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Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species

L. H. COMAS†* and D. M. EISSENSTAT

Department of Horticulture and Plant Physiology & Ecology Intercollege Graduate Programs, The Pennsylvania State University, University Park, PA 16802, USA

Summary

1. There is limited understanding of patterns of variation that exist among root traits of different species, especially under field conditions. We contrasted 11 fast- and slow-growing species paired within five evolutionary lineages to investigate whether root traits associated with soil resource acquisition were related to species' potential growth rate.

2. Measurements of root morphology, architecture, nitrogen and phenolic concentration, respiration and phosphorus uptake were taken on fine, non-woody roots sampled from forest stands in central Pennsylvania, USA.

3. Across all five contrasts, roots of fast-growing species generally had higher specific root length, smaller diameters, greater degree of branching, and lower phenolic concentrations than those of slow-growing species. This suggests differences in potential soil exploration and root defences among species differing in potential growth rate.

4. There were no significant differences between fast- and slow-growing species in root tissue density, respiration or P uptake. Lack of root physiological differences between species differing in growth rate contrasted with previous research on chamber-grown seedlings.

5. These results imply that, while roots of fast-growing species may be constructed for more rapid soil exploration and shorter life span than those of slow-growing species, root physiology is either more closely tied to overall plant physiology, which is more similar among mature trees, or masked by variation in soil microsites, root age or interactions with mycorrhizal fungi.

Key-words: fine root morphology, fine root architecture, SRL, root physiology, ecological strategies, comparative plant ecology

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Introduction

While roots vary widely in morphology and physiology, little is known about what selection pressures govern this variation or how this variation may be related to plant function. Ecologists have developed theories on plant growth strategies to explain variation in plant traits such as tissue morphology, metabolic activity and chemical defence (Grime 1977; Chapin 1980; Coley, Bryant & Chapin 1985; Tilman 1988). In particular, plant potential growth rate is recognized as a trait of key importance to a plant's growth strategy that varies widely among plants and helps to define overall life history strategy (Lambers & Poorter 1992; Chapin, Autumn & Pugnaire 1993). Theoretically there should be a suite of morphological and physiological traits associated with tissues of fast- and slow-growing plants due to trade-offs among traits related to the optimization of tissue function (Grime 1977; Chapin 1980; Tilman 1988). An underlying assumption is that allocation of biologically expensive resources to tissue structure and function is governed by biotic and abiotic selection pressures. Broad patterns in tissue structure and function correlating with potential growth rate have been found in leaves (Reich *et al*. 1999), but broad studies of root traits have been limited.

In general, roots of fast-growing species appear to be constructed for fast growth into new areas of soil, either by having high specific root length (SRL), thin roots or low root-tissue density (Eissenstat 1991; Wright & Westoby 1999; Wahl & Ryser 2000; Comas, Bouma & Eissenstat 2002). In three important families of temperate forest trees, roots of fast-growing species

†Author to whom correspondence should be addressed. E-mail: lhc105@psu.edu
*Present address: USDA-ARS, PSWMRU, Curtin Road, Bldg 3702, University Park, PA 16802, USA.

also had fast respiration rates, indicating higher metabolic activity than in roots of slow-growing species (Comas *et al*. 2002). Roots of fast-growing hardwoods had higher phosphorus-uptake rates than slow-growing hardwoods; however, little difference in P uptake was found in roots of fast- and slow-growing conifers (Comas *et al*. 2002). There may be some basic differences in the root systems of gymnosperms and angiosperms. For example, evergreen conifers typically have thicker roots and lower SRL than coexisting deciduous angiosperms (Reich *et al*. 1998; Bauhus & Messier 1999). Roots of evergreen conifers are also often found at low densities in soil which, combined with their morphological characteristics, may indicate greater dependency on mycorrhizas for acquisition of soil resources compared to hardwoods (Bauhus & Messier 1999).

Although ecologists have begun comparative investigations of root systems of different species, more studies of this type are needed to understand trade-offs in root form among different ecological strategies (Peterson 1992). Of the few studies that have examined how root traits are related to plant growth strategy, most have been done on seedlings (Poorter *et al*. 1991; Reich *et al*. 1998; Scheurwater *et al*. 1998; Wright & Westoby 1999; Craine *et al*. 2001; Comas *et al*. 2002) or mature herbaceous plants in pots (Wahl & Ryser 2000). Furthermore, fewer woody species than herbaceous species have been studied. Comparative root studies have rarely been carried out on field-grown plants because of the difficulty of obtaining root material. Consequently few comparative root studies have been done with mature trees (but see Pregitzer *et al*. 2002). Finally, of the traits that have been examined across broad species comparisons, root physiology has been particularly neglected because it is difficult to measure (Poorter *et al*. 1991; Reich *et al*. 1998; Scheurwater *et al*. 1998; Comas *et al*. 2002).

Measurements of root systems in comparative studies pose particular challenges. Examining traits associated with specific ecological strategies among species in phylogenetically independent contrasts (*sensu* Wright & Westoby 1999) may be the most efficient way to examine patterns of trait differences, because this controls for taxonomic differences. When investigating patterns of convergent evolution in ecological strategies, it is also important to choose contrasts that control for adaptation to local habitats. Finally, due to the complexity of the root systems of woody plants and the potential multiple functions of their roots, it is also necessary to select carefully consistent root material of specific orders of branching so that analogous material is compared (Pregitzer *et al*. 2002).

