# SPECIES-SPECIFIC PATTERNS OF FINE ROOT DEMOGRAPHY AND HYDRAULIC LIFT AMONG TREES OF THE FALL-LINE SANDHILLS

# By

# Javier F. Espeleta

# (Under the direction of Lisa A. Donovan)

# ABSTRACT

Belowground processes, such as fine root demography and soil water redistribution, can alter carbon, nutrient and water cycles in terrestrial ecosystems. Although these processes are known to differ significantly across broad spatial scales and plant functional types, little is known about the differences among species in narrow geographical scales. Studies were conducted in a group of five tree species that grow in the sandhills of the fall-line region of southeastern United States. Four *Quercus* species (O. laevis, O. incana, O. margaretta and O. marilandica) and the longleaf pine (*Pinus palustris*) co-occur in areas of intermediate fertility, but have different distribution along soil resource gradients. Species differences in fine root demography and hydraulic lift were studied by growing roots of adult trees in field rhizotrons and recording fine root production, death and lifespan and the water potential of the soil near the roots. The effect of variation in resource availability (water and nutrients) on fine root demography was also studied in greenhouse studies using seedlings. The species able to colonize xeric habitats (Q. laevis and Q. incana) exhibited fine roots with greater longevity but lower rates of production, death and percent mortality than species dominant in mesic habitats (O. margaretta and O. marilandica). The generalist species (*P. palustris*) exhibited intermediate fine root demography. Fine root death increased under high resources and under localized drought, especially in mesic species. Fine root production in mesic species was greater at high resource availability and after re-enrichment of dry surface soil. Only xeric Quercus species and the generalist P. palustris exhibited hydraulic lift ability. Consistent with optimality theory, these results suggest that greater fine root lifespan and hydraulic lift ability in xeric and generalist species may favor root persistence in dry soils. potentially reducing rates of resource loss. In contrast, greater fine root growth in mesic and generalist species may favor competition for resources. Results also indicate that species differences can be substantial even across congeners and narrow spatial scales. Hence, speciesspecific belowground processes deserve further investigation in order to understand how carbon and nutrient cycling respond to environmental change and shifts in species composition.

INDEX WORDS: Fine root death, Fine root density, Fine root diameter, Fine root growth, Fine root lifespan, Fine root morphology, Fine root mortality, Fine root production, Hydraulic lift, *Quercus incana, Quercus laevis, Quercus marilandica, Quercus margaretta, Pinus palustris*, Sandhills, Specific root length, Surface drought.

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### DEDICATION

To my wife Adriana, who has been my sole companion for about a decade of graduate studies. Such a long time of constant change, challenges and sometime even hardship, has helped to deepen and solidify our relationship. My hope is that a future of more stability will help us thrive in the increased parental responsibilities we will face ahead.

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#### CHAPTER 1

# INTRODUCTION AND LITERATURE REVIEW

Most of the deterministic theory of plant ecology indicates that species differences in certain plant characteristics are associated with adaptation to different environments. Although stochastic processes such as differential dispersal ability and random speciation may explain in part species diversity (Hubble 2001), niche partitioning and habitat specialization are also likely to be major factors (Grime 1979). In the search for specialized plant strategies, suites of plant traits have been characterized as part of "adaptive syndromes" that are unique for different types of environment. By describing global patterns in some of these characteristics it has been possible to define basic strategies of plant adaptation that involve some basic plant traits governed by universal tradeoffs (Grime 1997). For instance, the abilities of growing fast and of tolerating resource limitation are proposed to be inherently antagonistic, and this tradeoff defines a basic classification of plants into competitors and stress-tolerating species (Grime 1977).

Optimality theory has also been applied here to explain this association, assuming that optimal (therefore, adaptive) strategies are those that maximize the efficiency in the use of resources, and a wide range of hypotheses have been formulated for many plant traits (Givnish 1986 and included chapters). This has created a big interest to describe more detailed patterns of variation of plant traits under different environments, as a starting point for studying the potential adaptive value of plant traits. Similarly, in the context of global environmental change and shifts in species composition in natural plant communities, the study of these patterns helps to gain a better understanding of the effects of single species on ecosystem processes (Hooper and Vitousek 1997). Plants do not only respond to the environment by developing adaptive strategies, but also plant responses can modify the environment by altering the geochemistry of the ecosystems (Hobbie 1992; Aerts and Chapin 2000)

Historically, the first species-specific processes were characterized in aboveground structures. For instance, patterns of variation in tissue demography (i.e. production, death and lifespan of leaves), leaf morphology (size, thickness) and growth rates have been characterized aboveground in different plants and environments without major technical difficulties (Chabot and Hicks 1982; Reich et al. 1999; Lambers and Poorter 1992; Reich et al. 1999). Some of these patterns have been characterized by simple observation of aboveground structures. The simplest of these cases are the differences in leaf phenology, easily observed between plants with evergreen and deciduous growth habit.

Due to the difficulties observing plant roots, the state of the knowledge on belowground traits is still primitive. In general, belowground environments tend to be more variable for many environmental factors than aboveground environments (an exception are factors of light quality and intensity, but there is already vast information on this topic). Belowground factors such as nutrient and water availability exhibit very large spatial and temporal heterogeneity. This is especially true at small scales. If plants are known to respond indirectly to these different soil conditions with changes aboveground (such as leaf demography), it is expected that root responses would be more sensitive.

For a long time, ecologists and nature observers have known that different plant species tend to occur in specific environments that do not differ much aboveground, suggesting that belowground heterogeneity is a driving factor of community composition (Atkinson 1991). Characterization of the species-specific response to the differences in belowground environments could then provide an insight of the potential adaptive value of root traits, as well as of the species-specific effects on belowground processes in the ecosystem (Brown 1995). The dynamics of root growth and death have profound consequences on the cycling of water, carbon and nutrients in ecosystems. Processes of water acquisition and transport by roots can control overall water budgets of single plants and entire ecosystems (Horton and Hart 1998; Jackson et al. 2000), while root decay may determines the rates of carbon and nutrient cycling in the soil (Fogel and

Hunt 1979; Aerts et al. 1992). Clearly, there is a need for a better characterization of the variation in belowground traits across species and environments.

This study is an attempt to characterize the degree of differentiation in species-specific belowground traits in a natural community and their specific response to variation in environmental factors. For this purpose, we compared five species of trees that inhabit a sandhill habitat but show differential ecological distributions. By comparing these co-occurring species that exhibit differential distribution, we formulated hypotheses using the deterministic theory of plant adaptation (sensu Grime 1979), based on the different resource availabilities of the habitats they dominate. This study is focused on two belowground processes: fine root demography and hydraulic lift (also called hydraulic redistribution in a general sense). The study looks at the species-specific patterns in adult trees in a natural community (Chapters 3 and 4) and the differences in the responses to variation in resource supply. In particular, resource variation was studied through differences in intensity and frequency of resources (Chapter 1) and spatial and temporal variation (Chapter 2).

# Fine root demography

Fine root production and death are significant components of belowground carbon budgets (Caldwell and Richards 1986; Bloomfield et al. 1996; Eissenstat and Yanai 1997). Globally, fine roots (which make up to 2.5% of total terrestrial biomass) have been estimated to comprise about 33% of Net Primary Productivity (NPP= 20 Gtons of C per year) (Jackson et al. 1997) and about 50% of NPP in forest ecosystems (Vogt et al. 1996), assuming that fine roots live for one year. Fine root mortality and decomposition represent a large carbon cost to the plant as well as an important source of organic matter to the soil. The relative importance of root demography in carbon budgets may be greater in habitats with greater C allocation belowground, such as grasslands (Seastedt 1988), some tropical forests (Vogt et al. 1986, Nepstad et al. 1994; Silver et al. 2000), and resource-poor habitats where allocation to belowground structures is

greater (Caldwell and Richards 1986). Fine root death and decomposition also are a relevant source of nutrients to the soil. The effects of decomposing roots on nutrient cycles are more profound than those of aboveground structures, mainly because of the minimal retranslocation of nutrients from roots during senescence (Nambiar 1987; Gordon and Jackson 2000). For instance, death and decomposition of fine roots may contribute from 18 to 50 % more nitrogen to the soil than litterfall (Vogt et al. 1986).

Understanding environmental controls of fine root demography is crucial 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 and Yanai 1997). Despite the importance of fine root demography to carbon and nutrient cycling, few studies have examined factors controlling fine root demography, and patterns of root demography across species and environments are still unclear (Eissenstat and Yanai 1997; Eissenstat el al. 2000; Gill and 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 (Chabot and Hicks 1982; Bloom et al. 1995; Givnish 1986; Eissenstat and Yanai, 1997; Eissenstat *et al.* 2000). 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.1995). The balance of tissue costs and benefits may change in response to changes in resource availability and differences in tissue morphology and physiology (Eissenstat *et al.* 2000), and optimal tissue longevity may also adjust to such changes. Efficiency may be maximized by reducing costs of tissues under low resources and by increasing tissue benefits under high resources (Eissenstat and Yanai 1997). Low costs are normally associated with traits that guarantee resource retention, such as lower growth rates and long lifespan of tissues, whereas high benefits are associated with traits that lead to a greater competitive ability, such as greater tissue growth rates and resource uptake ability (Berendse

1994; Aerts 1999). Optimality theory has been used to understand patterns of leaf demography (Chabot and Hicks 1982). For leaves, it has been demonstrated that longevity tends to be greater for species adapted to infertile habitats (Schläpfer and Ryser 1996; Reich et al. 1992; Reich et al. 1999). Root efficiency models predict that root longevity should also increase at low resources (assuming constant nutrient uptake ability, Eissenstat and Yanai 1997). However, empirical information on how root demography should adjust to changes in root efficiency is still lacking (Eissenstat and Yanai 1997).

# Fine root demography and resource variation

Fine root longevity may change as a consequence of resource variation because root resource uptake (benefits) decrease under low resource availability. The 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 and Yanai 1997). The theory also identifies a tradeoff between longevity and growth rates of roots, 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. In ecological time scale, 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 and Grime 1989). Predictions on tissue demography based on resource variation have been confirmed aboveground. Greater leaf longevity was linked to reduction in resource availability (i.e. light and/or nutrients) (Chabot and Hicks 1982; Coley 1988; Reich et al. 1992; Schläpfer and Ryser 1996). However, root demographic patterns with soil resource variation are still controversial (Nadelhoffer et al. 1985; Hendrick and Pregitzer 1992; Pregitzer et al. 1993; Ryan et al. 1996; Eissenstat and Yanai 1997; Burton et al. 2000; Eissenstat et al. 2000).

#### Fine root demography and morphology

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 and Yanai 1997; Ryser 1996). Other variables being constant, relatively thick, dense roots tend to be more costly to construct per unit root length (Eissenstat 1991; 1992). Thicker roots should maximize lifetime efficiency by increasing longevity. 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 less than 10 species (Eissenstat et al. 2000). In leaves, tradeoffs between tissue morphology and demography are present. A positive relationship has been identified between high specific leaf area (SLA) and shorter longevity of leaves (Lambers and Poorter, 1992; Reich et al. 1992; Ryser and Urbas 2000). Information about the existence of similar tradeoffs in root longevity is still lacking. Root morphology traits, such as root diameter, specific root length (SRL) and root density (Eissenstat 1991, 1992; Ryser and Lambers 1995) have been proposed as important factors associated with root longevity. In this case, SRL has been considered an analog of specific leaf area (Reich et al. 1992). The identification of root morphological traits as surrogates for root longevity is especially important due to the comparatively more difficult task of determining demography of roots (Eissenstat et al. 2000).

#### Fine root demography and spatial and temporal variation in resource availability

Environmental factors, such as surface drought and rewetting, may have a strong effect on root demography because a major fraction of the total root length occurs in the surface soil, where nutrients are usually more abundant (Eissenstat and van Rees 1994, Fahey and Hughes 1994). Nonetheless, the application of optimality theory may be more difficult than in conditions spatially and temporally homogenous.

In root efficiency models, the effect of soil resource availability on lifespan also depends on how the benefits of resource acquisition changes with changing levels of resources, and this reflects species differences in uptake ability and resource patch characteristics. This may explain in part conflicting empirical data about the effects of nutrient availability on root lifespan in forest communities (Burton et al. 2000). For instance, root demographic responses to localized drought may be different than under low resource availability because under very low water availability, nutrient and water uptake cease and root benefits are minimal. Fine roots may be selectively shed in dry soil as part of a strategy to avoid costs of root maintenance under periods of reduced root benefits because of impaired nutrient and water uptake in dry soil. Following this expectation, species adapted to frequent droughts may be more capable of reducing maintenance costs of roots under dry soil, thereby increasing root survival (Eissenstat and Yanai 1997). Survival of roots in dry soil vests a future advantage in quicker resource uptake after rewetting and avoidance of costs of new root construction. (Aerts and Chapin 2000).

A different interpretation can be made if the extent of root death under dry soil is related to the likelihood of the drought's duration (Eissenstat and Yanai 1997). Phreatophytic species adapted to prolonged droughts may favor root shedding in dry soil (e.g. surface roots of *Agave deserti*, Huang and Nobel 1992) and proliferation of deeper roots with access to soil moisture, whereas species from habitats with brief droughts may favor greater tolerance (Molyneux and Davies 1983, Jupp and Newman 1987, Meyer et al. 1990). Root death in dry soil may be related also to carbohydrate starvation (Marshall and Waring 1985; Marshall 1986) or be the direct cause of desiccation of tissues (Stasovski and Peterson 1991). Plant species may not only vary in their ability to maintain roots alive under resource-poor patches but also in the deployment of new roots in resource-rich patches (Caldwell 1994). In addition, under surface drought, stresstolerating species from xeric habitats should allocate more roots to deeper wet soil layers (Campbell et al. 1991) and species from mesic habitats should response faster to resource enrichment (Campbell and Grime 1989). Clearly, more species-specific information about plant

responses to localized drought and enrichment is needed in order to clarify how fine root demography changes upon spatial and temporal variation in resources.

# Hydraulic redistribution

Hydraulic redistribution refers to the differential ability of plant root systems to redistribute water from wet to dry layers of the soil (Caldwell et al. 1998). "Hydraulic lift" indicates the particular case of upward transport of water from moist deep soil to dry surface soil via plant roots, and "reverse hydraulic lift" for the downward transport of water when an opposite pattern of moisture is present in the soil profile (Burguess et al. 1998; Schulze et al. 1998). Since hydraulic lift was first described in field plants of *Artemisia tridentata* by Richards and Caldwell (1987), more than 60 new cases have been reported in a series of species and habitats (about 43 woody species and 16 herbaceous species, Millikin and Bledsoe 2000; Jackson et al. 2000).

Hydraulic redistribution has been linked to the improvement of the effectiveness of water-uptake by deep roots (Caldwell and Richards 1989), of nutrient uptake in otherwise dry surface soils (Matzner and Richards 1986; Dawson 1998), to facilitation of water to neighboring plants (Caldwell and Richards 1989; Dawson 1993), and the alteration of the water balances of single plants (Emerman and Dawson 1996; Caldwell et al. 1998; Burguess et al. 1998), of stands of single species (Ryel et al. 2002) and of entire forests and regions (Jackson et al. 2000). Hydraulic lift can facilitate transpiration by supplying water overnight to upper soil layers where it can be utilized the following day (Caldwell et al. 1998). Simulations also showed that HL can potentially increase whole canopy transpiration in *Artemisia tridentata* stands (Ryel et al. 2002). In a sugar maple (*Acer saccharum*) forest with root access to groundwater hydraulically lifted water may account for up to one third of water loss via transpiration (Emerman and Dawson 1996) and may increase annual water use in the forest by 19-40% (Dawson 1996; Jackson et al. 2000). Simulations also suggest that, as sugar maple has become more abundant in the northeastern USA (with the abandonment of agriculture and the onset of chestnut blight), the

region's hydrological cycle might have changed through greater transpiration (Jackson et al. 2000). This suggests that single species can have a profound effect on forest hydrology via differential hydraulic redistribution ability.

Differences in hydraulic lift among species can be interpreted by optimality theory (Givnish 1986). This is to assume that there has to be a benefit from hydraulic lift that counteracts the costs paid by a plant in terms of water given up to the surrounding soils, and potentially via evaporation, drainage or uptake by neighboring plants. Caldwell et al. (1998) suggest that transpiration, nutrient acquisition, root longevity and biogeochemical processes can all likely benefit from water lifted into upper, otherwise dry soil layers. These authors suggest, however, that hydraulic lift may just be an inevitable consequence of roots without rectification properties (sensu Nobel 1994) that cannot prevent passive water efflux to the soil (in analogy to stomates that cannot selectively admit  $CO_2$  while preventing loss of water).

# The importance of species-specific belowground dynamics

Shifts in species composition of natural communities that are occurring globally can alter cycles of water, carbon and nutrients (Connin et al. 1997; Gill and Burke 1999). Gill and Jackson (2000) found substantial differences in the rates of root turnover between divergent plant functional types, such as grasslands and shrublands, and hypothesized that shifts in plant life form might also influence rates of root turnover in ecosystems. This effect has been implicated in shrub invasions of semiarid and arid grasslands of western United States (Schlesinger et al. 1990), and it has been predicted that biomass turnover (and carbon and nutrient cycling, consequently) should decrease as shrub invasion progresses, because of the differences in root turnover among shrubs and grasses (Gill and Jackson 2000). Although global patterns of fine root turnover have been described for major vegetation types and biomes (Vogt et al. 1996; Gill and Jackson 2000), little is known, however, about how different species-specific patterns might be within single environments.

Studies on fine root demography have been concentrated in indirect estimations of fine root turnover based on sequential coring and soil monoliths (Gill and Jackson 2000). Estimations based on direct observation of roots now prevail because of the technical breakthroughs with minirhizotron cameras. Nonetheless, most of the information being gathered in natural communities does not yet resolve for species-specific fine root demography, due to the difficulties of identifying the species for the fine roots in the soil of multi-specific communities. Table 1.1 provides a summary of the different studies of root demography that have used minirhizotrons. The record shows that studies of single species using seedlings in the greenhouse or monocultures have prevailed. In some studies of adult species in natural communities, patterns of fine root demography observed have been attributed to a single species when that species dominates the community. When more complex multi-specific communities are studied, fine root demographic data obtained with minirhizotrons represent only a community-level measurement, and the relative contribution of each species in the system is unknown. Clearly, there is a need for identifying the contributions of single species to the dynamics of fine root demography in entire plant communities.

Although species differences in hydraulic redistribution ability may be related to differences in water budgets of entire communities, information on species differences is also scarce and insufficient for predictive models of ecosystem water flux (Millikin and Bledsoe 2000). Table 1.2 summarizes the most recent studies on hydraulic lift reported in the literature. Most of the data available have been obtained from greenhouse studies with seedlings (Baker and van Bavel 1988; Sakuratani et al. 1999; Song et al. 2000; Wang et al. 2000) and from investigations of individual species in monospecific stands (Wan et al. 1993; Caldwell et al. 1998; Ryel et al. 2002) or in habitats where the spacing between different species was large enough to reduce intermixing of roots from different species (Dawson 1993, 1996; Yoder and Novak 1999).

The importance of hydraulic lift in communities with very low plant densities may be reduced because in such conditions plant-plant interactions are less likely to occur. Differences in

hydraulic lift ability among coexisting species in a plant community have usually been inferred from previous knowledge of spatial and temporal partitioning of root activity. Generally this has sufficed to detect differences in hydraulic lift ability between trees and understory vegetation, such as differences in phenology between *Quercus douglasii* trees and annual grasses in a California blue oak woodland (Millikin and Bledsoe 2000) or differences in rooting depth between sugar maple and neighboring understory plants (Dawson 1993). Spatial separation of roots from trees and grasses allowed the identification of species-specific effects in soil water use in African savannas (Ludwig 2001), but few studies have attempted to make comparisons within spatially co-ocurring trees and co-ocurring grass species. Measurements of stem flow in individual roots (Burguess et al. 1998) have identified differences between two species of *Eucalyptus* in nighttime water flow that are indicative of differential HR ability. However, this technique is very meticulous and is not suitable for simultaneous comparisons of larger number of species.

This study is the first field investigation on the species-specific patterns of fine root demography and hydraulic lift within coexisting tree species in their natural habitat. In order to circumvent the problems of interpreting the specificity of the data of fine root demography and hydraulic lift in a mixed-species community, we isolated each single species by growing roots of individual adult trees inside root chambers or "rhizotrons" (Figs 1.1a and 1.1b). This method was used successfully in the field to compare root demography between adult trees and seedlings (Espeleta and Eissenstat, 1998) and between mycorrhizal and non-mycorrhizal roots of adult trees (Espeleta, Eissenstat and Graham 1999) and for measuring field root respiration.

