

Tree species fine-root demography parallels habitat specialization across a sandhill soil resource gradient

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Abstract. Single species can substantially alter belowground processes in ecosystems via differential root production and death. However, information on species differences in fine-root demography is virtually absent for natural communities. In this field study, we recorded species-specific fine-root (<2 mm in diameter) demography in adults of four tree species (*Pinus palustris*, *Quercus laevis*, *Q. incana*, and *Q. margaretta*) that are distributed differentially along soil resource gradients in the fall-line sandhills of the southeastern United States. At a subxeric habitat where all four species co-occur, roots of individual trees of each species were isolated in rhizotrons and tracked individually for three years. *Quercus* species had similar fine-root morphology but differed substantially for fine-root demography and architecture. *Quercus laevis* and *Q. incana*, the species from xeric habitats, showed lower fine-root production, death, percentage mortality, turnover rates, and risk of death, and greater life span and mean root segment length (MRS�) than *Q. margaretta*, the species from subxeric habitats. Fine roots of *P. palustris* (a generalist) showed high production and intermediate mortality, turnover rate, longevity, and MRS�. Fine-root survival increased with root order (first to fourth in centripetal order), but the degree of change was species specific. *Q. margaretta* showed greater increases in survival with order, but all species had similar demography of third- and fourth-order roots. Mycorrhizal roots had greater longevity than non-mycorrhizal roots only in *Q. laevis*. Species differences were also seasonal. Although these *Quercus* species are leaf deciduous, some growth of fine roots occurred in *Q. margaretta* during the “leaf-dormant” season. In our narrow-scale species comparison, species differences in ecological distribution were consistent with the observed variation in fine-root demography and architecture with greater resolution than leaf characters or other root traits such as morphology. Our results also show that narrow-scale variation in fine-root demography (including intra-generic differences) can be as large as broad-scale variation across biomes and vegetation types. Hence, small shifts in community composition have the potential to produce substantial changes below ground.

Key words: ectomycorrhizas; fine-root architecture, longevity, and turnover; *Pinus palustris*; *Quercus incana*; *Quercus laevis*; *Quercus margaretta*; root order.

INTRODUCTION

Fine-root dynamics are a critical component of plant performance and nutrient relations. At larger scales fine-root turnover contributes substantially to annual ecosystem production and respiration (Vogt et al. 1996, Jackson et al. 1997). Although changes in fine-root demography can significantly affect aspects of ecosystem function such as productivity and element cycling rates (Eissenstat and Yanai 1997, Gill and Jackson 2000), our current understanding of root patterns across plant species and environments is still

limited. Targeted studies of belowground differences across species and resource gradients can advance our understanding of dynamic responses of terrestrial ecosystems to change, including shifts in species composition of natural communities.

The adaptive value of tissue demographic responses to resource variation has been explored via optimality theory (Chabot and Hicks 1982, Bloom et al. 1985, Givnish 1986), based on the premise that tissue longevity should be a function of time to recover the investment in tissue construction and maintenance, thereby maximizing tissue efficiency (i.e., the balance of benefits to costs). Most empirical studies testing root functional ecological theory have concentrated on isolated plants in greenhouses, and more information is needed on adult plants growing under natural conditions in multispecies communities (Hodge 2004). This is critical since theoretical expectations for other root traits (e.g., foraging ability) have not found support when tested for multiple species in natural conditions (Kembel and Cahill 2005).

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There are obvious methodological difficulties in measuring root demography in a wide range of species and environments (Gill and Jackson 2000). A survey of studies on fine-root demography using direct observation methods found that approximately two thirds of all studies were restricted to seedlings in the greenhouse or to adult plants in monospecific stands or plantations (Espeleta 2002). When natural multispecies communities have been studied, effects were attributed to one or two dominant species if the community was simple enough, such as in forests dominated by *Acer saccharum* (Hendrick and Pregitzer 1993), or *Quercus ilex* (López et al. 2001), or in certain heathlands dominated by dissimilar species (Aerts et al. 1992). Studies comparing mixed-species communities were less abundant (<10%), and all of them lacked the ability to resolve species-specific patterns (Ruess et al. 1998, Tierney and Fahey 2001). Some recent studies with planted tree plots are still unable to provide species-specific root demography because of the inclusion of understory vegetation (Valverde-Barrantes et al. 2007). To date, we are not aware of any published comparative studies of fine-root demography between co-occurring trees in natural communities.

In an attempt to derive proxies for root trait variation, root trait covariation and leaf/root parallelisms have been explored across species and biomes to circumvent tedious measurements of root demographic parameters (Comas and Eissenstat 2004, Craine et al. 2005, Tjoelker et al. 2005). Both leaf and fine-root life span can reflect whole-plant strategies for resource acquisition and conservation (sensu, Reich et al. 2003). However, the empirical evidence for a positive correlation between leaf and root traits is relatively weak (Burton et al. 2000), and it is possible that the phylogenetic and environmental scale of variation differs between fine roots and leaves (Withington et al. 2006). This apparent asymmetry could be explained by selective forces acting at different scales above and below ground, so that leaf life span relates more to broad climatic factors (such as growing season length; Cavender-Bares 2004b), and root demography responds mainly to narrow-scale variation in soil resource availability.

In order to investigate the degree of fine-root demographic divergence across narrow phylogenetic and spatial scales, we made intra- and intergeneric comparisons among the dominant trees of a fall-line sandhill ecosystem in the southeastern United States. We measured the range of intra-generic variation in fine-root demography across three *Quercus* species and compared it with a phylogenetically distant co-dominant *Pinus* species. We also tested whether species variation in fine-root demography was associated with local environmental gradients. The fall-line sandhills are characterized by sandy soils of varying depth with poor water and nutrient retention (Peet and Allard 1993, Christensen 2000, Goebel et al. 2001). Concomitant variation in topography and soil depth in the sandhills produces a

gradient of xeric (deep sand ridges), subxeric (slopes), and mesic habitats (bottom lands) with resource availability tending to increase from xeric to subxeric and mesic habitats (Goebel et al. 2001, West et al. 2004). Many dominant sandhill tree species coexist in subxeric habitats, but have different distributions along the gradient. *Quercus laevis* Walt. (turkey oak), *Q. incana* Bartr. (bluejack oak), and *Q. margaretta* Ashe (sand post oak) are differentially distributed along a xeric to subxeric gradient, with *Q. laevis* and *Q. incana* typically associated with the more xeric habitats, and *Q. margaretta* with the subxeric habitats (Wells and Shunk 1931, Weaver 1969, Mavity 1986, Jacqmain et al. 1999). *Pinus palustris* L. (longleaf pine) can dominate the overstory in all habitats but can be absent as well (Wells and Shunk 1931). The three *Quercus* species in this study differ in aboveground resource use strategies (Vaitkus and McLeod 1995, Donovan et al. 2000), but exhibit very similar root morphology (specific root length, diameter, and tissue density; Espeleta 2002, Espeleta and Donovan 2002). Differences in fine-root growth and mortality were evident among these species in a greenhouse study of seedlings (Espeleta 2002, Espeleta and Donovan 2002), but these findings do not necessarily predict adult root demography since this can change across plant developmental stages (Espeleta and Eissenstat 1999).