In this study a comparative approach was used to examine roots collected from mature trees in a common forest community of fast- and slow-growing species in five taxonomic contrasts. We investigated if morphological, chemical and physiological patterns in fine lateral roots of fast- and slow-growing species in mature trees were similar to those previously measured at the seedling stage (Comas *et al*. 2002). Seven root traits were examined related to root morphology, chemical defences, metabolic activity and nutrient uptake. Mycorrhizal colonization was also examined. The hypotheses tested were that, compared to slow-growing species, fast-growing species have roots with: (1) smaller diameters and greater length per mass of tissue; (2) lower phenolic concentrations; and (3) higher physiological activity as indicated by higher nitrogen concentration, respiration rate and P-uptake capacity.

Methods

SPECIES CONTRASTS

At least one fast- and one slow-growing species in each of five phylogenetic lineages were selected, representing a broad range of growth rates and taxonomic groups common in temperate north-eastern forests of North America (Table 1). Contrasts were limited to species that could be found within the same forest and habitat (e.g. ridge top, lowland). Species were identified as potentially fast- or slow-growing based on contrasting maximum reported trunk growth rate (TGR_{lit}), which was referenced from Burns & Honkala (1990), and by observations of tree seedlings planted at the same time in a common garden near State College, PA, USA (Table 1). Three contrasts were found within genera (*Acer*, *Quercus* and *Carya*) and another within taxonomic family (Pinaceae). One of the fastest growing species in north-eastern forests is *Betula lenta*, but its closest relative with a slow growth rate and similar habitat that could be found at the study site was *Fagus americana*. This contrast within sister clades was included because of the well established proximity of the taxonomic relationship of *Betula* and *Fagus* (Jones 1986; Manos & Steele 1997) and the difficulty we had in finding pairs of species with extremely dissimilar growth rates that were taxonomically related. *Betula* and *Fagus* were considered a pair, distinct from *Quercus*, which is also in the order Fagales, because *Betula* is a closer relative to *Fagus* than to *Quercus* (Manos & Steele 1997) and because *Quercus* is more typical of drier habitats than *Betula* and *Fagus*. Because of concerns of the relaxed phylogenetic controls in the *Betula–Fagus* contrasts, statistical analyses were analysed with and without inclusion of this contrast, and reported when different.

FIELD SITES AND ROOT COLLECTION

The primary sampling location in 1999 and 2000 was at the Penn State Stone Valley Experimental Forest located in Barree Township of Huntingdon County, except 1 year of measurements for the *Pinus* species (*P. virginiana* and *P. strobus*), which was done in 1997 on private property in Hughesville, PA (Muncy Township, Lycoming County). Trees sampled had either

Table 1. Physiological characteristics of 11 temperate tree species that differ in potential growth rate paired within five phylogenetically independent contrasts

Species	Abbr	Common name	TGR_{lit} cm $year^{-1}$	TGR_{sap} cm $year^{-1}$	TGR_{site} cm $year^{-1}$	d.b.h. range cm	Leaf N mg g^{-1}	Root N mg g^{-1}	Root respiration nmol O_2 g^{-1} s^{-1}	K_m of P uptake μM	V_{max} of P uptake pmol cm^{-2} s^{-1}
Deciduous AM trees											
Acer negundo	AN	Boxelder	2·50	1·56	0·80	24–37	3·03	1·67	49·7	28·1	1·00
Acer saccharum	AS	Sugar maple	0·48	0·83	0·41	11–37	1·88	1·42	33·8	37·9	3·05
Deciduous EM trees											
Betula lenta	BL	Sweet birch	0·65	–	0·54	7–32	2·46	1·89	38·1	12·5	1·84
Fagus grandifolia	FG	American beech	0·18	–	0·20	16–45	2·13	1·37	42·6	22·2	4·91
Quercus rubra	QR	Red oak	0·50	1·21	0·64	24–60	2·30	1·34	29·2	35·7	6·56
Quercus alba	QA	White oak	0·35	0·96	0·48	32–69	2·29	1·42	45·9	123	11·67
Carya ovata	CO	Shagbark hickory	0·35	–	0·28	25–48	1·97	1·67	33·5	17·1	3·97
Carya glabra	CG	Pignut hickory	0·25	0·51	0·19	13–32	1·88	1·38	51·1	8·19	2·77
Evergreen EM trees											
Pinus virginiana	PV	Virginia pine	0·86	1·73	0·19	23–33	1·18	1·36	11·3	15·3	9·62
Pinus strobus	PS	White pine	0·54	0·86	0·48	30–63	1·28	1·82	10·0	14·9	7·33
Tsuga canadensis	TC	Eastern hemlock	0·58	–	0·66	40–75	1·22	1·51	–	–	–
Pooled SE			–	0·15	0·37	–	0·19	0·36	11·5	–	–

Maximum trunk growth rate (TGR_{lit}) observed across the species' range was collected from Burns & Honkala (1990). Trunk growth rates of saplings (TGR_{sap}) were measured on 6-year-old saplings growing in a common garden plantation near the Penn State Experimental Forest. Trunk growth rates of mature trees (TGR_{site}) and trunk diameters at breast height (d.b.h.) were measured on the same trees used for root measurements in the Penn State Experimental Forest. Root N was measured in 1999 in the Penn State Experimental Forest. Respiration and P-uptake kinetics were measured in 2000 for trees in the Penn State Experimental Forest for all species except *P. virginiana* and *P. strobus*, which were measured in 1997 from trees in the Hughesville location. Pooled standard errors (SE) for each measured trait are given.

leaves in the forest upper canopy, or open canopy. Trunk diameters of sampled trees ranged from 7 to 75 cm at breast height across species (Table 1).

