m g^{-1} in *Carya glabra*, while N : C ratio was more constrained and ranged from 0.034 in *P. tremuloides* to

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Table 2 Summary of root diameter and survivorship results for 12 tree species grown in a common garden in central PA, USA

Species	Average diameter[a] (mm)	Diameter range[b] (mm)	Median days	Lower 95%	Upper 95%	Mean time (d)	Number observed[c,d]	Number censored
Populous tremuloides	0.22	0.06–0.29	95	84	111	153	429	93
Acer negundo	0.28	0.11–0.43	190	163	193	252	271	82
Juglans nigra	0.30	0.11–0.45	207	169	252	204	55	22
Quercus rubra	0.23	0.07–0.34	235	112	319	277	104	40
Carya glabra	0.22	0.06–0.28	247	235	267	254	305	97
Acer rubrum	0.29	0.09–0.43	259	234	283	293	507	149
Pinus virginiana	0.30	0.11–0.44	283	271	303	315	194	57
Pinus strobus	0.31	0.11–0.49	296	263	407	341	50	24
Sassafras albidum	0.56	0.41–0.90	317	291	324	322	159	87
Liriodendron tulipifera	0.64	0.45–1.16	323	294	350	332	118	49
Acer saccharum	0.30	0.10–0.46	324	280	364	359	185	80
Quercus alba	0.25	0.07–0.33	336	291	356	319	257	90

Species are arranged in order of shortest to longest lifespan. Upper and lower 95% refer to confidence intervals for median lifespan. 'Number censored' refers to roots whose birth was observed but whose death was not directly observed because the experiment ended or because of shifts in the soil that resulted in roots no longer being able to be observed.

[a]Average diameter observed in minirhizotron images.

[b]Diameter range of first- and second-order roots determined from scans of field collected roots.

[c]Total number of roots observed for each species and included in the analysis after removal of all roots outside of determined diameter range for first- and second-order roots.

[d]Dividing the number of roots observed by 560 cm^2 (total minirhizotron viewing area per species) yields a relative root density measure (e.g. root density equals 0.91 roots cm^{-1} for *A. rubrum* and 0.46 roots cm^{-1} for *Q. alba*).

0.063 in *S. albidum*. Other root traits tended to vary three- or fourfold across the species.

Diameter at breast height at 10 yr ranged from 9.4 to 27.6 cm (*S. albidum* and *P. tremuloides*, respectively), and wood density ranged from 518 to 926 kg m^{-3} (*Pinus strobus* and *Q. alba*, respectively). Variability in whole-plant traits was relatively large both within the genus and across all 12 species (Table S2). Fine root lifespan was positively correlated with wood density and negatively correlated with DBH at 10 yr ($P = 0.003$, Table 3). The apparent effect of increasing DBH at 10 yr was greater than that of wood density, as indicated by the unit risk ratios. The risk of root mortality increased by *c.* 6% with a 1.0 cm increase in DBH.

Table 3 Summary of proportional hazards fit for effects of plant and root traits on root survivorship

Factor	χ^2	$P > \chi^2$	Risk ratio
Root traits			
Diameter	52.5	**<0.001**	0.11
Depth	13.2	**<0.001**	0.98
SRL	26.2	**<0.001**	1.02
Ca content	5.4	**0.02**	0.91
Sugars	0.5	0.26	–
Carbohydrates	1.8	0.29	–
N : C Ratio	9.8	**0.002**	> 2.0
Tissue density	0.8	0.18	–
Respiration	0.6	0.45	–
Plant traits			
Wood density	7.9	**0.003**	0.998
DBH at 10 yr	0.1	**0.002**	1.06

Risk ratios < 1.0 indicate a positive relationship with lifespan and risk ratios > 1.0 indicate a negative relationship. Risk ratios are only reported for factors that are significant ($P < 0.05$). Bold values represent significant results.

SRL, specific root length; DBH, trunk diameter at breast height.