Retention of roots (i.e., reduction in tissue loss) is expected to be more advantageous in low resource, xeric environments, and high root production rates should be more important in mesic environments (Grime 1977, Aerts and Chapin 2000). We predicted that species that dominate xeric habitats would have greater fine-root longevity and that species that dominate subxeric habitats should have greater root production. We also recorded demography specific to root branching orders based on recent studies linking root branching order with root chemistry, longevity, and morphology (Pregitzer et al. 1997, 2002, Wells et al. 2002, Guo et al. 2004, 2008a, b, Majdi et al. 2005), and proposed that differences in root demography should be observed mainly in lower order roots, with putatively greater resource uptake and maintenance costs (sensu Eissenstat and Yanai 1997). The species in our study also differ in aboveground phenology, but this trait does not closely track the soil resource gradient. The evergreen habit of the generalist *P. palustris* contrasts with the *Quercus* species, which tend to be winter deciduous. Only the xeric *Q. incana* is brevideciduous (leaves persist during mild winters; Duncan and Duncan 1988) in comparison to the strictly winter deciduous xeric *Q. laevis* and subxeric *Q. margaretta*. Although nutrient use efficiency can be regulated by tissue demography both above and below ground (Aerts 1990), we hypothesized an asymmetry in tissue demography and phenology in leaves and fine roots, because of selection acting at different scales (sensu Cavender-Bares 2004a, b).

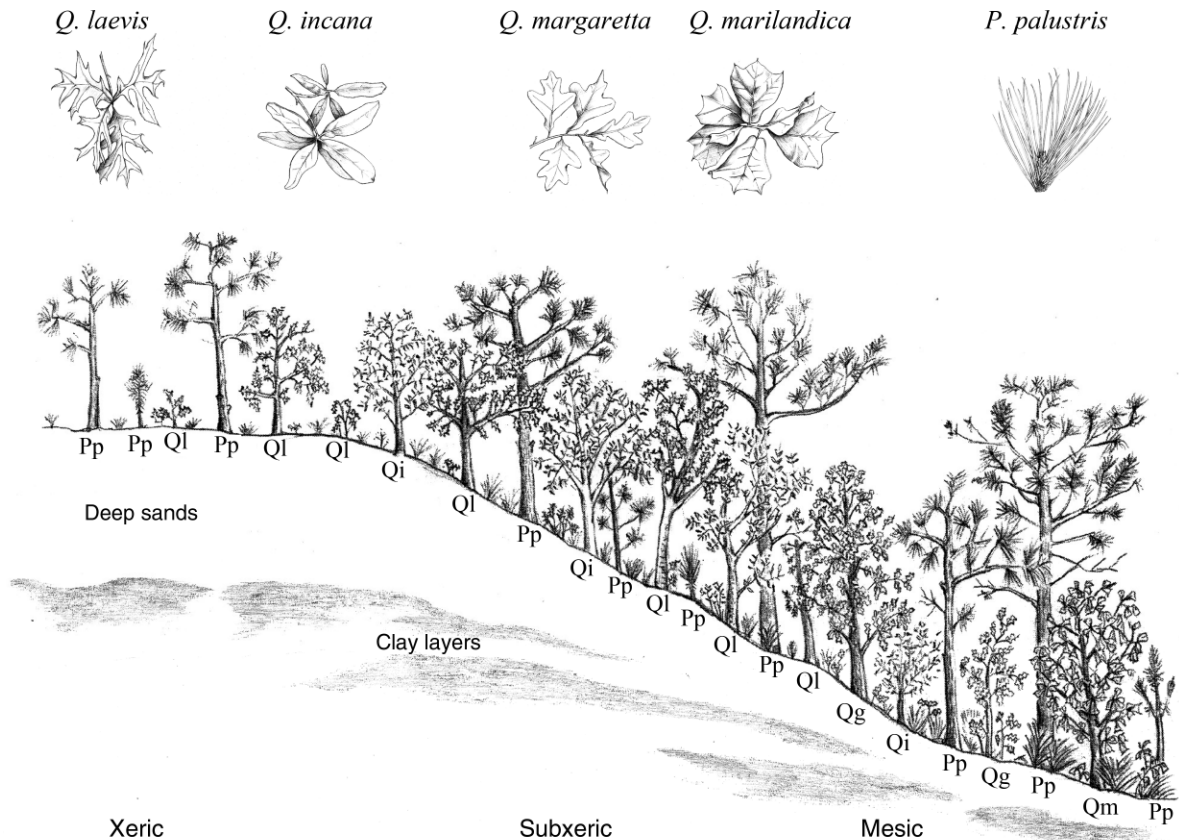


FIG. 1. Schematic representation of a fall-line sandhill habitat in the southeastern United States, showing differences in tree species distribution across a topographic gradient. These sandhills are characterized by sandy soils with varying depth to a relatively impermeable subsurface clay layer. Differences in water and nutrient availability create a transition from xeric (ridge tops) to subxeric (mid slopes) and mesic habitats (slope bottoms). Three oak species, *Quercus laevis* (Ql), *Q. incana* (Qi), and *Q. margaretta* (Qg) partition this gradient in this order but overlap in subxeric habitats. A pine species, *Pinus palustris*, is a generalist distributed evenly across the gradient. Our study compared fine-root demographic patterns in a subxeric habitat where all tree species coexisted. A fourth oak species, *Q. marilandica* (Qm) is only found in mesic habitats and was not included in the study. Leaves of each species are shown in detail to help identification.

MATERIALS AND METHODS

Study site

The investigation was conducted at the Carolina Sandhills National Wildlife Refuge (CSNWR) located near McBee, South Carolina, USA (34°33'18" N, 80°13'48" W). This site is located at ~100 m above sea level and has a temperate climate with a mean annual temperature of 16°C and a mean annual precipitation of 1234 mm, without a clear seasonality in rainfall. Appendix A shows temperature and precipitation data for the study period as well as 30-yr averages. The study site was located in a subxeric habitat at the lower half of a hill slope (Fig. 1). Our study plot consisted of ~0.1 ha (50 m in width × 20 m in length) in the subxeric habitat, where three *Quercus* species (*Q. laevis*, *Q. incana*, and *Q. margaretta*) and one *Pinus* species (*P. palustris*) coexist. The soil consists of deep coarse sand on top of a clay layer of sedimentary origin (Typic quartzzammint; USDA 1995). Understory vegetation is sparse and

mainly composed of wiregrass, *Aristida stricta*, and little bluestem, *Schizachyrium scoparium* (both C4 bunchgrasses), and dwarf huckleberry (*Gaylussacia dumosa*).

Isolation of species effects: rhizotron installation

Studying species-specific root demography in natural multispecific communities poses many difficulties. Some techniques for estimating root life span by direct observation, such as minirhizotrons and traditional underground rhizotrons, are not suitable for collecting species-specific root demography from mixed-species communities, especially when species exhibit similar root appearance. In this study, we used species-specific "rhizotrons" to isolate the responses of roots transplanted from single tree species in their natural community. Species-specific rhizotrons are more feasible and less intrusive alternatives to root trenching and complete species removal (Burch et al. 1997). The rhizotrons consisted of PVC semicylindrical chambers (diameter = 60 cm, depth = 60 cm, volume = 89 L), with

open tops and bottoms, that prevented colonization by any roots other than those being transplanted. The rhizotrons had a Plexiglas acrylic window (50×50 cm) that was used for root observation. The gap in front of the observation window was filled with insulation and the window covered with white over black plastic between observations to prevent light and temperature artifacts from affecting the roots growing against the window. We selected roots of six adult individuals (dbh: 20–70 cm) of each study species (*Q. laevis*, *Q. incana*, *Q. margaretta*, and *P. palustris*) and transplanted them into rhizotrons on 19 February 1999. Two lateral roots (1–2 m in length and 0.5–1.0 cm thick) of each tree were excavated from the soil and inserted through lateral holes into a rhizotron. Each rhizotron was buried next to the tree (distance = 1–2 m from the bole of the tree) and the volume above the roots was filled with the original soil, maintaining the original vertical stratification. New root growth was observed in all 24 rhizotrons during the 1999 growing season. Soil water potential (ψ_s) and soil temperature (T_s) were measured continuously (every hour at a depth of 25 cm) inside the rhizotrons with thermocouple psychrometers (details in Espeleta et al. 2004).