At the Penn State Experimental Forest trees were sampled in two even-aged stands composed predominately of hardwoods. These stands were approximately 65 years old and located in basins along north-west-facing slopes ≈ 2·25 km apart. Soil in one stand was an Ernest silt loam (fine-loamy, mixed, superactive, mesic Aquic Fragiudult) and in the other, a Newark silt loam (fine-silty, mixed, active, non-acid, mesic Aeric Fluvaquent). Both stands in the Stone Valley Experimental Forest were traversed by a stream, and the sites were long and narrow. A sampling transect was oriented parallel to the stream through the stands. A random point on each transect was picked as the centre of that site. Trees of each species nearest to this point within a narrow flood plain of the stream were selected to minimize microsite differences. One stand was larger than the other. Therefore in 1999, when three root samples were collected for each species, two trees were sampled at the larger stand and one at the smaller. In 2000, when four samples were collected for each species, two trees at each of the two stands were sampled. Species were generally distributed along the entire transect of each site.

At the Hughesville location trees sampled were from three stands: two mature stands with trees >60 years old, and one young stand with trees <20 years old, located within 1 km. The soil was a Weikert shaly silt loam (loamy-skeletal, mixed, active, mesic Lithic Dystrudept). A centre point of each stand was chosen and random coordinates were used to select sampled trees. More than one sample was taken in larger stands so that four or five samples per species, depending on analysis, were taken.

In the 1999 sampling at the Penn State Experimental Forest, six samples from six different species were collected daily until all species were sampled once. Root collection was completed when three plants of all species were sampled, which was done over a 6-week period in June and early July 1999. Root samples were collected by excavating roots from the top 20 cm of soil and tracing them back to the tree trunk for species identification. Roots were misted with deionized water and kept on ice in a cooler until they could be washed. Samples were used for morphology and chemistry. The 1997 sampling was similar, except that all samples were collected on one day in July for morphology and respiration, and on one day in August for P uptake.

In 2000, root bags constructed from porous nylon landscape fabric, 23 × 20 cm, were installed in early May at the Penn State Experimental Forest for *Acer negundo*, *Acer saccharum*, *Quercus rubra*, *Quercus alba*, *Betula lenta*, *Fagus grandifolia*, *Carya ovata* and *Carya glabra*. Eight root bags were installed under four trees of each species (two bags per tree). Woody roots >4 mm in diameter were traced back to an identified tree before being planted in root bags filled with one part silica sand and three parts sieved field soil by volume. Bags were buried under 2 cm mineral soil, covered with leaf litter, and watered. For each tree one bag was collected for morphology and respiration measurements, the

other for P-uptake kinetics. Approximately 5 weeks later one root bag was recovered from each species, woody roots were cut at the entrance of the root bag, and intact bags were brought to the laboratory in coolers.

During all sampling, fine non-woody roots were left attached to large-diameter woody roots (0·5–1 cm) until roots could be washed in the lab. Samples from all years were cleaned in tap water in the lab. The finest clusters of roots in each sample were selected. This generally included the finest two orders of roots, which are functionally the most similar among different species. Samples of roots with dry segments or swollen new roots were discarded.

ROOT MEASUREMENTS

Root morphology and chemistry

Root structure (diameter, tissue density, SRL, number of root tips per root length), root N concentration, and phenolic (tannic acid) concentration for the finest two root orders were examined for all 11 species in 1999, and for all species except the conifers in 2000, collected from the Penn State Experimental Forest. Morphology of *P. virginiana* and *P. strobus* was also measured using samples collected from Hughesville in 1997.

Roots used for morphological and architectural measurements were stored in distilled water until imaged with a desktop scanner (WinRhizo software, Regent Instruments, Quebec, Canada). Roots were spread out in water with minimal overlap and scanned in grey scale at 450 dpi with a filter of 1·0 mm^2 and an automatic threshold (brightness) method appropriate for each sample (automatic methods specific for pale, normal or dark roots; Bouma, Nielsen & Koutstaal 2000). Staining roots was not necessary. Root length, diameter, volume and tip counts were determined using WinRhizo. Root samples were then dried and weighed. Root-tissue density was calculated from dry mass and estimated root volume.

Roots used for N and phenolic analysis were immediately freeze-dried after cleaning and ground using a mortar and pestle. The stele that could not be ground was cut into 1 mm or smaller pieces with scissors (ground tissue stored at 4° C). Total N concentration was determined with an elemental analyser (EA 1108 CHNS-O, Fisons Instruments, Mt Pleasant, NJ, USA). Total phenolic concentration was determined with the Folin–Denis assay for total phenolics (Waterman & Mole 1994) after acetone extraction for 30 min at 4° C.

