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Linking root traits to potential growth rate in six temperate tree species

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Abstract There is an extremely limited understanding of how plants of different potential growth rate vary in root traits, especially in woody species. We contrasted fine root morphology, physiology, and elemental construction between a fast- and a slow-growing species in each of three families: Aceraceae (maple), Fagaceae (oak), and Pinaceae (pine). Measurements were primarily made on 1-year-old seedlings growing in a growth chamber. Across all three families, first- and second-order roots of fast-growing species had greater specific root length, thinner diameters, and faster respiration rates than those of slow-growing species. These fine roots of fast-growing species in Aceraceae and Fagaceae also had faster phosphorus (P) uptake on a surface area basis than those of slow-growing species, whereas little difference in P uptake was found between Pinaceae species. On a dry weight basis, roots of fast-growing species in Aceraceae and Fagaceae had higher nitrogen concentrations, lower carbon:nitrogen ratios and higher tissue construction costs than roots of slow-growing species (data were unavailable for Pinaceae). Tissue density did not vary in a consistent pattern between fast- and slow-growing species across all three families (P=0.169). To better understand the ecological significance of differences in these root characteristics, a root efficiency model was used to compare P uptake and root carbon (C) cost of each species in simulated field situations in two soils, one with low P buffering capacity (loamy sand) and another with relatively high P buffering capacity (silt loam). For the soil conditions modeled, fast-growing species of Aceraceae and Fagaceae were 17–70% more efficient (defined as cumulative P gain divided by cumulative C cost) at nutrient capture than slow-growing species while the fast-growing Pinaceae species was 20–24% less efficient than the slow-growing species. However, among all three families, roots of fast-growing species reached maximum lifetime efficiency 5–120 days sooner, depending on soil type. Thus, modeling results indicated that root traits of fast- and slow-growing species affected P acquisition in simulated field soil although soil type also had a strong impact.

Keywords Root form and function · Phosphorus acquisition strategies · Comparative plant ecology · Root efficiency modeling

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Introduction

There is considerable interest in the functional role of vegetation both at the ecophysiological and ecosystem level (Chapin et al. 1992). Our understanding of how roots vary among species of different life-history strategies is still only in its infancy. Plant-growth-strategy theory suggests that fast-growing species have short-lived leaves and roots of high absorptive capacity, whereas slow-growing species have long-lived leaves and roots of low absorptive capacity (Grime 1977; Chapin 1980; Tilman 1988). Leaf studies among species differing in relative growth rate largely support these theories on plant growth strategy, and correlate fast growth with short-lived leaves of high leaf area:mass ratio, high nitrogen concentration, fast photosynthetic rate and low tissue density (e.g. Poorter et al. 1990; Ryser and Aeschlimann 1999; Wright and Westoby 2000). These correlations in leaf traits have been found across plants from different biomes, suggesting global convergence in plant functioning (Reich et al. 1999).

Although few studies have compared roots of different species, there is some evidence indicating that broad

suites of root traits are linked to plant growth strategies at the plant level; specifically, to plant potential growth rate. Compared to slow-growing species, fast-growing species often exhibit greater ratios of root surface area: dry weight (specific root surface area, SRA) and root length: dry weight (specific root length, SRL), although this has not been consistently shown in all species comparisons (Poorter and Remkes 1990; Bernston et al. 1995). Often high SRA and SRL are achieved through smaller root diameter (woody species: Eissenstat 1991; Wright and Westoby 1999) and lower root tissue density (grasses: Ryser and Lambers 1995; trees: Eissenstat 1991). As well, fast-growing species exhibit faster specific rates of nutrient uptake and root respiration than slow-growing species (herbs: Lambers and Poorter 1992 and references therein; trees: Reich et al. 1998).

There also may be trade-offs between plants investing in root tissue versus supporting mycorrhizal fungi, as it has been seen that early-successional species, which tend to be faster growing than later successional species, typically have lower mycorrhizal dependency than mid- and late successional species (Huante et al. 1993). Root lifespan has also been tentatively linked to root morphology; more roots died over a growing season in grasses with roots of low tissue density than those with roots of high tissue density (Ryser 1996). In addition, physiological traits such as root maintenance respiration and nutrient uptake rates may influence root lifespan if plants selectively shed roots that are costly to maintain after function of these roots becomes hampered (Eissenstat and Yanai 1997). In general, although there is some indication of trade-offs in root form and function, few species have been examined making a broad assessment of these trade-offs difficult. Species comparisons provide a means of testing general trade-offs in root form and function but multiple species comparisons are rarely made (Peterson 1992).

In northeastern temperate forests, slow-growing trees that tolerate low light as seedlings persist for long periods of time in forest understories until gaps form. Because of inherent differences in establishment strategies of early and later successional species and their growth rate as seedlings, we expected seedlings of fast- and slow-growing trees to have different strategies for acquiring nutrients. We contrasted fine root traits of a fast- and slow-growing species in each of three families to identify characteristics associated with seedling growth rate. We focused on factors that influence phosphorus (P) acquisition because of the importance of root length to the acquisition of P (Andrews and Newman 1970). We investigated the influence of root traits on P acquisition through model simulations of a single root in a soil environment. While we acknowledge the role of mycorrhizae in the uptake of P, we focused on comparisons of root traits of different species because there has been little examination of the diversity of root characteristics and this is the first step of examining different strategies of plants for P acquisition.

