

# Fine root demography and morphology in response to soil resources availability among xeric and mesic sandhill tree species

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## Summary

1. Optimality theory suggests that roots should be kept alive until the efficiency of resource acquisition is maximized (i.e. a maximum ratio of benefits to costs). Because root efficiency may vary with environmental conditions, ecological distributions of plant species may be linked to different patterns of root demography.

2. In a greenhouse study, we investigated fine root turnover (growth and death) for three woody species from the fall-line sandhills of the south-eastern USA. *Pinus palustris* Mill. is a generalist in this habitat, whereas *Quercus marilandica* Muenchh. occurs in more fertile, mesic habitats relative to *Quercus laevis* Walt. Seedlings were grown under four resource treatments (water + nutrients) for 7 months: high resources, low resources, and short-term exposure (last 2 months of the study) to resource enrichment or depletion.

3. Increasing fine root longevity may be optimal in resource-poor sites because root efficiency may be maximized by less root turnover and resource loss. As expected, fine root death and growth was less in species from xeric habitats (*Q. laevis*), but greater in species from mesic habitats (*Q. marilandica*). The generalist species *P. palustris* exhibited high growth but little death of fine roots.

4. When soil resources decrease, less root turnover may reduce resource loss. Fine root growth of all three species decreased at low resources. Fine root death decreased at low resources in *Q. marilandica*, the only species with significant root death.

5. Demographic responses differed between fine roots and leaves. Although leaf and fine root death were greater in *Q. marilandica* than in *Q. laevis*, leaf death, unlike root death, did not change with resource availability. Short-term resource enrichment or depletion affected leaf production but not fine root demography in the *Quercus* species.

6. Given that fine root morphology affects root maintenance and construction costs, we expected greater fine root growth and death in species with thinner roots of high specific root length (SRL) and low density. However, the species with the greatest root turnover, *Q. marilandica*, had thick and dense roots of low SRL.

7. Results from our study with woody species indicate that fine root demography, but not fine root morphology, was linked to ecological distribution in a narrow geographical range. Differences in fine root turnover under different resource availability were consistent with the optimality theory, and may reflect trade-offs between tolerance and competitive ability below ground: less root turnover of xeric species under low fertility may conserve resources, whereas faster root growth of mesic species potentially maximizes resource uptake in more fertile soils.

*Key-words:* *Pinus palustris*, *Quercus laevis*, *Quercus marilandica*, root death, root growth, specific root length

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## Introduction

Fine root turnover is a significant component of below-ground carbon budgets (Bloomfield, Vogt & Wargo 1996; Caldwell & Richards 1986; Eissenstat & Yanai 1997), and affects nutrient cycles due to the minimal retranslocation of nutrients from roots during senescence (Gordon & Jackson 2000; Nambiar 1987). Understanding controls of fine root demography is crucial in order to predict how carbon and nutrient cycling, plant water and nutrient acquisition, plant growth and productivity, and plant competition and fitness vary under environmental change (Eissenstat & Yanai 1997). Despite the importance of fine root demography, few studies have examined its controlling factors, and patterns of root demography across species and environments are still unclear (Eissenstat & Yanai 1997; Eissenstat *et al.* 2000; Gill & Jackson 2000).

Demographic patterns of plant tissues may be explained using optimality theory, assuming that optimal tissue longevity maximizes tissue efficiency, defined as the ratio of lifetime benefits divided by lifetime costs of a given tissue (Bloom, Chapin & Mooney 1985; Chabot & Hicks 1982; Eissenstat & Yanai 1997; Eissenstat *et al.* 2000; Givnish 1986). Tissue benefits include the amount of resources acquired by a given tissue, while tissue costs include the resources used for tissue construction and maintenance (Bloom *et al.* 1985). The balance of tissue costs and benefits may change due to factors such as resource availability and tissue morphology and physiology (Eissenstat *et al.* 2000), and optimal tissue longevity may also adjust to such changes. The optimality theory has been used to understand patterns of leaf demography (Chabot & Hicks 1982). However, its use to understand how root demography should adjust to changes in root efficiency is still incipient (Eissenstat & Yanai 1997).

Fine root longevity may change as a consequence of resource variation because resource uptake (benefits) decreases under low resource availability. Optimality theory predicts that lower tissue turnover rates are more prevalent in plants from resource-poor habitats (Grime 1994). Long-lived roots may maximize efficiency in infertile soils by increasing the ratio of lifetime resource uptake to construction and maintenance costs (Eissenstat & Yanai 1997). The theory also identifies a trade-off between longevity and growth rates of roots (Aerts 1999), because carbon used in root maintenance over longer life spans limits growth. Hence, plants adapted to infertile habitats should exhibit less fine root growth and death than species from fertile habitats. Over ecological time-scales, increase in resources should also lead to greater fine root growth and death, mainly in plants adapted to fertile habitats, where resource pulses are more abundant (Campbell & Grime 1989). Predictions of tissue demography based on resource variation have been confirmed above ground. Greater leaf longevity was linked to reduction in resource availability (light and/or nutrients) (Chabot

& Hicks 1982; Coley 1988; Reich, Walters & Ellsworth 1992; Schlöpfer & Ryser 1996). However, root demographic patterns with soil resource variation are still controversial (Burton, Pregitzer & Hendrick 2000; Eissenstat & Yanai 1997; Eissenstat *et al.* 2000; Hendrick & Pregitzer 1992; Nadelhoffer, Aber & Melillo 1985; Pregitzer, Hendrick & Fogel 1993; Ryan *et al.* 1996).