Root physiology

Root physiology of *P. virginiana* and *P. strobus* was measured at Hughesville in 1997, and of the remaining species at the Penn State Experimental Forest in 2000. Samples were taken from four or five trees of each species in early June (Penn State Forest) or July and August (Hughesville) for respiration and ^{32}P uptake. Once removed from woody roots, selected fine roots were rinsed with distilled water and placed in calcium–MES buffered solution (1 mM $CaSO_4$, 5 mM MES adjusted with KOH to pH 5·5). Respiration (using a Clark-type oxygen electrode; Hansatech, King's Lynn, UK) and ^{32}P uptake rates were determined as described by Comas *et al*. (2002), with the exception that uptake rates were measured at 1·6, 7·8, 16, 80 and 400 μmol l^{-1} P in 1997, and at 1, 10, 25 and 50 μmol l^{-1} P in 2000. Respiration was measured 30 min after fine root separation from woody roots and within 5–6 h of field collection, and P uptake within 2 h of fine root separation and within 4–7 h of field collection.

Mycorrhizal colonization

Roots used in respiration measurements of the eight species sampled in 2000 (*A. negundo*, *A. saccharum*, *B. lenta*, *F. grandifolia*, *Q. rubra*, *Q. alba*, *C. ovata*, and *C. glabra*) were examined for mycorrhizal colonization after being dried and weighed. Dried roots were boiled in 10% KOH until roots became clear, but for no longer than 90 min. Roots of *A. saccharum* were soaked in 30% H_2O_2 for 10 min because they were still very dark. Other roots that were not clear after boiling in KOH were soaked in 1% H_2O_2 for 10 min. All roots were then washed three times with distilled water, soaked in 5% HCl for 5 min, and boiled in 0·01% Trypan Blue stain for 45 min. For arbuscular mycorrhizal (AM) species, the total percentage of root length colonization by fungi was determined using the magnified intersections method (McGonigle *et al*. 1990). For ectomycorrhizal (EM) species, the percentage of root tips that were covered by fungi was determined for each sample. The total percentage of root length colonization by fungi was also estimated using gridline intercept methods (McGonigle *et al*. 1990 and references therein).

TREE GROWTH AND SHOOT ACTIVITY

Tree growth at the site was assessed by measuring annual trunk growth rate (TGR_{site}) for the past 5 years in autumn 2000 at the Penn State Experimental Forest site. Two cores were taken from the trunk of each plant sampled for root measurements with an increment borer. Plants were cored ≈ 1·4 m from the ground (breast height) from the north and south direction if the plant was on level ground, and perpendicular to the slope if the plant was on a slope. Cores were oven-dried at 65 °C and mounted on wooden blocks. Cores were then sanded with 220, 320, 400 and 600 grit sandpaper and rubbed with 800 grit crocus cloth and white calcium carbonate chalk. The last five growth rings were measured with a calibrated micrometer on a dissecting scope. Trunk growth rate of saplings (TGR_{sap}) was also evaluated at a common garden plantation established in 1996 with 1-year-old seedlings at the Russell E. Larson Experiment Station, Penn State University, located near the Penn State Experimental

Forest. Trunk diameters were measured 10 cm from the ground in 2001.

As an estimate of photosynthetic capacity, leaf N concentration was determined for trees sampled at the Penn State Experimental Forest from canopy leaves collected in June 2000, using ropes and climbing equipment where required. Only leaves exposed to direct sunlight were chosen. For conifers, leaves were sampled from the youngest cohort of needles. Two subsamples were taken per plant, each comprising multiple leaves. Leaf petioles were not included. Leaves were transported to the lab in a plastic bag with a damp paper towel in a cooler. After washing the leaves in distilled water, leaves were freeze-dried, weighed and ground with a sample mill equipped with a 0·5 mm screen (Cyclotec 1093, Tecator, Sweden). Total N concentrations of each sample were determined with a CHNS-O elemental analyser (Model EA 1108, Fisons Instruments, Beverly, MA, USA).

STATISTICAL ANALYSES

All data were tested for normality with the Shapiro–Wilk test within species, and examined for homogeneity of variance among species with Levene's test. Non-normality and heterogeneity of variance were corrected with either logarithmic or square-root transformations. Traits were examined between fast- and slow-growing species across closely related pairs of species with a nested ANOVA design where fast and slow growth was nested within taxonomic contrast, observations were nested within the interaction between taxonomic contrast and fast and slow growth, and the design was replicated by year when 2 years' data were available (SAS Institute, Cary, NC, USA). Interactions between year, taxonomic contrast, and fast and slow growth were not significant, so were not included. As taxonomic contrasts and species within contrasts were fixed terms, the mean-square error used to test the effect of fast and slow growth was that of the observations nested in the interaction between taxonomic contrasts and fast and slow growth. Differences at $P = 0{\cdot}05$ were considered clearly significant. Differences between $P = 0{\cdot}10$ and $P > 0{\cdot}05$ were considered marginally significant to allow for the large variation typical of field data and the challenges of using numerous phylogenetic contrasts in a field root study. Experiment-wide pooled standard error for individual species was calculated from the square root of the mean-square error in the nested ANOVA used to test the effect of fast and slow growth (observations nested in the interaction between taxonomic relationships and fast and slow growth).