Sandhills habitats are routinely subjected to controlled fires. In March 2000, a prescribed burn crossed a fire line around the plot and burned its periphery. The fire was fast moving and burned the window of one *P. palustris* rhizotron that was subsequently removed from the study. The fire did not reach the other trees or the rhizotrons and was not detected as an increase in temperature by any of the thermocouple psychrometers placed inside or outside the rhizotrons.

Root observation

All roots visible through the observation window were traced onto transparent acetates (50 cm deep \times 50 cm wide) for a total of 13 time intervals during the 2.5-yr study period (19 February 1999 to 1 October 2001, sampling interval of about one and two months in growing and dormant seasons, respectively). Initial observations at shorter time intervals showed no need for greater sampling frequencies, especially in the dormant season. Only fine roots (diameter < 2 mm) were considered for this study. Fine roots of the sandhill tree species were relatively thick (mean diameter of 0.3–0.4 mm; Espeleta 2002, Espeleta and Donovan 2002) and so they were easily identified from the soil background. When needed, a magnifying glass and a light source were used to facilitate root identification. Roots appearing on each individual mapping date were considered part of the same cohort and were identified with a unique pen color. Root death was also recorded with the respective date and cohort information. Roots were considered dead when they showed clear symptoms of decay (shriveling, softening, and/or partial decomposition) and were followed until visible signs of decomposition confirmed the observation. The number of live

and dead roots was quantified from the tracing acetates for each root branching order, cohort, and mapping date. Lateral roots were counted as new roots when longer than 2 mm. Individual roots were assigned a root order category, following Pregitzer et al. (2002): increasing root branching order from distal to more basal segments (i.e., the apical, more distal, and unbranched segments were considered first-order roots, the following links were second-order roots, and so forth). Our root maps never showed more than four branching orders. Because of low total root counts, the group of fourth-order roots was pooled with third-order roots before calculating demographic indices. The ectomycorrhizal roots were identified by distinctive morphological features easily identified in our rhizotron windows: “coralloid” architecture (short, thick, profusely branched roots), “V-shaped” root tips, and presence of hyphal sheath (outer mantle) on root surface (Smith and Read 1997, Peterson et al. 2004). These roots were always composed of apical segments with no more than three orders of branching. The difference between these roots and the rest of the root orders was substantial so they were considered a different root order, and distinctively labeled in our study as “mycorrhizal” vs. “non-mycorrhizal” roots. We cannot rule out some degree of mycorrhizal colonization in roots not showing distinctive mycorrhizal morphology and architecture, so the interpretation of results of this study is limited to roots showing these distinctive features. All species in our study showed evidence of mycorrhizal colonization, both inside and outside the rhizotrons.

Demographic indices

Total root production, death, and percentage mortality (total root death divided by total root production \times 100) were calculated on the numbers of all roots of each species during the study and separated by root branching order, seasonal cohort, and year. Fine-root turnover was estimated in three ways: (1) total number of roots produced per year/maximum standing pool of live roots (Gill and Jackson 2000), (2) total number of roots produced per year/mean standing pool of live roots, and (3) total number of roots dying per year/mean standing pool of live roots (Burton et al. 2000). Because the first root cohort (spring and summer of 1999) can reflect the effect of soil disturbance after chamber installation (giving altered root production and death rates), we only used root demography data from the last two years (September 1999 to September 2001) to calculate turnover rates (Joslin and Wolfe 1999, Burton et al. 2000). We also combined all root orders and seasons to calculate turnover rates. Species effects were tested by one-way ANOVA and differences compared by post hoc Tukey hsd multiple comparisons test. Fine-root turnover rates showed normal distribution of residuals, but total root production, root death, and percentage mortality were normalized, respectively, by square root, logarithmic, and arcsine transformation.

Root length measurement and architectural relationships

We retraced the acetates used for root counts in order to measure fine-root lengths. The length of root tracings was measured using Delta-T Scan image analysis software (Delta-T Devices, Cambridge, UK). Images were scanned using Hewlett-Packard's "Precision Scan Pro" software (Hewlett-Packard, Palo Alto, California, USA). Image lengths were pre-calibrated with Delta-T Scan image standards. We used a brightness of 200 and a resolution of 400×400 dpi, according to the sensitivity requirements of Bouma et al. (2000). We developed length to number relationships for each species, root class, and date, and calculated the mean root segment length (MRS�) following Crocker et al. (2003). We compared the MRS� derived from the regressions by analysis of confidence intervals ($\alpha = 0.05$). We also estimated the length of dead roots for each species and root order from the number of dead roots by using the MRS� as the linear slope (Crocker et al. 2003). Species differences in total fine-root lengths (mycorrhizal plus non-mycorrhizal) were compared by one-way ANOVA.

Root survival analysis

Root life spans were calculated as the time between birth and death of each root. The birth date was considered as the mapping date when the root was visible for the first time. The death date was considered as the mapping date when a root showed first symptoms of senescence. Root survival tables were constructed by calculating the number of roots for each longevity class and cohort. Roots that did not reach death at the end of the study were considered right-censored data and were treated as such by the survival model. Root survival functions for each species and root order class (mycorrhizal, first order, second order, and third–fourth orders) were produced via survival analysis using the product-limit (Kaplan-Meier) method for roots from all cohorts (Andersson and Majdi 2005, Baddeley and Watson 2005), and median life span values for each species, order class, and cohort were estimated (see Black et al. [1998] for discussion). Median longevity was used because a large proportion of roots were not followed until their death and it was computed with data from the entire year, since the dormant season was short and still showed some root mortality (sensu Andersson and Majdi 2005). We considered fine roots from all cohorts in the survival analysis, including those from the final cohort that had a relatively short tracking period (spring–summer 2001).

Log-rank chi square statistics were computed to test for homogeneity of the survival functions across species and orders (Prentice and Kalbfleisch 1979). We fitted exponential, Weibull, and lognormal distributions to our survivorship data, but present the Weibull distribution because it provided the best fit (sensu Black et al. 1998). The Weibull distribution is described by two parameters: a scale parameter α , and a shape parameter β . The main determinant of the degree of hazard and the

average life span is α . The shape parameter β corresponds to the change in the degree of hazard over time. When $\beta = 1$ the hazard is constant and the probability of a living root surviving until the end of a given time period is constant for that time period. When $\beta > 1$ the risk increases with age, whereas when $\beta < 1$ the risk decreases with age. The Weibull fitting was done separately for each species, seasonal cohort, and year. Parameters of each survival curve were compared by their 95% confidence intervals.

Risk analysis

A proportional hazards model (Cox 1972, Wells and Eissenstat 2001, Anderson et al. 2003) was used to examine the effect of tree species and season and/or root order class (mycorrhizal, first order, second order, and third–fourth orders), and their interactions on survival times. For analysis of species and season effects, cohorts of each species were consolidated into two groups: spring and summer (growing season) and fall and winter (dormant season), and analyzed separately for 1999 and 2000. The growing season is defined as the period between mapping dates when winter deciduous trees (all *Quercus* species in this study) had green leaves and the dormant season as the period between mapping dates when their leaves were largely senesced. The last growing season date for 1999 was 25 September. The 2000 growing season comprised mappings from 13 March to 2 October. The 2001 growing season began on 14 March and the final mapping date of the study was 1 October 2001. The analysis was performed separately for root cohorts from the first two complete years (1999–2000 and 2000–2001), which included the roots produced between the spring of 1999 and the end of the winter of 2000. The proportional hazards model included the effects of three covariates: species (each species relative to *Q. margaretta*), season (growing season relative to dormant season), and a species \times season interaction term (the season effect of each species relative to the season effect of *Q. margaretta*). Species and interaction term effects were referred somewhat arbitrarily to *Q. margaretta*, because this is the only species unable to colonize xeric habitats. Consistent divergence in fine-root survival patterns of all species from *Q. margaretta* might provide insight into the fine-root demographic strategies that are involved in colonization of xeric habitats. The proportional hazards model was fitted using a maximum likelihood method to estimate the regression parameters associated with the explanatory variables and their standard errors (β coefficient). A chi-square statistic was used to test the null hypothesis that each parameter is equal to zero. A conditional risk ratio (or hazard ratio, e^β) and its confidence limits were also computed from the parameter estimates. A risk ratio >1 indicates increasing risk for that variable, and <1 decreasing, and $=1$ no difference in mortality risk.