Responses of the different tree species to resource variation were investigated by exposing seedlings in the greenhouse to variation in the intensity and frequency (Experiment 1, Chapter 1) and space and timing (Experiment 2, Chapter) of water and nutrient supply.

#### Study system: the fall-line sandhills of southeastern United States.

The fall-line sandhills are distributed in southeastern US along the geographic region where the southeastern coastal plain meets the piedmont area. This ecosystem is characterized by rolling hills with deep sandy soils, with poor water and nutrient retention capacity (Wells and Shunk 1931; Peet and Allard 1993; Christensen 2000; Goebel et al. 2001). Coarse texture of the soil and abundant rainfall interact to produce frequent and intense surface droughts of short durations. Gradients of xeric to mesic areas are generally associated with variation in topography (Peet and Allard 1993). Xeric sites occur on sandhill ridges where surface sands are deeper, subxeric sites occur in sandhill slopes and mesic sites occur on bottomlands where clay layers are closer to the surface. Mesic and subxeric sites exhibit denser canopy cover and higher species diversity (Christensen 2000). Water and nutrient availability tend to increase from xeric to more mesic sites (Goebel et al. 2001; J. West, unpublished data). The distribution of *Quercus* species has been linked to such soil resource gradients (Weaver 1969; Mavity 1986); especially water availability (Jacqmain et al. 1999; Donovan et al. 2000). The *Quercus* species have also shown differential ability to respond to resource variation in aboveground traits, such as photosynthesis and water-use efficiency (Donovan et al. 2000; Vaitkus and McLeod 1995). Figure 2.1 shows an artistic representation of how tree species are differentially distributed along the gradient. Four *Quercus* species are differentially distributed in order from a xeric to mesic habitats. *Q. laevis* Walt. (turkey oak) is the dominant species in xeric habitats. *O. incana* Bartr. (bluejack oak)and *O. margaretta* Ashe ex Small (sand post oak) have intermediate distribution and are found primarily in subxeric sites. Q. incana can colonize xeric habitats but Q. margaretta has a more mesic distribution. *Q. marilandica* Muenchh (blackjack oak) is the only species restricted to mesic sites, and do not colonize subxeric habitats, where the rest of the species may co-occur. A generalist *Pinus* species, *P. palustris* Mill. (longleaf pine) is the dominant overstory tree across the gradient. The differences between the sandhill tree species in the ecological distributions along the sandhill gradient allow the formulation of hypotheses based on tissue efficiency optimization. Applying

optimality theory to roots, the following predictions were made (the number of the chapters that address each question are indicated after each prediction):

1. a) Root persistence increases root efficiency under low-resource conditions by reducing nutrient losses. Therefore, root retention rates should be greater under low resource supply (Chapter 1). Also, species that colonize xeric habitats (*Q. laevis, Q. incana*) should exhibit less turnover and longer lifespan of fine roots than species that dominate mesic habitats but do not colonize xeric habitats (*Q. margaretta* and *Q. marilandica*). We expect the generalist *P. palustris* to show intermediate fine root longevities (Chapters 1, 2 and 4)

b) Rapid root turnover increases root efficiency under high resources because it facilitates quick root growth responses to spatial or temporal pulses in resources. Hence, species that dominate mesic habitats (*Q. margaretta* and *Q. marilandica*) should exhibit greater growth of roots under high resource supply (Chapter 1) or after an enrichment of resources (Chapter 2). Because *P. palustris* also dominates in mesic habitats, fine root growth rates should also be high in *P. palustris* (Chapters 1, 2 and 4)

c) Because a tradeoff exists often between persistence and growth ability of roots, species with long-living roots should also have slow growth rates in field conditions (Chapter 4), especially under high resources (Chapter 1) or as a response to resource enrichment (Chapter 2). In contrast, species with short-living roots should exhibit greater growth rates but lower survival ability under stress conditions (e.g. surface drought, Chapter 2)

2. Because thicker roots may live longer, species with longer fine root lifespan should exhibit thicker and more dense roots (Chapters 1 and 2).

3. Hydraulic lift may be advantageous for increasing root longevity and facilitating nutrient uptake in otherwise dry surface soils. Species that colonize xeric habitats (where surface drought

is more intense and frequent) should exhibit hydraulic lift ability compared to species unable to colonize these habitats (Chapter 3).

The fall-line sandhills are nearly unique in that several tree species of the same genus can be compared while coexisting within the same habitat. In addition, species can be compared across the resource availability gradient. Comparisons of root traits between co-occurring congeneric species with different ecological distribution may allow relating trait variation to adaptation without the interference of phylogenetic constraints or large-scale environmental noise (Long and Jones 1996). On the other hand, comparisons of root traits between the *Quercus* species and the longleaf pine can give an idea of the extent of the optimality predictions about tradeoffs in root traits and responses to resource variation. Comparisons of closely related species have been made for grass species (Garnier 1992); however, this study is the first attempt to compare belowground traits between several coexisting, congeneric tree species.

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Vegetation type	Species studied	Root observation technique	Reference
Single species			
Greenhouse			
Herbaceous	Festuca rubra Arachis hypogaea	minirhizotrons Observation tubes	Partel and Wilson (2001) Kraus and Deacon (1994)
Woody	Citrus spp.	Observation windows	Kosola and Eissenstat (1994)
	Prunus avium. Acer pseudoplatanus Picea sitchensis Populus x canadensis	Borescopes	Black et al. (1998)
	Populus generosa.	Borescopes	Hooker et al. (1995)
Field			
Herbaceous	Sorghum bicolor Medicago sativa Fragaria x ananassa	Minirhizotrons Minirhizotrons Rhizotrons	Cheng et al. (1990) Goins and Russell (1986) Atkinson (1985)
Woody	Malus domestica	Rhizotrons Minirhizotrons	Atkinson (1985) Wells and Eissenstat (2001)
	Actinidia deliciosa	Rhizotron – minirhizotrons	Reid et al. (1993)
	Citrus volkameriana	Observation windows	Espeleta and Eissenstat (1999) Espeleta et al. (1999)
		Minirhizotrons	Kosola et al. (1995)
	Vitis vinifera	Minirhizotrons	Comas et al. (2000)
Monospecific tree stands			
	Pinus ponderosa Picea abies	Minirhizotrons Minirhizotrons	Johnson et al. (2000) Majdi (2001), Maidi et al. (2001)
	Populus spp.		Dickmann et al. (1996)
	Eucalyptus globulus Pinus resinosa + Populus sp	Minirhizotrons Minirhizotrons	Katterer et al. (1995) Coleman et al. (2000)
	Pseudotsuga menziesii Liquidambar	Rhizotron Minirhizotrons	Keyes and Grier (1981) Price and Hendrick (1998)
	Pinus eliottii	Minirhizotrons	Schroeer et al. (1999)

Table 1.1. Summary of the species-specific information on fine root demography estimated by direct observation methods.

Vegetation type	Species studied	Root observation technique	Reference			
Communities with few species						
Temperate						
Broadleaf	Sugar maple	Minirhizotrons	Hendrick and Pregitzer (1992) Burton et al. (2000)			
	Prunus pensylvanica Acer saccharum-Betula alleghaniensis	Rhizotron minirhizotrons	Pregitzer et al. (1993) Tierney et al. (2001)			
	<i>Quercus ilex</i> in NE Spain	Minirhizotrons	Lopez et al. (2001)			
Grassland	Deschapsia flexuosa, Molinia caerulea	Minirhizotrons	Aerts et al. (1992)			
	Festuca ovina, Nardus stricta, Juncus squarrosus	Minirhizotrons	Fitter et al. (1997)			
Boreal/alpine						
Conifer	Pinus banksiana, Picea mariana, Populus sp	Minirhizotrons	Steele et al. (1997)			
Grassland	Carex eriphorum, Dupontia fisherii, Carex-oncophorus, Carex-poa	Rhizotron	Miller et al. (1980)			
	Carex aquatilis, Dupontia fisherii	Rhizotron	Shaver and Billings (1975) Shaver and Chapin (1991)			
Multi-specific communities						
Temperate- Broadleaf	NE hardwood SE Upland hardwood	Minirhizotrons Minirhizotrons	Tierney and Fahey (2001) Joslin and Wolfe (1998) Joslein et al. (2001)			
Boreal	Alaskan taiga	Minirhizotrons	Ruess et al. (1998)			

Table 1.1 (cont.). Summary of the species-specific information on fine root demography estimated by direct observation methods.
Vegetation type	Species	Detection technique	Reference					
Single specie	28							
Laboratory/G	Laboratory/Greenhouse							
Herbaceous								
	Triticum vulgare (wheat)	Soil water content in	Breazeale (1930)					
	and Zea mays (maize)	different compartments	Preszenie and Crider (1024)					
	(tomato)	different compartments	Breazeare and Crider (1934)					
	Phaseolus vulgaris (bean)	Water efflux from hypocotyl	Schippers et al. (1967)					
	Medicago sativa (alfalfa)	Soil water content in different compartments	Corak et al. (1987)					
	<i>Buchloe dactyloides</i> and <i>Zoysia japonica</i> (grasses)	Soil water content, split-pot	Huang (1999)					
	<i>Cynodon dactylon</i> and <i>C. transvaalensis</i> (bermudagrass)	Soil water content in different compartments	Baker and van Bavel (1986)					
	Pennisetum glaucum (pearl millet)	Microtensiometer	Vetterlain and Marschner (1993)					
	Sorghum bicolor	Soil water content in	Xu and Bland (1993)					
	(sorghum) Zag mays (maize)	different compartments	Topp et al. $(1006)$					
	Maize hybrids	TDR. split-pot	Wan et al. $(2000)$					
	Helianthus annus (sunflower)	DPHP sensor	Song et al. (2000)					
Woody								
ý	<i>Circidium torreyana</i> (palo verde), <i>Acacia greggii</i> (catclaw)	Soil water content in different compartments	Breazeale and Crider (1934)					
	Gossypium hirsutum (cotton)	Soil water content, split-pot	Baker and van Bavel (1998)					
	Prunus persica (peach)	Soil water content in different compartments	Glenn and Welker (1993)					
	Eucalyptus viminalis	Soil water content in different compartments	Phillips and Riha (1994)					
	Sesbania rostrata	Constant power heat	Sakuratani et al. (1999)					
	Gutierrezia sarothrae Artemisia tridentata	TDR TP	Wan et al. (1993) Matzner and Richards (1986)					

Table 1.2. Summary of the literature on species-specific patterns of hydraulic redistribution among plant species (TP: thermocouple psychrometers, TDR: time-domain reflectometry, DPHP: dual-probe heat-pulse technique, HRM: heat ratio method).

Vegetation type	Species	Detection technique	Reference	
Single speci	es			
Field (Mon	ospecific stands or isolated specie	es)		
Herbs/ Shrubs	Artemisia tridentata	TP	Richards and Caldwell (1987); Williams et al. (1993) <sup>:</sup> Ryel et al. (2002)	
	<i>Gutierrezia sarothrae</i> (transplants)	TDR	Wan et al. (1993)	
Trees	<i>Grevillea robusta</i> , reverse flow <i>Eucalyptus</i> spp.	Sap flow gauges Sap flow gauges, HRM	Smith et al. (1999) Burguess et al. (1998, 2001)	
	<i>Acer saccharum</i> (sugar maple), isolated individuals	TP, isotopes	Dawson (1993)	
Multiple sp	ecies			
Grasses/ shrubs	Mojave desert shrubs (one CAM plant)	TP	Yoder and Novak (1999)	
Grasses vs. trees	<i>Quercus douglasii</i> (blue oak) and understory grasses	TP	Millikin and Bledsoe (2000)	
	Acacia trees and African savanna grasses	TP	Ludwig et al. (2001)	

Table 1.2 (cont.). Summary of the literature on species-specific patterns of hydraulic redistribution among plant species (TP: thermocouple psychrometers, TDR: time-domain reflectometry, DPHP: dual-probe heat-pulse technique, HRM: heat ratio method).



Figure 1.1a. Diagram of the root observation chambers ("rhizotrons") used to isolate roots from adult trees of known species identity in a subxeric habitat of the fall-line sandhills.



Figure 1.1b. Top view of the rhizotrons showing the positioning of lateral roots and thermocouple psychrometers used to record species-specific data of fine root demography and hydraulic lift from adult. Fine roots were observed and mapped on a transparent plexiglass window.



Figure 1.2. Artistic depiction of tree species distribution along a topographical and resource availability gradient in the fall-line sandhills. The intensity of the bar's color indicates the approximate relative distribution of each species along the gradient (from white color=no presence to black color=greatest abundance). Small letters indicate species identity: Pp (*Pinus palustris*), Ql (*Quercus laevis*), Qi (*Q. incana*), Qg (*Q. margaretta*), Qm (*Q. marilandica*).

### CHAPTER 2

# FINE ROOT DEMOGRAPHY AND MORPHOLOGY IN RESPONSE TO SOIL RESOURCES AVAILABILITY AMONG XERIC AND MESIC SANDHILL TREE SPECIES<sup>1</sup>

<sup>&</sup>lt;sup>1</sup>Espeleta, J.F. and L.A. Donovan. 2002. *Functional Ecology*. 16:113-121.

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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 south-eastern US. *Pinus palustris* Mill. is a generalist in this habitat, whereas *Quercus marilandica* Muenchh.occurs in more fertile, mesic habitats relative to *Q. laevis* Walt. Seedlings were grown under four resource treatments (water + nutrients) for seven months: high resources, low resources, and short-term exposure (last two 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 tradeoffs between tolerance and competitive ability belowground: 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.

#### Introduction

Fine root turnover is a significant component of belowground carbon budgets (Caldwell & Richards 1986; Bloomfield, Vogt & Wargo 1996; Eissenstat & Yanai 1997), and affects nutrient cycles due to the minimal retranslocation of nutrients from roots during senescence (Nambiar 1987; Gordon & Jackson 2000). Understanding controls of fine root demography is crucial 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 el 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 (Chabot & Hicks 1982; Bloom,

Chapin & Mooney 1985; Givnish 1986; Eissenstat & Yanai, 1997; Eissenstat *et al.* 2000). 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, Chapin & Mooney 1995). The balance of tissue costs and benefits may change by 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 and 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 tradeoff 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 aboveground. Greater leaf longevity was linked to reduction in resource availability (i.e. light and/or nutrients) (Chabot & Hicks 1982; Coley 1988; Reich, Walters & Ellsworth 1992; Schläpfer & Ryser 1996). However, root demographic patterns with soil resource variation are still controversial (Nadelhoffer, Aber & Melillo 1985; Hendrick & Pregitzer 1992; Pregitzer, Hendrick & Fogel 1993; Ryan et al. 1996; Eissenstat & Yanai 1997; Burton, Pregitzer & Hendrick 2000; Eissenstat et al. 2000).

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; 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 less 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 simultaneously leaf and fine root demography and morphology 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 southeastern US, which are characterized by rolling hills with deep sandy soils, with poor water and nutrient retention capacity (Peet & Allard 1993; Christensen 2000; Goebel *et al.* 2001).

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 and 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 overstory 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 (Weaver 1969; Jacqmain, Jones & Mitchell 1999) and species differences in water stress tolerance (Mavity 1986; Donovan, West & McLeod 2000).

#### Plant material and experimental setting

Seeds of the three species were collected at the end of the fall of 1998 near Columbus, Georgia, USA. Seeds were stratified over the winter at 5 °C for four 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 minutes. Seedlings were planted in 2-L plastic pots filled with sand and subjected to different resource supply treatments (see below) for seven 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  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> 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 seven months (from July 1999 to February 2000): a "HIGH" treatment consisted of 1/10 modified Hoagland's solution applied every two days; a "LOW" treatment consisted of 1/40 modified Hoagland's applied once per 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 two 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 ca. 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 x 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 (shriveling, 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 one, four, six and seven 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 pen colour. 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 seven months (February 2000), plants from all treatments were harvested and root and leaf morphology were recorded. Three sub-samples 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 (Delta-T Devices Ltd, Cambridge, UK). 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 a 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 belowground 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 hours. The root: shoot ratio was calculated as the total aboveground biomass (stem and leaves) divided by the total belowground biomass (coarse and fine roots).

#### Statistical Analysis

The experiment was designed as a completely randomized, 3 species x 4 treatments, fullfactorial experiment. The species, treatment and interaction (species x treatment) effects on root and leaf demography and morphology, and biomass allocation were analyzed 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 and 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 analyzed by pairwise comparisons of means. Species comparisons within treatments comprised a total of 12 comparisons (3 comparisons at each treatment: *Quercus marilandica* vs. *Q. laevis*, *Q. marilandica* vs. *Pinus palustris*, and *Q. laevis* vs. *P. palustris*). Treatment comparisons for each species comprised a total of 9 comparisons (3 comparisons for each species). We only compared treatment differences between HIGH vs. LOW, HIGH vs. DEPLETION and LOW vs.ENRICHMENT. In total, 21 comparison pairs were analyzed 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 3 treatment comparisons per species). All mean contrasts were analyzed by two-tailed t-tests after Bonferroni correction, using Statistical Analysis System, MULTTEST procedure (SAS, Release 8.00, SAS Institute, NC, USA).

The effects of time and the differences in fine root growth among species and treatments during the experiment were analyzed 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 x species, time x treatment and time x species x treatment). Multivariate analyses were performed using JMP Data Analysis Software (version 4.0.2, SAS Institute, NC, USA).

#### Results

#### Fine root demography

Species differed in fine root growth, death and mortality (Figs 2.1, 2.2a, 2.2b and 2.2c). In general, *P. palustris* and *Q. marilandica* exhibited more fine root growth than *Q. laevis* (Table 2.1; Fig. 2.1 and Fig 2.2a), 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. 2.2b and 2.2c).

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* (Figs 2.1 and 2.2a). Fine root death was also greater under HIGH than LOW resources for *Q. marilandica*, the only species that exhibited significant fine root death (Fig. 2.2b). Although not significant, fine root mortality tended to be less at LOW resources (Fig. 2.2c). Fine root death was observed during the last two 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 (Figs 2.2a, 2.2b and 2.2c). Except for *Q. laevis* DEPLETION tended to reduce fine root growth (Fig. 2.2a).

#### Leaf demography

Contrary to fine root growth, leaf production was similar between the *Quercus* species (Fig. 2.2d). 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* (Figs 2.2b, 2.2c, 2.2e and 2.2f). However, leaf death was similar across treatments (Fig. 2.2e) but fine root death increased at HIGH resources (Fig. 2.2b). In addition, leaf mortality in *Q. marilandica* was greater at LOW resources (Fig. 2.2f), but the opposite trend was observed in fine root mortality (Fig. 2.2c). 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 (Figs 2.2a and 2.2d).

#### 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 2.2 and 2.3). 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. 2.2a), produced fine roots with greatest thickness and density and lowest SRL (Figs 2.3a, 2.3b and 2.3c). Third, root morphology was constant across treatments, except for two instances. First, SRL of *Q. laevis* increased at ENRICHMENT (Fig. 2.3a). Second, fine root thickness and fine root density tended to be less in *P. palustris* (Fig. 3.3b and 3.3c) at LOW than HIGH resources. There was not any effect of resource supply on fine root diameter and density for the *Quercus* species (Fig. 3.3b and 3.3c).

#### Leaf morphology

In general, we observed analogous patterns between leaf and fine root morphology. Both *Quercus* species had similar SLA and SRL (Fig. 2.3d). SLA and SRL were similar across resource supply treatments (Figs. 2.3a and 2.3d), except for the ENRICHMENT treatment, where only SLA of *Q. laevis* increased compared to the LOW treatment (Figs. 2.3a and 2.3d). The DEPLETION treatment was not significantly different than the HIGH treatment for SLA and SRL (Figs 2.3a and 2.3d).

#### Allocation belowground

Fine root and leaf biomass were similar among the *Quercus* species and significantly less than *P. palustris* at HIGH resources (Figs 2.4a and 2.4b). At LOW resources, species differences in fine root and leaf biomass decreased (Figs 2.4a and 2.4b). Proportional allocation belowground (root:shoot ratio) was similar among the *Quercus* species and greater than *P. palustris* at all resource levels, except for the ENRICHMENT treatment, where all species were similar (Fig. 2.4c). 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.2.4c). Similar to leaf number, leaf biomass but not fine root biomass was greater at ENRICHMENT compared to LOW treatments, especially in *Q. marilandica* (Figs 2.4a and 2.4b). In all species, DEPLETION did not significantly change fine root and leaf biomass and root:shoot ratio (Figs 2.4a and 2.4c).