Differences in root longevity may be linked to different costs of tissue construction and maintenance, which in turn are associated with different fine root morphology (Eissenstat 1992; Eissenstat & Yanai 1997). Other variables being constant, relatively thick, dense roots tend to be more costly to construct per unit root length (Eissenstat 1991; Eissenstat 1992). Thicker roots should maximize lifetime efficiency by increasing longevity; therefore they should exhibit lower rates of growth and death. Although leaf demography and morphology have been characterized in hundreds of species (Reich *et al.* 1999), fine root demography and morphology have been described together in fewer than 10 species (Eissenstat *et al.* 2000).

In this study we investigated the predictions from the optimality analysis of root demography. In a greenhouse experiment using seedlings we compared root turnover (growth and death) of congeneric and non-congeneric woody species that inhabit the same area but have different ecological distributions. First, we tested the hypothesis that fine root growth and death are greater in mesic species compared to xeric species. Second, subjecting seedlings to different resource supply treatments, we tested if high resources increase turnover (growth and death) of fine roots. Third, we investigated whether differences in fine root morphology explained differences in fine root demography. We hypothesized that finer roots have higher turnover than thicker roots. Last, we compared demography and morphology of leaves and roots. Because the theory explaining fine root demography and morphology is adapted from studies on leaves, it is important to study leaf and fine root demography and morphology simultaneously, to test if functional analogies exist between leaves and fine roots (*sensu* Eissenstat *et al.* 2000).

## Materials and methods

### SPECIES AND HABITAT DESCRIPTION

The species studied in our experiment are native inhabitants of the fall-line sandhills of south-eastern USA, which are characterized by rolling hills with deep sandy soils, with poor water and nutrient retention capacity (Christensen 2000; Goebel *et al.* 2001; Peet & Allard 1993). Xeric and mesic areas are generally associated with variation in topography (Peet & Allard 1993). Xeric sites occur on sandhill ridges where surface sands are deeper; mesic sites occur in sandhill slopes and bottomlands where clay layers are closer to the surface. Mesic sites exhibit denser canopy cover and higher species diversity and soil resource availability

than xeric sites. *Pinus palustris* Mill. (longleaf pine) is the dominant overstorey tree in xeric and mesic areas. Two *Quercus* species, *Q. laevis* Walt. (turkey oak) and *Q. marilandica* Muenchh (blackjack oak), are distributed in xeric and mesic sites, respectively, co-occurring sometimes in mesic sites. The distribution of *Quercus* species has been linked to site differences in soil resource availability (Jacqmain, Jones & Mitchell 1999; Weaver 1969) and species differences in water stress tolerance (Donovan, West & McLeod 2000; Mavity 1986).

#### PLANT MATERIAL AND EXPERIMENTAL SETTING

Seeds of the three species were collected at the end of autumn 1998 near Columbus, Georgia, USA. Seeds were stratified over the winter at 5 °C for 4 months and later germinated in 'concrete sand' media in the greenhouse. The media consisted of washed, graded sand material free of organic matter and fine clay particles. The sand material met ASTM-C33 standards for sieve analysis. Before being used in the experiment, the sand was sterilized by steaming at 82.5 °C for 45 min. Seedlings were planted in 2 l plastic pots filled with sand and subjected to different resource supply treatments (see below) for 7 months (July 1999 to February 2000). The greenhouse provided control of air temperature (20–30 °C), and additional light was provided during the entire course of the experiment with sodium halide lamps that provided additional 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a 14 h photoperiod per day.

#### TREATMENTS

We studied the effects of different resource availabilities by changing the frequency of application and the concentration of a modified Hoagland's solution (Epstein 1972). Four different treatments were applied to groups of eight plants for a total of 7 months (from July 1999 to February 2000): a 'HIGH' treatment consisted of 1/10 modified Hoagland's solution applied every 2 days; a 'LOW' treatment consisted of 1/40 modified Hoagland's applied once a week; a 'DEPLETION' treatment consisted of shifting from HIGH to LOW; and an 'ENRICHMENT' treatment that shifted from LOW to HIGH. The last two treatments shifted resource supply during the last 2 months of the experiment (from December 1999 to February 2000). The HIGH treatment produced a gravimetric water content of the sand of approximately 10% (with a minimum above 8%), whereas the LOW treatment fluctuated between 5 and 2.5% (field capacity corresponded to a gravimetric moisture content of  $\approx$  12%).

#### FINE ROOT AND LEAF DEMOGRAPHY

The growth and death of fine roots (diameter <1 mm) was measured by mapping the fine roots visible through

one transparent plastic window (7 × 7 cm) in the wall of each pot. The root maps of each date were later retraced on transparent plastic, scanned, and their length measured using image analysis software (DELTA-T SCAN, Delta-T Devices Ltd, Cambridge, UK). Fine roots were considered dead when they disappeared or showed symptoms of senescence (shrivelling, blackening and decomposition of cortex and stele). Fine root growth was recorded as the total length of visible roots, and fine root death as the total length of dying roots. Fine root mortality was calculated as the percentage of total death divided by total growth. Fine root growth, death and mortality were recorded for each of eight plants per species and treatment combination, in intervals extending from the beginning of the experiment (July 1999) until 1, 4, 6 and 7 months after treatment initiation. The time intervals allowed the analysis of demography over most of the seedlings' growing season in the greenhouse. Fine roots growing and dying within a single interval were mapped with the same colour pen. Fine roots were mapped in biweekly intervals to ensure recording all events of root birth and death. For all seedlings, root turnover was slow and did not require more frequent observations. Except for short periods during root tracing, the windows were covered by opaque plastic to avoid light penetration.

Leaf demography was recorded by tagging individual leaves and by recording their fate from production until senescence. Leaf death was defined by necrosis of at least 75% of the leaf blade. Leaf mortality was calculated at the end of the experiment as the percentage of total leaf death divided by total leaf production. Leaf demographic variables were recorded for only the *Quercus* species.