For analysis of species and root order class effects, we ran an additional proportional hazards test to compare

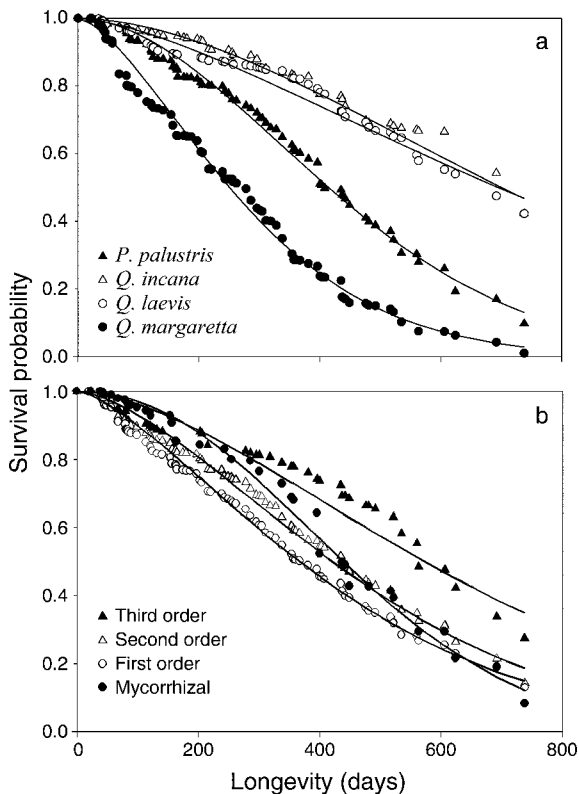


FIG. 2. Fine-root survival curves of (a) four tree species (pooling all root orders), and (b) four root orders (pooling all species), during the study period (from February 1999 to September 2001), as calculated by the product-limit (Kaplan-Meier) method. Data are based on a total of 1584, 1674, 3255, and 3314 roots of *Quercus laevis*, *Q. incana*, *Q. margaretta*, and *Pinus palustris*, respectively, and a total of 1843, 6187, 1529, and 228 roots of mycorrhizal, first-, second-, and third- plus fourth-order roots. The “y-axis” value corresponds to a survival ratio calculated with the product-limit analysis, and it gives an indication of the survival probability on a scale of 0 to 1.0, with 1.0 being the highest possible probability of survival. The censored observations are included in the estimation of the survival probabilities; therefore the survival curves are not equivalent to the empirical distributions. A two-factor Weibull distribution was fitted to the data to estimate the mean root life span for each species and root order (see Table 1 for details on curve parameters).

survival risks of species and root order classes. The proportional hazards model included the species effect (as before, each species relative to *Q. margaretta*), the root order effect (each root order relative to first-order roots), and a species \times root order interaction term (the root order effect of each species relative to the root order effect of *Q. margaretta*). This proportional hazards model was also fitted using a maximum likelihood method to estimate the regression parameters associated with the explanatory variables and their standard errors. The conditional risk ratio (or hazard ratio) and its confidence limits were also computed from the parameter estimates. All statistical analyses were done using

JMP statistical discovery software, Version 4.0 (SAS Institute 2000).

RESULTS

Species differences

The tree species exhibited significant differences in survival and fine-root longevity (Fig. 2a, Table 1a). Median life span of *Q. laevis* roots (692 d) and *Q. incana* roots (738 d) were ~ 2.6 times greater than that of *Q. margaretta* roots (278 d). Median life span of *P. palustris* fine roots was intermediate (408 d). These species differences in longevity were consistent for all cohorts in both years, and they tended to decrease for the younger cohorts (Appendix B). The slope of the species-specific root survival curves (Fig. 2a), interpreted as the age-dependent risk of root death (β), also differed across the tree species in this study (Table 1a). Fine roots from all cohorts were more likely to die as they aged ($\beta > 1$, for all species), indicating that young roots of the study species are very resilient and do not go through a period of high susceptibility early in their development, at least for periods longer than the observation intervals. However, the relative risk of death with root age differed across species (Table 1a) and cohorts (Appendix C). For all cohorts together, *Q. margaretta* and *Q. laevis* had a significantly lower β , indicating comparatively lower risk of root death at later ages (Table 1a). Nonetheless, species differences in β varied across individual cohorts: β was lower in *Q. laevis* and *Q. incana* relative to *Q. margaretta* and *P. palustris* for older cohorts, but the pattern tended to reverse for more recent (younger) cohorts (Appendix B).

The species also differed in total fine-root production, death, percentage mortality, and turnover rates (Fig. 3, Tables 1a and 2). The species that dominates subxeric habitats (*Q. margaretta*) and the generalist *P. palustris* exhibited greater total fine-root production and death than xeric *Quercus* species. *Quercus margaretta* had the greatest percentage fine-root mortality and *P. palustris* was intermediate. Fine-root production and total death and mortality based on root lengths (Appendix D) showed similar patterns as the root numbers (Appendix C). In both cases (numbers and lengths), xeric species exhibited 1.5–2 times lower production and nearly 5–6 times lower death than *Q. margaretta*. Species also showed different patterns of fine-root demography with cohort age (Appendices C and D). Percentage mortality of fine roots in *Q. margaretta* was $>95\%$ for the first two seasonal cohorts, close to 80% in the two following cohorts, and only decreased to 50% in the most recent cohort. In contrast, percentage mortality was consistently lower in the xeric *Quercus* species, both in root numbers and estimated root lengths.

The relationships between numbers and lengths of fine roots were species specific for both non-mycorrhizal and mycorrhizal roots (Table 3). The mean root segment length (MRSLS) of non-mycorrhizal roots (first to fourth

TABLE 1. Analysis of fine-root survivorship data across: (a) four sandhill tree species, and (b) four root branching orders.

Species or root order	Number of roots			Survival analysis†				Weibull curve fitting‡			
	Failed§	Censored¶	Total	Median life span (days)	Median turnover (yr ⁻¹)	χ^2	<i>P</i>	α	Confidence interval (95%)	β	Confidence interval (95%)
a) Species											
<i>Quercus laevis</i>	357	1227	1584	692 ^a	0.53 ^c	2037.9	<0.0001	886.0 ^a	813–976	1.51 ^b	1.38–1.65
<i>Q. incana</i>	416	1258	1674	738 ^a	0.49 ^c			860.0 ^a	808–921	1.79 ^a	1.65–1.94
<i>Q. margaretta</i>	2474	781	3255	278 ^c	1.31 ^a			319.5 ^c	311–328	1.52 ^b	1.50–1.56
<i>Pinus palustris</i>	2045	1269	3314	408 ^b	0.89 ^b			504.5 ^b	493–516	1.87 ^a	1.80–1.94
Total	5292	4535	9827								
b) Root order											
First	3547	2640	6187	381 ^c	0.96 ^a	100.03	<0.0001	472.6 ^c	462–483	1.45 ^b	1.42–1.49
Second	825	744	1569	437 ^b	0.84 ^b			530.9 ^b	509–555	1.58 ^b	1.49–1.66
Third–fourth	99	129	228	563 ^a	0.65 ^c			713.8 ^a	634–820	1.66 ^b	1.39–1.95
Mycorrhizal	821	1022	1843	400 ^b	0.91 ^b			521.1 ^{bc}	505–539	2.14 ^a	2.02–2.26
Total	5292	4535	9827								

Notes: Roots correspond to five root cohorts produced between the spring of 1999 and the end of the summer of 2001 (144 weeks). See the *Materials and methods* for a complete explanation of terms.