Materials and methods

Plant material

A fast- and slow-growing species were chosen in each of three families: Aceraceae (maple), Fagaceae (oak), and Pinaceae (pine) (Table 1). Fast-growing species were *Acer negundo* L. (box elder), *Pinus virginiana* Mill. (Virginia pine) and *Quercus rubra* L. (red oak). Slow-growing species were *A. saccharum* Marsh. (sugar maple), *Tsuga canadensis* (L.) Carr. (Eastern hemlock), and *Q. alba* L. (white oak). Species were chosen for within-family contrasts using available information on tree lifespan, sapling growth rate and shade tolerance, keeping other aspects of plant adaptation such as nutrient and drought stress tolerance as similar as possible within contrasts (Table 1). Typical habitat of the two Pinaceae species is least similar, *P. virginiana* typically considered well adapted to poor soils and *T. canadensis* to moist sites. However, *T. canadensis* also co-occurs with drought-resistant species on dry ridge tops in Pennsylvania and West Virginia (personal observation).

One-year-old dormant bare-root seedlings were obtained in spring of 1996 from local Pennsylvanian nurseries specializing in plants for conservation purposes for all species except for *Acer negundo*, which was started from cuttings in early spring before the growing season. Plants were genetically distinct. Seedlings acquired from nurseries were started from seed. Cuttings were collected from different seedlings established naturally from seeds.

Because of the difficulty with field-grown plants of sampling roots quickly enough for physiological measurements, all measurements other than elemental analysis of roots were taken on seedlings grown in a growth chamber (Environmental Growth Chambers, Chagrin Falls, Ohio). Nine seedlings of each species were planted in 650 ml Deepots (Stuewe, Corvallis, Ore.) in autoclaved silica sand in June 1996. Pots were laid out in a completely randomized design and adjusted as plants grew so that no plant was shaded. Photon flux density in the chamber was programmed such that the intensity was 480 µmol m^{-2} s^{-1} for 14.5 h per day with an additional 0.5 h immediately before and after this period at 245 µmol m^{-2} s^{-1}. Temperature and relative humidity were 25°C and 63%. Approximately every 2–3 days as needed, seedlings were given distilled water alternately with nutrient solution [in µM: 900 KNO_3, 600 $Ca(NO_3)_2$, 300 $NH_4H_2PO_4$, 37.5 $MgSO_4$, 6.67 KCl, 3.33 H_3BO_3, 0.27 $MnSO_4$, 0.27 $ZnSO_4$, 0.07 $CuSO_4$, 0.07 $(NH_4)_6Mo_7O_{24}$, and 6.67 Fe-EDTA]. After growing for 6 months, plants were sampled for root P uptake, respiration and morphological measurements.

Elemental analysis was done on roots collected from seedlings grown at a field site in the Russell E. Larson Experimental Station, Penn State University (40° 85′ N, 77° 83′ W), located near State College, Pennsylvania. Soil type was a silt loam (Hagerstown series). The experimental layout was a completely randomized design. Six seedlings of each species were planted in the field individually into mesh bags filled with sieved field soil in June 1996. Bags were constructed from tulle nylon fabric with mesh openings of 1.0 mm. Bags were approximately 18 cm in diameter and 20 cm deep with a smaller pouch approximately 10×14 cm constructed from the same material that enclosed the original roots of each seedling. Bags were open on top and were buried with the upper 1 cm of mesh exposed. Plants were watered at the time of planting but no subsequent water or fertilizer was added. Plants were harvested in July and August 1996 by bringing the seedlings still in mesh bags back to the laboratory for root cleaning.

For each root trait, samples were replicated using different plants. At the time of harvest, roots were cleaned with tap water to remove soil or sand, and then rinsed with distilled water. Two nonwoody root classes were separated based on branching order. Root orders were counted from root tips with first-order roots being the finest roots ("functional method", sensu Fitter 1987). The "very fine" class collected comprised the finest two orders of roots of each species and the "fine" class comprised third-order roots. Separations of roots were made between these root orders because the largest difference in root diameters appeared to occur between

Table 1 Description of the six northeastern tree species used in this study. All information was collected from Burns and Honkala (1990)

Family	Species	Common name	Sapling shade tolerance	Tree lifespan	Growth r sapling	Maximum DBH increase (cm year^{-1})
Aceraceae	*A. negundo*	Box elder	Intolerant	<100 years	Fast	2.5
	A. saccharum	Sugar maple	Tolerant	>350 years	Slow	0.76
Fagaceae	*Q. rubra*	Red oak	Intolerant	<250 years	Faster than *Q. alba*	1.02
	Q. alba	White oak	Tolerant	>400 years	Slow	0.35
Pinaceae	*P. virginiana*	Virginia pine	Intolerant	<120 years	Fast	0.86
	T. canadensis	Eastern hemlock	Tolerant	>450 years	Slow	0.58

the second and third orders and there was variation in branching frequency of second-order roots off of third-order roots. Thus, separations at this scale controlled sample uniformity as these first- and second-order roots are most likely to serve primarily in nutrient absorption where as the function of higher order roots may vary more widely among species. While physiological and morphological differences may also exist between first- and second-order roots, root pieces cut at the level of individual branching orders would have been too small for physiological measurements. We included third-order roots with first- and second-order roots for elemental analysis because this material was collected prior to sampling for root morphology and differences in root system morphology were not yet apparent. However, third-order roots comprised a smaller percentage of these samples since these root systems were small.

Roots of growth-chamber grown seedlings selected for physiological and morphological measurements were healthy in appearance without visibly swelling from initial root growth and expansion. Roots of field-grown seedlings selected for elemental analysis were from those that had grown out from the inner bag into the outer bag. Visual inspection of pot-grown Fagaceae and Pinaceae roots indicated that roots of these seedlings growing during the experiment were non-mycorrhizal. Mycorrhizal infection was not checked on *A. negundo* or *A. saccharum* roots.