#### FINE ROOT AND LEAF MORPHOLOGY

After 7 months (February 2000), plants from all treatments were harvested and root and leaf morphology were recorded. Three subsamples of fine roots per replicate were used to estimate: fine root thickness (mean diameter), tissue density, and specific root length (SRL). Samples were suspended in water on top of a desktop scanner and the length of the images and mean diameter was measured using DELTA-T SCAN image analysis software. After calibrating with DELTA-T SCAN image standards for length and thickness, images were scanned using Hewlett-Packard's PRECISION SCAN PRO software (Hewlett-Packard, Palo Alto, CA, USA), with settings of 200 for brightness and 400 dpi for resolution (Bouma, Nielsen & Koutstaal 2000). After scanning, root samples were oven-dried and the SRL estimated as the mean length divided by dry weight. Tissue density was calculated by the inverse of the SRL divided by the mean cross-sectional area of the fine roots (estimated from the mean diameter and assuming cylindrical root geometry). Specific leaf area (SLA) was calculated at the end of the experiment as the leaf area divided by leaf dry biomass. Leaf area was

measured with an LI-3100 leaf area meter (LiCor Inc., Lincoln, NE, USA). SLA was recorded for only the *Quercus* species.

#### BIOMASS ALLOCATION

In February 2000, plants from all treatments were harvested and above- and below-ground measurements were recorded for only living tissue: leaf and stem biomass, biomass of coarse roots (diameter >1 mm) and fine roots (diameter <1 mm), and root : shoot ratio. Biomass was measured after oven-drying plant parts at 60 °C for 48 h. The root : shoot ratio was calculated as the total above-ground biomass (stem and leaves) divided by the total below-ground biomass (coarse and fine roots).

#### STATISTICAL ANALYSIS

The experiment was designed as a completely randomized, three species  $\times$  four treatments, full factorial experiment. The species, treatment and interaction (species  $\times$  treatment) effects on root and leaf demography and morphology, and biomass allocation were analysed by a two-way ANOVA at the end of the experiment. Variables were transformed (square root, logarithmic and Box–Cox transformations) as necessary to meet ANOVA assumptions of normal distribution of residuals (Kolmogorov–Smirnov–Lillifor test) and variance equality (Bartlett's test) (Sall & Lehman 1996). Box–Cox transformations and tests of normality, variance inequality and ANOVAs were performed using JMP DATA ANALYSIS software (version 4.0.2, SAS Institute, NC, USA).

Differences between treatments for each species and differences between species within each treatment were analysed by pairwise comparisons of means. Species comparisons within treatments comprised a total of 12 comparisons (three comparisons at each treatment: *Q. marilandica* versus *Q. laevis*; *Q. marilandica* versus *P. palustris*; *Q. laevis* versus *P. palustris*). Treatment comparisons for each species comprised a total of nine comparisons (three comparisons for each species). We only compared treatment differences between HIGH versus LOW, HIGH versus DEPLETION, and LOW versus ENRICHMENT. In total, 21 comparison pairs were analysed for all fine root demography, morphology and biomass variables. Because we did not record leaf demography and morphology in *P. palustris*, there were only 10 comparisons for these variables (one species comparison at each treatment and three treatment comparisons per species). All mean contrasts were analysed by two-tailed *t*-tests after Bonferroni correction, using STATISTICAL ANALYSIS SYSTEM, MULTTEST procedure (SAS, Release 8.00).

The effects of time and the differences in fine root growth among species and treatments during the experiment were analysed by a multivariate, repeated-measures analysis (MANOVA; von Ende 1993) after

logarithmic transformation of the data. Only HIGH and LOW treatments were included in the analysis. Pillai's trace was used as the multivariate test of significance, and it is the statistic we report for within-subject effects (time, time  $\times$  species, time  $\times$  treatment, and time  $\times$  species  $\times$  treatment). Multivariate analyses were performed using JMP DATA ANALYSIS Software (version 4.0.2).

## Results

#### FINE ROOT DEMOGRAPHY

Species differed in fine root growth, death and mortality (Fig. 1; Fig. 2a–c). In general, *P. palustris* and *Q. marilandica* exhibited more fine root growth than *Q. laevis* (Table 1; Fig. 1; Fig. 2a) at HIGH and LOW resources. Fine root death and percentage mortality were significantly higher in *Q. marilandica* than in *Q. laevis* and *P. palustris* at HIGH resources, but did not differ at LOW resources (Fig. 2b,c).

At the end of the experiment, total fine root growth was significantly less in the LOW than HIGH treatments for *Q. marilandica* and *P. palustris*, and followed the same trend for *Q. laevis* (Fig. 1; Fig. 2a). Fine root death was also greater under HIGH than LOW resources for *Q. marilandica*, the only species that exhibited significant fine root death (Fig. 2b). Although not significant, fine root mortality tended to be less at LOW resources (Fig. 2c). Fine root death was observed