† Median life span and turnover rate (=life span⁻¹) were estimated by product-limit (Kaplan-Meier) survival analysis. We used a log-rank homogeneity test to compare survival differences between species. Different letter superscripts indicate differences in median life span at 95% confidence.

‡ Mean life span of the 62% percentile (α) and the magnitude of the risk slope (β) were estimated by fitting a Weibull distribution to the survival data. Different letter superscripts indicate significant differences at $P < 0.05$.

§ The number of failed roots corresponds to the number of roots that died before the end of the study.

¶ The number of censored roots corresponds to the number of roots that were still alive at the end of the study.

root orders) was significantly greater in the xeric *Quercus* species than in *Q. margaretta* and *P. palustris*, suggesting species differences in fine-root architecture (lower branching per volume of soil in *Q. laevis* and *Q. incana*). Similar ranking of species differences in MRSI (*Q. incana* \geq *Q. laevis* = *P. palustris* > *Q. margaretta*) were also observed in mycorrhizal roots (Table 3).

Species differences were also observed in four different estimates of fine-root turnover rates. These differences were significant in three of those estimates: the inverse of median life span (Table 1a) and the ratios of “production : maximum standing stock” and “death : mean standing stock” (Appendix E).

Differences by root branching order

Different root orders exhibited significant differences in longevity and turnover rate (Fig. 2b, Table 1b) and production, death, and mortality (Fig. 3, Table 2). Pooling all four species, median life span of first-order roots (381 d) was 1.2 and 1.5 times shorter than second (437 d), and third–fourth order roots (563 d), respectively. Mycorrhizal roots (median life span of 400 d) exhibited a significant, but relatively small, increase in longevity compared to first-order roots. The age-dependent risk of root death (β) also differed across root orders (Table 1b). In general, mycorrhizal roots exhibited greater risk of death over time, as evidenced by a greater slope in the root order-specific survival curves (Fig. 2b) and higher β values for all species together (Table 1b). Inspection of these curves revealed dissimilar survival patterns of mycorrhizal vs. non-mycorrhizal roots (all orders). Although showing initially a survival pattern similar to the longer lived and slow dying third–

fourth order roots, mycorrhizal roots exhibited an abrupt decrease in survival after the first 200 days of life (Fig. 2b).

Species \times root order interactions

Fine-root demography depended strongly on species identity. We observed significant effects of species \times root order interactions in fine-root production and death (Table 2). The demography of first and second order classes exhibited two distinct species groups (Fig. 3). The xeric species (*Q. laevis* and *Q. incana*) had low proliferation, death, and mortality, but the subxeric *Q. margaretta* and the generalist *P. palustris* had high proliferation, death, and mortality. Similar species patterns were exhibited by the third–fourth order class, but only for percentage mortality (species had similar production and death of third- and fourth-order roots). In addition, demography of mycorrhizal roots did not show a clear xeric–subxeric dichotomy, and differences were observed even among xeric species. For instance, mycorrhizal roots had greater mortality in *Q. incana* than in *Q. laevis* (Fig. 3).

Survival patterns of the different root orders also varied across species. Contrary to most species, where longevity increased with root order, demography of *Q. margaretta* roots was more similar across root orders. For instance, the median life span and the age-dependent risk of root death (β) were not significantly different for all root orders in *Q. margaretta* (Appendix F). Although generally longer lived than first-order roots, mycorrhizal roots showed greater demographic variability across species. Compared to first-order non-mycorrhizal roots, mycorrhizal roots were longer lived in *Q. laevis*, had

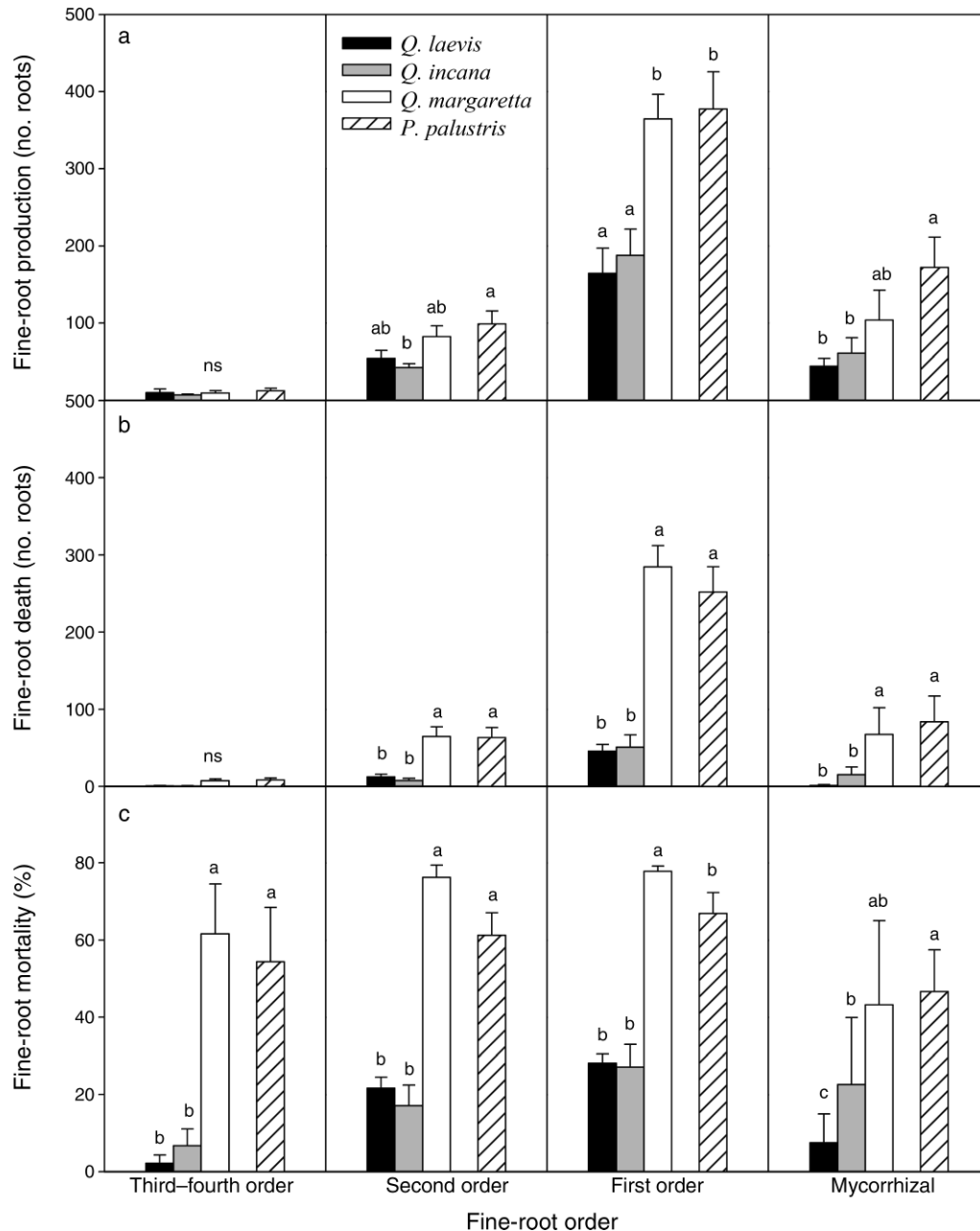


FIG. 3. Mean production, death, and percentage mortality (\pm SE) of fine roots of different branching order classes (first, second, third plus fourth, and mycorrhizal) and among four sandhill tree species: *Quercus laevis*, *Q. incana*, *Q. margaretta*, and *Pinus palustris*. Data are based on the number of roots produced from 19 February 1999 to 30 September 2001 ($n = 6$ *Quercus* trees and $n = 5$ trees of *P. palustris*). For statistical analysis of species and root order effects see Table 4. Different letters indicate significant differences between species means in each root order at $P < 0.05$ by Tukey's multiple comparison test.