#### Discussion

Our study demonstrates different patterns of belowground 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 the *Quercus* species 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 tradeoff 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* 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 aboveground 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 lifespans 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 lifespans and less root turnover at high fertility (Keyes and Grier 1981; Vogt, Grier & Vogt 1986; Pregitzer, Hendrick & Fogel 1993; Burton, Pregitzer & Hendrick 2000). 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 belowground 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 aboveground 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 the 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, 1992; Ryser & Lambers 1995) based on relationships between high specific leaf area and shorter leaf lifespan (Lambers & Poorter 1992; Reich et al. 1992, 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 found a poor association also between leaf demography and morphology. As with fine roots, leaf morphology (SLA) was similar but leaf demography was different 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 belowground were significantly lower in species from xeric habitats when more species of the southeastern US coastal plain were also compared (Long & Jones 1996).

Our results provide circumstantial evidence that root turnover may be reduced in habitats of low fertility, 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 suggest also that tradeoffs may exist between tolerance and competitive ability belowground (Grime 1977; Aerts 1999). 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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Table **2.1.** 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 numerator denominator		F statistic	P > F
Between subjects				
Species	2	84	21.52	< 0.0001
Treatment	3	84	9.30	< 0.0001
Species x Treatment	6	84	1.75	0.1204
Within subjects				
Time	3	82	339.0	< 0.0001
Time x Species	6	166	2.46	0.0267
Time x Treatment	9	252	3.12	0.0014
Time x Species x Treatment	18	252	1.86	0.0195

Fine root growth data was analyzed after logarithmic transformation (n=8 plants per species x treatment combination).



**Fig. 2.1.** Time course of fine root growth of *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings exposed to different treatments: (a) high resource supply ('HIGH'), and (b) low resource supply ('LOW'). Note that the graphs do not share the same scale in 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 ± SE, n=8 plants per species and treatment combination).



**Fig. 2.2.** Demography of aboveground and belowground tissues in *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for seven 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 analyzed 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.



**Fig. 2.3.** Morphology of fine roots and leaves of *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for seven 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 analyzed 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.



**Fig. 2.4.** Allocation to fine roots and leaves and root:shoot ratio in *Q. laevis*, *Q. marilandica* and *P. palustris* seedlings grown for seven 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 analyzed 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.

## CHAPTER 3

# FINE ROOT DEMOGRAPHY IN RESPONSE TO SURFACE DROUGHT AND REWETTING DIFFERS AMONG TREE SPECIES FROM A SOIL RESOURCE GRADIENT $^1$

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<sup>&</sup>lt;sup>1</sup>Espeleta, J.F. and L.A. Donovan. To be submitted to *New Phytologist*.

#### Summary

• We studied how ecological distribution (xeric to mesic habitats) relates to fine root demographic responses to resource variation for tree species from a soil resources gradient in the fall-line sandhills of southeastern US.

• In a greenhouse experiment with seedlings, we compared the responses of five different tree species to different treatments (control, surface drought and surface rewetting) in fine root demography (growth, death and percentage mortality), allocation and fine root morphology (mean diameter, specific root length and tissue density).

• Fine root demography mirrored the ecological distribution of species. Species known to colonize xeric habitats (*Quercus laevis* and *Q. incana*) exhibited greater survival in dry surface soil and less proliferation after rewetting tended to allocate less to surface roots, greater fine root survival in dry surface soil and less proliferation after rewetting than mesic species (*Q. marilandica*). Species with intermediate distribution (*Q. incana* and *Q. margaretta*) showed intermediate levels of fine root turnover. Contrary to *Quercus* species, which exhibited a tradeoff between fine root persistence and proliferation, the generalist *Pinus palustris* showed high survival ability under dry soil and high growth ability after rewetting. Fine root morphology was very similar among *Quercus* species and was not associated with fine root demography.

• Our results confirmed predictions from the theory of resource-use-efficiency optimization. Responses to low or high resource availability were linked to conservation or fast turnover of fine roots, respectively. Differences in tissue turnover rates may also indicate differences in resource cycling across environments: xeric habitats exhibiting slower resource cycling than mesic habitats

#### Introduction

The turnover rate of belowground tissues is a major controlling factor in resource budgets in most ecosystems (Caldwell & Richards, 1986; Bloomfield *et al.*, 1996; Vogt *et al.*, 1996). In

order to estimate productivity of different ecosystems, the dynamics of fine root demography in response to environmental change needs to be investigated (Eissenstat et al., 2000; Norby & Jackson, 2000). Studies have compared root demography of species from different environments in order to search for patterns of ecological variation (Black et al., 1998; review by Gill & Jackson, 2000). Other studies examined aspects of root demography of single species, e.g., variation in root lifespan, proliferation and death (Eissenstat & Yanai, 1997; Tingey et al. 2000), and root allocation responses in heterogenous soil (Campbell et al., 1991; Einsmann et al., 1999). Due to the difficulties in directly observing roots to estimate root demography, other studies have examined root traits, other than root demography, that can serve as surrogates (Ryser & Lambers, 1995; Ryser & Eek, 2000; Eissenstat et al., 2000). Potential links between root form and function (Eissenstat & Yanai, 1997) may allow predictions of root demography based on differences in root morphology (Eissenstat, 1991). Nonetheless, few studies have looked simultaneously at root demography, morphology and allocation responses between species with different ecological distribution as affected by change in the environment (Eissenstat et al., 2000). This study compares root demography and morphology of species with different ecological distribution as affected by drying and rewetting of surface soil. Environmental factors such as surface drought and rewetting may have a strong effect on root demography because a major fraction of the total root length is found in the surface soil, where nutrients are usually more abundant (Eissenstat & van Rees, 1994; Fahey & Hughes 1994).

Theoretical predictions have been formulated to explain the variation of root demography and morphology. Most of these predictions have been extrapolated from optimality analysis that was first applied to leaves (Chabot & Hicks 1982; Givnish 1986; Reich *et al.*, 1992; Eissenstat & Yanai, 1997). Economic models interpret tissue demography by relating the optimal lifespan of tissues with the maximization of lifetime tissue efficiency (defined as the ratio of benefits to costs of tissues, Bloom *et al.*, 1985). Efficiency may be maximized by reducing costs of tissues under low resources and by increasing tissue benefits under high resources (Eissenstat & Yanai 1997).

Low costs are normally associated with traits that guarantee resource retention, such as slow growth rates and long lifespan of tissues, whereas high benefits are associated with traits that lead to a greater competitive ability, such as greater tissue growth and resource uptake rates (Berendse, 1994; Aerts, 1999). For leaves, it has been demonstrated that longevity tends to be greater for species adapted to infertile habitats (Schläpfer & Ryser, 1996; Reich et al., 1999). Root efficiency models predict that root longevity should also increase at low resources (assuming constant nutrient uptake ability, Eissenstat & Yanai, 1997). However, under localized drought, when nutrient and water uptake cease and root benefits are minimized, the outcome may be different. As part of a strategy to avoid costs of root maintenance under periods of reduced root benefits, fine roots may be selectively shed in dry soil. Species adapted to frequent droughts may be more capable of reducing maintenance costs of roots under dry soil, thereby increasing root survival (Eissenstat & Yanai, 1997). Persistence of roots in dry soil can be more critical among plants of infertile habitats, because it avoids future costs of root reconstruction (Aerts & Chapin, 2000) and prevents loss of nutrients due to the small re-translocation from roots during senescence (Nambiar, 1987; Gordon & Jackson, 2000). To the contrary, in resource-rich habitats, shedding of roots in dry soil followed by rapid construction of new roots after rewetting may be essential for rapid resource uptake (Robinson, 2001), which favors competitive ability of species growing in fertile habitats (Aerts & Chapin, 1999). Plant species may not only vary in their ability to maintain live roots under resource-poor patches but also in the deployment of new roots in resource-rich patches (Grime, 1994). Under surface drought, stress-tolerating species from xeric habitats are expected to allocate more roots to deeper wet soil layers (Grime, 1977; Campbell et al., 1991).

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; 1992). Thicker roots should

maximize lifetime efficiency by increasing longevity; therefore, they should exhibit lower rates of growth and death. Similar relationships between leaf morphology (thickness) and leaf lifespan have already been described (Reich *et al.*, 1999; Ryser & Urbas, 2000). A empirical test of these predictions is not possible because the information on root demography and morphology has been described together in no more than 10 species (compared to hundreds of species with leaf demography studies), most of which are crop and annual plants (Eissenstat *et al.*, 2000).

The present study explores the variation in root demography and morphology as affected by surface drought and re-wetting in a group of congeneric species that have different ecological distribution. Comparisons of root demography between co-occurring congeneric species with different ecological distribution may provide a system for relating trait variation to environment without the interference of phylogenetic constraints or large-scale environmental noise (Long & Jones, 1996). We compared fine root demography of five tree species (four congeneric Quercus species and one *Pinus* species) that coexist in a fall-line sandhill habitat but show differential ability to colonize habitats of different resource availability (Fig. 3.1). The fall-line sandhills of southeastern United States are characterized by rolling hills with deep sandy soils, with poor water and nutrient retention capacity (Peet & Allard, 1993; Christensen, 2000; Goebel et al., 2001). The coarse texture of the sandy soil and the abundant precipitation interact to produce frequent and intense surface droughts but of short durations. Variation in topography is associated to a gradient of xeric to mesic habitats. Mesic and subxeric sites exhibit denser canopy cover and greater species diversity and soil resource availability (e.g. greater nitrogen mineralization) than xeric sites (J. West, unpublished data). The distribution of sandhill *Quercus* species has been linked to such soil resource gradients (Weaver, 1969; Mavity, 1986); especially water availability (Jacqmain et al., 1999; Donovan et al. West & McLeod 2000). Four *Ouercus* species are differentially distributed from a xeric to mesic habitats. Q. laevis Walt. (turkey oak) is the dominant species in xeric habitats. Q. incana Bartr. (bluejack oak) and Q. margaretta Ashe ex Small (sand post oak) have intermediate distribution and are found primarily in subxeric sites. Q.
incana can colonize xeric habitats but Q. margaretta has a more mesic distribution. Q. marilandica Muenchh (blackjack oak) is the only species restricted to mesic sites, and do not colonize subxeric habitats, where the rest of the species may co-occur. A generalist *Pinus* species, P. palustris Mill. (longleaf pine) is the dominant overstory tree across the gradient. In a greenhouse study using seedlings we recorded responses of fine root demography (growth, death and percentage mortality), morphology and allocation of trees exposed to surface drought and rewetting and made comparisons across species according to their ecological distribution. We hypothesized that species would differ in fine root demography as a response to surface drought. In particular, we predicted that: 1) species able to colonize xeric habitats would have less fine root growth, death and percentage mortality than species from mesic habitats, and that, 2) fine root growth and death would increase under dry versus wet surface soil, especially in mesic species. Because resource pulses are more abundant in mesic habitats we predicted: 3) that mesic species had less root survival in dry surface soil but greater root growth response after rewetting than xeric species. We also predicted: 4) that allocation to deep roots in wet soil was greater for species able to colonize xeric habitats. We also investigated whether differences in fine root morphology explained differences in fine root demography. Because finer roots have greater growth and death rates than thicker roots, we predicted that mesic species would have finer roots than xeric species.

## Materials and methods

## Plant material and experimental setting

Seeds of the five tree species (*Quercus laevis* Walt., *Q. incana* Bartr., *Q. margaretta* Ashe ex Small, *Q. marilandica* Muenchh and *Pinus palustris* Mill.) were collected in the fall of 1999 at the Carolina Sandhills National Wildlife Refuge (CSNWR), McBee, South Carolina. Seeds were stratified over the winter at 5 °C for four months and later germinated in 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 minutes. On 1 June, 2000, seedlings were transplanted into split-pot systems consisting of two vertically arranged 2-L plastic pots filled with sand and separated as top and bottom compartments (Fig. 3.2). Each bottom and top pot had a 70-cm (7 x 10 cm) transparent window that allowed root observation. Root observation windows were covered by a double-layer of black and white plastic to prevent light penetration and excessive heating, respectively. A 5-cm deep layer of perlite separated top and bottom compartments and served as a barrier for vertical ascent of water in the soil from bottom to top sections, while still allowing downward movement and root penetration. Liquid fertilizer was delivered by an automated fertilization system that supplied ca. 300 ml of 1/10 modified Hoagland's solution (Epstein, 1972) independently each top and bottom pots every two days via separate irrigation tubes (Fig. 3.2). This rate and concentration was considered to be an ample supply of water and nutrients for the plant species studied, and reproduced the application rate of a high resource treatment used in a previous study (Espeleta & Donovan 2002).

Seedlings of all species were grown in the greenhouse and fertilized in top and bottom sections for 9 weeks (June to August, 2000) until the start of the experimental treatments. Air temperature was controlled (20-30 °C) and additional light was provided with sodium halide lamps (300  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> for a 14-h daily photoperiod).

#### Treatments description

We studied species differences in the response to two successive treatments. First, species differences under localized drought were studied by comparing the species-specific responses to a surface drought treatment relative to a well-watered control. Last, species previously exposed to surface drought were compared in their response to a rewetting treatment.

## a. Surface drought experiment

We first studied the effects of surface drought by partially restricting the delivery of liquid fertilizer in a subset of plants of every species, while the remaining plants were fertilized regularly. In treated plants, water and nutrients were applied only to bottom pots and in the soil of top pots was allowed to dry. Control pots had continued uniform application to top and bottom pots. Surface drought treatment began when seedling growth was sufficiently advanced so a large number of roots were visible in the windows of bottom pot sections. The surface drought treatment of the sand in top pots was approximately 12% (with a minimum above 10%) for controls, and below 2% for the surface drought treatment. Field capacity corresponded to a gravimetric moisture content of ca. 12%. A total of ten plants per each treatment (well-watered controls and plants exposed to surface drought) were harvested entirely at the end of the surface drought experiment.

## b. Surface re-wetting experiment

Second, we studied species differences in the response to rewetting by re-application of liquid fertilizer to top pots in a subset of ten plants that were previously exposed to the surface drought treatment. Rates of re-application in top pots were the same as for the well-watered controls of the previous experiment (300ml of 1/10 modified Hoagland's every other day). Application of water and nutrients to bottom pots remained unchanged. The re-wetting treatment was applied at the end of the surface drought treatment (November 2000) and was continued for 9 weeks until the end of the experiment (January 2001).

## Root measurements

## a. Fine root demography

We recorded the effect of the experimental treatments on the demography (growth, death and mortality) of fine roots (diameter < 1 mm) of the five species studied. Fine root growth was

recorded as the total length of visible roots, and fine root death as the total length of dead roots. Fine root mortality was calculated as percent fine root death divided by fine root growth. The growth and death of fine roots was measured by mapping the fine roots visible through the transparent plastic window in the wall of each top and bottom pot section. Fine root maps of each date were later retraced in transparent plastic, scanned, and measured for length 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 (shriveling, blackening or decomposition). Fine roots were mapped biweekly and different pen colors were used to distinguish every single interval. Fine root turnover was slow and did not require more frequent observations. Fine root demography was recorded before the start of the surface drought and re-wetting treatments and throughout the application of treatments until the end of the experiment. Total fine root growth was calculated for the surface drought and rewetting periods separately for treated and control plants. During the surface drought experiment, fine root growth was recorded for top and bottom pots, and fine root death and mortality were recorded for top pots only. During the rewetting experiment, only fine root growth was recorded.

## b. Fine root allocation

Fine root allocation was calculated at the end of the experiment as the ratio of fine root growth (in length) in bottom to top pots of each plant seedling of every species under wellwatered (control) and surface drought treatments.

## c. Fine root morphology

A group of plants (10 plants per species and treatment combination) were harvested at the end of the surface drought and rewetting experiments. Three sub-samples per replicate of fine roots inside the top pots 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 (Delta-T Devices Ltd, Cambridge, UK). 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). We used a brightness of 200 and a resolution of 400 x 400 dpi, according to the sensitivity requirements listed by Bouma *et al.* (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).

## Statistical Analysis

The surface drought experiment was designed as a completely randomized block, fullfactorial design (2 blocks x 5 species x 2 treatments, n=10 seedlings per species). The effect of species, treatment (surface drought vs. control) and the interaction (species x treatment) effect on fine root demography (fine root growth, fine root death and percentage mortality), fine root morphology (diameter, specific root length and tissue density) and allocation were analyzed by a two-way ANOVA (species levels = 5, treatment levels = 2). The differences between species and treatment combinations were compared by a Tukey-HSD multiple comparison test.

The surface re-wetting experiment was designed as a completely randomized block, fullfactorial design (2 blocks x 5 species, n=10 seedlings per species). A control was not included this time and only the effect of species on fine root growth was analyzed by two-way ANOVA. Differences in root growth after rewetting between species were compared by a Tukey-HSD multiple comparison test.

All 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). Data

transformations, tests of normality, variance inequality, ANOVAs and multiple comparison tests were performed using JMP Data Analysis Software (version 4.0.2, SAS Institute, NC, USA).

## Results

#### Surface drought experiment

## a. Fine root demography

Fine root growth, death and percentage mortality were significantly different between the species (significant 'species' effect, Table 2.1a). Fine root death and mortality were significantly different between wet and dry surface soil treatments (significant 'treatment effect', Table 2.1a).

Fine root death and percentage mortality was greatest in the species restricted to mesic and subxeric habitats (*Q. marilandica* and *Q. margaretta*) than in the species able to colonize xeric habitats (*Q. laevis*, *Q. incana and P. palustris*) (Fig. 3.3b,c). *Quercus marilandica* and *Q. margaretta* exhibited greater fine root death and percentage mortality compared to *Q. laevis*, *Q. incana* and *P. palustris*, which showed the greatest survival (Fig. 3.3c). Fine root death was significantly greater in *Q. marilandica* and *Q. margaretta* in dry surface soil and there was a similar tendency under wet soil (Fig. 3.3b,c). Fine root growth was greater in *Q. marilandica* in the well-water control and there was a similar trend for the generalist *P. palustris* (Fig. 3.3a). *Quercus margaretta*, the mesic species that also colonizes subxeric habitats exhibited lower fine root growth, similar to *Q. laevis* and *Q. incana*.

Exposure to dry surface soil increased fine root death and percentage mortality (significant treatment effect, Table 2.1a). The effect of surface drought on percentage fine root mortality varied among species (significant species\*treatment interaction term, Table 2.1a). Surface drought increased percentage fine root mortality in *Q. marilandica* and *Q. margaretta*, but it did not affect fine root demography of species able to colonize xeric habitats (*Q. laevis*, *Q. incana* and *P. palustris*). *Quercus marilandica* exhibited the largest increase in fine root death and percentage mortality after exposure to dry surface soil (Figs 3b and 3c). Fine root death and

percentage mortality was very low in wet and dry surface soil in *Q. laevis*, *Q. incana* and *P. palustris* (Fig. 3.3c). Surface drought did not significantly alter root growth for most species (Table 2.1a). Only in *Q. marilandica* and *P. palustris*, root growth was reduced in dry surface soil (Fig. 3.3a).

## b. Allocation to deep roots

Allocation of growth to deeper roots in wet soil tended to be greater in xeric than mesic *Quercus* species (marginally significant species effect, Table 2.1a). The effect may be attributed mainly to the most xeric species, *Q. laevis*, which tended to exhibit greater allocation to deep roots (Fig. 3.4). No change in the pattern of growth allocation between top and bottom pot sections was observed when surface roots were exposed to dry soil (Fig. 3.4).

## c. Fine root morphology

Fine root morphology (mean fine root diameter, specific root length and fine root tissue density) was significantly different in *P. palustris* when compared to the *Quercus* species (Table 2.1b, Figs. 5a-c). On the other hand, fine root morphology was very similar among the *Quercus* species. Surface drought decreased fine root diameter (Table 2.1b), but the effect was of little magnitude and it was only significant in *Q. incana* (Fig. 3.5a). Surface drought did not change any of the other fine root morphology variables: specific root length or tissue density (Fig. 3.5b,c).