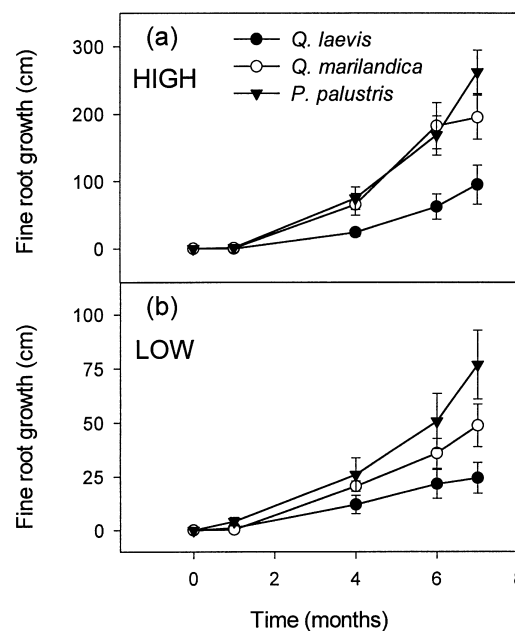
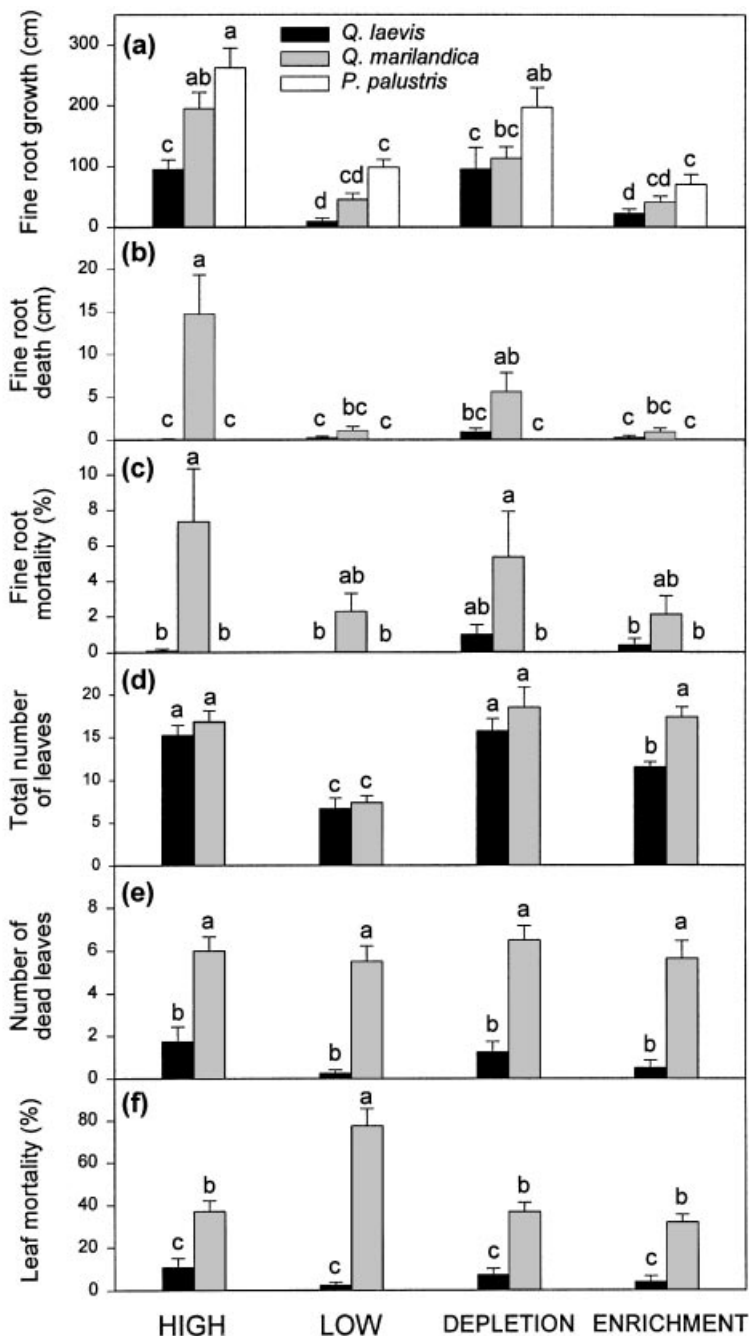


Fig. 1. Time course of fine root growth of *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings exposed to different treatments: (a) high resource supply ('HIGH'); (b) low resource supply ('LOW'). The graphs do not share the same scale on the y axis. Fine root growth was significantly less in *Q. laevis* ( $P < 0.001$ ) at HIGH resources. There were not significant differences between species ( $P > 0.05$ ) at LOW resources (means  $\pm$  SE,  $n = 8$  plants per species and treatment combination).



**Fig. 2.** Demography of above-ground and below-ground tissues in *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for 7 months in the greenhouse. The plants were exposed to different resource supply treatments: HIGH, LOW, ENRICHMENT and DEPLETION (means  $\pm$  SE,  $n = 8$  plants per species and treatment). Species differences across treatments and treatment differences for each species were analysed by Bonferroni-corrected pairwise comparisons. Different letters indicate significant differences between species at each treatment and between treatments of a single species at  $P < 0.05$ . (a) Fine root growth; (b) fine root death; (c) percentage fine root mortality; (d) leaf production; (e) leaf death; (f) percentage leaf mortality.

during the last 2 months and it was similar across treatments and species a month prior to harvest (data not shown). Compared to HIGH and LOW treatments, ENRICHMENT and DEPLETION treatments did not change significantly fine root death or percentage mortality (Fig. 2a–c). Except for *Q. laevis*, DEPLETION tended to reduce fine root growth (Fig. 2a).

## LEAF DEMOGRAPHY

Contrary to fine root growth, leaf production was similar between the *Quercus* species (Fig. 2d). The demographic responses to resources were also different between leaves and fine roots. Similar to fine roots, death and mortality of leaves were greater in *Q. marilandica* than *Q. laevis* (Fig. 2b,c,e,f). However, leaf death was similar across treatments (Fig. 2e), but fine root death increased at HIGH resources (Fig. 2b). In addition, leaf mortality in *Q. marilandica* was greater at LOW resources (Fig. 2f), but the opposite trend was observed in fine root mortality (Fig. 2c). Finally, fine root growth and leaf production were less at LOW than HIGH resources, but there was a positive response of leaf production to ENRICHMENT in *Q. marilandica* that was not observed for growth of fine roots (Fig. 2a,d).