Across all species, fine root lifespan significantly increased with increasing root diameter, depth in soil, and Ca content and significantly decreased with increasing SRL and N : C ratio ($P \leq 0.02$, Table 3). Of these traits, the unit risk ratios indicated that root diameter, Ca content, and N : C ratio had the greatest effect on root lifespan. Accordingly, a 0.1 mm increase in root diameter and a 1.0 mg g^{-1} increase in root Ca content each resulted in a *c.* 9% decrease in the risk of root mortality, while the negative effect on root lifespan of increasing N : C ratio was also substantial. Because diameter and depth were measured for each root observed in the study, we also tested whether these traits were significant at the individual species level. Eight out 12 species showed a significant increase in lifespan with increases in diameter (*A. negundo*, *C. glabra*, *P. tremuloides*, and *S. albidum* were not significant). Only four of the 12 species showed a significant increase in lifespan with depth (*A. negundo*, *C. glabra*, *L. tulipifera,* and *P. strobus* were significant; $P \leq 0.05$). Sugar content, carbohydrate content, root tissue density, and root respiration were not significantly related to fine root lifespan ($P > 0.25$).

Mycorrhizal status (AM associate vs EM associate) was not associated with shorter or longer lifespan (log-rank $P = 0.95$, Wilcoxon $P = 0.08$). Each tree species was associated with only one type of mycorrhizal fungi, except for *P. tremuloides* which, though dominantly associated with AM fungi during the time of the study, was also observed to commonly associate with EM fungi. As such, *P. tremuloides* was omitted from the analysis of mycorrhizal status and fine root lifespan.

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Combined model of fine root lifespan

Of the seven variables that were significantly related to fine root lifespan according to Cox proportional hazards (Table 3), we selected four potential candidate variables to describe fine root lifespan: DBH at 10 yr, observed root diameter, N : C ratio, and Ca content. The variables wood density and SRL were not included because of strong covariance with other variables (DBH at 10 yr with wood density and observed root diameter with SRL, Table S3). Depth was not used as it was not relevant for describing fine root lifespan of an entire population. The best model based on lowest AICc scores included observed diameter and DBH at 10 yr (Fig. 2, Table S4). The model explained less variation (R^2 = 0.62) than did the second ranked model, which included observed root diameter and DBH at 10 yr as well as N : C ratio (R^2 = 0.76, ΔAICc = 0.894). The full model, including all four variables, only explained *c.* 4% more of the variation and had a distinctly higher AICc score.

Discussion

Plant species vary widely in fine root lifespan, creating formidable challenges for scaling root longevity and turnover to broader spatial scales. To address these challenges, we took advantage of a long-term common garden experiment and developed a unique data set by directly observing fine root lifespan separately for 12 diverse species of temperate trees over 4 yr. Observations of fine root lifespan were compared with a suite of measured fine root and above-ground plant traits. We then used observed relationships between plant and root traits to identify generalizable indices of root lifespan across species.

At our site, median fine root lifespan ranged from 95 to 336 d (Table 2, Fig. S1). Our observed root lifespans for each species are broadly consistent with previously published minirhizotron data, with pines, oaks and some maples typically having roots of moderate to longer lifespan (Coleman *et al.*, 2000; Withington *et al.*, 2006; Pritchard *et al.*, 2008; Espeleta *et al.*, 2009; McCormack *et al.*, 2010; Stover *et al.*, 2010). Addressing our first objective, we examined whether fine root traits were correlated with fine root lifespan and found that, consistent with our hypothesis, fine root diameter and Ca content were correlated positively with fine root lifespan, whereas N : C ratio and SRL were correlated negatively with fine root lifespan. Previous studies of temperate trees have identified a positive relationship between root diameter and fine root lifespan. However, this has most commonly been observed *within* the root system of plants of a single species (Wells & Eissenstat, 2001; Withington *et al.*, 2006; Guo *et al.*, 2008). Here we found that diameter of the lowest two root orders significantly explained the differences in fine root lifespan *across* species. Species with larger-diameter first- and second-order roots tended to have longer root lifespans than those with smaller diameter roots. For example, *P. tremuloides* and *L. tulipifera* have similar whole-plant traits (i.e. fast growth and low wood density), but *P. tremuloides* has smaller-diameter fine roots, and correspondingly shorter fine root lifespan, than *L. tulipifera*. A few previous studies have observed fine root lifespan in mixed forests that contain tree species with roots of contrasting diameter sizes (relatively thicker and thinner fine roots) (Tierney & Fahey, 2002; Strand *et al.*, 2008). In these studies, root diameter was found to be related significantly to root lifespan, which likely was caused by a combination of both variation within root systems of roots of different orders and variation across species. The concept that larger-diameter roots live longer supports a resource optimization concept, as the greater C investment per unit root length required by larger-diameter roots should be coupled with longer lifespan to ensure a favorable nutrient and water return on the higher carbon investment compared with smaller-diameter roots (Eissenstat & Yanai, 1997).