## Surface re-wetting

Species were significantly different (F  $_{4,35}$ , p = 0.0198) in the length of new roots produced in the top pot in response to rewetting. Re-application of water and nutrients to the surface soil produced greater fine root growth in mesic than xeric *Quercus* species. Fine root growth ranged

from greatest in *Q. marilandica*, intermediate in Q. margaretta and Q.incana, to least in *Q. laevis*. In *P. palustris* fine root growth after rewetting was high, similar to *Q. marilandica* (Fig. 3.6).

## Discussion

The ability of roots to survive in dry soil and proliferate after rewetting was closely linked to the ecological distribution of the species in our study. Species able to colonize xeric habitats (Q. laevis, P. palustris and Q. incana) shared the ability for greater survival of roots under dry soil than mesic species. On the other hand, species that dominate mesic habitats (Q. marilandica and Q. margaretta) exhibited greater ability to grow fine roots after rewetting. Less plasticity of xeric than mesic oaks in response to resource variation also agrees with results of previous studies with sandhill oak species on fine root demography (Espeleta & Donovan, 2002), and photosynthesis and water use efficiency (Vaitkus & McLeod, 1995). Fine root demographic strategies appeared also to be part of a continuum because species that occupy intermediate habitats (Q. margaretta and Q. incana) exhibited intermediate survival and proliferation. For instance, *O. incana*, a species that colonizes intermediate and xeric sites, exhibited low mortality but a trend of greater root growth after rewetting than the most xeric species, Q. laevis. Similarly, Q. margaretta, a species that colonizes mesic and intermediate sites, exhibited less fine root death and growth than the more mesic species, *Q. marilandica*. On the other hand, generalist distributions may be related with generalist strategies. For instance, P. palustris colonizes mesic and xeric habitats and exhibited high root growth after rewetting together with little root death in dry soil. Because our study was carried out among closely related species that inhabit the same geographical area, our results indicate that root demography may reflect evolutionary responses to habitat fertility (Eissenstat & Yanai, 1997), similar to studies on aboveground growth and allocation patterns in congeneric grasses (Garnier 1992) and sandhill oaks (Long & Jones 1996).

Results from this study are consistent with our expectations based on economy of resource use: the efficiency of resource use may be maximized for plants adapted to fertile and infertile habitats in different ways. In xeric habitats, persistence of roots in dry soil avoids future costs of root reconstruction and the loss of resources (sensu Eissenstat & Yanai, 1997), whereas in mesic habitats, shedding of roots in dry soil followed by rapid construction of new roots after rewetting may be essential for rapid resource uptake (sensu Robinson, 2001) and greater competitive ability (Aerts & Chapin, 1999). Our results demonstrate the existence of a tradeoff between the ability of fine root to persist in dry soil and the ability to proliferate after rewetting among the *Quercus* species: none combined high root growth and persistence to the same extent. The divergent fate of roots of mesic and xeric species in dry soil (and the tradeoff between persistence and growth) may be determined by the inability of plants to construct roots that combine characteristics of high longevity, proliferation ability and tolerance to drought. Similar tradeoffs were discovered for fine roots of *Q. laevis* and *Q. marilandica* growing under high and low resources in a previous study (Espeleta & Donovan, 2002). Although this tradeoff did not seem to hold when comparing *Quercus* species and *P. palutris* (greater fine root persistence was associated with greater fine root growth), this does not indicate necessarily that *P. palustris* is free of any root tradeoff. High growth ability of thick roots with low turnover rates may be related to the evergreen growth form (Aerts, 1995), to developmental constraints during juvenile tree growth (sensu Espeleta & Eissenstat, 1998) or to other tradeoffs, such as greater susceptibility to herbivory and root pathogens (as observed in field roots of adult *P. palustris*, unpublished data).

Root demographic responses to localized drought may be very different to those due to low nutrient availability in the absence of severe drying of the soil. We observed substantially greater root death of mesic species under surface drought than previously recorded for the same species when exposed to low resource supply but without severe drought (Espeleta & Donovan, 2001). On the other hand, results of both studies were strikingly similar for the control treatments that applied high resource supply under continuous wet soil. Root efficiency models predict that the effect of soil resources availability on lifespan depends on how the benefits of resource acquisition change with changing levels of resources, which may reflect the availability of

resources and also species differences in uptake ability (Eissenstat & Yanai, 1997). Root demographic responses to localized drought may be different than under low nutrient availability because under very low water, nutrient and water uptake cease and root benefits are minimal.

Differences between responses to localized drought or to low nutrient supply may contribute to the conflicting empirical data about the effects of nutrient availability on root lifespan in forest communities: low fertility has been linked to less fine root turnover (Aber *et al.*, 1985; Nadelhoffer *et al.*, 1985; Pregitzer *et al.*, 1995) or to greater fine root turnover (Keyes & Grier, 1981; Vogt *et al.*, 1986; Pregitzer *et al.*, 1993; Burton *et al.*, 2000).

Consistent also with our hypothesis of efficiency maximization in roots, we observed an increase in death and mortality as a consequence of exposure to dry soil only in fine roots of mesic *Quercus* species. In mesic species, fine roots may be selectively shed in dry soil to reduce costs of root maintenance when nutrient and water uptake are impaired. On the other hand, xeric species (adapted to more frequent droughts) may be capable of reducing maintenance costs of roots under dry soil and maintain the roots alive, because costs of reconstruction of roots would be excessive if root shedding occurs at every episode of soil drying (Eissenstat & Yanai, 1997). Our results with xeric tree species contradict the observations in some desert plants that tend to shed surface roots during severe drought (Nobel, 1994). Additionally, our results with mesic species contradict the high tolerance to dry soil observed in some crop species not adapted to drought (tomato: Portas & Taylor, 1976; wheat: Meyer et al., 1990; corn: Stasovski & Peterson, 1991). The differences in root lifespan strategies in different xeric environments may depend on the intensity and frequency of drought events. Seasonal long droughts may select for species with specialized fine roots that are only deployed during the rainy season and shed at the onset of the drought, such as the "rain roots" of Agave deserti (Huang & Nobel, 1992). In contrast, xeric environments like those in the southeastern sandhills, with abrupt and unpredictable changes in soil water availability, may select for roots with longer lifespan that reduce resource loss and

allow exploitation of short-term resource pulses, similar to the strategy displayed by slowgrowing species of infertile soils such as *Festuca ovina* (Campbell & Grime, 1989).

Fine root growth was also not affected by exposure to surface drought in the species found in xeric and subxeric habitats (*Q. laevis*, *Q. incana*, *Q. margaretta* and *P. palustris*, which suggests that growth of surface roots in very dry soil can be sustained by water and nutrient supply to deep roots (Portas & Taylor, 1976). Only *Q. marilandica*, the species restricted to mesic habitats, showed a significant decrease (~50%) in fine root growth in dry surface soil as compared to roots in wet surface soil. Allocation to deep roots tended also to be greater from xeric to mesic species (although in lesser degree), in a continuum similar to fine root death and proliferation (Fig. 3.5). Thus, xeric species may be able to sustain roots in dry surface soil by having a larger fraction of deep roots with access to moist soil. Processes like hydraulic lift could be implicated in improving tolerance of surface roots to soil drying in xeric species. Preliminary evidence suggests that hydraulic lift ability may also decrease for mesic species in the field (J. Espeleta, unpublished data).

Selective root shedding may occur via reducing carbon exports to fine roots in dry surface soil and subsequent carbohydrate starvation (Marshall & Waring 1985; Marshall 1986). Nonetheless, root death may be directly caused by desiccation of tissues (Jupp & Newman, 1987; Stasovski & Peterson 1991). More detailed studies about physiology (sensu Kosola & Eissenstat, 1994, Eissenstat *et al.*, 1999, Bouma *et al.*, 2000b) and anatomy (sensu Eissenstat & Achor, 1999) of senescing roots in these species are needed to investigate the mechanisms explaining the results observed in this study with sandhill tree species.

Coinciding with previous studies on a smaller number of sandhill tree species (Espeleta & Donovan, 2002), we observed a lack of correspondence between fine root morphology and demography. Average diameter, specific root length and tissue density of fine roots were very similar among the *Quercus* species, but fine root demography was very different. Other studies with grasses and forb species (Ryser, 1996) found a correspondence between root death and fine

root density that we did not observe in our study with tree species. Also, greater plasticity of mesic species was not associated with finer roots, a relationship found for other tree species (Eissenstat, 1992; Mou *et al.*, 1997). On the other hand, root morphology was very different in *P. palustris* when compared to the *Quercus* species. These results, similar to findings with leaves (Reich, 1993), suggest that root morphology may not be a factor associated with fine root demography among closely related species (sensu Eissenstat *et al.* 2000).

Our findings of divergent root demographic strategies among species adapted to different resource availabilities are not only relevant for plant adaptation theory. Differences in tissue turnover rates may potentially indicate differences in resource cycling across environments. In resource-poor areas, greater lifespan of roots may lead to greater resource conservation but lower ability for exploiting ephemeral resource enrichment. Slow root turnover, combined with low productivity, low litter production and decomposability may lead to slow rate of nutrient cycling, which would prevent invasion of highly competitive, low nutrient-efficient species (Chapin, 1993). In resource-rich areas, greater root proliferation ability but greater root death may lead to faster rate of resource cycling. This may exclude slow-growing nutrient-efficient plants from fertile habitats, promoting ecosystem stability (Aerts, 1999).

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**Table 3.1a** Analysis of variance of the effects of species, treatment (surface drought vs. wellwatered control) and interaction effects on fine root demography (growth, death and percentage mortality) and fine root allocation (growth bottom/top) of *Quercus* spp. and *P. palustris* seedlings exposed to surface drought for 9 weeks. Bold print shows p < 0.05.

Source	df	Fine root growth		Fine root death		Fine root mortality (%)		Fine root allocation (bottom/top)	
		F	p > F	F	p > F	F	p > F	F	p > F
Block	1	0.648	0.4232	1.910	0.1706	0.248	0.6194	2.266	0.1364
Species	4	3.015	0.0225	13.77	<0.0001	13.85	<0.0001	2.306	0.0659
Treatment	1	0.398	0.5297	6.222	0.0146	6.797	0.0108	0.690	0.4087
Sp x Treat	4	0.254	0.9067	4.400	0.0200	2.848	0.0288	0.157	0.9585

**Table 3.1b** Analysis of variance of the effects of species, treatment (surface drought vs. wellwatered control) and interaction effects on fine root morphology (mean diameter, specific root length and tissue density) of *Quercus* spp. and *P. palustris* seedlings exposed to a surface drought for 9 weeks. Bold print shows p < 0.05.

Source	df	Mean fine root diameter (mm)		Specific root length (mg <sup>-1</sup> )		Fine root tissue density (mgm <sup>-3</sup> )	
		F	p > F	F	p > F	F	p > F
Block	1	1.318	0.2554	0.200	0.6561	3.546	0.0616
Species (Sp)	4	93.09	<0.0001	11.96	<0.0001	13.48	<0.0001
Treatment (Treat)	1	10.13	0.0023	0.371	0.5450	1.686	0.0935
Sp x Treat	4	1.805	0.1397	0.054	0.9945	1.157	0.2913



**Fig. 3.1** Distribution of five tree species inhabitants of the fall-line sandhills of southeastern US. The soils of the fall-line sandhills present a top layer of coarse sands on top of sedimentary clays. Xeric habitats occur on sandhill ridges where surface sands are deeper, subxeric habitats occur in sandhill slopes and mesic habitats occur in bottomlands where clay layers are closer to the surface. The intensity of the bar's color indicatives approximate relative distribution of each species along the gradient (from white color = no presence to black color = highest density).



Fig. 3.2 Diagram of the vertically split pot design used to study surface drought effects on fine root demography. The pot consisted in two vertical compartments: top and bottom, each one with a separate irrigation line and transparent window (7 x 10 cm) for observing and mapping roots. When roots were not being mapped, the plastic window was covered with black plastic to prevent light penetration and with while plastic to reflect excessive heat.



**Fig. 3.3** Fine root demography of five sandhill tree species recorded at the end of an experiment consisting of a surface drought treatment that lasted for 9 weeks and a well-watered control: a) Total fine root growth, b) Total fine root death, c) Percentage fine root mortality. The effects of species, treatment and species\*treatment interaction were analyzed by a two-way ANOVA. Results are reported in Table 3.1a. Different letters indicate significant differences between LS means by Tukey-HSD multiple comparison test (p < 0.05, n =10 replicates per species and treatment combination). Qd: *Quercus marilandica*, Qm: *Q. margaretta*, Qi: *Q. incana*, QI: *Q. laevis*, Pp: *Pinus palustris*.



**Fig. 3.4** Allocation of fine roots of five sandhill tree species recorded at the end of an experiment consisting of a surface drought treatment that lasted for 9 weeks and a well-watered control. The effects of species, treatment, and species\*treatment interaction were analyzed by a two-way ANOVA. Results are reported Table 3.1a. Different letters indicate significant differences between LS means by Tukey-HSD multiple comparison test (p < 0.05, n =10 replicates per species and treatment combination). Qd: *Quercus marilandica*, Qm: *Q. margaretta*, Qi: *Q. incana*, QI: *Q. laevis*, Pp: *Pinus palustris*.



**Fig. 3.5** Fine root morphology of five sandhill tree species recorded at the end of an experiment consisting of a surface drought treatment that lasted for 9 weeks and a well-watered control: a) Average fine root diameter, b) Specific root length, c) Fine root tissue density. The effects of species, treatment and species\*treatment interaction were analyzed by a two-way ANOVA. Results are reported in Table 2. Different letters indicate significant differences between LS means by Tukey-HSD multiple comparison test (p < 0.05, n =10 replicates per species and treatment combination). Qd: *Quercus marilandica*, Qm: *Q. margaretta*, Qi: *Q. incana*, QI: *Q. laevis*, Pp: *Pinus palustris*.



**Fig. 3.6** Total fine root proliferation after a 9-week re-wetting in five sandhill tree species subjected previously to surface drought for other 9 weeks. The species effect was analyzed by a two-way ANOVA. Different letters indicate significant differences between LS means by Tukey-HSD multiple comparison test (p < 0.05, n =8 replicates per species and treatment combination). Qd: *Quercus marilandica*, Qm: *Q. margaretta*, Qi: *Q. incana*, Ql: *Q. laevis*, Pp: *Pinus palustris*.

## CHAPTER 4

# SPECIES-SPECIFIC RHIZOTRONS REVEAL DIFFERENCES IN HYDRAULIC LIFT AMONG ADULT TREES AND GRASSES FROM A SANDHILL COMMUNITY

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## Summary

Individual species may have profound effects on ecosystem water balances by affecting the redistribution of water by roots; however, little field evidence is available on the degree in which species differ in their ability for hydraulic redistribution (HR). In a field study using rhizotrons that isolated roots from single species we compared species-specific HR activity (specifically hydraulic lift, HL) of four species of adult trees and two species of grasses that co-occur in the fall-line sandhills of southeastern US. After three years of continuous hourly records of soil water potentials ( $\psi_s$ ) at 25 cm depth, we found that three of the tree species (a generalist species, *Pinus*) palustris, and two xeric species, Quercus laevis and Q. incana) exhibited HL activity, whereas Q. margaretta, a species with more mesic distribution, exhibited none. Simultaneous measurements of  $\psi_s$  outside of the rhizotrons showed that adequate soil moisture was continuously available at a depth of one meter, and that differences in HL among the tree species were not likely caused by differential access to subsurface water by deep roots. Species with HL activity tended also to show the most intense drying of the soil inside the rhizotrons, similar in frequency and magnitude to the patterns of  $\psi_s$  in the surface soil (25 and 50 cm) outside the rhizotrons. For the shallow rooted grasses, (where soil droughts were sometimes intense but not as frequent) we did not observe significant differences in mean  $\psi_s$  between the more stress tolerant species, Aristida stricta, and the species unable to colonize xeric habitats, Schizachyrium scoparium. However, A. stricta exhibited HL activity (but probably minimized by the limited access to deeper soil moisture). We argue that HL activity could be linked to the species ecological distribution and the demographic responses of surface fine roots to drying soil because the tree and grass species not showing HL (*Q. margaretta* and *S. scoparium*) do not colonize xeric habitats and exhibit the least fine root survival in dry soil (in other studies). Xeric species may have a strong effect in water balance of sandhill plant communities (xeric and mesic) by redistributing water from the deep soil to the rapidly drying surface sands.

*Key-words: Aristida stricta*, hydraulic lift, hydraulic redistribution, *Pinus palustris*, *Quercus laevis*, *Quercus incana*, *Quercus margaretta*, *Schizachyrium scoparium*, soil water potential.

*Abbreviations*: HL: hydraulic lift; HR: hydraulic redistribution; TP: thermocouple psychrometer;  $\psi_s$ : soil water potential.

## Introduction

Many studies of water flux in ecosystems describe seasonal and diurnal patterns of soil water availability (Horton and Hart 1998; Joffre and Rambal 1993). Careful examinations of diurnal patterns of soil water potential ( $\psi_s$ ) in some plant communities have revealed the phenomenon of "hydraulic redistribution" (HR), defined as the nighttime transfer of water from wet to dry soil via plant roots). Hydraulic redistribution is also called "hydraulic lift" (HL) in the strict sense, to refer the upward transfer of deep soil water to dry surface soil (Richards and Caldwell 1987); or "reverse hydraulic lift" for the downward transport of water when an opposite pattern of moisture is present in the soil profile (Burguess et al. 1998; Schulze et al. 1998; Smith et al. 1999). Since the first case of HR was precisely described for plants in the field (Richards and Caldwell 1987), more than 60 new cases have been reported in a series of species and habitats (about 43 woody species and 16 herbaceous species, Millikin and Bledsoe 2000; Jackson, Sperry and Dawson 2000). Hydraulic redistribution has been demonstrated to facilitate water to neighboring plants (Caldwell and Richards 1989; Dawson 1993). It has also been suggested that HL may potentially improve of nutrient uptake in otherwise dry surface soils (Matzner and Richards 1986; Dawson 1998; deKroon et al. 1998), and alter the water balances of single plants (Emerman and Dawson 1996; Caldwell, Dawson and Richards 1998; Burguess et al. 1998), of stands of single species (Ryel et al. 2002) and of entire forests and regions (Jackson, Sperry and Dawson 2000). Simulations also showed that HL can potentially increase whole canopy transpiration in Artemisia tridentata stands (Ryel et al. 2002). In a sugar maple (Acer saccharum)

forest with root access to groundwater, hydraulically lifted water may account for up to one third of water loss via transpiration (Emerman and Dawson 1996) and may increase annual water use in the forest by 19-40% (Dawson 1996; Jackson, Sperry and Dawson 2000). Simulations also suggest that as sugar maple has become more abundant in the northeastern USA (with the abandonment of agriculture and the onset of chestnut blight), the region's hydrological cycle might have changed through greater transpiration (Jackson, Sperry and Dawson 2000). This suggests that single species can have a profound effect on forest hydrology via differential HR ability.

Although species differences in HR ability may affect water budgets of entire communities, information on species differences is scarce and insufficient for predictive models of ecosystem water flux (Millikin and Bledsoe 2000; Meinzer, Clearwater and Goldstein 2001) and for understanding the specificity of plant interactions (Callaway 1998). Most of the data available have been obtained from greenhouse studies with seedlings (Baker and van Bavel 1988; Sakuratani et al. 1999; Song et al. 2000; Wan et al. 2000) and from investigations of individual species in monospecific stands (Wan et al. 1993; Caldwell, Dawson and Richards 1998; Ryel et al. 2002) or in habitats where the spacing between different species was large enough to reduce intermixing of roots from different species (Dawson 1993, 1996; Yoder and Novak 1999); however, in these environments the potential role of HL in plant-plant interactions may not be fully appreciated because of the spatial separation of roots between different species.

Differences in hydraulic lift ability among coexisting species in a plant community have usually been inferred from previous knowledge of spatial and temporal partitioning of root activity. Generally this has sufficed to detect differences in HL ability between trees and understory vegetation, such as differences in phenology between *Quercus douglasii* trees and annual grasses in a California blue oak woodland (Millikin and Bledsoe 2000) or differences in rooting depth between sugar maple and neighboring understory plants (Dawson 1993). Root trenching experiments have been used to separate roots from trees and grasses and for

determining species-specific effects in soil water use in African savannas (Ludwig 2001), but few studies have attempted to make comparisons within co-ocurring trees and co-ocurring grass species. Measurements of xylem flow in individual roots (Burguess et al. 1998) were used to characterize differences between two species of *Eucalyptus* in nighttime water flow that are indicative of differential HR ability. However, this technique is very labor intensive and is not suitable for simultaneous comparisons of larger number of species.