Results

ROOT MORPHOLOGY AND ARCHITECTURE

Fast-growing species had 27·9% overall larger SRL and 10·4% overall thinner roots than slow-growing species across species contrasts (SRL, $F_{5,10} = 3{\cdot}33$, $P < 0{\cdot}05$; diameter, $F_{5,10} = 7{\cdot}68$, $P < 0{\cdot}05$; Fig. 1a,b). There was no significant pattern in tissue density between fast- and slow-growing species ($F_{5,10} = 0{\cdot}50$, $P = 0{\cdot}77$; Fig. 1c). Year-to-year variation was smallest for root diameter and largest for tissue density. Root diameters were very similar between years (overall 1·3% difference in the

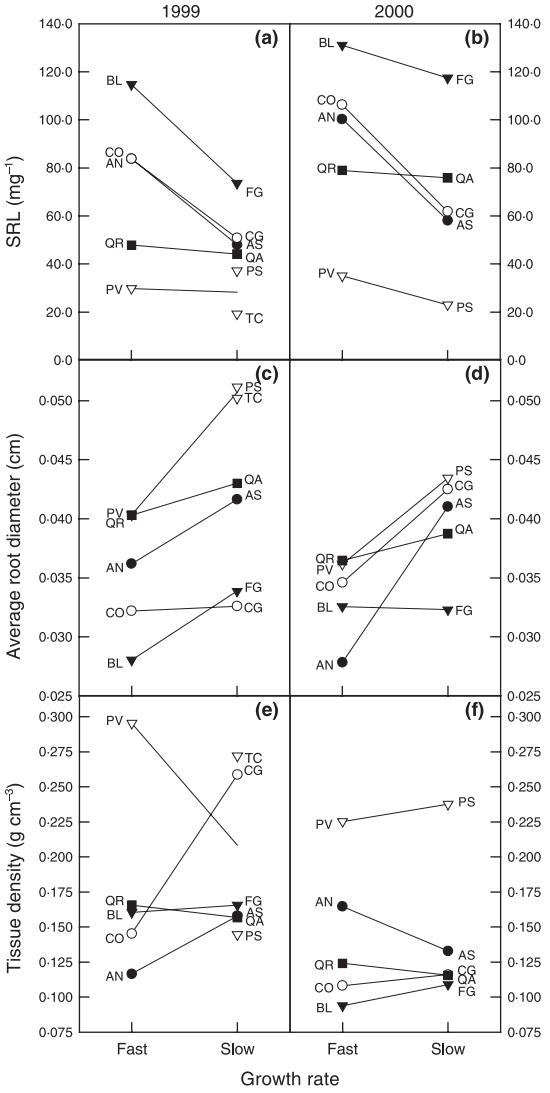

Fig. 1. (a,b) Specific root length (SRL); (c,d) root diameter; (e,f) root-tissue density compared within pairs of closely related fast- and slow-growing species. Species abbreviations: AN, *Acer negundo*; AS, *A. saccharum*; QR, *Quercus rubra*; QA, *Q. alba*; BL, *Betula lenta*; FG, *Fagus grandifolia*; PV, *Pinus virginiana*; PS, *Pinus strobus*; TC, *Tsuga canadensis*. Measurements in (a,c,e) taken in 1999 at the Penn State Experimental Forest; those (b,d,f) taken in 2000 for all species except *Pinus*, which were measured in 1997 at the Hughesville location. TC was measured only in 1999. In 1999 Pinaceae contrasts the line is drawn through the average of PS and TC, but both species are shown. Differences in SRL and root diameter between fast- and slow-growing species across contrasts were significant ($P < 0{\cdot}05$) but differences in tissue density were not ($P = 0{\cdot}77$). Pooled SE = 14·5 for SRL; 0·0042 for root diameter; 0·077 for tissue density (calculated for SRL and tissue density before transformation for statistical analyses).

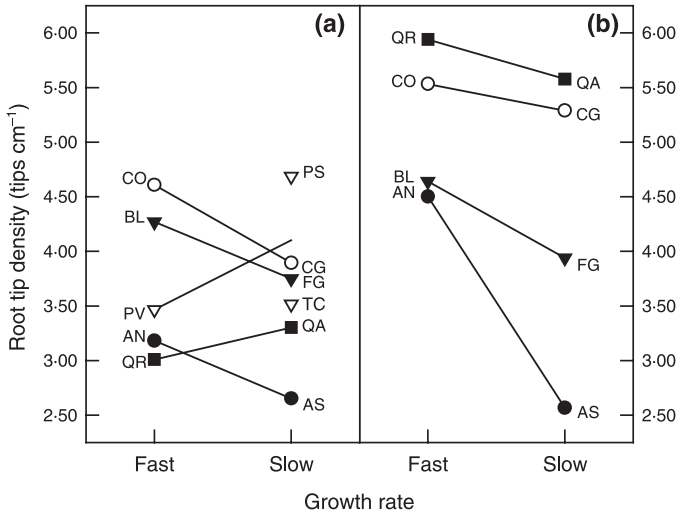

Fig. 2. Root-tip density (number of root tips per unit root length) compared within pairs of closely related fast- and slow-growing species measured in 1999 (a) and 2000 (b). Species abbreviations are as described for Fig. 1. In 1999 Pinaceae contrasts the line is drawn through the average of PS and TC, but both species are shown. Differences between fast- and slow-growing species across contrasts were marginally significant ($P < 0{\cdot}08$); pooled SE = 0·74 (calculated before transformation for statistical analyses).