Phosphorus uptake

Roots of very fine and fine classes were collected from five greenhouse-grown plants of each species over 2 days; three plants of each species measured the first day and two plants of each species measured the second day. Each day, stems of harvested plants were cut at mid-day in order to standardize the amount of carbohydrates each root system received from the shoots. Cleaning order of species was rotated between the 2 days. For each plant, approximately three roots of each root class were placed in each of two Histoprep tissue cassettes (Fisher Scientific, Pittsburgh, Pa., USA); one cassette was used for P uptake measurements at 2 µM P and the other at 20 µM P. Cassettes were stored in a calcium-MES buffer solution (1 mM $CaSO_4$, 5 mM MES, adjusted with KOH to pH 5.5) in the dark until all plants of that day's harvest were cleaned; about 9 h. Excised roots of corn have been found to require 4 h after excision for their P uptake to recover from disturbance and wounding (Gronewald and Hanson 1982). As well, P uptake in eucalyptus roots was similar up to 3 days after excision (Keith 1998).

Phosphorus uptake was measured using the modified "tea-bag" technique (Epstein et al. 1963; Eissenstat et al. 1999). Excised roots were given a 10-min incubation period in 2 and 20 µM P + calcium-MES buffer solution labeled with ^{32}P. During the incubation period, the solution was kept at 25°C and bubbled with air for thorough mixing. Following incubation with labeled solution, roots were flushed twice with unlabeled solution of the same P concentration to remove any label not taken up by the roots. Samples were then weighed and ashed in a muffle furnace for 6 h at 495°C. The ash was dissolved in 10 ml of 0.1 M HCl and measured with a TriCarb-100 liquid scintillation analyzer (Packard Instruments, Meriden, Conn., USA). To account for any contributions of root morphology on uptake, P uptake was calculated per unit surface area based on root morphology determined on separate plants of each species.

Root respiration

Root respiration was determined using excised roots of chamber-grown plants and a Clark-type oxygen electrode (Walker 1993). Measurements were taken on four plants of each species in late November to early December 1996. Respiration measurements were made over 4 days from four plants of each species, one plant measured per day. Roots were collected in the same manner as described for P uptake measurements. Again, cleaning order of species was rotated each day of harvest. Excised roots were stored in calcium-MES buffer (described above) until measurements were taken. Respiration was measured about 4 h after excision, so roots had time to recover from perturbation. Respiration measurements were taken with a Hansatech oxygen electrode (Hansatech, King's Lynn, UK) in aerated calcium-MES buffer at 25°C with chamber volume adjusted to 2.75 ml. Respiration was determined on a dry mass basis (nmol O_2 g^{-1} s^{-1}) to indicate the maintenance cost of the tissue.

Root morphology

After respiration measurements were taken, roots were stained with neutral red (0.16 g l^{-1}; 20 min soaking followed by 2 rinses with distilled water). Roots were imaged with a CCD camera and digitized using Snappy Video Snapshot (Play Streaming Media Group, Rancho Cordova, Calif., USA) at a resolution of 118 pixels/cm. Root length, diameter and volume were obtained by analyzing images with Delta-T SCAN software (Delta-T Devices, Cambridge, UK). Modal root diameter, the diameter associated with the greatest amount of root length in each sample, was used rather than average observed root diameter of each sample because root diameter within samples had a non-normal left-skewed distribution.

Nitrogen concentration, C:N ratio and construction cost

Roots from the seedlings in the field were collected in July and August 1996 from six plants of each species. Prior to analysis, root samples were freeze-dried. Samples were then ground with a sample mill equipped with a 0.5 mm screen (Cyclotec 1093, Tecator, Sweden). The percentage of carbon, nitrogen, hydrogen, sulfur, and oxygen in the root tissue was determined with a CHNS-O elemental analyzer (Model EA 1108, Fisons Instruments, Beverly, Mass., USA). Construction cost was calculated by the McDermitt and Loomis (1981) method from the ratio of elements. Calculations require input of the source of nitrogen taken up by the plants because of the difference in assimilation costs between nitrate and ammonia. Since the fast- and slow-growing species within Aceraceae and Fagaceae are found in similar soil conditions, there was no reason to suspect that their nitrogen sources would differ within contrasts. Tree species, especially slow-growing species,

Table 2 Symbols and parameter values used in the root efficiency model

Symbol	Parameter	Units	Lilly loamy sand		Hagerstown silt loam
			Values	(both)	Value
SRL	Specific root length	m g^{-1}		70.8–272.8[a]	
r_o	Root radius	cm		0.009–0.020[a]	
α	Root absorbing power	cm s^{-1}		Calculated[b]	
C_o	Concentration of nutrient at root surface	mol cm^{-3}		Calculated[b]	
t	Model time step, time	days		1	
C_{GE}	Construction cost from glucose equivalent of root	mol C (g DW)$^{-1}$		0.00634–0.00738[a]	
$R_{M(w)}$	Maintenance respiration	mol C (g DW)$^{-1}$ s^{-1}		17.2×10^{-9} – 40.7×10^{-9} [a]	
V_{max}	Maximum nutrient influx rate	mol P cm^{-2} s^{-1}		2.57×10^{-13} – 9.02×10^{-13} [a]	
K_m	Half-saturation constant for uptake	mol P cm^{-3}		1.64×10^{-9} – 8.13×10^{-9} [a]	
C_{av}	Average nutrient concentration in soil solution	mol cm^{-3}		2.16×10^{-9} at t=0 [d]	
v_o	Inward radial velocity of water at root surface	cm s^{-1}	5.66×10^{-7} [c]		4.45×10^{-6} [e]
r_x	Average half-distance between roots	cm	2.0 [c]		1.98[f]
D_e	Effective diffusion coefficient of solute through soil	cm^2 s^{-1}	8.17×10^{-7} [c]		4.96×10^{-9} [e]
b	Soil P-buffer power; used to calculate C_o	Dimensionless	5.84 [c]		176.2 [e]

[a] Range of values from data on the very fine root class of species presented in this paper
[b] Equation given in Yanai (1994);
[c] From Kelly et al. (1992);
[d] From Yanai (1991);
[e] From Bouma et al. (2001);
[f] Value determine for Hubbard Brook, NH, mixed hardwood forest (R. Yanai, personal communication)

typically preferentially take up ammonium over nitrate (Zerihun and BassiriRad 2001). However, construction costs presented here were calculated assuming 50% of the nitrogen in the roots came from ammonium and 50% from nitrate because we could not rule out that none of these species would take up nitrate. Calculations were also made assuming the nitrogen source was 100% nitrate and 100% ammonium to check if differences between species held.