## FINE ROOT MORPHOLOGY

Fine root morphology was not closely associated with fine root demography. First, morphology but not demography of fine roots was similar between the *Quercus* species (Figs 2 and 3). Second, fine roots of lower SRL and greater density and thickness did not always exhibit less growth and death: *P. palustris*, the species with greatest root growth (Fig. 2a), produced fine roots with greatest thickness and density and lowest SRL (Fig. 3a–c). Third, root morphology was constant across treatments except for two instances. First, SRL of *Q. laevis* increased at ENRICHMENT (Fig. 3a). Second, fine root thickness and fine root density tended to be less in *P. palustris* (Fig. 3b,c) at LOW than HIGH resources. There was no significant effect of resource supply on fine root diameter and density of the *Quercus* species (Fig. 3b,c).

## LEAF MORPHOLOGY

In general, we observed analogous patterns between leaf and fine root morphology. Both *Quercus* species had similar SLA and SRL (Fig. 3d). SLA and SRL were similar across resource supply treatments (Fig. 3a,d), except for the ENRICHMENT treatment, where only SLA of *Q. laevis* increased compared to the LOW treatment (Fig. 3a,d). The DEPLETION treatment was not significantly different than the HIGH treatment for SLA and SRL (Fig. 3a,d).

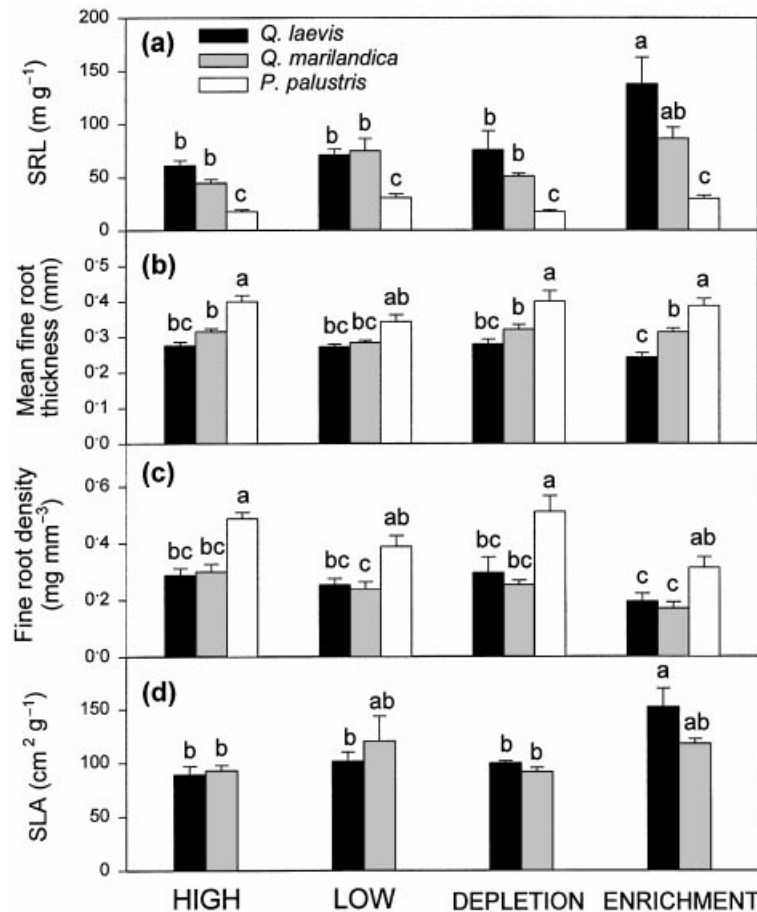
## ALLOCATION BELOW-GROUND

Fine root and leaf biomass were similar among the *Quercus* species, and significantly less than *P. palustris* at HIGH resources (Fig. 4a,b). At LOW resources, species differences in fine root and leaf biomass decreased (Fig. 4a,b). Proportional allocation below ground (root : shoot ratio) was similar among the *Quercus* species and greater than *P. palustris* at all

**Table 1.** Multivariate repeated measures analysis of time, species and treatment effects on the time course of fine root growth for *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown under HIGH and LOW resource supply

Source	Degrees of freedom		F	P > F
	Numerator	Denominator		
Between subjects				
Species	2	84	21.52	<0.0001
Treatment	3	84	9.30	<0.0001
Species × treatment	6	84	1.75	0.1204
Within subjects				
Time	3	82	339.0	<0.0001
Time × species	6	166	2.46	0.0267
Time × treatment	9	252	3.12	0.0014
Time × species × treatment	18	252	1.86	0.0195

Fine root growth data were analysed after logarithmic transformation ( $n = 8$  plants per species × treatment combination).