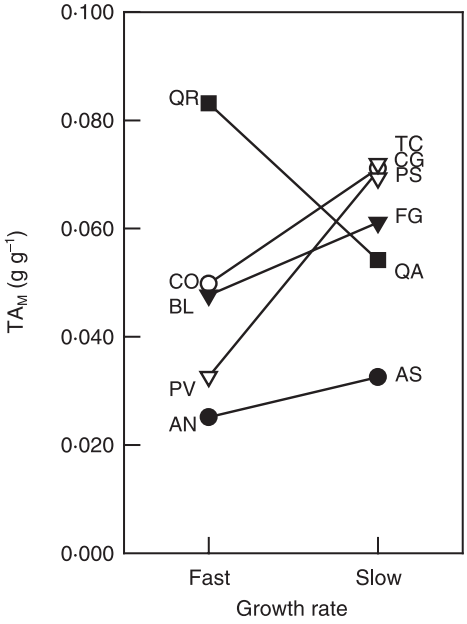

Fig. 3. Root phenolic (tannic acid) concentration per unit root mass (TA_M) compared within pairs of closely related fast- and slow-growing species. Species abbreviations are as described for Fig. 1. Differences between fast- and slow-growing species across contrasts were significant ($P < 0{\cdot}02$); pooled SE = 0·014.

species measured in both 1999 and 2000 at the Penn State Experimental Forest), whereas SRL and tissue density were 43% different.

Roots of fast-growing species had more tips per length of root (greater root tip frequency, 13·4% more overall) across species contrasts than roots of slow-growing species ($F_{5,10} = 2{\cdot}69$, $P < 0{\cdot}08$; Fig. 2). The one exception to this pattern was the conifer contrast. Fast-growing *P. virginiana* had fewer root tips per root length than *P. strobus*, which could be related to the decline in vigorous growth of *P. virginiana* at the site (Table 1). If the *Betula–Fagus* contrast was not included then differences in root architecture across contrasts were not significant ($F_{4,8} = 2{\cdot}24$, $P < 0{\cdot}15$), although fast-growing species in most contrasts (three out of four) still had more tips per length of root.

Qualitatively, species contrasts that had greater differences in growth rates between fast- and slow-growing species (such as the Aceraceae and *Betula–Fagus* contrasts) tended to have greater differences in SRL, root diameter and tips per root length than those with smaller differences in growth rates (such as the *Quercus* and *Carya* contrasts). However, the correlations of differences in traits and potential growth rate among contrasts (SRL and TGR_{lit}, $r = 0{\cdot}46$; root diameter and TGR_{lit}, $r = 0{\cdot}61$; number of root tips per unit length and TGR_{lit}, $r = 0{\cdot}66$; $n = 5$, df = 3), with so few degrees of freedom, were not significant.

ROOT-DEFENCE CHEMISTRY

Roots of fast-growing species generally had 24·7% overall lower concentration of tannic acids than those of slow-growing species across species contrasts ($F_{5,9} = 3{\cdot}74$, $P < 0{\cdot}05$; Fig. 3). Fast-growing species in all taxonomic groups except *Quercus* were consistent with this trend.

ROOT PHYSIOLOGY

Within all contrasts except the Pinaceae, the roots of fast-growing species tended to have higher N concentrations than those of slow-growing species in 1999 (without Pinaceae, $F_{4,6} = 3{\cdot}74$, $P = 0{\cdot}07$; with Pinaceae, $F_{5,8} = 0{\cdot}93$, $P = 0{\cdot}51$). The fast-growing species *P. virginiana* was probably in decline when roots were sampled at the Penn State Experimental Forest, as trunk growth rates measured on site were extremely small (Table 1). In the following year the fast-growing species in the Aceraceae contrast had higher respiration rates than slow-growing species. However, fast-growing species in *Betula–Fagus*, *Quercus* and *Carya* contrasts had lower respiration compared to slow-growing species. Thus no overall pattern in respiration rates emerged between fast- and slow-growing species ($F_{5,9} = 1{\cdot}48$, $P = 0{\cdot}29$; Table 1). Respiration per unit N was not examined because measurements were taken in different years.

Phosphorus uptake rate was lower in fast- than slow-growing species in Aceraceae and *Betula–Fagus* contrasts, and similar between fast- and slow-growing species of other contrasts; thus there was no significant overall pattern (P uptake at 50 μM P, $F_{5,10} = 1{\cdot}36$, $P = 0{\cdot}32$; Fig. 4).

As there was no general pattern between root physiology and life history, we examined the potential