similar life spans in *Q. margaretta* and *P. palustris*, but were shorter lived in *Q. incana*. The age-dependent risk of root death (β) in *Q. laevis* was considerably lower in mycorrhizal roots than in other root orders, but it was greater in *Q. incana* and *P. palustris* (Appendix F). The differences in mortality risks (proportional hazards model, Appendix G) between mycorrhizal and first-order roots were also greater in *Q. incana* and *P.*

palustris. In contrast, third-order roots were less likely to die than first-order roots, but the difference in risks was lower in *Q. incana* relative to *Q. margaretta*, and similar in the other species (Appendix G).

Seasonal differences

We studied the different seasonal cohorts via proportional hazards analysis (Table 4). Survival of roots

TABLE 2. Species differences in mean root segment length (MRSL) for two different root order classes (mycorrhizal and non-mycorrhizal).

Root order class and species	<i>F</i>	df	<i>P</i>	<i>r</i> ²	MRSL (cm segment ⁻¹)	Confidence interval (95%)
Non-mycorrhizal						
<i>Q. laevis</i>	627.65	1, 72	<0.0001	0.90	1.89	1.76–2.01
<i>Q. incana</i>	1070.84	1, 67	<0.0001	0.94	2.02	1.89–2.14
<i>Q. margaretta</i>	555.23	1, 72	<0.0001	0.89	1.44	1.35–1.54
<i>P. palustris</i>	667.81	1, 59	<0.0001	0.92	1.65	1.55–1.76
Mycorrhizal						
<i>Q. laevis</i>	47.05	1, 11	<0.0001	0.81	0.44	0.37–0.52
<i>Q. incana</i>	80.71	1, 9	<0.0001	0.91	0.74	0.60–0.88
<i>Q. margaretta</i>	59.67	1, 14	<0.0001	0.81	0.32	0.27–0.37
<i>P. palustris</i>	146.85	1, 26	<0.0001	0.85	0.43	0.38–0.49

Notes: MRSL was estimated as the slope of the linear regression (intercept through zero) of root length vs. numbers for each of four sandhill tree species. Each point in the linear regression represents one cohort of each individual rhizotron per species. MRSLs per species and order class were compared by confidence intervals. Different letter superscripts show significant differences at $P < 0.05$.

depended not only on species identity (roots of xeric oak trees had lower risk of death), but also on the season of cohort production. For both 1999 and 2000 there was a significant effect of season (risk ratio, $e^{\beta} > 1$), indicating a higher risk of death for roots produced in the dormant season (fall and winter) than those produced in the growing season (spring and summer). There were also significant species \times season interactions, indicating that the differences in risk of death between dormant and growing season cohorts differed across species. In particular, fine roots of *P. palustris* were more likely to die than fine roots of *Q. margaretta* if they were produced in the dormant season. Cohorts of different years exhibited differences between *Quercus* species. For the 1999 cohort, fine roots of *Quercus laevis* were more likely to die in the growing season than *Q. margaretta* fine roots, but the relationship was opposite with *Q. incana* fine roots. For the younger cohort of 2000, fine roots from all *Quercus* species did not differ in their relative risk of death if produced in dormant vs. growing seasons.

We also compared the time courses of the different seasonal cohorts (Appendix H). There were differences between species and years in the production and death of each seasonal cohort. Declines in the number of live roots were steeper in *Q. margaretta* and *P. palustris*, especially during the growing season. The number of live roots in xeric *Quercus* species was virtually unaltered in the dormant season and showed lower declines in the

growing season than the other species. *Pinus palustris* consistently produced more roots than *Q. margaretta*, but roots of both species exhibited similar precipitous declines for all cohorts (Appendix H). In addition, fine-root demographic curves also showed species-specific seasonal patterns. In general, root production and death cumulative curves flattened during the dormant season (Appendix I), but the response was species specific. Subxeric species (the “leaf-deciduous” *Quercus margaretta* and the “leaf-evergreen” *P. palustris*) exhibited more continuous growth and death of fine roots during growing and dormant seasons. In contrast, more xeric *Quercus* species (the “leaf-deciduous” *Q. laevis* and the “leaf-brevideciduous” *Q. incana*) showed little fine-root growth and death during the dormant season. Greater rates of fine-root production and death in all species were associated with greater fluctuation in soil water potentials and higher soil temperatures during the growing season (Appendix I: lower graphs).

DISCUSSION

Our results provide, to our knowledge, the first report of fine-root demographic differences across congeneric tree species that co-occur in a single ecosystem. Large intrageneric variation in fine-root life span tracked the differential distribution of the *Quercus* species along a resource-availability gradient in spite of the proportionally smaller variation in leaf life span. These differences rival the variation in fine-root demography across

TABLE 3. Results of two-way ANOVA of the effects of species identity and root order on fine-root production, death, and percentage mortality (see Fig. 3).

Source	df	Fine-root production		Fine-root death		Fine-root mortality (%)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species	3, 73	13.57	<0.0001	38.40	<0.0001	25.41	<0.0001
Order	3, 73	114.78	<0.0001	70.49	<0.0001	8.43	0.0001
Species \times order	9, 73	2.50	0.0151	4.30	0.0002	0.83	0.5898

Note: Data are based on the number of roots produced between the spring of 1999 and the summer of 2001.

TABLE 4. Analysis of mortality risks of fine-root cohorts produced in different seasons ("growing," spring and summer; "dormant," fall and winter) using a proportional hazards regression for root survivorship data.

Variable	df	Parameter estimate	SE	Wald χ^2	P	Risk ratio	Confidence interval (95%)	
a) 1999–2000 cohort								
Species (Pp)	1	0.2345	0.0519	455.225	<0.0001	1.264	1.142	1.400
Species (Qi)	1	-0.9253	0.1112	455.225	<0.0001	0.396	0.313	0.486
Species (Ql)	1	-0.3093	0.0811	455.225	<0.0001	0.734	0.626	0.860
Season (dormant)	1	0.1720	0.0466	11.597	0.0007	1.188	1.084	1.297
Pp \times season	1	0.1240	0.0519	17.050	0.0007	1.132	1.023	1.253
Qi \times season	1	-0.3891	0.1112	17.050	0.0007	0.678	0.535	0.831
Ql \times season	1	0.1962	0.0811	17.050	0.0007	1.217	1.038	1.426
b) 2000–2001 cohort								
Species (Pp)	1	0.2345	0.0519	845.048	<0.0001	1.536	1.416	1.667
Species (Qi)	1	-0.9253	0.1112	845.048	<0.0001	0.568	0.496	0.651
Species (Ql)	1	-0.3093	0.0811	845.048	<0.0001	0.410	0.352	0.478
Season (dormant)	1	0.1720	0.0466	111.238	<0.0001	1.559	1.451	1.675
Pp \times season	1	0.1240	0.0519	5.126	0.1628	0.915	0.843	0.993
Qi \times season	1	-0.3891	0.1112	5.126	0.1628	1.106	0.966	1.266
Ql \times season	1	0.1962	0.0811	5.126	0.1628	1.025	0.879	1.194