Unlike diameter, the relationship between Ca content and root lifespan has not been identified in previous studies. However, the broader role for Ca from the tissue level and the ecosystem level is increasingly being recognized (Juice, 2006). An interesting area of future study may be in understanding the role of Ca in maintaining root function and longevity under stress and how this impacts whole-plant or ecosystem function.

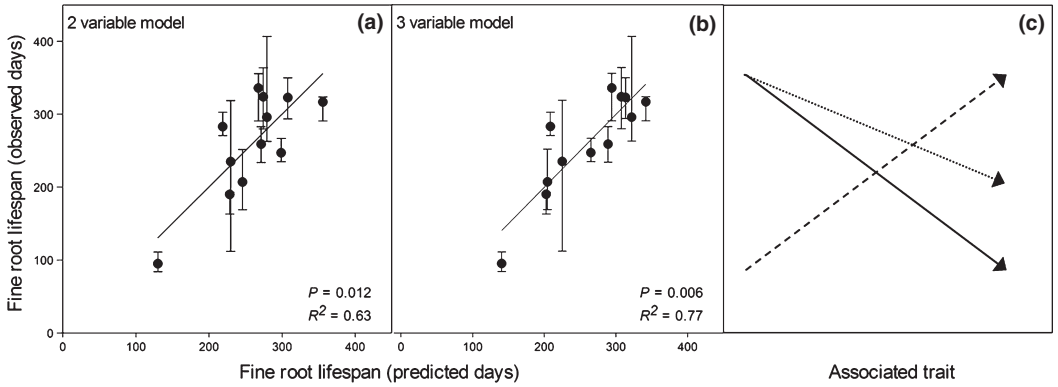

Fig. 2 Relationships between fine root lifespan and fine root and whole-plant traits. (a, b) Regression plots of observed fine root lifespan (± 95% CI) vs predicted fine root lifespan based on a two-variable (diameter at breast height (DBH) at 10 yr and root diameter) or three-variable (DBH at 10 yr, root diameter, and root N : C ratio) model. Parameter estimates for each model are contained in Table S5. (c) Conceptual model of the direction and relative strength of relationships of plant growth rate (solid line), root diameter (dashed line), and root N : C ratio (or similarly root N content; dotted line) with fine root lifespan.