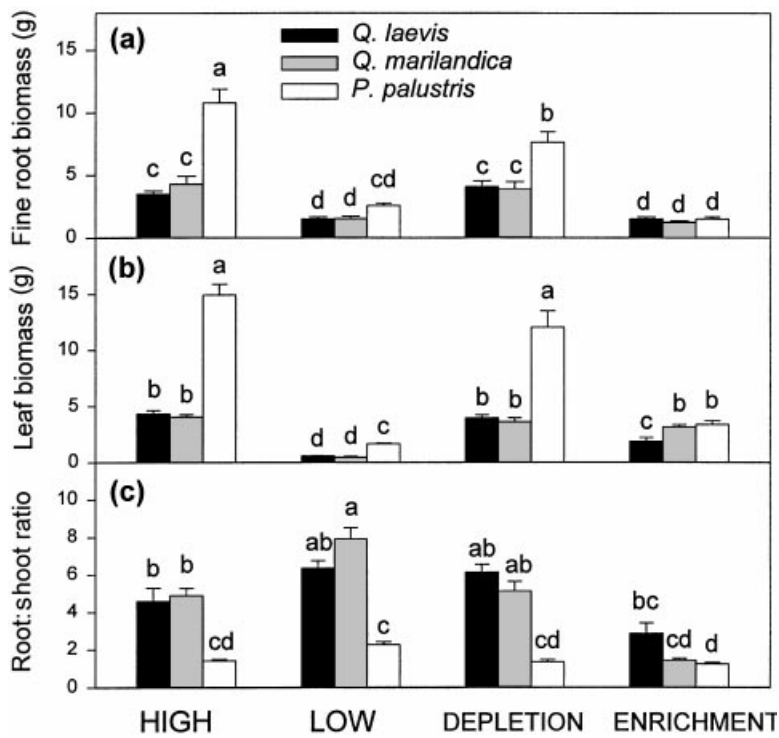
**Fig. 3.** Morphology of fine roots and leaves of *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for 7 months in the greenhouse. The plants were exposed to four different treatments of resource supply: HIGH, LOW, ENRICHMENT and DEPLETION (means ± SE,  $n = 8$  plants per species and treatment). Species differences across treatments and treatment differences for each species were analysed by Bonferroni-corrected pairwise comparisons. Different letters indicate significant differences between species at each treatment and between treatments of a single species at  $P < 0.05$ . (a) Specific root length, SRL; (b) mean fine root thickness; (c) fine root density; (d) specific leaf area, SLA.

resource levels, except for the ENRICHMENT treatment, where all species were similar (Fig. 4c). Contrary to the *Quercus* species, root : shoot ratio was uniform in *P. palustris* across treatments. For the *Quercus* species root : shoot ratio was greater at LOW than HIGH resources and less in response to ENRICHMENT (Fig. 4c). Similar to leaf number, leaf biomass but not fine root biomass was greater at ENRICHMENT compared to LOW treatments, especially in *Q. marilandica* (Fig. 4a,b). In all species, DEPLETION did not significantly change fine root and leaf biomass and root : shoot ratio (Fig. 4a,c).

## Discussion

Our study demonstrates different patterns of below-ground demography in tree species from a narrow environmental and geographical range. According to our expectations, fine root demography was associated with the ecological distribution of the congeneric oak species. Fine root growth and death were less in the *Quercus* species from xeric sites (*Q. laevis*) compared to those from more fertile, mesic sites (*Q. marilandica*). Slow fine root turnover in species from infertile habitats may maximize efficiency by increasing resource conservation under resource limitation (Eissenstat & Yanai 1997). This indicates a strategy of stress tolerance that favours *Q. laevis* under low resources, but constrains its growth when resources are abundant (Grime 1977). On the contrary, greater fine root growth and death in *Q. marilandica* may confer competitive advantage under more fertile conditions because faster root turnover allows the potential for rapid foraging for nutrients (Grime 1977). This is consistent with our findings that growth and death of fine roots were greater in *Q. marilandica* than *Q. laevis* only at HIGH resources. Less plasticity of *Q. laevis* than *Q. marilandica* in fine root growth and death also agrees with results of a previous study with sandhill oak species that investigated physiological plasticity in response to fertilizer and water addition (Vaitkus & McLeod 1995). In that study, juvenile trees of *Q. laevis* exhibited less plasticity in photosynthetic capacity and water-use efficiency than juvenile trees of *Q. hemisphaerica*, a mesic species with similar distribution to *Q. marilandica*.

For the generalist pine species, *P. palustris*, we did not observe a trade-off between persistence and proliferation ability of roots: absence of fine root death and less plasticity in allocation patterns (traits of stress tolerance) were associated with lower root : shoot ratio and greater root growth rates (competitive traits, *sensu* Grime 1977). This may be related to the widespread distribution of the pine species. Less root death can contribute to better tolerance of resource-poor xeric sites by *P. palustris* and *Q. laevis* rather than *Q. marilandica*. Higher root growth rates at high-resource mesic sites can contribute to the dominance of *P. palustris* and *Q. marilandica* over *Q. laevis*. Less fine root death in *P. palustris* than in *Q. marilandica*



**Fig. 4.** Allocation to fine roots and leaves and root : shoot ratio in *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for 7 months in the greenhouse. The plants were exposed to four different treatments of resource supply: HIGH, LOW, ENRICHMENT and DEPLETION (means  $\pm$  SE,  $n = 8$  plants per species and treatment). Species differences across treatments and treatment differences for each species were analysed by Bonferroni-corrected pairwise comparisons. Different letters indicate significant differences between species at each treatment and between treatments of a single species at  $P < 0.05$ . (a) Leaf biomass; (b) fine root biomass; (c) root : shoot ratio.

may reflect the continuous growth of the pine species throughout the year, and stronger nutrient retention, a trait associated with nutrient-poor environments (Aerts 1995). Differences in root demography between *Pinus* and *Quercus* species could not only be related to ecological distribution and evergreen growth habit of *Pinus*, but also be a consequence of comparing very distinct taxonomic groups (e.g. *Quercus* and *Pinus*). In our study, the comparison of congeneric *Quercus* species provides better evidence that root demography reflects evolutionary responses to habitat fertility, similar to studies on above-ground traits, growth and allocation patterns in congeneric grass species (Garnier 1992) and sandhill oaks (Long & Jones 1996).