Notes: The analysis was performed separately for root cohorts from the first two complete years (1999–2000 and 2000–2001) and tested the effects of three covariates (species, season, and species \times season interaction) on root life span. All risk estimates are relative to the risk of *Q. margaretta* (species effect) and to the risk of growing season cohorts. The proportional hazards model was fitted using a maximum likelihood method to estimate the regression parameters associated with the explanatory variables and their standard errors (β coefficient). A chi-square statistic was used to test the null hypothesis that each parameter is equal to zero. The risk ratio is interpreted as the ratio of the hazard of a given species vs. *Q. margaretta* (e.g., <1 indicates lower mortality risk of roots of each given species), "dormant season" (fall and winter) vs. "growing season" (spring and summer), and the interaction of species \times season. The significant interaction term suggests greater (risk ratio >1) or lower (risk ratio <1) divergence of risk between seasons for *Q. margaretta* as compared to each one of the other species. Bold numbers indicate values significantly different from 1.0 at 95% confidence. Species identifiers: *Quercus laevis* (Ql), *Q. incana* (Qi), *Q. margaretta* (Qm), *Pinus palustris* (Pp).

considerable geographic and phylogenetic ranges, such as between grasses and forests or tropical and temperate regions (Gill and Jackson 2000). Furthermore, fine-root demographic differences were specific to root order class and growing season. These findings have many potential implications. First, they complement current information about trait divergence in co-occurring plant phylogenies such as *Quercus* (Cavender-Bares et al. 2004a, b) and suggest a central role of belowground traits in ecological sorting at small geographic scales. Second, they emphasize previous observations that belowground dynamics are critically important components of ecosystem carbon cycling and its responses to shifts in community composition (Partel and Wilson 1992).

Degree of oak species differentiation in fine-root demography

Interspecific variation in fine-root demography included variables such as the median and mean longevity (α parameter) and the age-dependent risk of death (β parameter), total production and death and percentage mortality, the mortality risk and the rates of fine-root turnover. The range of variation in all these root demographic variables between three congeneric oak species far exceeded the differences with a taxonomically unrelated conifer, *P. palustris*. For instance, fine-root turnover rates varied from 1.5-fold to fivefold among *Quercus* species (range due to different fine-root turnover estimates; Table 1 and Appendix E), but

variation was only onefold to threefold when comparing any oak species with longleaf pine.

Species demographic patterns across root branching orders and classes

Our results provide support for the growing body of evidence linking root demography (King et al. 2002, Pregitzer et al. 2002, Joslin et al. 2006) and anatomy and physiology (Guo et al. 2008a, b) with the position on the root branching system or "root order" and with mycorrhizal association (Espeleta et al. 1999, Eissenstat et al. 2000). Here, fine-root longevity increased generally with root order and with mycorrhizal colonization. First-order roots without typical mycorrhizal morphology were also more likely to die at an early age, particularly in comparison to mycorrhizal roots (greater age-dependent risk of root death, β , or greater slope of the survival curve). Furthermore, these results demonstrate that root order–life-span relationships can vary substantially across species, similar to recent observations of tree species differences in the degree of anatomical development with increasing root branching order (Guo et al. 2008b). Increasing root order was generally associated with greater longevity and greater age-dependent risk of death, but the relative change over order number was high in *Q. laevis* and nearly absent in *Q. margaretta*. Our results also indicate that species differences in fine-root demography are mainly in apical roots and tend to disappear centripetally. Mycorrhizal root demography was far more variable: compared to first-order non-mycorrhizal roots, mycorrhizal roots had

greater longevity in *Q. laevis* and *Q. margaretta*, were similar in *P. palustris*, but lower in *Q. incana*. Similarly, the age-dependent risk of root death increased in mycorrhizal roots only in *Q. incana*, and in *P. palustris* to a lesser extent. These results suggest that effects of ectomycorrhizas on fine-root demography strongly depend on host species identity (even between congeneric host species), and may explain the conflicting views either in favor (Newsham et al. 1995, Espeleta et al. 1999) or against (Hooker et al. 1995) positive effects of mycorrhizas on fine-root longevity.

Association of demography with morphology and architecture

Previous studies have described differences in root morphology across large geographic ranges (Ryser 1996, Craine et al. 2005) or among tree functional types (i.e., slow-growing vs. fast-growing species; Comas and Eissenstat 2004). In our study of sandhill oak trees with similar fine-root diameter, specific length, and tissue density (Espeleta 2002, Espeleta and Donovan 2002), belowground differences were observed in fine-root demography and architecture. Here, species with lower mean root segment length (MRSL) exhibited lower fine-root longevity, suggesting that root systems with shorter fine-root internodes (i.e., more highly branched) are likely to be shorter lived. Previous studies have indicated that species identity is more important than environmental conditions (Crocker et al. 2003) and these results now show a direct link between fine-root demography and species differences in MRSL. This relationship between fine-root architecture and demography was not sensitive to mycorrhizal status. Although mycorrhizal roots had comparatively lower MRSL than non-mycorrhizal roots, the species with shorter root longevity (*Q. margaretta*) also showed lower MRSL in mycorrhizal roots.

Species-specific seasonal patterns

Our study showed that cohorts produced in the dormant season had greater mortality risk, and that root death tended to be higher, during the growing season. It is possible that dormant season cohorts were more susceptible to death factors acting in the growing season (such as summer droughts) than cohorts produced during these stress periods (growing season cohorts). Indeed, a simultaneous study showed that greater fine-root death occurred in summer months, especially in *Q. margaretta*, a species unable to rewet surface soil via hydraulic lift (Espeleta et al. 2004). Likewise, low fine-root mortality in *Q. laevis* and *Q. incana* could result from alleviation of surface drought via hydraulically lifted water (Caldwell et al. 1999) or by the maintenance of vitality of first-order roots in dry soil via internal hydraulic redistribution (Bauerle et al. 2008). These processes of water transport from roots in wet soil layers might confer an increased ability to colonize xeric habitats (Espeleta et al. 2004).

Contrary to our expectations based on aboveground observations, root phenological patterns differed strongly among species. Although previous studies with non-woody species showed variation in leaf and root demography varying in concert across productivity (Schläpfer and Ryser 1996) and altitudinal (Craine and Lee 2003) gradients, the observed variation in fine-root demography in sandhill oaks is not paralleled by similar variation in leaf demography. Although *Q. incana* is the only oak species showing some degree of leaf persistence during the dormant season (brevideciduous species), both *Q. laevis* and *Q. incana* exhibited considerable persistence of fine roots as well. In contrast, we observed year-round root growth and death in the subxeric, deciduous oak *Q. margaretta* and in the evergreen generalist *P. palustris*. The lack of correspondence between fine-root and leaf phenology in the oak species contradicts assertions that leaf persistence habit (i.e., the “evergreen” hypothesis; sensu Monk 1966, Chapin 1980, Aerts 1995) might be a general adaptive response to low resources applicable to belowground tissues. Non-parallel leaf and fine-root phenology also suggests important limits to the extrapolation of leaf trait variation to root tissues, as recently evidenced by global comparisons of grass species (Craine et al. 2005) and common gardens studies with temperate trees (Withington et al. 2006).