This study is the first field investigation on the species-specific effects on  $\psi_s$  patterns and differences in HR ability within coexisting trees and grass species in their natural habitat. In order to circumvent the problems of interpreting the data of  $\psi_s$  in a mixed-species community, we isolated the effects of each single species by growing roots of individual plant species inside root chambers ("rhizotrons"). Soil water potentials ( $\psi_s$ ) were measured every hour with thermocouple psychrometers (TP) during three growing seasons.

The species in this study included two grasses and four trees native to the fall-line sandhills of the southeastern US. These sandhills consist of deep sandy soils with poor water and nutrient retention capacity (Peet and Allard 1993; Christensen 2000; Goebel et al. 2001) that are ideal for studying HR (specifically hydraulic lift, HL) to rapidly drying surface soil and for doing root manipulations. This system is also suitable for answering questions about the association between species-specific effects on  $\psi_s$  patterns and HR and species differences in rooting strategies and ecological distribution. Previous studies with sandhill species indicate species differences in belowground resource use strategies, root demography (Donovan, West and McLeod 2000, Espeleta and Donovan 2002; West, Espeleta and Donovan, unpublished data) and distribution (Weaver 1969; Mavity 1986; Jacqmain et al. 1999). The divergent strategies of resource use of the species within each functional group (e.g. trees and grasses) have been linked to differential species distribution across xeric to mesic habitats (Donovan, West and McLeod 2000, Espeleta & Donovan 2002; West, Espeleta & Donovan unpublished data). Variation in topography in the sandhills produces a gradient of xeric habitats (deep sand ridges), subxeric (slopes) and mesic

habitats (bottomlands) and water and nutrient availability tends to increase from xeric to more mesic sites (Goebel et al. 2001; J. West, pers. Obs.). All the species in this study coexist in subxeric habitats but have different distribution along the resource gradient. Three sandhill oak species: turkey oak (*Quercus laevis* Walt.), bluejack oak (*Q. incana* Bartr.) and sand poast oak (*Q. margaretta* Ashe) are differentially distributed in xeric, subxeric and mesic sites, respectively (Wells and Shunk 1931). Longleaf pine (*P. palustris* L.) dominates the overstory in all sites. In studies with seedlings and adult trees, *Q. laevis* exhibited very little fine root production and death (Espeleta and Donovan 2002), and *Q. incana* and *Q. margaretta* exhibited intermediate and high fine root turnover, respectively (Espeleta and Donovan, unpublished results). *Pinus palustris* exhibits intermediate root longevity and greater rates of root growth (Espeleta and Donovan 2002). The understory is dominated by two native C4 bunchgrasses: wiregrass (*Aristida stricta* Minchx.) and little bluestem (*Schizachyrium scoparium* Minchx.). *Aristida stricta* is a winterperennial grass that exhibits a more stress-tolerant strategy than *S. scoparium*, which is winterdeciduous perennial grass, and its dominance tends to increase on the most nutrient-poor, xeric sites where *S. scoparium* does not colonize (West, Espeleta and Donovan, unpublished data).

Hydraulic lift should be more prevalent among species from xeric environments that exhibit frequent surface drought but have access to deep water (Horton and Hart 1998; Jackson, Sperry and Dawson 2000). We predicted that sandhill tree and grass species differ in HL activity and that patterns of HL and water use in the top soil will reflect the ecological distribution of the species in the sandhills: xeric tree species with roots able to tolerate surface drought will exhibit greater HL activity in comparison to species unable to colonize xeric areas or in comparison to species without deep rooting like grasses.

#### **Materials and Methods**

## Study site

The investigation was conducted at the Carolina Sandhills National Wildlife Refuge (CSNWR) located in McBee, South Carolina at approximately 100 meters above sea level. This site has a temperate climate with a mean annual temperature of 16 °C and a mean annual precipitation of 1234 mm, without a clear seasonality. Temperature and precipitation data for the study period and 30-year averages are shown in Fig.4.2. Our study plot was located in the middle of the slope in an intermediate, subxeric community where all tree and grass species co-occurred. The tree community consisted of P. palustris, Q. laevis, Q. incana and Q. margaretta. The understory vegetation was sparse and composed mainly by the C4 bunchgrasses: wiregrass (A. stricta) and to a lesser extend by S. scoparium (little bluestem) and Gaylussacia dumosa (Andr.) Torr. & Gray (dwarf huckleberry). The soil consisted of a deep layer of coarse sands on top of clay sediments (Typic quartizamment, USDA 1995). Analysis of a soil core in our site revealed a top layer of about 1m of very coarse white sands, followed by a deep layer of yellow sands with little clay content, extending down to 4 meters of depth. A layer of compact and hydrophobic red clay appears after that depth. For a single coring in the summer we observed at least 50 cm of water standing on top of the clay layer together with a thin layer of white sands. This suggests that rain water most likely moves rapidly through the surface sandy layer then flows laterally as subsurface water along the slope on top of the clay layer. This subsurface runoff might cause leaching of the soil just above the clay formation, as observed by Oliver (1978). Observations of a big soil pit in the vicinity (about 100 meters away from our field site) revealed that tree roots do not grow beyond the compact clay layer, either because of excess water or the impenetrability of the subsurface formation.

#### Experimental design and methods

Our study plot consisted of an area of approximately 0.1Ha (50 m wide x 20 m long) within the subxeric habitat. Soil temperature ( $T_s$ ) and  $\psi_s$  were measured every hour for three years in our study plot by using screen- caged Peltier-type thermocouple psychrometers (TP) (J.R.D. Merrill Specialty Equipment, Logan, UT, USA) interfaces with a data logger (CR7; Campbell Scientific, Inc., Logan, UT, USA). Thermocouple psychrometers were placed at six locations in the study plot and three different soil depths: 25, 50 and 100 cm, for a total of six TPs per depth. Three of these locations were contiguous to plants of *A. stricta* and the other three were located in the bare soil between plants. Hourly measurements of air temperature and photosynthetic flux density (quantum sensor, LICOR Inc., Lincoln, NE, USA) complemented the measurements of  $\psi_s$ in the study plot.

In order to collect species-specific data of  $\psi_s$  and HR, root systems of the species studied were isolated in the field by growing them for three years in "rhizotrons". The rhizotrons consisted of PVC semi-cylindrical chambers (diameter= 60 cm, depth= 60 cm, volume= 89 liters) with open tops and bottoms that prevented colonization of any roots besides those transplanted into the rhizotrons. The rhizotrons had a plexiglass window (50 x 50 cm ) that was used for root observation in order to assess root colonization of the rhizotrons and to measure root demography (in a separate study).

Six individuals per grass and tree species were selected in the study plot:

a) For the four tree species (*Q. laevis*, *Q. incana*, *Q. margaretta* and *P. palustris*), six adult trees (dbh: 20-70 cm) were selected for each rhizotron. On February 19, 1999, two lateral roots (length of 1-2 m and thickness of 0.5-1.0 cm) of each tree were excavated from the soil and inserted through lateral holes into the rhizotrons. Each rhizotron was buried next to the tree (distance = 1-2 m from the bole of the tree) and the rhizotron volume was filled with the original soil, maintaining the original stratification. Two TPs were placed in the center of each rhizotron at 25-cm depth and at about 5 cm of distance from each lateral root (and 20 cm from each other).

The roots were left to re-colonize the soil inside the rhizotron. Based on observations of roots visible on the plexiglass window, we confirmed that all 24 chambers containing tree roots had produced new roots before the end of the growing season of 1999.

b) For the grass species (*A. stricta* and *S. scoparium*) adult grass plants of similar size were selected in the study plot (4 plants each of *S. scoparium* and *A. stricta*; one *S. scoparium* plant died after transplant and was not replaced). On February 19, 1999, each plant was carefully excavated form the soil together with a semi-cylindical soil monolith containing the root system (diameter= 60 cm, depth= 20 cm). The remaining soil just below the monolith was excavated to a depth of 60 cm and a rhizotron was placed in the pit. One Peltier-type screen-caged thermocouple psychrometer was placed in the center of the chamber at 25-cm depth and covered with 5 cm of soil. The plant and the soil monolith were placed immediately above, and were left to re-colonize the rest of the soil. We observed new roots in the plexiglass windows as early as the spring of 1999.

In March 2000 a prescribed burn crossed a fire line around the plot and burned inside of it. The fire was fast moving and did not damage the rhizotrons, and was not detected as an increased temperature by any of the TPs placed inside or outside the rhizotrons at the more shallow depth of 25 cm. Although the trees in the study plot did not burn, grass plants in five of the seven chambers were burned and two were untouched (one of each species). Close comparison of the  $\psi_s$  curves of each TP of unburned and burned grasses did not reveal any response of water potential to the fire. As a result, we included all chambers in the analysis and make the assumption that the fires did not substantially alter our results with the grasses.

#### Calibration of thermocouple psychrometers and analysis of soil water potential data

A total of 80 individually calibrated TPs were connected in the field to two CR7 data loggers. Prior to installation each TP was calibrated with three standard solutions of known water potential at constant temperature (25 °C), and by using a calibration model (Brown & Bartos

1982) for a 30-minute cooling time. Rhizotrons were insulated to prevent temperature gradients. Insulation rapidly corrected problems of temperature fluctuations at the beginning of the experiment and offset values were found to be within the range of -5 to +5 microvolts, within the adequate range necessary to prevent inaccurate readings of water potential (Brown and Bartos 1982). Data of TPs with offset values beyond that range were discarded. Data of  $\psi_s$  were recorded every hour during three years and was analyzed in detail for the presence of patterns indicating hydraulic lift events (Caldwell, Dawson and Richards 1998). The criteria used for detecting the presence of HL were fluctuations of at least 0.01 MPa corresponding to decreases in  $\psi_s$  during the day and increases in  $\psi_s$  at night (Millikin and Bledsoe 2000).

Several variables were calculated using data of  $\psi_s$  for each year and for all years together at the end of the experiment. For calculating these indexes only data from the months of April to November were used because soil inside and outside the rhizotrons was continuously wet during the winter months. The average daily  $\psi_s$  was calculated by averaging the minimum  $\psi_s$  for each day. This index was considered to estimate the magnitude of the soil drought. The average daily fluctuation in  $\psi_s$  was calculated by averaging the amplitude of each HL wave across all days with HL events. This index was considered to estimate the magnitude of HL. The number of dry days and the number of days with HL were computed after careful examination of the curves of each TP for each year of the study. The "number of dry days" were counted as the days with  $\psi_s$  more negative than -0.1 MPa. Variation in  $\psi_s$  below -0.1 MPa was considered to be out of the range of best sensibility of the TPs. The percentage of dry days with HL was calculated by dividing the number of days with HL by the total number of dry days. This index estimates the relative importance of HL during soil drying for each TR. Species means were calculated for the indexes of psychrometers inside the rhizotrons (trees and grasses) and at each depth in the intact soil. In the case of the trees that contained two TPs per rhizotron, only the rhizotron with the most HL signals was used as a single replicate for calculating the species means. Differences between species and between depths in the soil outside of the rhizotrons were analyzed by one-way
ANOVA using JMP Statistical Discovery Software (version 4.0, SAS Institute, Cary, NC). Maximum values of the replicates of each species are also reported. They are considered to reflect the maximum potential of soil drying and hydraulic ability each single species.**Results** 

Soil water potentials of the topsoil (25 cm depth) in the study plot fluctuated widely, especially during the summer months, but never reached values below -2.0 MPa (Fig. 4.1). Substantial soil drying was observed from late April to mid November; however it was more prevalent during the summer months (June to September). Droughts were usually short, lasting not more than one month and followed by quick recharge of the soil by rainwater. Total precipitation in the area was less than average during the three years of the study (Fig. 4.2). Comparison of daily precipitation (Fig. 4.1a) and  $\psi_s$  (Fig. 4.1b, c and d) indicates a close correspondence of periods of soil drought and lack of precipitation, the former usually recorded as steep increases in  $\psi_s$ . For instance, in the summer of 1999, we observed three distinctive drought events in early June, early August and early September coincident with lack of precipitation. The end of these dry periods coincided with rain events in mid June, mid August and mid September. In general, rain was likely to increase  $\psi_s$  only when precipitation totals exceeded 20 mm. Rain deficits were associated with more severe soil drying at the end of the summer, when the air temperature was greater (Figs 4.1a and 4.2). A substantial rain deficit in May and June of 2000 also coincided with low  $\psi_s$  in the month of June. Nonetheless, a sharp increase in  $\psi_s$  at the end of June 2000 indicated significant rain event at our field site, since it was not recorded in the precipitation records from the CSNWR headquarters (approx. 7 Km away from the study site. Figs 4.1a and 4.2). Two major soil drought events occurred in the summer of 2001, both ending simultaneously in late May to early June, and late August to early September (Fig. 4.1a and 4.2).

Normal patterns of  $\psi_s$  in the soil outside of rhizotrons show that soil drying occurs mainly in the top 25 cm of the soil with some drought being experienced still at 50 cm of depth. At 1 m of depth  $\psi_s$  was consistently higher (Fig 4.1b).

Diurnal fluctuations in  $\psi_s$  at 25 and 50 cm depth were indicative of hydraulic lift (i.e. nighttime increase in  $\psi_s$  suggestive of water efflux from roots, Figs 4.3 and 4.5a). At 50 cm, diurnal fluctuations were sometimes opposite to the normal pattern of hydraulic lift (Fig. 4.3). The fluctuation in  $\psi_s$  closely tracked the curve of soil temperature, indicating a strong correlation at nighttime between rapid temperature drops and increasing values of  $\psi_s$  (Figs 3 and 5b). This phenomenon was first reported by Millikin and Bledsoe (2000) and named as "offset fluctuations". After exhaustive review of the techniques, these authors concluded that the offset fluctuations were likely an artifact caused by soil temperatures overcorrecting the  $\psi_s$  values in the empirical model developed by Brown and Bartos (1982) and used extensively to calculate water potentials from TP microvolt ouputs. Like in Millikin and Bledsoe (2000), offset fluctuations were mostly observed at high water potentials (above -0.1 MPa) or during winter months, contrary to HL fluctuations, which were observed only at lower  $\psi_s$  (below -0.1 MPa). This artifact is likely to cause the comparatively lower  $\psi_s$  recorded during the winter of all years (Figs 4.1b, c and d) and is probably associated with inaccuracy of the Brown and Bartos model at very low temperatures (below 10°C). We believe that the winter drop was not reported before because studies that measure  $\psi_s$  for several entire years are very uncommon.

Hydraulic lift was a common phenomenon in our study and was observed in a maximum of 100 days during three growing seasons (Table 4.1) and from the months of May until November (Fig. 4.4). The occurrence of HL was associated with periods of lower  $\psi_s$  at 25 cm soil depth. During the drier months, HL could occur in up to 25 days per month (Fig. 4.4). In the soil outside of rhizotrons, we recorded lower water potentials at 25 than 50 cm of depth; however, HL was frequently also recorded at 50 cm. Even when the soil at 100 cm depth had lower number of dry days than the surface soil (Table 4.2,  $F_{2,14}=3.7378^*$ ), HL was still recorded in few instances at 100 cm (Table 1, Fig. 4.4).

Rhizotron data showed considerable species differences in hydraulic lift activity (Figs 4.4, 4.6 and 4.8) and seasonal average  $\psi_s$  (Fig. 4.7). As expected, most of the tree species showed HL

activity (Table 4.1, Fig. 4.4). The exception was *Quercus margaretta*, the only tree species studied that does not colonize xeric habitats, did not show any HL activity during the three years of the study. Tree species were significantly different the percentage of dry days with HL and the average daily  $\psi_s$  (Table 4.2). A trend was also observed in the number of days with HL. In general, HL was not recorded in the grass species. However, we observed a few putative HL signals in one TP placed inside a rhizotron with roots of *A.stricta* (but not of *S. scoparium*) during two drought events from June 10 to June 22 in 2000 (2 days with clear HL fluctuations) and from May 20 to May 27 in 2001 (3 days with clear HL fluctuations) (Figs 4.1d, 4 and 8). HL was not recorded in the summer droughts of 1999 (Fig. 4.1d) for any grass species (Fig. 4.4). HL appeared to be a very important factor in the hydrology of the plot: HL could be present in up to 90% of all drying cycles of the soil in the species with HL activity (*P. palustris, Q. incana* and *Q. laevis*), not only inside the rhizotrons but also outside in the intact soil (Table 4.1). Amplitude of the HL wave (daily fluctuation), which may give an idea of the magnitude of the HL, reached in some instances values up to 0.3 MPa (Fig. 4.5) or even 0.5 MPa (data not presented).

The intensity and frequency of the soil droughts were greater in *P. palustris* but very similar among the *Quercus* species (Figs 4.1c and 7). Rhizotrons with roots of *P. palustris* had significantly lower average  $\psi_s$  and lower number of dry days than the *Quercus* species (Tables 4.1 and 4.2; Figs 4.4, 4.7 and 4.8). The number of drought events during the three years of the study was also greater for *P. palustris* than any other species (Fig. 4.1c). Among the *Quercus* species, the magnitude of the soil drought tended to be greater in rhizotrons with *Q. laevis* roots but very similar between *Q. incana* and *Q. margaretta* (Figs 4.1c and 4.7). For the grass species, although soil drying tended to be more intense in rhizotrons with *S. scoparium* than *A. stricta* plants (Figs 4.1d and 4.7, lower minimum and average  $\psi_s$ , Table 4.2) the differences were not significant (Table 4.2). Among all species, *P. palustris* exhibited the greatest HL activity, especially during the second and third years (2000 and 2001, Figs 4.1 and 4.4). Soil drought and HL activity were also extended over a longer period in rhizotrons of *P. palustris* and in the external soil than in the

rhizotrons of the other *Quercus* species (Fig. 4.4). The increase in soil drying and HL activity of the pine roots inside the rhizotrons was associated with a significantly greater root proliferation in *P. palustris*, as found in a simultaneous study of species differences in root demography (Espeleta, West and Donovan, unpublished results). This relationship was not present for the species that did not exhibit HL, *Q. margaretta*, that showed the second largest fine root proliferation of all tree species inside the rhizotrons.

Water uptake by roots was likely to be the main factor determining decreases in  $\psi_s$  because some TPs (inside and outside of rhizotrons) never showed significant soil drying. This was also indicated by the continuously high  $\psi_s$  recorded in one rhizotron that was left aside containing only soil without grass or tree roots (data not shown). The large variation among replicates in the intensity of drought and the occurrence of HL (Table 4.1, see Standard Errors), may also indicate variation in water uptake and HL activity of individual roots. However, it most likely reflected the TPs not being in close proximity to roots and the very small volume of soil sampled by the TPs (Caldwell, Dawson and Richards 1998; Ludwig 2001). In our system this may be accentuated by low root densities in the intact soil, something we observed while excavating roots for the installation of the rhizotrons. HL was only detected in two thirds of the rhizotrons with roots of *Q. incana* and *P. palustris*, and one third of the rhizotrons with roots of *Q. laevis* (Table 4.1). We do not believe that the absence of HL activity was related to little root proliferation inside the rhizotron, because a large number of roots colonizing the plexiglass windows of all rhizotrons with tree and grass roots, as early as the first growing season after the installation.

### Discussion

This three-year study is among the first to describe differences in HL among dominant canopy and understory species in a single plant community. Collect species-specific information by transplanting roots of adult trees into field rhizotrons proved to be successful in our study. Like other investigations that compared across different functional types, such as trees and

understory plants (Dawson 1993), and trees and grasses (Ludwig 2001), we found different effects on  $\psi_s$  and different HL activity among overstory trees and grasses that dominate the understory vegetation. Our results suggest that trees were the best contributors in the redistribution of water to the surface soil. Nonetheless, we also found differences within the species of trees and grasses studied, including significant differences between *Quercus* species. Differences in HL activity found between congeneric tree species suggest that species differentiation in HL activity can occur at even finer scales than previously thought. This suggests that even small changes in species composition of plant communities could potentially alter the hydraulic redistribution patterns and the water balance of entire ecosystems (sensu Jackson, Sperry and Dawson 2000). Differences in HL activity were also associated with the ecological distribution of the species. Our results demonstrate the existence of species differences in HL activity for a group of species that co-inhabit a subxeric sandhill habitat but are differentially distributed in a resource availability gradient at a larger scale. Colonization of xeric habitats may benefit from HL because HL activity was recorded in all species except for Q. margaretta and S. scoparium, the only species in the study that do not colonize xeric habitats. Hydraulic lift may be involved in the differential ability of the species to tolerate resource limitation or compete for soil resources (sensu Grime 1977; Aerts 1999). Quercus species from mesic sandhill habitats have shown a larger response to resources in root demography (Espeleta and Donovan 2002) and photosynthesis and water use efficiency (Vaitkus and McLeod 1995). On the other hand, species from xeric habitats (Q. laevis and Q. incana) were more conservative in water use than the mesic Q. margaretta (Donovan, West and McLeod 2000). Analogous differences have been found in the grass species, between the stress-tolerant A. stricta that dominates the understory of xeric habitats and S. scoparium that is restricted to subxeric and mesic habitats (West, Espeleta and Donovan, unpublished data). It is possible that HL may contribute to tolerance of more frequent and severe droughts in xeric habitats by reducing root death in dry soil and increasing the length of time in which soil nutrients are available (Caldwell, Richards and Beyschlag 1991).