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Of the remaining root traits examined, we found no apparent relationship between these traits and fine root lifespan. Although traits like root respiration and carbohydrate content have logical connections to lifespan (Notes S1), they are also variable through time and with local environmental conditions (Comas & Eissenstat, 2004; Sayer & Haywood, 2006; Drake *et al.*, 2008). It is possible that the high variability in these traits makes detecting consistent relationships with root lifespan difficult. Previous work has also shown that nonstructural carbohydrates may be mobilized from higher-order roots to support fine root metabolism, alleviating limitations of carbohydrate reserves to fine root lifespan (Guo *et al.*, 2004). In either case, because variability through time or mobilization of carbohydrates forms higher-order roots, we find no support for the hypothesis put forth by Marshall & Waring (1985) that fine root lifespan should be determined by their carbohydrate content and respiration rates. In addition, we detected no relationship between fine root lifespan and root tissue density ($P = 0.64$, $R^2 = 0.02$), despite finding a strong correlation between root lifespan and stem wood density. This was somewhat surprising because we expected root tissue density to be correlated with whole-plant measures of stem wood density and growth. Furthermore, root tissue density has been found to relate to root longevity and many other root and plant traits (Ryser, 1996; Roumet *et al.*, 2006). However, these patterns were mostly observed in nonwoody species, the investigators did not separate roots by order, and trends may not apply to comparisons across the finest roots in trees. Our field observations also suggest that our measures of root tissue density might not capture all aspects of the toughness (e.g. fiber strength) of the roots. In the field, fine roots of both *Quercus* species and *Carya glabra* roots were noticeably more difficult to break, which would be consistent with the relatively long lifespan of these species despite their small diameters. Other measures, such as stele to cortex ratio, or other indicators of mechanical strength may be needed to better capture the presumed linkages between root toughness (defense) and lifespan.

Evaluating our second objective, we showed that plant growth rate (measured by DBH at 10 yr) was negatively related to root lifespan, with faster-growing species having shorter fine root lifespan. Wood density was positively related to lifespan and qualitatively explained a similar portion of variation in fine root lifespan as DBH at 10 yr, which is not surprising as wood density and growth rate are often correlated (Zhang, 1995; King *et al.*, 2006). Because whole-plant traits like potential growth rate and wood density are not directly linked to root-level processes, it is somewhat difficult to discern any direct mechanistic connection between growth rate and fine root lifespan. It is more likely that these traits are representative of a syndrome of correlated traits at the whole-plant and organ level (e.g. slow growth, greater investment in tissue construction and defense, lower photosynthetic/metabolic rates, etc.).

Previous research has shown root traits such as root diameter and SRL to be relatively conserved within a given phylogeny (Comas & Eissenstat, 2009). We found this to be true in our data, which might limit our ability to predict differences in root lifespan based solely on root traits. However, we were still able to explain much of the variation in lifespan within a genus based on the life history traits (plant growth rate and wood density) of each species. This was particularly true for the *Acer* and *Quercus* genera. In each case, large variation in fine root lifespan among congeneric species could be explained based on growth rate and wood density differences, despite similar patterns in root traits. Unlike in *Acer* and *Quercus*, differences in growth rates and wood densities of our two *Pinus* species (*Pinus strobus* and *Pinus virginiana*) do not clearly indicate that one species should have longer-lived roots than the other. The faster growth of *P. virginiana* suggests shorter fine root lifespan, whereas the greater wood density of *P. virginiana* suggests longer fine root lifespan than that of *P. strobus*. The similarity in observed fine root lifespan for *P. strobus* and *P. virginiana* (median of 296 and 283 d, respectively) were consistent with the mixed signal associated with their life history strategy.

In addition to whole-plant traits, previous research has attempted to link root lifespan with leaf lifespan (Schlapfer & Ryser, 1996; Withington *et al.*, 2006). Although we did not directly address connections between leaf and root lifespan, we found little to support the idea that the two traits would be correlated across temperate tree species. While the pine species at our site had substantially longer leaf (needle) lifespan than deciduous species, their root lifespans were roughly average across all 12 species. Even within the deciduous species, there was little evidence for any correlation. For example, *P. tremuloides* and *A. negundo* leaves emerged early in the season and remained until roughly the same time as the other deciduous species at the common garden, yet they had the shortest root lifespan. Correlations of leaf and root lifespan may still possibly exist in woody tree species within constrained phylogenies (i.e. angiosperms vs gymnosperms) but likely require substantially more species than used in this study for detection. Alternatively, root and leaf lifespan may be uncorrelated in woody trees. Unlike leaves, root function can be strongly influenced by its symbiotic relationship and mycorrhizal fungi, and this symbiosis can dramatically alter the ability of roots to acquire limiting resources. In addition, roots are often exposed to considerably different environmental constraints than leaves experience above ground, leading to different selection pressures for root lifespan and leaf lifespan (Eissenstat & Yanai, 1997). Thus, in seasonally dry environments, evergreen species such as those in the Proteacea, may have short-lived cluster roots near the soil surface for nutrient foraging (Skene *et al.*, 1998), and species in the genus *Picea* may cope with low and episodic nutrient availability in boreal environments with long-lived leaves but short-lived roots (Ruess *et al.*, 2003; Withington *et al.*, 2006).