Our results also provide evidence of different patterns of root demography under variation in resource availability. Fine root growth and death responses to different regimes in resource supply were generally consistent with the theory of efficiency optimization. Fine root growth was greater in all species under high resource supply. Fine root death was also greater at high than low resource supply for *Q. marilandica*, the only species that exhibited significant root death in the study. There was a trend of higher mortality also in *Q. marilandica* under high resources. Our results suggest that root turnover increased at higher resource availability, similar to findings of decreased fine root

life spans and higher turnover in more fertile soils (Aber *et al.* 1985; Nadelhoffer *et al.* 1985; Pregitzer *et al.* 1995), but contrary to findings of longer life spans and less root turnover at high fertility (Burton, Pregitzer & Hendrick 2000; Keyes & Grier 1981; Pregitzer, Hendrick & Fogel 1993; Vogt, Grier & Vogt 1986). Responses of leaf demography to resource availability differ from root responses. Although leaf and fine root death were greater in *Q. marilandica* than in *Q. laevis*, leaf death, unlike root death, was not affected by resource availability. Differences observed in the demographic responses of fine roots and leaves limit the simultaneous application of the optimality theory to above- and below-ground structures.

Contrary to our expectations, fine root growth and death did not change significantly after short-term resource enrichment or depletion, although leaf production in the *Quercus* species increased after enrichment. This suggests that short-term shifts in resource supply affect first above-ground growth rather than root demography in these species. Because *Q. laevis* also tended to increase SLA and SRL after enrichment, the *Quercus* species may differ in morphological plasticity, similar to findings in congeneric grass species (Ryser & Eek 2000).

Root morphological traits were previously proposed to be potential surrogates of root longevity (Eissenstat 1991; Eissenstat 1992; Ryser & Lambers 1995) based on relationships between high SLA and shorter leaf life span (Lambers & Poorter 1992; Reich *et al.* 1992; Reich *et al.* 1999; Ryser & Urbas 2000), and the assumption that SRL and SLA may be analogous (Eissenstat *et al.* 2000). On the contrary, our results indicate that fine root demography was not predicted by fine root morphology. Ryser (1996) found poor correspondence of SRL and fine root thickness with fine root death in grasses and forbs, but a good association between fine root density and death. We did not find good correspondence in any root morphological variable, nor between leaf morphology and demography. Similar to studies on leaf longevity and morphology of similar species within single communities (Reich 1993), our study with the sandhill oaks also found a poor association between leaf demography and morphology. As with fine roots, leaf morphology (SLA) was similar but leaf demography differed between the *Quercus* species. Variation in morphology of leaves and roots may occur over wider ecological ranges, and it may not be a factor associated with demography in closely related species. Eissenstat *et al.* (2000) proposed that better correspondence between root demography and morphology may be found only when comparing broad ranges of species that vary widely in these traits. For instance, SLA and allocation below ground were significantly lower in species from xeric habitats when more species of the south-eastern US coastal plain were also compared (Long & Jones 1996).

Our results provide circumstantial evidence that root turnover may be reduced in habitats of low fertil-

ity, possibly as a strategy to maintain roots alive until the efficiency of resource acquisition is maximized (Eissenstat & Yanai 1997). The greater fine root turnover under high resources of the *Quercus* species from the more fertile habitat, but the slower turnover of the species from infertile habitats, also suggest that trade-offs may exist between tolerance and competitive ability below ground (Aerts 1999; Grime 1977). Even though observed patterns of fine root demography were consistent with those suggested for species adapted to fertile and infertile habitats, generalizations based solely on a comparison of few species must be regarded with caution. Our conclusions should not be extrapolated to adult trees because seedlings are likely to have less root mortality than adult trees (Espeleta & Eissenstat 1998). Because establishment of seedlings is important in vegetation development, and juvenile traits have potentially adaptive value, our results still support the use of optimality and cost-benefit approaches to understand leaf and root demography of these sandhill tree species.

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### References

- Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McLaugherty, C.A. & Pastor, J. (1985) Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* **66**, 317–321.
- Aerts, R. (1995) The advantage of being evergreen. *Trends in Ecology and Evolution* **10**, 402–407.
- Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* **50**, 29–37.
- Bloom, A.J., Chapin, F.S. III & Mooney, H.A. (1985) Resource limitation in plants; an economic analogy. *Annual Review of Ecology and Systematics* **16**, 363–392.
- Bloomfield, J., Vogt, K. & Wargo, P.H. (1996) Tree root turnover and senescence. *Plant Roots, the Hidden Half* (eds Y. Waisel, A. Eshel & U. Kafkafi), pp. 363–382. Marcel Dekker, New York.
- Bouma, T.J., Nielsen, K.L. & Koutstall, B. (2000) Sample preparation and scanning protocol for computerised analysis of root length and diameter. *Plant and Soil* **218**, 185–196.
- Burton, A.J., Pregitzer, K.S. & Hendrick, R.L. (2000) Relationships between fine root dynamics and nitrogen