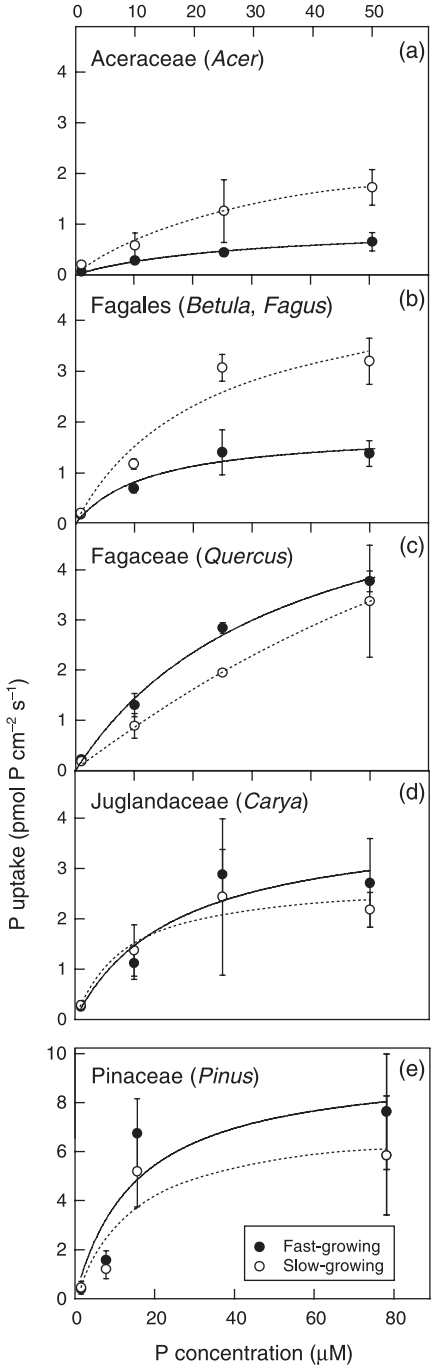

Fig. 4. Phosphorus-uptake rates at different P concentrations compared between fast- and slow-growing species of (a) Aceraceae (*Acer negundo*, *Acer saccharum*); (b) Fagales (*Betula lenta*, *Fagus grandifolia*); (c) Fagaceae (*Quercus rubra*, *Quercus alba*); (d) Junglandaceae (*Carya ovata*, *Carya glabra*); (e) Pinaceae (*Pinus virginiana*, *Pinus strobus*). Michaelis–Menten curves [$y = a \times x/(b + x)$] were fitted through averages of uptake measurements at each concentration. Measurements were taken on roots collected at the Stone Valley Experimental Forest for all species except *P. virginiana* and *P. strobus*, which were collected from Hughesville, PA. Differences between fast- and slow-growing species across contrasts were not significant ($P = 0{\cdot}32$ for highest concentration shown).

contributing effects of tree growth rate, leaf activity, tree size and mycorrhizal colonization on root physiology. Annual trunk diameter at breast height (d.b.h.) increase at the field site (TGR_{site}) was used as a surrogate for tree growth rate, leaf N concentration for leaf activity, and trunk d.b.h. for tree size. There was no correlation of TGR_{site}, leaf N concentration or trunk d.b.h. with respiration, nor were any of these factors significant as covariates when differences in respiration rates among species were analysed (data not shown). However, there was a clear decrease in respiration with increased fungal colonization that explained a significant portion of the variation in respiration ($r = 0{\cdot}53$, $P < 0{\cdot}05$; Fig. 5). Fungal colonization was a significant covariate when differences in respiration rates among species were analysed ($F_{2,11} = 6{\cdot}59$, $P < 0{\cdot}05$) but there was still no consistent pattern in respiration between fast- and slow-growing species ($F_{4,8} = 2{\cdot}33$, $P = 0{\cdot}14$).

Discussion

Patterns of root morphology, architecture and chemistry among the fine roots of fast- and slow-growing tree species in north-eastern temperate forests suggest that plants with high potential growth rates constructed their finest orders of roots for quick exploration of soil resources, short life span and rapid decomposition. Roots of fast-growing species generally had greater SRL, smaller diameters, more root tips per unit root length, and lower phenolic defences than slow-growing species, as originally hypothesized. However, hypotheses that roots of fast-growing species would have higher physiological activity than slow-growing species were not supported.

Greater SRL, smaller diameter and more root tips per unit root length permit plants to increase the volume of soil explored per unit biomass invested in fine roots. Root morphology, especially SRL, is theoretically important for nutrient foraging based on solute transport models (Yanai, Fahey & Miller 1995; Eissenstat & Yanai 1997). Greater SRL has been correlated with faster root proliferation rates in other studies, for example where rootstocks were grafted with the same scion (shoot) to control for shoot effects (Eissenstat 1991). In another study, when elongation rates of individual roots did not differ, root systems of fast-growing species had more root tips than those of slow-growing species (Nicotra, Babicka & Westoby 2002). However, factors other than root morphology and architecture influence root growth rates, such as carbohydrate supply and environmental conditions.

Total phenolics were generally less concentrated in roots of fast-growing than in those of slow-growing species, suggesting that roots of fast-growing species may have higher turnover rates, as roots with fewer defences are more likely to be attacked by soil organisms and to have faster decomposition rates. In leaves, species with fewer chemical and structural defences per unit mass are usually more susceptible to herbivory and decompose more quickly (Wardle, Bonner & Barker 2002).

Patterns in root morphology between fast- and slow-growing trees appeared to be robust against different

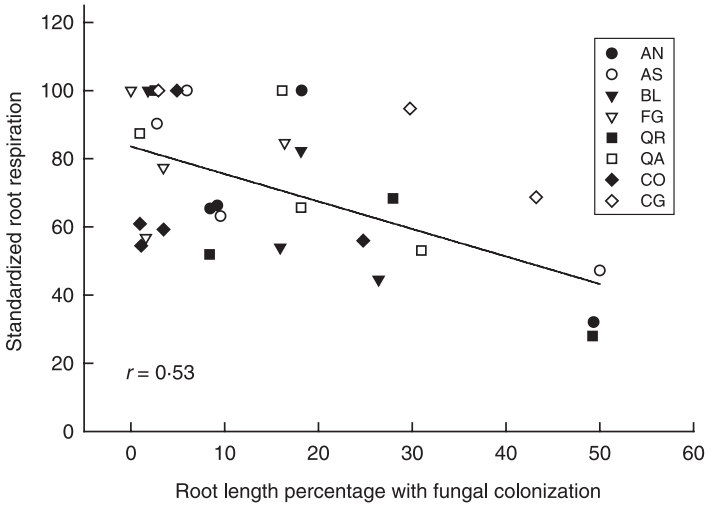

Fig. 5. Standardized root respiration (respiration standardized within species as a percentage of the measured for that species) correlated with percentage of root length colonized by fungi ($P < 0{\cdot}05$). Species abbreviations are as in Fig. 1. Each data point is an individual observation ($n = 33$). Correlations within species are negative for every species except *Fagus grandifolia*, which had low colonization percentages.

environmental conditions, as the 2 years of this study varied in moisture availability (total precipitation in May–June recorded for valley, 9·5 cm in 1999; 22·5 cm in 2000). Patterns in SRL and root diameter between fast- and slow-growing species in the present study were generally consistent with a seedling study that included many of the same species (Comas *et al*. 2002), indicating the generality of these patterns in morphological traits across ontogenetic stages.