The comparatively higher  $\psi_s$  in the rhizotrons of *Q. margaretta* could indicate that HL was absent in this species because there was not a sufficient gradient in water potential between deep and surface soil in order to drive water efflux from roots. We believe that all tree species experienced adequate access to subsurface water during the course of the investigation, because  $\psi_s$  was generally high at depths of one meter and the trees never showed evidence of water stress. Measurements of predawn leaf water potentials of the trees during periods of low  $\psi_s$  in late summer of 2001 (data not shown) also suggest that trees probably had continuous access to wet soil layers and were free of water stress. On the other hand, rhizotrons with roots of *Q. incana* and *Q. margaretta* exhibited similar intensity of soil drying; however, HL activity was only observed in *Q. incana*. This suggests that a gradient might have existed between the soil in contact with deep and surface roots in both species, and the differences may be attributed to inherent inability to perform HL due to hydraulic constraints.

We speculate that root death in *Q. margaretta* might be an explanation of the differences in HL activity. In a greenhouse study using seedlings, fine surface roots in *Q. margaretta* and another mesic species (*Q. marilandica*) are susceptible to surface drought (Espeleta and Donovan, unpublished data). Hence, in the field substantial death could have occurred at comparatively higher  $\psi_s$  in mesic than xeric species. Fine roots in surface soil of some tree species have shown to be susceptible to even moderate drying (fine root death in Sitka spruce can be triggered just below -0.01 MPa, Deans 1979), and this response could be found predominantly in the mesic sandhill species of our study. In fact, concomitant field studies of species differences in root deemography using the rhizotrons from this study, indicate that *Q. margaretta* did exhibit greater rates of fine root mortality in the summer than any other tree species (Espeleta, West and Donovan, unpublished data). Shedding of fine roots in the summer may reduce the population of new roots, which are known to exhibit greater water efflux rates during HL events (Dawson 1998). The absence of HL activity in *Q. margaretta* may also reflect the loss of root-soil contact and hydraulic conductivity that results of root senescence (Nobel 1994). Among grass species,

HL might be limited by a shallow root system that does not access deeper wetter soil, especially in the most xeric species, *A. stricta*, which exhibited some potential HL ability and is also known to show high root longevities in dry soil (West, Espeleta and Donovan, unpublished data). Otherwise, absence of HL activity in *S. scoparium* might also reflect inherent HL inability due to greater rates of fine root death (West, Espeleta and Donovan, unpublished data). Cavitation and death of surface fine roots upon incipient drying of the topsoil may also function as a "hydraulic fuse" that prevents water efflux into the soil in mesic species unable to lift water from wet soil layers (Jackson, Sperry and Dawson 2000). This type of drought-deciduousness has been reported previously in succulent desert species in which water efflux from roots increases as  $\psi_s$  decreases (Nobel 1994). For sandhill species not exhibiting HL ability, early root shedding might prevent excessive water loss due to the rapidly decreasing water potentials of drying sandy soils.

The profuse occurrence of HL in the surface soil, as detected by the TPs placed outside of the rhizotrons, indicates that tree roots are important colonizers of the topsoil, along with the grass species. Moreover, the frequency and magnitude of soil drying in the external soil resembles more the patterns observed in the rhizotrons of *P. palustris* and *Q. laevis* (to a lesser degree), than those of the grass chambers (Fig. 4.1). This suggests that these tree species may be key determinants of the patterns of  $\psi_s$  of the entire subxeric community and that there is potential for competition for water and nutrients and/or facilitation in the surface soil between grasses and trees. Our results also support previous studies (Le Roux et al. 1995; Ludwig 2001) that did not find evidence of niche differentiation between roots of trees and grasses in savanna ecosystems via differential vertical deployment of roots, also called the two-layer hypothesis (Sala et al. 1989; Scholes and Archer 1997).

Our results with continuous monitoring of  $\psi_s$  at 1-m depth for up to three growing sesons contradict the expectations that substantial soil drying might occur at intermediate depths in the deep sands of sandhill ridges and slopes (Christiansen 1993). It is likely that surface drought is the predominant type of water stress experienced by the tree species in subxeric habitats like the one in our study, and that trees have continuous access to adequate moisture in the soil at relatively shallow depths. Nonetheless, surface drought may constrain the growth of grass species with shallow root systems, the establishment of tree seedlings and the carbon economy of surface fine roots that are deployed for nutrient uptake in the more nutrient-rich shallow soil (sensu Eissenstat and Yanai 1997). These conclusions should not be extrapolated to other habitats of the sandhills. It is likely that deep soil might desiccate substantially in more xeric areas. During the summer of 2001 we observed a very severe drought in the xeric community uphill from our study site that resulted in the death of *A. stricta* plants and massive leaf abscission in *Q. laevis* trees. As a consequence of some intermittent rains, new leaves flushed out immediately after the drought, only to be shed again in a subsequent drought. During this time, no sign of water stress was apparent in the tree species in our study site (based on the appearance of the plants and predawn leaf water potential measurements). In more mesic habitats with access to wet soil in shallower layers, grass species such as *A. stricta*, which showed some potential ability for HL, might play a more significant role in the redistribution of water to the surface soil.

Hydraulic lift ability may not only be important for the colonization of xeric habitats, but it may also affect belowground processes in other habitats. Species with HL ability may colonize mesic habitats, such as the case of *P. palustris*, which has generalist distribution in the sandhills. Thus, HL may be relevant not only in habitats with intense droughts, but also in those where only transient drying occurs in the surface soil. In mesic habitats with adequate supply of subsurface water, HL may potentially be important for nutrient acquisition in the more fertile surface soil (Dawson 1998). All hydraulic-lifting species in this study are also characterized by slower root turnover. Because slow turnover of roots may increase root efficiency in resource-poor habitats (Eissenstat and Yanai 1997), the coupling of HL and surface fine root survival in xeric species may be part of a strategy to assure conservation of resources via maintenance of fine roots in dry soil. Since fine root turnover is estimated to represent a large fraction of primary productivity in many ecosystems (Caldwell, Richards and Beyschlag 1991), the association between HL and fine

root demography deserves more attention in future of studies of plant communities under limiting resources.

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Table 4.1. Soil water potential ( $\psi_s$ ) and hydraulic lift (HL) variables recorded after three years of continuous measurements with soil psychrometers placed inside and outside rhizotrons containing roots of different sandhill tree and grass species (N: number of samples, Min: minimum value, Max: maximum value, SE: standard error of the mean).

		Average daily ψ <sub>s</sub> (MPa)			# of dry days $(\psi_s <-0.2 \text{ MPa})$		% of Total number of samples days with HL (3-year period)		Average nightly recovery of $\psi_s$ via HL (MPa) <sup>a</sup>			Percentage of dry days with HL					
	N	Min.	Mean	SE	Max	Mean	SE	-	Max	Mean	SE	Max	Mean	SE	Max	Mean	SE
Trees																	
P. palustris	6	-0.332	-0.190	0.049	304	126.5	55.18	66.7	164	58.5	26.11	0.158	0.074	0.029	90.61	41.17	17.53
Q. laevis	6	-0.194	-0.089	0.026	121	30.0	23.43	33.3	71	27.2	11.88	0.108	0.036	0.229	59.50	20.18	12.68
Q. incana	6	-0.119	-0.078	0.012	93	36.2	15.80	66.7	72	16.8	13.99	0.107	0.066	0.224	94.12	61.91	16.14
Q. margaretta	5	-0.107	-0.076	0.010	20	7.80	4.78	0	0	0	0	0	0	0	0	0	0
Grasses																	
A. stricta	4	-0.107	-0.075	0.012	28	21.75	3.57	20	3	1.25	0.75	0.05	0.025	0.025	10.71	4.60	2.73
S. scoparium	3	-0.145	-0.104	0.022	41	22.3	11.98	0	0	0	0	0	0	0	0	0	0
External Soil																	
25 cm	6	-0.251	-0.102	0.031	141	46.67	21.46	66.7	44	15.17	7.07	0.250	0.082	0.038	76.92	28.33	11.53
50 cm	5	-0.288	-0.111	0.045	143	40.20	27.18	50.0	101	24.6	19.57	0.135	0.045	0.028	70.63	23.29	14.79
100 cm	6	-0.104	-0.070	0.011	13	0.98	0.98	16.7	13	2.17	2.17	0.084	0.014	0.014	100	16.67	16.67

<sup>a</sup>: Average nightly recovery of  $\psi_s$  consisted on the daily variation in  $\psi_s$  (the mean amplitude of the HL waves) and was calculated as the maximum minus minimum soil water potential during a 24 hour period corrected for the overall trend by substracting the absolute value of the measurements at 12:00 am at the beginning and at the end of the day).

<sup>b</sup>: The percentage of daily  $\psi_s$  recovered at night via HL was calculated as the average daily variation in soil water potential due to HL divided by the average daily  $\psi_s$ 

	A. Di	ifferences a	Inside r mong trees	hizotrons B. Dif	s ferences arr	nong grasses	Outside rhizotrons C. Differences across soil depth			
Variable	df	F	<i>P</i> < F	df	F	<i>P</i> < F	df	F	$P \leq F$	
Number of dry days	3	1.1221	0.3679	2	0.5304	0.4991	2	3.7378	0.0499	
Number of days with HL	3	3.0356	0.0577	2	2.0869	0.2082	2	1.2994	0.3036	
Percentage of dry days with HL	3	3.1512	0.0476	2	2.1252	0.2047	2	1.1325	0.3483	
Average daily $\psi_s$	3	3.1997	0.0499	2	1.7897	0.2216	2	0.4561	0.6429	
Average daily fluctuation in $\psi_s$ (magnitude of HL)	3	2.1788	0.128	2	2.1429	0.2031	2	1.2395	0.3194	

Table 4.2. Analysis of variance of the effects of tree species (A), grass species (B) and of soil depth (C) in the dynamics of soil water potential ( $\psi_s$ ) and hydraulic lift during three years of study in the sandhills. (*df*: degrees of freedom).



**Fig. 4.1a,b** Daily rainfall (mm) and soil water potentials ( $\psi_s$ ) measured throughout three consecutive years (1999-2001): a) daily precipitation in the CSNWR headquarters, approx. 7 Km from the study plot, b) hourly  $\psi_s$  outside rhizotrons at three different depths (25, 50 and 100 cm).



Fig. 4.1c Daily rainfall (mm) and soil water potentials ( $\psi_s$ ) measured throughout three consecutive years (1999-2001): c) hourly  $\psi_s$  inside rhizotrons with roots of tree species (*Pinus palustris, Quercus laevis, Quercus incana* and *Quercus margaretta*). Curves include data from all thermocouple psychrometers in the study.



**Fig. 4.1d** Daily rainfall (mm) and soil water potentials ( $\psi_s$ ) measured throughout three consecutive years (1999-2001): d) hourly  $\psi_s$  inside rhizotrons with roots of grass species (*Aristida stricta* and *Schizachyrium scoparium*). Curves include data from all thermocouple psychrometers used in the study.



**Fig. 4.2** Mean monthly temperature and total monthly rainfall for the study period plotted onto 30-year averages. The monthly data were collected at the Carolina Sandhills National Wildlife Refuge headquarters, approximately 7 Km from the field site. The average temperature and precipitation curves are from 30 years of data (1961-1990) collected in Cheraw, SC (approx. 20 Km from the field site).



**Fig. 4.3** Depth-specific soil water potential ( $\psi_s$ , solid line) and soil temperature ( $T_s$ , dashed line) during rapid drying of the soil outside of rhizotrons in June of 1999 (shade indicates nighttime). The thermocouple psychrometer (TP) at 25 cm showed the largest drought and a series of HL events, whereas the TP at 50 cm showed only "offset fluctuations" in  $\psi_s$  that tracked closely the fluctuations in  $T_s$ . The TP at 100 cm showed very uniform wet soil and little fluctuation in  $T_s$ .



**Fig. 4.4** Maximum number of dry days ( $\psi_s <-0.1$  MPa) and hydraulic lift (HL) days per month during three consecutive growing seasons (1999-2001) inside rhizotrons of tree and grass species: Pp (*Pinus palustris*), Ql (*Quercus laevis*), Qi (*Quercus incana*), Qm (*Quercus margaretta*), As (*Aristida stricta*), Ss (*Schizachyrium scoparium*), and outside rhizotrons (three different depths: 25, 50 and 100 cm). Data presented are the means of five to six replicates per tree species and depth in the intact soil, and 3-4 replicates of each grass species.



**Fig. 4.5** Typical patterns of soil water potential ( $\psi_s$ , solid line) indicative of a) HL fluctuations, and b) "offset fluctuations" (gray bars indicate nighttime). Contrary to HL fluctuations, the offset fluctuations tracked closely the soil temperature ( $T_s$ , dashed line). Data were obtained from the same psychrometer placed inside a rhizotron with roots of *Quercus laevis*, during: a)August to September of 1999, and (b) February of 2000.



**Fig. 4.6** Mean daily fluctuation in  $\psi_s$  (mean hydraulic lift amplitude +/- SE) during three consecutive years (1999-2001) inside rhizotrons of for tree and grass species: Pp (*Pinus palustris*), Ql (*Quercus laevis*), Qi (*Quercus incana*), Qm (*Q. margaretta*), As (*Aristida stricta*), Ss (*Schizachyrium. scoparium*), and outside rhizotrons (depths: 25, 50 and 100 cm). Data presented are the means of 5-6 replicates per tree species and depth in thesoil outside rhizotrons, and 3-4 replicates of each grass species.



**Fig. 4.7** Mean daily  $\psi_s$  (+/- SE) measured at three consecutive years (1999-2001) for roots of tree and grass species inside rhizotrons: Pp (*Pinus palustris*), Ql (*Quercus laevis*), Qi (*Quercus incana*), Qm (*Quercus margaretta*), As (*A. stricta*), Ss (*S. scoparium*), and outside rhizotrons (depths: 25, 50 and 100 cm). Data presented are the means of 5-6 replicates per tree species and depth in the soil outside rhizotrons, and 3-4 replicates of each grass species.



**Fig. 4.8** Yearly average in the number of dry days ( $\psi_s <-0.1$  MPa) and hydraulic lift (HL) days measured at three consecutive years (1999-2001) inside rhizotrons with roots of trees and grasses: Pp (*P. palustris*), Ql (*Q. laevis*), Qi (*Q. incana*), Qm (*Q. margaretta*), As (*A. stricta*), Ss (*S. scoparium*), and outside rhizotrons (depths: 25, 50 and 100 cm). Data presented are the means of 5-6 replicates per tree species and depth in soil outside of rhizotrons, and 3-4 replicates of each grass species.

# CHAPTER 5

# DIVERGENCE IN SPECIES-SPECIFIC FINE ROOT DEMOGRAPHY

# IN ADULT TREES OF A SANDHILL COMMUNITY

<sup>&</sup>lt;sup>1</sup>Espeleta, J.F.; West, J.B. and L.A. Donovan. To be submitted to *Ecology*.

#### Abstract

Single species can substantially alter belowground processes in ecosystems via differential root death and production; however, the information on species-specific differences in fine root demography is virtually non-existent for natural communities. In this field study, we recorded species-specific fine root demography in adult trees of four species (Quercus laevis, Q. incana, Q. margaretta and Pinus palustris) that inhabit a sandhill habitat in the fall-line of southeastern United States. At a site where all four species co-occur, roots of individual trees of known identity were isolated into root observation chambers (rhizotrons). Fine root demography (fine root production, death, percentage mortality and fine root longevity) was recorded throughout a period of three years. There were substantial differences in fine root demography. *Quercus laevis* and *Q. incana*, which are generally found in more xeric areas, showed less fine root production, death and percentage mortality and greater lifespan than O. margaretta, the species restricted to mesic habitats. Fine roots of *P. palustris* (a generalist) showed high proliferation and intermediate mortality and longevity. Species also differed in seasonal fine root demography. Although all *Quercus* species are leaf deciduous, fine roots of *Q. laevis* and *Q. incana* grew only during the growing season, whereas fine roots of *P. palustris* and *Q. margaretta* were produced year-round. Fine roots of all species were more likely to die if produced during the dormant season, but this likelihood also varied across species. Our results with a single habitat indicate that variation in fine root demography (including that between congeneric species) was as large as previously reported for broad-scale differences across biomes and vegetation types. Hence, small shifts in species composition in natural communities have the potential to bring about substantial changes in belowground processes.

# Introduction

Belowground net primary productivity accounts for 33 to 50% of total net primary production in most ecosystems (Vogt et al. 1996; Jackson et al. 1997). Although the turnover of fine roots is the main component of belowground net primary production (Jackson et al. 1997), very little information is available on the differences in fine root demography across plant species and environments (Vogt et al. 1996; Gill and Jackson 2000). Patterns of fine root demography have been described first for broad-scale comparisons of fine root turnover between major vegetation types and biomes (Gill and Jackson 2000). These authors reported significant differences across plant functional types and climatic regions (e.g. greater fine root turnover in grasslands versus shrub vegetation and in tropical versus high latitude forests), as well as a positive exponential relationship between fine root turnover and mean annual temperature. Nonetheless, little is known about the degree of variation in fine root demography at narrow spatial scales, such as the species differences within similar functional types that inhabit the same geographic region. Broad-scale patterns have proven to be poor predictors of inter-annual variability at individual sites (Gower et al. 1996; Gill and Jackson 2000). The problems scaling down from biomes to individual ecosystems could be due in part to very divergent speciesspecific responses that reduce the resolution of the data (Norby and Jackson 2000). Studying species-specific patterns of fine root demography in natural communities is necessary in order to gain a better understanding of the potential species effects on carbon and nutrient cycling in ecosystems (Hendricks et al. 1993; Hobbie 1992). This is relevant for the current debate about the effects of shifts in species composition on ecosystem processes (Gill and Jackson 2000) and species-specific responses to global environmental change (Norby and Jackson 2000).

Characterizing species differences in fine root demography is also important because species-specific patterns are a starting point for detailed studies on its potential adaptive value. Comparing species with different ecological distribution can elucidate associations between environmental factors and different belowground strategies. Optimality theory (Bloom *et al.* 

1985, Givnish 1986) predicts that tissue longevity should be the response of maximization in tissue efficiency. Because resources are more costly in infertile habitats, fine roots should be retained longer to avoid the loss of resources via fine root death and the costs of growing new roots thereafter. This should be more important in roots than leaves because the plants are less able to reabsorb nutrients from senescing roots than senescing leaves (Nambiar 1987; Gordon and Jackson 2000). Nonetheless, little empirical evidence exists about the direction in which factors like soil fertility may select for specific patterns of root demography (Eissenstat and Yanai 1997). Currently, it is controversial whether fine root longevity tends to be greater in fertile versus infertile habitats or vice versa (Burton *et al.* 2000). Part of this conflict can be explained by the variability introduced by the different techniques used to estimate root lifespan and by uncontrolled, interacting environmental variables. Additionally, the variability in species-specific responses within each plant community may difficult broad-scale generalizations on patterns of fine root demography (Norby and Jackson 2000).