Rhizotron data and comparability with other root demographic estimates

Although direct observation methods such as rhizotrons and minirhizotrons are considered good estimators of population-based parameters such as turnover (Smit et al. 2000), considerable differences may exist between these different direct observation techniques. Roots growing in mixed-species soils and observed with minirhizotrons may exhibit greater rates of turnover than those in single-species soils (Partel and Wilson 2002). The rates we report from single-species rhizotrons are intermediate between high estimates measured at the community level with minirhizotrons (up to three per year; West et al. 2004) and previous reports for this system using indirect methods (0.39 per year; Saterson and Vitousek 1984; but see King et al. 2002). Minirhizotrons have small observation areas (~1 cm²) and tend to sample a more ephemeral population of roots than rhizotrons with large observation windows (~2500 cm²). In contrast, larger observation areas allow tracking of more complete root branches that include roots of higher order with lower turnover rates. Indeed, mean turnover rates of first-order roots in our study (Table 1) are more similar to minirhizotron estimates (West et al. 2004) than those of the higher root orders. Fine-root turnover rates between the four tree species of our intermediate sandhill ecosystem spanned concurrent variation in fine-root turnover rates measured with minirhizotrons in the gradient from xeric to mesic sandhill habitats (~1.5-fold), suggesting that differences

across dominant tree species now observed with rhizotrons could in part explain the variation in the natural, mixed community across environments previously observed (West et al. 2004).

It is possible that discrepancies with previous mini-rhizotron data were related to comparatively higher soil and root disturbance after rhizotron installation, leading to excessive root proliferation (Joslin and Wolfe 1999). Together with the larger dimensions of the rhizotron, this could account for a greater "colonization" effect in rhizotrons compared to minirhizotrons. However, inspection of root production time courses in our rhizotrons (Appendices H and I) indicates an early stabilization of root production since the numbers of new roots were similar in years two and three. Therefore, we believe that our production-based turnover estimates (Appendix E) were not inflated (sensu Joslin and Wolfe 1999). Conversely, root death lagged root production indicating that death-based estimates probably underestimated real turnover rates (sensu Burton et al. 2000). It should also be noted that the different turnover metrics were more similar for *Q. margaretta* and *P. palustris* than for *Q. laevis* and *Q. incana*, suggesting that faster turnover rates in the former probably led to faster equilibration (i.e., when rates of fine-root production and death become equal). It is possible that species differences in fine-root demography could lead to differences in soil resource uptake, which would result in the rhizotrons of species with greater fine-root production rates exhibiting greater resource depletion. However, we think that the differences in root densities were insufficient to differentially affect resource availability. For instance, if water depletion rate is used as an indicator of soil resource competition, summer soil water potentials should have been lower in rhizotrons with species with high root growth rates. Although this might be the case for *P. palustris*, we did not find evidence of lower soil water potential in rhizotrons of *Q. margaretta*, compared to oaks with low root proliferation (Appendix I and Espeleta et al. 2004).

Species differences and differential ecological distribution

Although studies have shown significant phylogenetic conservation of other root traits such as foraging scale and precision (Kembel and Cahill 2005) and morphology (Espeleta 2002, Espeleta and Donovan 2002), our results show that root life span can vary substantially within relatively fine clades. Congeneric differences in fine-root longevity observed here rival those across distant phylogenetic groups, such as with the conifer *Pinus palustris* or with the grasses *Aristida stricta* and *Schizachyrium scoparium* (West et al. 2003). Root demographic and architectural traits can show strong plastic responses in response to environmental variation (Hodge 2006). Indeed, seedlings of the species in this study showed substantial variation in fine-root growth

and mortality at different resource levels (Espeleta 2002, Espeleta and Donovan 2002), suggesting that fine-root responses can differ across environmental gradients. Nonetheless, in that study, species differences were consistent in spite of species-specific plastic responses, with mesic species exhibiting greater fine-root turnover than xeric species at both high and low resources (Espeleta and Donovan 2002). This controlled-environment response is consistent with our field data reported here on adult trees coexisting in an intermediate, subxeric habitat.

Our results also provide empirical evidence that ecological sorting could be linked to root trait variation in plant communities, a finding that was previously suggested for those sandhill grass species (West et al. 2003). In the particular case of sandhill oaks, our results support findings of strong niche differentiation for this speciose genus (Cavender-Bares et al. 2004b). Our results provide empirical evidence that although leaf demography is highly conserved within phylogenies and correlates with broad geographic distributions (Cavender-Bares et al. 2004a, b), fine-root demography corresponds well with species distribution across local gradients, even between closely related species. Observed belowground differences may also follow subgeneric phylogenetic relationships, since more closely related oak species exhibited more similar root traits: species with persistent roots (*Q. incana* and *Q. laevis*) are both red oaks, whereas *Q. margaretta* is a white oak (Cavender-Bares et al. 2004a). Cavender-Bares et al. (2004a) proposed that southeastern oak species are overdispersed and that co-occurring species tend to be distantly related, promoting trait diversity and niche differentiation. In fact, the co-occurring oak species present in the intermediate, subxeric habitat of this study are widely spread across a phylogeny constructed for 17 Floridian oak species (Cavender-Bares et al. 2004a), with *Q. laevis* and *Q. margaretta* the more distantly related. Species differences in fine-root demography could then be associated with ecological sorting along the xeric to subxeric gradient, so that the species with greater longevity of roots dominates in xeric habitats, supporting existing theories of abiotic controls on tissue demography (Eissenstat and Yanai 1997).

We propose that sandhill xeric oak species (*Q. laevis* and *Q. incana*) share a distinct fine-root demographic "low-resource syndrome" characterized by a suite of root traits that confer tolerance of low water and nutrient availability (i.e., sparsely branched fine roots with high longevity but low production and turnover rates, analogous to low-resource tolerating strategies that prevent excessive resource loss; Grime 1977). In contrast, species dominating in subxeric habitats (both the congeneric oak, *Q. margaretta*, and the distantly related conifer, *P. palustris*) show a relatively "high-resource syndrome," characterized by shorter, more highly branched and ephemeral fine roots with high production rates to allow rapid nutrient foraging and

greater competitive ability in higher resource habitats (Grime 1977, Aerts 1999, Aerts and Chapin 2000). These two contrasting syndromes are consistent with a trade-off between the ability of roots to grow fast and their ability to persist alive, which is likely linked to optimization of resource acquisition and loss rates in species growing in habitats of different fertility (Eissenstat and Yanai 1997, Comas et al. 2002).

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APPENDIX A

A climate graph showing mean monthly temperature and total monthly rainfall for the study period, plotted onto 30-yr averages at the field site (*Ecological Archives* E090-125-A1).

APPENDIX B

Survival analysis of fine roots from different tree species from each seasonal cohort (*Ecological Archives* E090-125-A2).

APPENDIX C

A table showing fine-root demography (production, death, and mortality) based on root numbers (*Ecological Archives* E090-125-A3).

APPENDIX D

A table showing fine-root demography (production, death, and mortality) based on root lengths (*Ecological Archives* E090-125-A4).

APPENDIX E

A table comparing three different estimates of fine-root turnover rates across tree species (*Ecological Archives* E090-125-A5).

APPENDIX F

Survival analysis of different root branching orders from each tree species (*Ecological Archives* E090-125-A6).

APPENDIX G

Results of the proportional hazards regression for root survivorship data (species and root branching order effects) (*Ecological Archives* E090-125-A7).

APPENDIX H

A figure showing the species-specific time courses of the number of living roots pertaining to each seasonal cohort (*Ecological Archives* E090-125-A8).

APPENDIX I

A figure showing the cumulative curves of fine-root demography (total root proliferation and death), soil water potential (ψ_s), and temperature (T_s) in each species-specific root chamber (*Ecological Archives* E090-125-A9).