Root efficiency modeling

Lifetime root efficiency (cumulative benefits and costs of P acquisition at the single root-level) was determined for roots in the very fine class of each species. Root efficiency (E) was calculated as described in Yanai et al. (1995) and Eissenstat and Yanai (1997) with modifications to fit the data collected in this study:

$$E = \frac{\mathrm{P}_{\text{acquired}}}{\mathrm{C}_{\text{cost}}} = \frac{\mathrm{SRL}\; 2\pi r_o \alpha C_o}{\left[C_{GE} + t \times R_{M(w)}\right] t^{-1}};\ \text{mol P mol}^{-1}\text{C} \qquad (1)$$

where r_o= root radius (cm), α= root absorption power (cm s^{-1}), C_o= nutrient concentration at root surface (mol cm^{-3}), t= time (days), C_{GE}= construction cost from glucose equivalent of root (mol C g^{-1} DW), and $R_{M(w)}$= maintenance respiration (mol C g^{-1} DW day^{-1}). Both α and C_o are calculated as in Yanai (1994): α from Michaelis-Menton kinetics and C_o from steady-state equations estimating the supply rate of P from water influx at the root surface and P movement through the soil assuming a closed system for P. Phosphorus uptake parameters, K_m and V_{max}, which were used to calculate α, were determined for each species from a hyperbolic fit of a Michaelis-Menton curve through species averages of uptake measurements made at 2 and 20 µM P for each species. The numerator of Eq. 1 is a model of P acquisition accounting for the diffusion of P to the root surface (Baldwin et al. 1973; Nye and Tinker 1977; Yanai 1994). The cost of root production in mol C was calculated from root construction cost (the glucose equivalent of root tissue) instead of the sum of root carbon content and growth respiration (respiration cost for root production) used in Eissenstat and Yanai (1997). Average root construction cost of all Aceraceae and Fagaceae species was used for both Pinaceae species. Respiration measured in this study was substituted for maintenance respiration because respiration associated with ion and growth was assumed to be negligible as the solution used during respiration measurements did not contain any nitrogen, the uptake of which accounts for about 90% of ion uptake respiration (Veen 1981), and because root growth was presumed to have ceased for the roots selected for measurement. Roots measurements made on first- and second-order roots were used for all root parameters except for root construction cost, which were made on a pooled group of first-, second- and third-order roots. Soil and root parameters not collected in this study were obtained from the literature (Table 2). Parameters for two soil types were obtained, one soil type that was sandy (Lilly) and one that had high clay content (Hagerstown), because the P-buffering capacities of these soil types illustrate extremes found in northeastern soils. The model was run for both soil types.

Statistics

Data were tested for normality with the univariate procedure and for homogeneity of variance with Levene's test (SAS Institute, Cary, N.C., USA). Respiration (very fine class), SRL (both classes) and N concentrations were log transformed and root diameter (very fine class) was square-root transformed to correct for non-normality of residuals. All measurements were analyzed with nested AVOVA designs (SAS Institute, Cary, N.C., USA). Root traits were dependent variables on the effect of growth characteristics, which was nested within family relationships. Differences were considered significant at P=0.05.

Results

Root morphology

Among very fine roots, fast-growing species had roots with 30–56% more length per unit dry weight (SRL) and 10–35% thinner modal diameters than those of slow-growing species (SRL: P<0.05, diameter: P<0.05; df=1; Fig. 1). Similar patterns were found when the average root diameters of each sample were compared (P<0.05; df=1; data not shown) but differences between fast- and slow-growing species in the Pinaceae and Fagaceae were less pronounced than with modal diameters. When SRL and modal root diameter of the very fine root class were

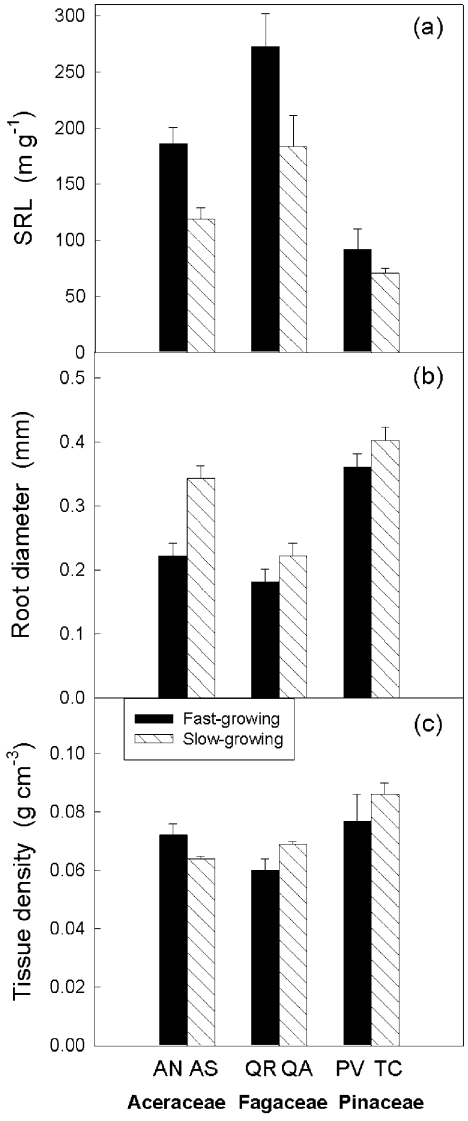

Fig. 1 **a** Specific root length [SRL, cm (g root dry weight) $^{-1}$] (+ SE); **b** modal root diameter (diameter associated with the greatest root length) (+SE); and **c** tissue density (gram root dry weight per volume) (+SE) of first- and second-order roots of fast- and slow-growing species of Aceraceae (maple), Fagaceae (oak) and Pinaceae (pine). Differences in SRL and root diameter were significant between fast- and slow-growing species across all three families (P=0.05; df=1). Differences in tissue density were not. Species abbreviations are *Acer negundo* (*AN*), *A. saccharum* (*AS*), *Quercus rubra* (*QR*), *Q. alba* (*QA*), *Pinus virginiana* (*PV*), *Tsuga canadensis* (*TC*)