Addressing our third objective, we developed two models that highlight potentially broad patterns of fine root lifespan in temperate trees. Both models used plant potential growth rate (DBH at 10 yr) and root diameter, which together account for 62% of the variation in our data. The second model also included root N : C ratio which explained a further 14% of the variation in the data. From this we determined three generalizable patterns of fine root lifespan that we suggest may be applicable across temperate trees species: trees with faster growth rates tend to have shorter fine root lifespan; trees with first- and second-order roots of

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smaller diameter tend to have shorter lifespan than trees with first- and second-order roots of larger diameter; and all else being equal, fine roots with higher N : C ratio (or N concentration) have shorter lifespan (Fig. 2c). Parameter estimates for both models are reported in Table S5. Although it is likely that these equations will not directly translate to other sites under different environmental conditions, we expect that the general patterns across species should be consistent. Identification of these patterns should enable forest ecologists and modelers to make simple observations of tree species in their field site and gain a useful first approximation of their average root demography. These simple generalizations are particularly important as we move forward in reducing the knowledge gap between above- and below-ground ecology. Furthermore, broad understanding of fine root lifespan enables more detailed descriptions of below-ground processes to be incorporated into ecosystem- and landscape-scale models. Importantly, the patterns we observed were largely independent of any single species, including *P. tremuloides*, which had the shortest root lifespan and fastest growth. Here, rather than change the general patterns, the removal of *P. tremuloides* from the analysis resulted in a change in the relative importance of different traits, with N : C ratio becoming more important and plant growth rate becoming less important. This can be observed in Fig. 2(b), as the spread amongst the points becomes more even with the addition of the N : C ratio to the model.

In this study, we compared fine root lifespan across 12 temperate tree species and identified novel patterns linking fine root lifespan to commonly measured root and whole-plant traits. We found that the simple traits of potential plant growth rate, fine root diameter and fine root N : C ratio explained a substantial amount of the variation observed in fine root lifespan. This work suggests that variation in root lifespan across species in similar environments might be estimated by easily measured root and plant traits. Although we explained up to 76% of the variation in fine root lifespan at our study site, we caution that the study was designed to minimize the influence of environmental variation in root lifespan. In fact, we have very little understanding of how environmental gradients will affect fine root lifespan or root traits in general. An interesting next step will be to determine how environmental factors (edaphic and climatic) alter fine root lifespan. A wealth of silvicultural literature has shown that soil and climate play a critical role in whole-plant traits, including growth rate and wood density, and root traits can likewise be affected by their environment (Comas & Eissenstat, 2004). It will be important for future work to discern if, and how, fine root lifespan will vary with changes in environment.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Fine root survivorship curves for 12 temperate tree species grown in a common garden in central Pennsylvania, USA.

Table S1 Life history traits of 12 temperate tree species used in a common garden in central Pennsylvania, USA

Table S2 Coefficient of variation (%) within three genera (*Acer*, *Pinus*, and *Quercus*) and across all 12 species for median lifespan, diameter at breast height (DBH) at 10 yr, wood density, and observed root diameter

Table S3 Pearson's correlations between root and plant traits

Table S4 Five best candidate models predicting fine root lifespan based on diameter at breast height (DBH) at 10 yr, observed root diameter (Diam), root respiration, root carbohydrate content, N : C ratio, root tissue density, and Ca content

Table S5 Parameter estimates for models 1 and 2 shown in Fig. 2

Notes S1 Variable justification

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