Studying species-specific root demography in natural multi-specific communities has been always a difficult task. Techniques currently available to estimate root lifespan by direct observation, such as mini-rhizotrons and underground rhizotrons are not suitable for distinguishing roots from different species, especially when root morphology is very similar. Therefore, most of the studies of root demography in natural communities provide only a community-level estimate that represents a combination of the root systems of all plant species that co-inhabit the area. In many cases, effects are attributed to one or a few species when there is a clear dominant in the community. This is impossible when studying more complex species assemblages. In a general review of the literature on fine root demography that included only studies using direct observation methods, we found that a majority of studies included observations of roots of seedlings in the greenhouse or adult plants in monospecific stands or plantations (~ two thirds of all studies). When natural multispecific communities were studied, effects were attributed to one or two dominant species if the community was simple enough, like

in forests dominated by *Acer saccharum* (Hendrick and Pregitzer 1993) or *Quercus ilex* (Lopez *et al.* 2001), or in certain grasslands (Aerts *et al.* 2002). Studies comparing mixed-species communities were less abundant (less than 10%), and all of them lack the ability to resolve species-specific patterns (Reuss *et al.* 1998; Tierney and Fahey 2001). Comparative studies of species-specific root demography for adult trees in mixed-species communities are virtually non-existent. In this study, we used species-specific rhizotrons to isolate the effect of single species in a natural community. This technique is more feasible and less intrusive than other methodologies used previously to study species effects in root demography, such as root trenching and complete species removal (Burch *et al.* 1997).

Four tree species native to the fall-line sandhills of southeastern USA were study. This ecosystem exhibits deep sandy soils with poor water and nutrient retention capacity (Peet and Allard 1993; Christensen 2000; Goebel et al. 2001). Previous studies with sandhill species indicate species differences in belowground resource use strategies (Vaitkus and McLeod 1997; Donovan et al. 2000), root demography (seedlings studies in the greenhouse: Espeleta and Donovan 2002; Espeleta and Donovan, unpublished data) and distribution (Weaver 1969; Mavity 1986; Jacqmain et al. 1999). These differences have been linked to differential species distribution across xeric to mesic habitats (Donovan, West and McLeod 2000, Espeleta and Donovan 2002; Espeleta and Donovan unpublished data). Variation in topography in the sandhills produces a gradient of xeric habitats (deep sand ridges), subxeric (slopes) and mesic habitats (bottomlands) and water and nutrient availability tends to increase from xeric to more mesic sites (Goebel et al. 2001; J. West, pers. obs.). All the species in this study coexist in subxeric habitats but have different distribution along the gradient. Three sandhill oak species: Quercus laevis Walt. (turkey oak), *Q. incana* Bartr. (bluejack oak) and *Q. margaretta* Ashe (sand post oak) are differentially distributed in xeric, subxeric and mesic sites, respectively (Wells and Shunk 1931). *Pinus palustris* L. (longleaf pine) dominates the overstory in all sites.

In greenhouse studies with seedlings, *Q. laevis* had very little fine root growth and death (Espeleta and Donovan 2002), and *Q. incana* and *Q. margaretta* exhibited intermediate and high fine growth and death, respectively (Espeleta and Donovan, unpublished results). *Pinus palustris* exhibits little root death and greater rates of root growth (Espeleta and Donovan 2002). Because retention of roots (i.e. reduction in tissue loss) should be more advantageous in xeric environments and high root growth rates should be more important in mesic environments (Aerts and Chapin 2000) we predicted that species that colonize xeric habitats will have greater fine root longevity and that species that dominate mesic habitats should have more root growth.

The species also differ in aboveground phenology. The evergreen habit of *P. palustris* contrasts with the *Quercus* species, that tend to be winter deciduous. Only *Q. incana* leaves persist during mild winters (Duncan and Duncan 1988) in comparison to the strictly winter deciduous *Q. laevis* and *Q. margaretta*. We expect that patterns of seasonal root demography should be associated with aboveground demography and that *P. palustris* and *Q. incana*, to a lesser extent, would have seasonality in patterns of root demography.

# **Materials and Methods**

#### Study site

The investigation was conducted at the Carolina Sandhills National Wildlife Refuge (CSNWR) located in McBee, South Carolina. This site is located at approximately 100 meters above sea level 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. Temperature and precipitation data for the study period and 30-year averages are shown in Figure 5.1. The study site was located in a subxeric habitat at the lower half of a hill slope. Our study plot consisted of an area of approximately 0.1 Ha (50 m wide x 20 m long) within the subxeric habitat, where three *Quercus* species (*Q. laevis, Q. incana and Q. margaretta*) and one *Pinus* species (*P. palustris*) coexisted. The soil consists of a very deep coarse sand layer on top of a clay layer of sedimentary

origin (Typic quartizamment) (USDA 1995). Understory vegetation is sparse and composed mainly by the C4 bunchgrasses: *Aristida stricta* (wiregrass) and to a lesser extend by *Schizachyrium scoparium* (little bluestem) and *Gaylussacia dumosa* (dwarf huckleberry).

#### Isolation of species effects: rhizotron installation

In order to collect species-specific data of tree root demography, roots from the four species studied were isolated in the field by growing them for three years in "rhizotrons". The rhizotrons consisted of PVC semi-cylindrical chambers (diameter= 60 cm, depth= 60 cm, volume= 89 liters) with open tops and bottoms that prevented colonization of any roots besides those transplanted into the rhizotrons. The rhizotrons had a plexiglass window (50 x 50 cm ) that was used for root observation and to record root demography. Six adult individuals (dbh: 20-70 cm) of each of four tree species (*Q. laevis*, *Q. incana*, *Q. margaretta* and *P. palustris*) were selected for the study. On February 19, 1999, two lateral roots (length of 1-2 m and thickness of 0.5-1.0 cm) of each tree were excavated from the soil and inserted through lateral holes into the rhizotrons. Each rhizotron was buried next to the tree (distance = 1-2 m from the bole of the tree) and the volume was filled with the original soil, maintaining the original stratification.

Two thermocouple psychrometers were placed in the center of each rhizotron at 25-cm depth and at about 5 cm from each lateral root. Soil water potential ( $\psi$ s) and soil temperature were measured every hour for three years in our study plot by using screen- caged Peltier-type thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, UT, USA) interfaces with a computerized data acquisition system (CR7; Campbell Scientific, Inc., Logan, UT, USA). Roots were left to re-colonize the soil inside the rhizotron. Based on observations of roots visible on the plexiglass window, we confirmed that all 24 chambers containing tree roots had produced new roots before the end of the growing season of 1999. In March 2000 a prescribed burn crossed a fire line around the plot and burned inside of it. The fire was fast moving and did not burn the trees of the study. Nonetheless it damaged the observation window of one rhizotron with roots of

*P. palustris*, therefore one of six replicates of *P. palustris* was taken out the study. The fire did not damage the other rhizotrons, and was not detected as an increased temperature by any of the thermocouple psychrometers placed in side or outside the rhizotrons at the depth of 25 cm.

#### Root observation

The rhizotrons contained a flat, transparent plexiglass window (60 x 60 cm) that allowed root observation. All roots visible through the observation window were traced on transparent acetates (50 cm depth x 50 cm width) for a total of 13 time intervals during the 2.5-year study period (from February 19, 1999 to October 1, 2001). Only fine roots (diameter < 2 mm) were considered for this study. Roots appearing on each individual mapping date were considered to be part of the same cohort and were identified with different pen colors. Death of roots was also recorded with the respective date and cohort information. Roots were considered dead when they started to show symptoms of decay (shriveling, softening and/or partial decomposition) and were followed until total decomposition to confirm the observation.

# Final demographic variables

The number of live and dead roots was quantified from the tracing acetates for each cohort and mapping date. Lateral roots were counted as new roots when they were longer than 2 mm. Total root production, death and percentage mortality (percentage of total death divided by total root production) were calculated for root numbers for each species, seasonal cohort and year at the end of the experiment. Differences between species in total number of roots produced, total number of dead roots and total percentage mortality (percentage of roots produced that died before the end of the study) were tested by ANOVA.

#### Root survival analysis

Lifespans 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 were estimated via survival analysis using the product-limit (Kaplan-Meier) method for roots from all cohorts and median lifespan values for each species and cohort were estimated (see Black et al., 1998 for a detailed discussion of survival analysis).

Log-Rank Chi Square statistics were computed to test for homogeneity of the survival functions across species (Prentice & Kalbfleisch, 1979). Because we had no prior knowledge of the root survival distributions, we fit exponential, Weibull and lognormal distributions to our data. We present the Weibull distribution because it provided the best fit (Black et al., 1998). The Weibull distribution is described by two parameters: a scale parameter  $\alpha$ , and a shape parameter  $\beta$ . The main determinant of the degree of hazard and the average life span is  $\alpha$ . The shape parameter  $\beta$  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 and the estimation of  $\alpha$  and  $\beta$  parameters was done separately for each species, seasonal cohort and year. Parameters of each survival curve were compared by the degree of overlap between the 95% confidence intervals. Unless otherwise noted, all statistical analyses were done using JMP Statistical Discovery Software (version 4.0, SAS Institute, Cary, NC).

#### Risk analysis

A proportional hazards model (Cox, 1972; Wells & Eissenstat, 2001) was used to examine the effect of season on survival times. For this analysis, cohorts of each species were consolidated in two groups: spring & summer (growing season) and fall & 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) are actively photosynthesizing and the dormant season as the period between mapping dates when their leaves are largely senesced. The last growing season date for 1999 was September 25. The 2000 growing season began on March 13 and ended October 2. The 2001 growing season began on March 14 and the final mapping date of the study was October 1. The proportional hazards model included the species effect (each species relative to *Q. margaretta*), the season effect (growing season relative to dormant season) and a species\*season interaction term (the season effect of each species relative to the season effect of Q. margaretta). Species and interaction term effects were referred arbitrarily to *O. margaretta*, because this is the only species unable to colonize xeric habitats. Consistent divergence in fine root survival patterns of all species with Q. margaretta, might provide clues on the fine root demographic strategies that could be 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. A conditional risk ratio (or hazard ratio) and its confidence limits were also computed from the parameter estimates.

# Results

The tree species studied exhibited significant differences in fine root longevity (Table 1, Figure 5.2). Median lifespan of *Q. laevis* roots (606 days) and *Q. incana* roots (738 days) was 2.5-3 times that of *Q. margaretta* roots (243 days). Median lifespan of *P. palustris* fine roots was intermediate (449 days). These species differences in longevity were consistent for all cohorts in

both years (Table 5.1), although they tended to decrease for the younger cohorts. The longevities observed in this study for fine roots (diameter < 2 mm) are generally greater than values reported on other species and habitats (Eissenstat and Yanai 1997), but they span over the range of variation observed for two sandhill C4 bunchgrasses that show distinct root demography (West, Espeleta and Donovan, unpublished results).

In addition, for all cohorts the risk of root death for a given time period increased as the roots aged for both species ( $\beta$ >1 for all species; Table 5.1). This suggests that most young roots are very resilient and that fine roots of these species do not go through a period of high susceptibility early in their development. The risk of death with root age was different among the species. For all cohorts together, *Quercus margaretta* had a significantly lower value of  $\beta$ , indicating that death at an early age was more likely in roots of *Q. margaretta* than the other tree species (Table 5.1). These differences were not constant for the different seasonal cohorts. For the first three seasonal cohorts there was a shift in the differentiation of  $\beta$  values: the first cohort (growing season 1999) showed lower values for the xeric *Quercus* species, the second cohort (dormant season 1999), showed no species differences, and the third cohort (Spring and Summer 2000) showed the inverse pattern (lower  $\beta$  values in the species dominant in mesic habitats, Q. margaretta and P. palustris). This again indicates that roots of mesic species were more likely to die young only when the more recent cohorts were considered. This is consistent with the observation that roots involved in early colonization of the rhizotrons are less ephemeral than roots from later cohorts (as evidenced by the decreasing trend in median root longevity with cohort age, Table 5.1). We do not have an explanation for the similar  $\beta$  value between mesic species and *Q. laevis* in the last recorded cohort (Fall and Winter 2000, Table 5.1). This may indicate differentiation between the *Quercus* species that can colonize xeric habitats and a greater likelihood of Q. laevis roots to die younger than Q. incana roots. Nonetheless, data for the last cohorts must be interpreted with caution due to the little number of measurements in time they include.
The species also differed in total fine root production, death and percentage mortality (Table 5.3). Species that dominate in mesic habitats (*Q. margaretta*) and the generalist *P. palustris* exhibited greater production and death of fine roots than xeric *Quercus* species. *Quercus margaretta* had the greatest percentage fine root mortality, and *P. palustris* was intermediate. Species also showed different patterns of fine root demography with cohort age. Percent mortality of fine roots was close to 100% for the first three seasonal cohorts in *Q. margaretta*, and only less for the most recent cohorts (78%), whereas it was consistently low in the xeric *Quercus* species. This again indicates that a sizeable group of roots in xeric species are remarkably long-lived, and such percentage seems to be constant over time.

Although not tested statistically, we also observed species-specific seasonal patterns in fine root production and death (Figure 5.3). *Quercus margaretta* and *P. palustris*, both species dominant in mesic habitats, exhibited more continuous growth and death of fine roots during growing and dormant seasons. In contrast, xeric *Quercus* species (*Q. laevis* and *Q. incana*), showed little fine root growth and death during the dormant season. We did not expect such pattern of seasonal differentiation in fine root demography among the *Quercus* species, only *Q. incana* tends to show more leaf persistence in the dormant season. *Pinus palustris* showed, as expected, continuous growth and death of fine roots during the dormant season (Figure 5.3). Greater rates of root production and death in all species during the growing season (indicated by the slope of the production and death curves in Figure 5.3) was associated with the occurrence of lower soil water potentials and greater soil temperatures, respectively, during spring and summer months (Figure 5.3). Contrary to *P. palustris*, where high rates of root death were associated with frequent and intense drought of the soil inside the rhizotrons (Figure 5.3), high rates of death of *Q. margaretta* were associated with less soil drying (Figure 5.3).

The cumulative production curves show a trend of distinct slowing of winter production in xeric *Quercus* species as compared to mesic *Q. margaretta* and *P. palustris* (Figure 5.3). There were differences between species and years in the production and death of each seasonal cohort

(Figure 5.4). 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 decline 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 (Figure 5.4). These patterns are consistent with the results of the proportional hazards analysis (Table 5.3). In 1999 and 2000 there was a significant effect of the xeric species (Q. laevis and Q. incana, both with risk ratios < 1), indicating lower risk for roots of xeric *Quercus* species compared to mesic *Q. margaretta*, and a significant effect of season (risk ratio > 1), indicating a higher risk of death for roots produced in the dormant season for all species. In both years there were significant species\*season interactions, indicating that the differences in risk of death between dormant and growing season cohorts differed across species. For the 1999 and 2000 cohorts, fine roots of P. palustris were more likely to die than fine roots of Q. margaretta if they were produced in the dormant season. Only for the 1999cohort, fine roots of Quercus laevis were also 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 species did not differ in their risk of death in the dormant versus growing seasons relative to Q. margaretta.

## Discussion

#### Species differences in fine root demography: implications for ecosystem function

Results from this study demonstrate that species differences in fine root demography can be substantial, even when comparing congeneric species that inhabit the same ecosystem. The degree of variation in fine root turnover between the *Quercus* species inhabiting the sandhill habitat of this study, together with previous results with two co-occurring C4 bunchgrasses (West et al. unpublished results) is of comparable magnitude to the broad-scale variation described previously for vegetation types and biomes (Gill and Jackson 2000). These authors had suggested

that shifts in plant functional types could imply changes in fine root turnover and carbon and nutrient cycling of ecosystems, such as the effect of shrub invasions in arid and semi-arid grasslands of western United States, which could potentially decrease fine root turnover. Our results suggest that more subtle changes in species composition have the potential to render similar or larger shifts in patterns of root turnover. Clearly, more investigation is needed to verify if these differential patterns result in changes in ecosystem processes of carbon and nutrient cycling. Expanding the studies on species differences to different ecosystems will help to include species-specific processes not accounted for in models of ecosystem response to global change.

#### Fine root demography and differential species distribution.

Our study also indicates that species-differences may be predicted to some extent with the existing theories of abiotic controls on tissue demography (sensu Eissenstat and Yanai 1997). Fine root longevity may potentially be associated with the different distribution of the species along the xeric to mesic gradient. Greater longevity in the Quercus species able to colonize xeric habitats (*Q. laevis* and *Q. incana*) is consistent with the expectations that plants from infertile habitats would tend to control excessive loss of resources by maintaining low rates of tissue loss. On the other hand, species that dominate mesic habitats, such as *Q. margaretta* and *P. palustris*, showed greater fine root growth rates, which might allow rapid foraging for nutrients and greater competitive ability in more fertile, mesic habitats (Grime 1977; Aerts 1999; Aerts and Chapin 2000). Our results also suggest that a tradeoff might exist between the ability of roots to grow fast and persist alive (sensu Eissenstat and Yanai 1997). The Quercus species with greater fine root longevities (Q. laevis and Q. incana) exhibited little fine root growth, while the species that dominate in mesic habitats showed the opposite response. This adds further support to the theory that optimal fine root lifespan might be the result of maximization of tissue efficiency. High construction costs of large numbers of fine roots may be advantageous only if the uptake of soil resources is augmented accordingly. On the other hand, costs of root maintenance can be

sustained only if root persistence prevents loss of comparatively more valuable resources in infertile conditions (Eissenstat and Yanai 1997). Therefore, the benefits of short root lifespan may be reduced in soils of low fertility, because there is little benefit of growing new roots into new, but yet infertile soil (Eissenstat et al. 2000).

Differences in tissue turnover rates may potentially indicate differences in resource cycling across environments. In xeric areas, greater fine root longevity may lead to greater resource conservation but lower ability to exploit ephemeral resource enrichment. Slow root turnover, combined with low productivity, low litter production and decomposability may potentially lead to slow rates of nutrient cycling, which would prevent invasion of highly competitive, low nutrient-efficient species (Chapin 1993). In mesic areas with greater resource availability, greater root proliferation ability but greater root death may lead to faster rate of resource cycling. This may exclude slow-growing nutrient-efficient plants from fertile habitats, promoting ecosystem stability (Aerts, 1999).

The results of our study with "in-growth" rhizotrons, specifically with the first root cohorts, may also indicate different strategies for colonization of new soil volumes. The species showed differences in this "colonization" effect: xeric species colonized more slowly but produced remarkably long-lived roots, so the percentage of roots surviving in each cohort was more similar (Table 5.1). This is consistent with observations from other studies indicating enormous differences in fine root longevity (very short-lived versus very long-lived fine roots) among fine roots (Gaudinski et al. 2001), which have been attributed in part to differences in fine root order and diameter (Eissenstat et al. 2000; Wells and Eissenstat 2001). Our results suggest that differences in fine root longevity among fine root classes may be species-specific and that species from xeric habitats may exhibit larger differentiation.

### Analogies between roots and leaves

Most of the optimality theory applied to roots has been adapted from patterns observed in leaves (Chabot and Hicks 1982; Reich et al. 1999). Although species differences in fine root demography agrees the observations for leaves and roots of grasses from a productivity gradient (Schläpfer and Ryser 1996), our results with trees of the sandhill gradient provide contradictory evidence that aboveground patterns could be mirrored precisely belowground. First, differences in seasonal fine root demography did not match patterns of leaf phenology. Also, the seasonality of root demography exhibited by xeric *Quercus* species contrasted with more constant root growth and death around the year for the mesic Q. margaretta and the generalist P. palustris. This contradicts assertions that tissue persistance habit might be an adaptive response to low resources (Monk 1966; Aerts 1995). Contrary to *Quercus margaretta*, *Q. incana* tends to exhibit more leaf persistence in the winter, but little root production during the winter months. On the other hand, the evergreen and generalist P. palustris exhibits little seasonality in root demography. Second, leaf morphological patterns do not parallel fine root morphology. Although previous studies described differences in specific leaf area (SLA) that closely follow the ecological distribution of the *Quercus* species (i.e. greater SLA in mesic species), fine root demography was found to be virtually the same in greenhouse studies with seedlings (for three root morphological variables: specific root length, SRL, average fine root diameter and tissue density). This supports previous views indicating a low ability to resolve differences in root morphology in intra-specific comparisons (Ryser 1996, issenstat et al. 2000).

Relationships between tissue morphology and demography have also been borrowed from leaf lifespan theory to explain belowground patterns (Eissenstat and Yanai 1997). Our results suggest the lack of a positive relationship between fine root longevity and fine root thickness and diameter (or an inverse relationship with SRL): greater fine root longevity in xeric *Quercus* species was associated with no differences in root morphology. Furthermore, comparing morphology and demography among xeric *Quercus* species and *P. palustris*, we found an

opposite pattern: fine roots of *P. palustris* were thicker but grew faster and died sooner than xeric *Quercus* species. It is likely that optimal efficiency in tissues might be achieved in different ways above- and below-ground. Based on our results and reports from other plant species from other habitats, adjustments of fine root lifespan rather than fine root morphology may be the primary mechanism of adaptation via maximizing efficiency under different resource availability.