examined across all six species without accounting for taxomomic groups, there was no relationship between root morphology and shoot growth rate (SRL: r^2=0.09, P=0.58; diameter: r^2=0.14, P=0.47; n=6; data not shown). Among third-order roots, no significant differences were found in SRL or in diameter between fast- and slow-growing species even after accounting for phylogeny (SRL: P>0.47; diameter: P>0.90; df=1; Table 3). Across all three families, tissue density did not vary between fast- and slow-growing species in a consistent direction or by a large magnitude in either very fine or fine root classes (very fine: P=0.17, Fig. 1c; fine: P=0.47, df=1; Table 3). However, within Pinaceae and Fagaceae, fast-growing species tended to have slightly less dense first- and second-order roots than slow-growing species (Fig. 1c).

Root physiology

Very fine roots of fast-growing species in Aceraceae and Fagaceae had 80–200% faster P uptake on an area basis than those of slow-growing species, but little difference in P uptake was found between Pinaceae species. Across all three families, differences in P uptake rate at 20 µM P within the very fine root class was only marginally significant between fast- and slow-growing species due to the lack of difference between Pinaceae species (P=0.09; df=1; Fig. 2). Differences in P uptake rate at 2 µM P across all three families, however, were not significant between fast- and slow-growing species (P=0.16; df=1; Fig. 2). Patterns of P uptake on a mass basis were similar between species (data not shown). Respiration rates within the very fine root class were consistently faster in fast- than in slow-growing species across all three families (P<0.05; df=1; Fig. 3a). When P uptake and respiration rates of the very fine root class were examined across all six species without accounting for taxonomic groups, there was no relationship between root physiology and shoot growth rate of the species (annual trunk growth rate from the *Silvics of North America* used as a measure of shoot growth rate; P uptake: r^2=0.19, P=0.39; respiration: r^2=0.01, P=0.86; n=6; data not shown).

In Aceraceae and Fagaceae, mean differences in P uptake between fast- and slow-growing species were gener-

Table 3 Specific root length (*SRL*), root diameter, tissue density, phosphorus (*P*) uptake at 20 mM P, and respiration of the coarse class of fine roots (third-order roots) of six woody species common to northeastern forests. Standard errors are given in parenthesis. Traits are compared experiment-wide between fast- and slow-growing species, nesting within the respective families (df=1)

Family	Species	SRL (m g^{-1} DW)	Modal diameter (mm)	Tissue density (g cm^{-3})	P uptake (pmol P cm^{-2} s^{-1})	Respiration (nmol O_2 g^{-1} s^{-1})
Aceraceae	*A. negundo*	16.9 (3.5)	0.645 (0.057)	0.192 (0.022)	0.778 (0.311)	8.15 (1.38)
	A. saccharum	15.2 (3.0)	0.685 (0.070)	0.191 (0.019)	0.447 (0.184)	5.87 (1.00)
Fagaceae	*Q. rubra*	16.9 (2.2)	0.605 (0.052)	0.185 (0.029)	0.746 (0.308)	12.15 (2.14)
	Q. alba	31.7 (6.7)	0.504 (0.060)	0.15 (0.004)	0.324 (0.034)	13.37 (2.33)
Pinaceae	*P. virginiana*	32.5 (5.9)	0.741 (0.064)	0.084 (0.007)	0.550 (0.169)	25.01 (5.65)
	T. canadensis	28.6 (3.1)	0.783 (0.021)	0.082 (0.007)	0.616 (0.072)	15.01 (1.58)
	P	0.47	0.90	0.47	0.63	<0.05