There has been much discussion of the best morphological metric that distinguishes species' differences in comparative studies. Of particular interest is whether tissue geometry (root diameter, leaf thickness) or tissue density best captures structural differences in tissues among species (Wilson, Thompson & Hodgson 1999; Garnier *et al*. 2001). At issue are: (1) which traits should be used in multiple species comparisons where time and ease of measurement are important practical factors (Garnier *et al*. 2001); and (2) whether there are convergent patterns governing tissue construction among different species (Reich *et al*. 1999; Meinzer 2003). Among grasses, which have relatively fine roots, root-tissue density often best describes morphological differences between fast- and slow-growing species, with roots of slow-growing species being denser (Ryser 1996; Wahl & Ryser 2000). Grassland species associated with nutrient-poor habitats, which are typically slow-growing species, also have high tissue density in their roots (Craine *et al*. 2001). This general pattern in tissue density, however, does not seem to hold in fast- and slow-growing woody species and is variable among woody species in years that differed in moisture availability. When controlling for phylogeny, root diameter (or SRL) appears to be the best indicator of differences in potential growth rate among woody species. Fast-growing species had larger SRL than slow-growing species, either with little consistent difference in tissue density (Wright & Westoby 1999; Comas *et al*. 2002; present study) or where SRL described the combined effects of root diameter and tissue density (Eissenstat 1991). Constraints in tissue structure, such as root diameter and tissue density, may be different in herbaceous and woody vegetation, the important convergent pattern being that fast-growing species invest less biomass in the construction of root absorptive surface area or length.

Physiological measurements such as P uptake, respiration and N concentration did not show trends between fast- and slow-growing species, in contrast to previous research on seedlings grown in a controlled environment (Comas *et al*. 2002). However, there are many reasons why patterns of root physiology among seedlings should not be the same as those in mature trees of fast- and slow-growing species. First, root physiology is closely tied to whole-plant physiology. Patterns of faster respiration and P uptake in roots of fast- *vs* slow-growing species were observed at the seedling stage, when differences in plant growth rates between species would be greatest (Comas *et al*. 2002). Differences in plant growth rates between fast- and slow-growing species observed at seedling or sapling stages were less pronounced at mature stages (Table 1). In one species contrast – Pinaceae – the plant growth rate of the fast-growing species (*P. virginiana*) at the site (TGR_{site}) was actually slower than those of the slow-growing species (*P. strobus* and *T. canadensis*), possibly because most of the *P. virginiana* trees at the site had reached their maximum expected life span (Table 1). Second, root physiology can vary sharply with root age, and the relationship between age and physiology can also vary between species (Comas, Eissenstat & Lakso 2000; Bouma *et al*. 2001). While we sampled from only the first cohort of roots that proliferated at the start of the growing season, so that no roots were older than 5 weeks, we could not control for the precise age of roots. Although roots were collected around the same time for both fast- and slow-growing species, new root initiation of fast- and slow-growing species may occur at slightly different times so that the ages of roots of the different species may have differed by several weeks. Finally, soil microsite differences within the same forest could also affect root physiology, especially nutrient-uptake kinetics (Jackson, Manwaring & Caldwell 1990). Although roots were sampled randomly from the same forest, different trees can change the soil differently over time (Zinke 1962; Boettcher & Kalisz 1990). Thus there may have been systematic microsite differences between species that sampling techniques could not capture.

To our knowledge this is the first report of a correlation of decreased respiration rate with increased mycorrhizal colonization. One explanation for this relationship is that, while mycorrhizal colonization may have increased with root age, respiration may have decreased more rapidly with age. If mycorrhizal roots

had higher respiration rates than non-mycorrhizal roots when roots were relatively young, as typically found in seedling studies (Peng *et al*. 1993; Nielsen *et al*. 1998), then a potential decline in respiration with root age might have masked this mycorrhizal effect in the present study.

In conclusion, there are systematic differences in the structure of the finest roots of fast- and slow-growing species in north-eastern forests. Differences in root morphology and chemistry provide evidence for divergent patterns in root deployment by fast- and slow-growing species: fast-growing species have fine lateral roots that are cheaper to build, but are less well defended and presumably shorter-lived compared with the roots of slow-growing species. Patterns in root structure were found in the finest order roots, which are the most biologically active and ephemeral portion of the root system (Pregitzer *et al*. 1998; Wells, Glenn & Eissenstat 2002). Differences between fast- and slow-growing trees were apparent only when controlling for phylogeny; phylogeny exerted as large an effect on structural traits as did growth rate within phylogeny (Figs 1–3). Expanding these results to more families in other biomes would reveal whether the same kinds of generalities associated with leaf structure and potential growth rate also exist for the finest order roots.

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