- availability in Michigan northern hardwood forests. *Oecologia* **125**, 389–399.
- Caldwell, M.M. & Richards, J.H. (1986) Competing root systems: morphology and models of absorption. *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 251–269. Cambridge University Press, London.
- Campbell, B.D. & Grime, J.P. (1989) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist* **112**, 261–267.
- Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**, 229–259.
- Christensen, N.L. (2000) Vegetation of the southeastern coastal plain. *North American Terrestrial Vegetation* (eds M.G. Barbour & W.D. Billings), pp. 397–448. Cambridge University Press, New York.
- Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**, 531–536.
- Donovan, L.A., West, J.B. & McLeod, K.W. (2000) *Quercus* species differ in water and nutrient characteristics in a resource-limited fall-line sandhill habitat. *Tree Physiology* **20**, 929–936.
- Eissenstat, D.M. (1991) On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytologist* **118**, 63–68.
- Eissenstat, D.M. (1992) Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* **15**, 763–782.
- Eissenstat, D.M. & Yanai, R.D. (1997) The ecology of root lifespan. *Advances in Ecological Research* **27**, 2–60.
- Eissenstat, D.M., Wells, C.E., Yanai, R.D. & Whitbeck, J.L. (2000) Building roots in a changing environment: implications for root longevity. *New Phytologist* **147**, 33–42.
- von Ende, C.N. (1993) Repeated-measures analysis: growth and other time-dependent measures. *Design and Analysis of Ecological Experiments* (eds S. Scheiner & J. Gurevitch), pp. 113–137. Chapman & Hall, New York.
- Epstein, E. (1972) Mineral nutrition of plants. *Principles and Perspectives*. John Wiley & Sons, New York.
- Espeleta, J.F. & Eissenstat, D.M. (1998) Responses of citrus fine roots to localized soil drying: a comparison of seedlings with adult fruiting trees. *Tree Physiology* **18**, 113–119.
- Garnier, E. (1992) Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology* **80**, 665–675.
- Gill, R.A. & Jackson, R.B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* **147**, 13–32.
- Givnish, T.J. (1986). *On the Economy of Plant Form and Function*. Cambridge University Press, London.
- Goebel, P.C., Palik, B.J., Kirkman, K., Drew, M.B., West, L. & Paterson, D.C. (2001) Forest ecosystems of a Lower Gulf Coastal Plain landscape: a multifactor classification and analysis. *Journal of the Torrey Botanical Society* **128**, 47–75.
- Gordon, W. & Jackson, R.B. (2000) Nutrient concentrations in fine roots. *Ecology* **81**, 275–280.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.
- Grime, J.P. (1994) The role of plasticity in exploiting environmental heterogeneity. *Exploitation of Environmental Heterogeneity of Plants: Ecophysiological Processes Above- and Belowground* (eds M.M. Caldwell & R.W. Pearcy), pp. 1–20. Academic Press, New York.
- Hendrick, R.L. & Pregitzer, K.S. (1992) The demography of fine roots in a northern hardwood forest. *Ecology* **73**, 1094–1104.
- Jacqmain, E.I., Jones, R.H. & Mitchell, R.J. (1999) Influences of frequent cool-season burning across a soil moisture

- gradient on oak community structure in longleaf pine ecosystems. *American Midland Naturalist* **141**, 85–100.
- Keyes, M.R. & Grier, C.C. (1981) Above- and belowground net production in 40 year old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* **11**, 599–605.
- Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **22**, 187–161.
- Long, T.J. & Jones, R.H. (1996) Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. *Trees* **11**, 1–8.
- Mavity, E.M. (1986) *Physiological ecology of four species of Quercus on the sandhills of Georgia*. MSc thesis, University of Georgia, Athens.
- Nadelhoffer, K.J., Aber, J.D. & Melillo, J.M. (1985) Fine roots, net primary productivity and soil nitrogen availability: a new hypothesis. *Ecology* **66**, 1377–1390.
- Nambiar, E.K.S. (1987) Do nutrients retranslocate from fine roots? *Canadian Journal of Forest Research* **17**, 913–918.
- Peet, P.K. & Allard, D.J. (1993) Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. *Proceedings of the Tall Timbers Fire Ecology Conference* **18**, 45–82.
- Pregitzer, K.S., Hendrick, R.L. & Fogel, R. (1993) The demography of fine roots in response to patches of water and nitrogen. *New Phytologist* **125**, 575–580.
- Pregitzer, K.S., Zak, D.R., Curtis, P.S., Kubiske, M.E., Teerie, J.A. & Vogel, C.S. (1995) Atmospheric CO<sub>2</sub>, soil nitrogen and turnover of fine roots. *New Phytologist* **129**, 579–585.
- Reich, P.B. (1993) Reconciling apparent discrepancies among studies relating leaf life span, structure and function of leaves in contrasting plant life forms and climates: 'the blind man and the elephant retold'. *Functional Ecology* **7**, 721–725.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**, 365–392.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**, 1955–1969.
- Ryan, M.G., Hubbard, R.M., Pongracic, S., Raison, R.J. & McMurtrie, R.E. (1996) Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* **16**, 333–343.
- Ryser, P. (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology* **10**, 717–723.
- Ryser, P. & Eek, L. (2000) Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany* **87**, 402–411.
- Ryser, P. & Lambers, H. (1995) Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil* **170**, 251–265.
- Ryser, P. & Urbas, P. (2000) Ecological significance of leaf life span among Central European grass species. *Oikos* **91**, 41–50.
- Sall, J. & Lehman, A. (1996) *JMP Start Statistics. A Guide to Statistical and Data Analysis Using JMP and JMP IN Software*. Duxbury Press, Belmont, USA.
- Schläpfer, B. & Ryser, P. (1996) Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos* **75**, 398–406.
- Vaitkus, M.R. & McLeod, K.W. (1995) Photosynthesis and water-use efficiency of two sandhill oaks following additions of water and nutrients. *Bulletin of the Torrey Botanical Club* **122**, 30–39.
- Vogt, K.A., Grier, C.C. & Vogt, D.J. (1986) Production, turnover and nutritional dynamics of above- and belowground detritus of the world forest. *Advances in Ecological Research* **15**, 303–307.
- Weaver, T.W. (1969) *Gradients in the Carolina fall-line sandhills: environment, vegetation, and comparative ecology of oaks*. PhD thesis, Duke University, Durham, North Carolina.

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