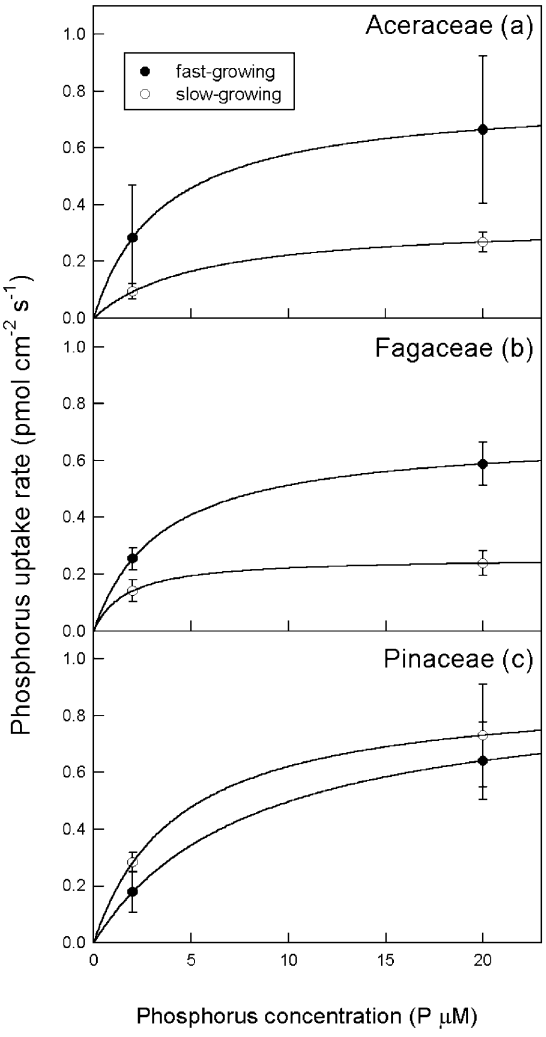

Fig. 2 Phosphorus uptake [pmol P absorbed (cm root) $^{-2}$ s^{-1}] (+SE) of first- and second-order roots of fast- and slow-growing species of **a** Aceraceae, **b** Fagaceae and **c** Pinaceae at 2 and 20 μM P. Differences in P uptake at 20 μM P were marginally significant between fast- and slow-growing species across all three families (P<0.090; df=1) but not at 2 μM P. The Michaelis-Menton parameters, V_{max} (pmol cm^2 s) and K_m (μM), derived from the data are as follows: 0.78 and 3.51 (*AN*); 0.34 and 5.23 (*AS*); 0.69 and 3.42 (*QR*); 0.26 and 1.64 (*QA*); 0.90 and 8.13 (*PV*); 0.89 and 4.29 (*TC*). Species abbreviations are as described for Fig. 1

ally greater than respiration differences. Phosphorus uptake measured at 20 μM P was 150–180% greater in fast-growing species than in slow-growing species (Fig. 2a, b), while root respiration was only 20–21% greater (Fig. 3a). Within the Pinaceae, however, P uptake was similar between the fast- and slow-growing species, while respiration was 52% faster in roots of the fast-growing species (Figs. 2c, 3a).

Comparing third-order fine roots, there were no significant differences in P uptake rates between fast- and slow-growing species across all three families (P=0.63; df=1; Table 3). Respiration rates in third-order roots of fast-growing species, however, were significantly faster than those of slow-growing species across all three families even though root respiration of the two oaks was similar in this root class (P<0.05; df=1; Table 3).

Table 4 Nitrogen concentrations and C/N ratio of the finest three orders of roots among four woody species common to north-eastern forests. Standard errors are given in parentheses. Traits are compared experiment-wide between fast- and slow-growing species, nesting within the respective families (df=1)

Family	Species	N concentration (% g g^{-1})	C/N ratio (g g^{-1})
Aceraceae	*A. negundo*	2.65 (0.20)	16.3 (1.1)
	A. saccharum	1.95 (0.09)	20.8 (0.9)
Fagaceae	*Q. rubra*	4.80 (0.99)	8.9 (1.0)
	Q. alba	1.64 (0.07)	23.8 (1.0)
	P	<0.05	<0.05

Nitrogen concentration, C:N ratio and construction cost

On a dry weight basis, fast-growing species of Aceraceae and Fagaceae had 36–190% higher N concentration and 22–63% lower C:N ratios (N concentration: P<0.05; C:N ratio: P<0.05; df=1; Table 4). Root tissue construction cost in fast-growing species was 4–21% higher than in slow-growing species of these families (P<0.05; df=1; Fig. 3b). This difference in construction cost was mainly due to fast-growing species having higher root N concentration. When construction costs were calculated with ammonium as the sole source of N, construction costs for each species were 4–10% lower but the same pattern was found between fast- and slow-growing species. If slow growing species primarily use ammonium as the sole source of N and fast-growing species use both ammonium and nitrate, the differences in construction cost between fast- and slow-growing species widen. Nitrogen concentrations and C:N ratios for roots of Pinaceae species could not be determined because of insufficient root material.

Root efficiency modeling

Lifetime P acquisition efficiency was higher in fast- than in slow-growing species of Aceraceae and Fagaceae with the magnitude of the difference depending on soil type: 34–70% higher in the less-buffered soil (Lilly) and 17–24% higher in the clay soil (Hagerstown) (Fig. 4 a, b, d, e). Within Pinaceae, however, P acquisition efficiency of the fast-growing species was lower (20–24%) than that of the slow-growing species (Fig. 4c, f). In sandy soil with low P-buffer capacity (Lilly), maximum P acquisition efficiency was reached within 120 days for all species because roots in the sandy soil could deplete exchangeable P quickly due to the lack of P adsorption to the sand (Fig. 4a–c). In clay soil with high P-buffer capacity (Hagerstown), maximum P acquisition efficiency was reached between 676 and 850 days; much later than in the sandy soil (Fig. 4d–f). Across all three families,

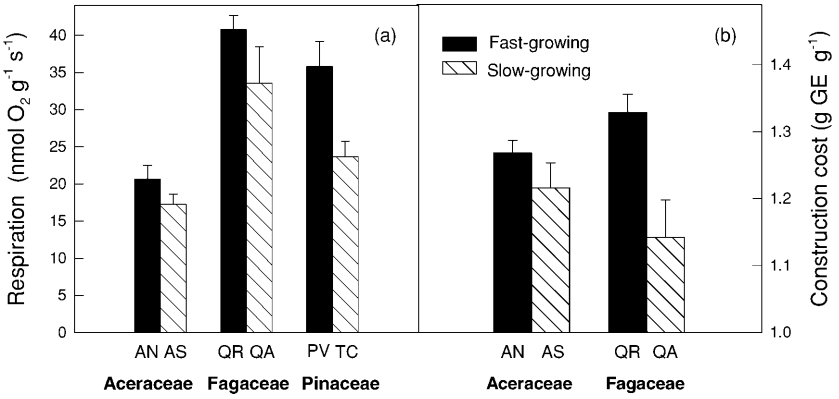

Fig. 3 a Respiration [nmol oxygen consumption (g root dry weight)$^{-1}$ s^{-1}] (+SE) of first- and second-order roots among fast- and slow-growing species of Aceraceae, Fagaceae and Pinaceae. Differences in respiration were significant between fast- and slow-growing species across all three families (P=0.05; df=1). **b** Construction cost (gram glucose equivalent per g root dry weight) (+ SE) of all fine roots combined. Data were available only for Aceraceae and Fagaceae. Differences in construction cost were significant between fast- and slow-growing species across all three families (P=0.05; df=1). Species abbreviations are as described for Fig. 1

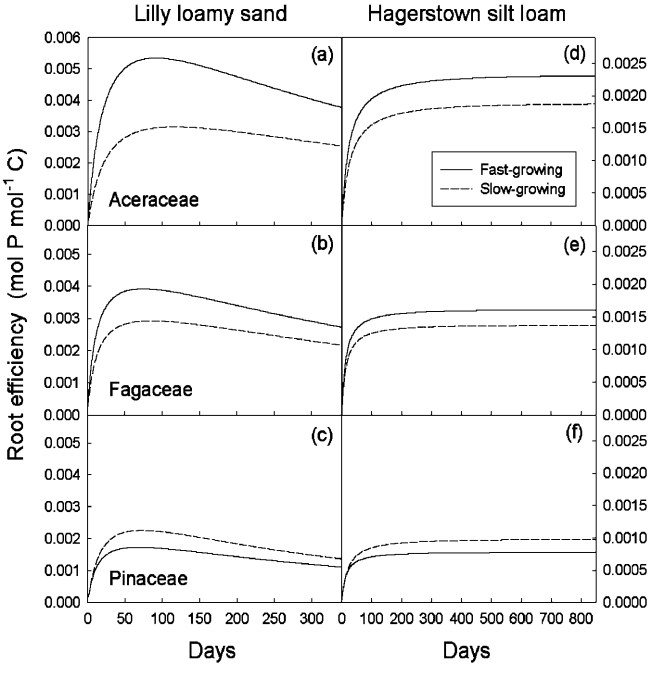

Fig. 4 Lifetime phosphorus acquisition efficiency of first- and second-order roots for fast- and slow-growing species of **a**+**d** Aceraceae, **b**+**e** Fagaceae and **c**+**f** Pinaceae in Lilly loamy sand (**a**, **b**, **c**) and in Hagerstown sitt loam (**d**, **e**, **f**). Root efficiency was calculated as cumulative P uptake divided by cumulative C cost (Eissenstat and Yanai 1997) from root characteristics determined from this study and values for soil parameters and remaining root traits needed taken from the literature (see Table 2)

however, roots of fast-growing species reached maximum lifetime P acquisition efficiency more quickly than roots of slow-growing species irrespective of soil type (Lilly: 5–28 days earlier; Hagerstown: 106–120 days earlier).

Discussion

Root characteristics

Fast-growing species consistently exhibited a suite of root traits consistent with their high potential growth rate. Roots of fast-growing species had greater SRL, smaller diameter, faster respiration and higher nitrogen concentration than those of slow-growing species, confirming hypotheses developed from plant growth theories on root morphological and metabolical differences between fast- and slow-growing species. Variation in root traits between fast- and slow-growing species was probably related to differences in their strategies for acquiring soil resources because the greatest variation was found in first- and second-order roots, whose primary function is resource acquisition. Traits of third-order roots, which are more likely to be part of the structural portion of root systems, were not significantly different between fast- and slow-growing species. During seedling establishment, root traits of fast-growing species were presumably selected under high light where fast growth would require rapid resource acquisition. Morphology that maximizes root surface area and length per biomass, and physiology and construction for high functional capacity would be beneficial for fast-growing plants (Grime 1977; Chapin 1980). In contrast, root traits of slow-growing species were presumably selected under low light where slow growth would have low metabolic demands for resources. In the case of slow-growing species, if high functional capacity were not necessary, metabolic costs may be lower. Thicker roots of slow-growing species may also have other benefits, such as extra fortification against desiccation and pests (Eissenstat and Anchor 1999; Huang and Eissenstat 2000).

First- and second-order roots of fast-growing species had consistently higher SRL than those of slow-growing species across all three families (Fig. 1a), which corresponded well with root diameters being thinner in fast-growing species across the three families (Fig. 1b). However, tissue density, another component of SRL, did not exhibit large differences or consistent patterns between fast- and slow-growing species (Fig. 1c). Other studies have found fast-growing species to have high SRL (e.g.

Eissenstat 1991; Ryser 1996; Wright and Westoby 1999), although this has not been consistently shown in all species comparisons (Poorter and Remkes 1990; Bernston et al. 1995). Similar to our study, Wright and Westoby (1999) found no correlation between root tissue density and species growth rate in a comparison of 28 woody Australian species. In contrast, comparisons of grass species often indicate that fast-growing species have lower tissue density than slow-growing species (Ryser 1996; Wahl and Ryser 2000). Whether this is a general difference between grasses and woody species, however, is unclear.

Assessing trade-offs in physiological costs and benefits is complicated. Maintenance respiration should be higher in roots with higher uptake capacity due to these roots maintaining more proteins (Bouma et al. 1994). However, fast-growing species in this study that had greater P uptake capacity had relatively small increases in respiratory costs, which is similar to comparisons of nitrogen uptake and respiration across fast- and slow-growing species (Poorter et al. 1991; Scheurwater et al. 1998). Like respiration, nitrogen concentration has also been found to be higher in root tissue with higher nutrient absorption capacity (sugar maple roots of different orders, Pregitzer et al. 1998; grape roots of different ages, Volder and Eissenstat, unpublished data). This correlation likely reflects a positive association of metabolism with protein concentration. Assuming other elements are constant, tissues with higher nitrogen concentrations generally have higher construction costs (McDermitt and Loomis 1981) as well as higher maintenance requirements (Penning de Vries 1975). In this study, modeling root efficiency indicated that benefits associated with roots of high uptake capacity outweighed respiration and construction costs of these roots, but it is possible that root respiration included metabolic energy expended for processes other than maintaining proteins and membrane potentials necessary for physiological function (Bouma et al. 1994). For example, energy from respiration may be used for purposes such as attracting symbiotic soil organisms (*VAM:* Phillips and Tsai 1992; *Ecto:* Sun and Fries 1992) that would enhance nutrient acquisition. Thus, we cannot account for all costs and benefits associated with fine roots.

Root interactions with mycorrhizal fungi need to be studied further and may be particularly important for nutrient uptake in Pinaceae species, which, in general, have relatively coarse first-order roots and have low root length densities in field soil (Bauhus and Messier 1999). Unlike in Aceraceae and Fagaceae, P uptake capacity was similar in the fast- and slow-growing Pinaceae species, which may reflect a high dependency on mycorrhizal fungi in this family. Both Pinaceae species may have similarly slow P uptake kinetics when non-mycorrhizal.

The importance of nutrient uptake kinetics for nutrient uptake in field conditions has been controversial (Clarkson 1985). When immobile nutrients such as P are in low supply, model simulations of root traits affecting nutrient acquisition indicate that increasing root length should be most beneficial for increasing nutrient acquisition (Silberbush and Barber 1983; Caldwell et al. 1992). Where nutrient availability is high, fast nutrient uptake kinetics are thought to be most beneficial for P acquisition (Caldwell et al. 1992; Jackson and Caldwell 1996). Nonetheless, crop cultivars successful under low nutrient conditions are found to have faster nutrient uptake kinetics than those successful under high nutrient conditions (Nielsen and Schjørring 1983; Siddiqi and Glass 1983). In this study, we found that roots of fast-growing species in Aceraceae and Fagaceae, which had higher P uptake capacity, also had higher SRL than roots of slow-growing species. Increases in SRL result in greater root length for the same biomass investment in root. Thus, these fast-growing species had both morphological and physiological root traits important for rapid P acquisition.

Root-level P acquisition efficiency modeling

Incorporating multiple root traits into a root efficiency model that simulated field conditions was valuable for assessing the relative effects of root morphology, construction costs and physiology on P acquisition. Root efficiency modeling indicated that root trait differences found between fast- and slow-growing species affected P acquisition in soils of both low and high buffering capacity (Fig. 4). Root death and re-growth in new areas of soil might be particularly important in optimizing P acquisition due to formation of depletion zones around roots in soil. Theoretically, roots should live until their lifetime efficiency begins to drop. Modeling indicated that roots of fast-growing species reached maximum lifetime efficiency sooner than those of slow-growing species within each family due to faster P acquisition regardless of soil type, suggesting that roots of fast-growing species should be shorter lived. Indirect evidence suggesting that roots of fast-growing species have shorter lifespan than those of slow-growing species can be assembled from studies where one or a small number of species were examined (*fast:* sweet cherry=19 days, poplar=42 days, Black et al. 1998; apple=34–57 days, Wells and Eissenstat 2001; *slow:* sugar maple=125–340 days, Hendrick and Pregitzer 1993; beech/sugar maple forest=180–195 days, Fahey and Hughes 1994). However, many factors, such as environmental conditions, can also influence root longevity (Eissenstat and Yanai 1997). The effects of nutrient depletion in soil patches for root deployment patterns may be more important for low P-buffered soil than for highly P-buffered soil where nutrient depletion of soil patches occurs more slowly.

In our modeling of P acquisition efficiency we made several assumptions. First, we assume that P efficiency in units of carbon is meaningful but this depends on the relative value of P and carbon in the whole plant (Yanai et al. 1995). We assumed that the success of these woody species would also be furthered by efficient deployment of carbon because carbon is an indirect measure of

energy gained and expended by plants and can be allocated to acquire limiting nutrients (Chapin 1989). If carbon were less valuable to fast-growing plants adapted to higher light levels, these species might expend more carbon per unit P acquired than slow-growing species but, in fact, we found that they do not. Secondly, the model used in this study considered root maintenance respiration and construction the main costs associated with P acquisition at the root level but there are other costs involved with maintaining fine roots, such as the production of defense compounds and root exudation (Eissenstat and Yanai 1997). These costs, however, should be accounted for, in part, by respiration. Finally, in our modeling of root efficiency we used average values for P uptake and respiration and assumed that these values were constant throughout the life of the root. We know, however, that root physiology is not constant with root age (Bouma et al. 2001). Furthermore, decline in root function with root age may not occur at the same rate in roots of both fast- and slow-growing species as decline did not occur similarly in the two species examined by Bouma et al. (2001). Thus, age-dependent changes in uptake and respiration of fine roots of these species should be examined if lifetime efficiency is to be more accurately described.

It remains to be seen if mycorrhizae may compensate for the difference in maximum root efficiency between the fast- and slow-growing species because our modeling did not include interactions with mycorrhizal fungi. Greater root efficiency has previously been found in species with fast relative growth rate (Poorter et al. 1991) but these studies also did not include mycorrhizae. Thicker roots may be less efficient for P acquisition than thinner roots when non-mycorrhizal but thicker roots may support more mycorrhizae per unit root length. Thus, root function of slow-growing species examined here may be less than optimal without mycorrhizae. However, while mycorrhizal relationships can greatly increase nutrient uptake (Colpaert et al. 1999; Van Tichelen and Colpaert 2000), mycorrhizae have added costs associated with maintaining the symbiosis (Peng et al. 1993). If roots of these slow-growing species typically support more mycorrhizae under natural conditions, there may be an even greater difference between timing of peak efficiency in roots of these fast- and slow-growing species because there is a lag time in the formation of mycorrhizal associations in new roots (Brundrett and Kendrick 1988). Now that root systems of these species have been examined under controlled conditions and differences in their morphological and physiological characteristics have been identified, further examination of the potential effects of mycorrhizal associations among these species would be informative.

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