## Water availability and fine root demography

Our results indicate potential interactions between seasonal patterns of fine root demography and soil water dynamics in the topsoil. In all species, but primarily in mesic (*Q. margaretta*) and generalist species (*P. palustris*), fine root death was greater during the summer months, in coincidence with the period of greatest drying of the surface soil. It is possible that species-specific responses to surface drought may account in part for the observed differences in root demography. Previous greenhouse studies with seedlings of all species suggest that mesic species are more plastic in response to surface drought and rewetting (Espeleta and Donovan, unpublished results). Fine roots of adult trees might respond similarly: fine roots might die by direct desiccation in the dry soil (Jupp and Newman 1987; Stasovski and Peterson 1991; but see Eissenstat and Achor 1999), or after selective root shedding in order to reduce maintenance costs under conditions where benefits are reduced because water and nutrient absorption is impeded (Espeleta and Eissenstat 1998).

Fine root demography might be implicated with species-specific patterns of water use and redistribution. Previous studies on water use strategies of the three *Quercus* species (Donovan *et al.* 2000) indicate that mesic species are less conservative in water use, maintaining greater stomatal water conductance even under periods of low soil water availability. Little control in aboveground water loss might induce cavitation of the stem and roots (Jackson *et al.* 2000), causing significant levels of root death in mesic species exposed to dry conditions. This characteristic may prevent mesic *Quercus* species from colonizing xeric habitats. Nonetheless, in

the subxeric habitat of our study we observed continuous ample supply of water at more than one meter of depth (Espeleta, West and Donovan, unpublished results) indicating that all trees should have good access to water throughout the entire three years of the study. More likely, root death may be less dependent on the entire water status of the plant and more on the conditions experienced by the roots found in different soil profiles. In a simultaneous 3-year investigation on hydraulic redistribution using the same rhizotrons of this study (Espeleta, West and Donovan, unpublished), we observed differential patterns of hydraulic lift. All species that colonize xeric habitats (*Q. laevis, Q. incana* and *Q. margaretta*) exhibited frequent hydraulic lift activity, in contrast to *Q. margaretta*, that showed none. If hydraulic lift contributes to fine root survival by rewetting the surface soil during periods of surface drought (Caldwell *et al.* 1991), speciesdifferences in root death during the growing season (Fig. 5.4) may be dependent on speciesdifferences in hydraulic lift ability.

From a different perspective, death of surface fine roots of *Q. margaretta* may be triggered during early stages of surface soil drying, perhaps as a strategy to prevent excessive loss of water, serving as "hydraulic fuses" that prevent hydraulic lift activity (Jackson *et al.* 2000). Whatever the causal relationship between hydraulic lift and demography of surface fine roots, there is a need to further investigate species-differences in concert for fine root demography and hydraulic lift in a series of environments. To our knowledge, this is the first time such associations have been observed in adult trees in a natural community.

### Species differences in fine root demography: implications

Our study demonstrates the feasibility of obtaining species-specific information about fine root demography in a natural community with multiple species. The lack of this type of information in the scientific literature reflects the enormous technical limitations of isolating species-specific processes in mixed-species communities. Characterizing the variation of speciesspecific root traits in single environments is important to gain a better understanding of the scale at which plant adaptive theory may be applicable (sensu Grime *et al.* 1991). Similarly, ecosystem responses to environment change will not be fully understood until a better idea exists on the degree of variation of species-specific responses at finer scales, because shifts in species composition within biomes may change previously observed broad-scale patterns of ecosystem function (Gill and Jackson 2000). We hope that in the future, perhaps via adaptation of techniques using species-specific molecular markers (Linder *et al.* 2000), it will be possible to obtain species identity simultaneously with indirect and/or direct methods of estimating fine root demography.

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**Table 5.1a** Field demography of fine roots of four species of adult trees during 1006 days (144 weeks). Data represents survival times of all root cohorts produced between the Spring of 1999 and the end of the Winter of 2000 (roots were tracked from February 19, 1999, until September 30, 2001).

<u>Cohort</u>	Species	Number of roots			Survival Analysis <sup>1</sup>			Weibull curve fitting <sup>2</sup>			
Season/year		Failed	Censored	Total	Median days	$\chi^2$	$P > \chi^2$	α	Confidence interval (95%)	β	Confidence interval (95%)
ALL Spring 1999 - Winter 2000	Q. laevis Q. incana Q. margaretta P. paluetris	351 427 2440	1163 1146 672	1514 1573 3112	606 <sup>a</sup> 738 <sup>a</sup> 243 <sup>c</sup>	2176.2	<0.0001	835.1 <sup>a</sup> 808.6 <sup>a</sup> 306.0 <sup>c</sup>	771 - 913 765 - 860 298 - 314	1.6 <sup>ab</sup> 1.89 <sup>a</sup> 1.54 <sup>b</sup>	1.45 - 1.76 1.74 - 2.04 1.49 - 1.59 1.73 - 1.87
	P. palustris	1760	1145	2905	449			515.7	502 - 529	1.80	1./3 - 1.8/

(1): Median lifespan was estimated by product limit (Kaplan-Meier) Survival Analysis. Log-Rank homogeneity test compares survival differences between the two species. Estimated median lifespan is provided with 95% confidence interval. (2): A Weibull distribution was fitted to the survival data, and the fitting parameters ( $\alpha$  and  $\beta$ ) were estimated. Mean lifespan of the 62% percentile ( $\alpha$ ) and the magnitude of the risk slope ( $\beta$ ) are listed with lower and upper 95% confidence intervals.

<u>Cohort</u>	Species	Number of roots			Survival Analysis <sup>1</sup>				Weibull curve fitting <sup>2</sup>			
Season/year		Failed	Censored	Total	Median days	$\chi^2$	$P > \chi^2$	α	Confidence interval (95%)	β	Confidence interval (95%)	
Spring and Summer 1999	Q. laevis Q. incana Q. margaretta P. palustris	63 171 485 425	65 163 5 123	128 334 490 548	>738 <sup>a</sup> 738 <sup>a</sup> 381 <sup>c</sup> 624 <sup>b</sup>	411.81	<0.0001	945.3 <sup>a</sup> 899.5 <sup>a</sup> 473.4 <sup>c</sup> 673.9 <sup>b</sup>	810 - 1154 835 - 981 456 - 491 653 - 696	1.60 <sup>b</sup> 2.09 <sup>c</sup> 2.51 <sup>c</sup> 3.02 <sup>a</sup>	$1.26 - 1.98 \\ 1.81 - 2.39 \\ 2.34 - 2.68 \\ 2.77 - 3.28$	
Fall and Winter 1999	Q. laevis Q. incana Q. margaretta P. palustris	59 10 241 318	31 56 6 127	90 66 247 445	563 <sup>a</sup> >606 <sup>a</sup> 206 <sup>c</sup> 517 <sup>b</sup>	200.34	<0.0001	631.6 <sup>b</sup> 2174 <sup>a</sup> 345.4 553.6 <sup>b</sup>	553 - 742 1145 - 9574 318 - 375 525 - 586	1.9 <sup>ns</sup> 1.38 1.60 2.01	$\begin{array}{c} 1.44 - 2.35 \\ 0.70 - 2.40 \\ 1.44 - 1.77 \\ 1.82 - 2.22 \end{array}$	
Spring and Summer 2000	Q. laevis Q. incana Q. margaretta P. palustris	131 178 741 662	423 300 87 281	554 478 828 943	>522 <sup>a</sup> 522 <sup>a</sup> 286 <sup>c</sup> 408 <sup>b</sup>	880.54	<0.0001	729.6 <sup>a</sup> 664.6 <sup>a</sup> 331.1 <sup>c</sup> 448.1 <sup>b</sup>	668 - 815 617 - 726 318 - 344 429 - 469	2.90 <sup>a</sup> 2.39 <sup>a</sup> 1.86 <sup>b</sup> 1.70 <sup>b</sup>	2.44 - 3.41 2.07 - 2.74 1.75 - 1.98 1.59 - 1.82	
Fall and Winter 2000	Q. laevis Q. incana Q. margaretta P. palustris	32 46 426 293	144 97 78 207	176 143 504 500	>357 <sup>a</sup> 311 <sup>a</sup> 243 <sup>b</sup> 301 <sup>ab</sup>	222.30	<0.0001	463.9 <sup>a</sup> 338.8 <sup>b</sup> 263.1 <sup>c</sup> 328.7 <sup>b</sup>	$\begin{array}{r} 401-583\\ 328-352\\ 255-272\\ 318-340 \end{array}$	3.02 <sup>b</sup> 8.52 <sup>a</sup> 3.20 <sup>b</sup> 3.57 <sup>b</sup>	2.22 - 3.95 6.82 - 10.43 2.97 - 3.45 3.24 - 3.93	

**Table 5.1b** Field demography of fine roots of four species of adult trees during 1006 days (144 weeks). Data represents survival times offour root cohorts produced between from February 19, 1999, until September 30th, 2001).

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(1): Median lifespan was estimated by product limit (Kaplan-Meier) Survival Analysis. Log-Rank homogeneity test compares survival differences between the two species. Estimated median lifespan is provided with 95% confidence interval. (2): A Weibull distribution was fitted to the survival data, and the fitting parameters ( $\alpha$  and  $\beta$ ) were estimated. Mean lifespan of the 62% percentile ( $\alpha$ ) and the magnitude of the risk slope ( $\beta$ ) are listed with lower and upper 95% confidence intervals.

**Table 5.2** Fine root demography (number of roots) of four adult tree species during the study period (1006 days): Least Significant Mean (and SE) root production, death, and mortality at the end of the experiment. Data are based on root counts for four successive seasonal cohorts. Species differences within each cohort were analyzed by one-way ANOVA. Percentage mortality data were analyzed after normalization with arcsine transformation (n = 6 for the *Quercus* species and n = 5 for *P. palustris*, df = 3,19).

COHORT (Season/year)	SPECIES	Total root production (root numbers)	$F_{(3,19)}$ ( $P < F$ )	Total root death (root numbers)	$F_{(1,5)}$ ( $P < F$ )	Final root mortality (%)	$F_{(1,5)}$ ( $P < F$ )
ALL Spring 1999 - Winter 2000	Q. laevis Q. incana Q. margaretta P. palustris	251.8 (42.6) 262.2 (36.8) 518.7 (64.6) 593.4 (92.0)	8.412 (0.0009)	58.0 (12.7) 71.2 (20.5) 406.7 (46.4) 352.0 (53.3)	26.745 <0.0001	22.3 (3.0) 25.4 (5.8) 78.8 (2.4) 59.8 (4.3)	46.829 <0.0001
Spring and Summer 1999	Q. laevis Q. incana Q. margaretta P. palustris	20.8 (13.2) 55.7 (34.0) 81.7 (29.9) 109.6 (61.9)	1.711 (0.1986)	10.0 (5.07) 28.5 (17.7) 80.8 (29.7) 85.0 (44.5)	3.580 (0.0332)	37.7 (13.2) 48.9 (11.1) 99.2 (0.68) 88.6 (7.0)	10.037 (0.0004)
Fall and Winter 1999	Q. laevis Q. incana Q. margaretta P. palustris	15.0 (7.80) 11.0 (2.85) 41.2 (17.7) 89.0 (29.3)	3.185 (0.0474)	9.83 (5.10) 1.67 (0.21) 40.2 (17.3) 63.6 (22.2)	8.8462 (0.0007)	57.6 (10.2) 29.3 (14.3) 98.7 (1.33) 79.4 (11.2)	8.464 (0.0009)
Spring and Summer 2000	Q. laevis Q. incana Q. margaretta P. palustris	92.3 (29.2) 79.7 (17.8) 138.0 (23.6) 201.0 (51.3)	2.9437 (0.0593)	21.8 (10.4) 29.7 (14.0) 123.5 (20.5) 132.4 (33.8)	8.4940 (0.0009)	22.9 (6.2) 30.1 (13.8) 90.3 (3.54) 62.0 (9.66)	12.027 (0.0001)
Fall and Winter 2000	Q. laevis Q. incana Q. margaretta P. palustris	29.3 (5.96) 23.8 (7.44) 84.0 (18.4) 100.0 (27.6)	6.6118 (0.0030)	5.33 (1.52) 7.67 (2.94) 71.0 (20.1) 58.6 (21.0)	10.884 (0.0002)	21.2 (7.02) 31.9 (11.3) 78.4 (6.25) 51.6 (9.02)	8.863 (0.0007)

**Table 5.3** Results of the proportional hazards regression for root survivorship data. The analysis was used to assess the effects of three covariates (species, season and species\*season interaction) on root life span. The analysis was performed separately for each year. A method of partial likelihood estimates the  $\beta$  coefficient associated with each covariate in the model. All effects are comparisons with *Quercus margaretta*. A negative parameter indicates that increasing values of the covariate are associated with a decreasing risk of mortality relative to *Q. margaretta*, and vice versa for positive parameter values. A chi-square statistic was used to test the null hypothesis that each  $\beta$  coefficient is equal to zero. Also reported is the risk ratio, defined as  $e^{\beta}$ . A risk ratio >1 indicates increasing risk for that variable, <1 decreasing, and =1 no difference in mortality risk. The risk ratio is interpreted as the ratio of the hazard of a given species versus *Q. margaretta* (e.g.,  $\beta$ <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 by season. The significant interaction term suggests greater divergence of risk between seasons for *Q. margaretta* as compared to each one of the other species.

a) 1999-2000 Variable	df	Parameter estimate	SE	Wald chi square	$P > \chi^2$	Risk ratio	Confidence (95 Lower	ce interval 5%) Upper
Species $(Pp)$ Species $(Qi)$ Species $(Ql)$ Season (dormant) Sp. $(Pp)$ * seas. (dormant) Sp. $(Qi)$ * seas. (dormant) Sp. $(Ql)$ * seas. (dormant)	1 1 1 1 1 1 1	0.2095 -1.0653 -0.1790 0.2094 0.1162 -0.5156 0.3128	0.0551 0.1249 0.0804 0.0502 0.0551 0.1249 0.0804	463.281 463.281 463.281 13.686 26.561 26.561 26.561	<0.0001 <0.0001 <0.0001 0.0002 <0.0001 <0.0001 <0.0001	1.233 0.345 0.836 1.233 1.123 0.597 1.367	$ \begin{array}{r} 1.111\\ 0.263\\ 0.714\\ 1.111\\ 1.012\\ 0.456\\ 1.168\\ \end{array} $	1.381 0.432 0.979 1.355 1.257 0.748 1.601
b) 2000-2001		Doromotor		337 11			C C 1	• • •
Variable	df	estimate	SE	wald chi square	$P > \chi^2$	Risk ratio	(95 Lower	Upper

Species identifiers: Quercus laevis (Ql), Q. incana (Qi), Q. margaretta (Qm), Pinus palustris (Pp)



**Fig. 5.1** Mean monthly temperature and total monthly rainfall for the study period plotted onto 30-year averages. The monthly data were collected at the Carolina Sandhills National Wildlife Refuge headquarters, approximately 7 km from the field site. The average temperature and precipitation curves are from 30 years of data (1961-1990) collected in Cheraw, SC (approx. 20 km from the field site).



**Fig. 5.2a** Time course of root demography (total root proliferation and death) and soil water potential and temperature in rhizotrons with Q. *laevis* roots (from February 1999 until September 2001; GS = growing season, DS = dormant season). Root demography data represent the mean of six replicate rhizotrons *s* taken at 13 different mapping dates. Soil water potential and soil temperature were recorded every hour with one thermocouple psychrometer placed inside each replicate rhizotron per species. Separate curves for each psychrometer are presented.



**Fig. 5.2b** Time course of root demography (total root proliferation and death) and soil water potential and temperature in rhizotrons with Q. *incana* roots (from February 1999 until September 2001; GS = growing season, DS = dormant season). Root demography data represent the mean of six replicate rhizotrons *s* taken at 13 different mapping dates. Soil water potential and soil temperature were recorded every hour with one thermocouple psychrometer placed inside each replicate rhizotron per species. Separate curves for each psychrometer are presented.



**Fig. 5.2c** Time course of root demography (total root proliferation and death) and soil water potential and temperature in rhizotrons with *Q. margaretta* roots (from February 1999 until September 2001; GS = growing season, DS = dormant season). Root demography data represent the mean of six replicate rhizotrons *s* taken at 13 different mapping dates. Soil water potential and soil temperature were recorded every hour with one thermocouple psychrometer placed inside each replicate rhizotron per species. Separate curves for each psychrometer are presented.



**Fig. 5.2d** Time course of root demography (total root proliferation and death) and soil water potential and temperature in rhizotrons with *P. palustris* roots (from February 1999 until September 2001; GS = growing season, DS = dormant season). Root demography data represent the mean of five replicate rhizotrons *s* taken at 13 different mapping dates. Soil water potential and soil temperature were recorded every hour with one thermocouple psychrometer placed inside each replicate rhizotron per species. Separate curves for each psychrometer are presented.



**Fig. 5.3** Survival curves of the four tree species during the course of the experiment, as calculated by the product-limit (Kaplan-Meier) method. Data is based on a total of 1514, 1573, 3112 and 2905 roots of *Quercus laevis, Q. incana, Q. margaretta* and *Pinus palustris*, respectively, and the censored observations are included in the estimation of the survival probabilities. A 2-factor Weibull distribution was fitted to the data to estimate the mean root lifespan for each species.



Fig. 5.4 Time course of the number of living roots of each seasonal cohort from the date of rhizotron installation (GS = growing season, DS = dormant season, shaded bars). Roots of each cohort were produced during the periods marked by shading (i.e., at the beginning of the season that cohort had zero roots).

### CHAPTER 6

### CONCLUSIONS

Our results suggest that species differences in fine root demography and hydraulic lift can be substantial, even when comparing congeneric species that inhabit the same ecosystem. The degree of variation in fine root turnover between the *Quercus* species inhabiting the sandhill habitat of this study, together with previous results with two co-occurring C4 bunchgrasses (West et al., unpublished results) is of comparable magnitude to the broad-scale variation described previously for vegetation types and biomes by Gill and Jackson (2000) (Figure 5.1). By comparing differences in fine root turnover between grasses and shrubs, Gill and Jackson (2000) suggested that shrub invasions in arid and semi-arid grasslands of western United States can lead to lower fine root turnover rates and carbon and nutrient cycling. Our results suggest that more subtle changes in species composition have the potential to render similar or larger shifts in patterns of fine root turnover. Differences in hydraulic lift activity found between congeneric tree species suggest that species can also differ in belowground water use patterns at even finer scales than previously thought, and that small changes in species composition of plant communities could potentially alter the patterns of hydraulic redistribution and the water balance of entire ecosystems (sensu Jackson et al. 2000). More investigation is needed in order to verify if these differential patterns result in changes in ecosystem processes of water, carbon and nutrient cycling. Notwithstanding, expanding the studies on species differences to different ecosystems will help to include species-specific processes not accounted for in models of ecosystem response to global change.

Differences in tissue turnover rates may potentially indicate differences in resource cycling across environments. In xeric areas, greater fine root longevity may lead to greater resource conservation but lower ability for exploiting ephemeral resource enrichment. Slow root turnover,

combined with low productivity, low litter production and decomposability may lead to slow rates of nutrient cycling, which would prevent invasion of highly competitive, low nutrientefficient species (Chapin, 1993). In mesic habitats with greater resource availability, greater root proliferation ability but greater root death may lead to faster rate of resource cycling. This may exclude slow-growing nutrient-efficient plants from fertile habitats, promoting ecosystem stability (Aerts, 1999).

Results of these studies also indicate that species differences may be predicted to some extent with the optimality theory (Givnish 1986). Differences in fine root demography and hydraulic redistribution were associated with the ecological distribution of the species in xeric to mesic habitats, suggesting a potential value of these belowground traits in adaptation to different habitat fertility. Based on our results it seems that variation in fine root demography and hydraulic lift may contribute to maximize the efficiency of resource use under different resource availability (sensu Eissenstat and Yanai 1997, and Caldwell et al. 1998). Greater fine root longevity and survival in dry surface soil in the Quercus species able to colonize xeric habitats is consistent with the expectations that plants from infertile habitats would tend to control excessive loss of resources by maintaining low rates of tissue loss. On the other hand, species that dominate mesic habitats, such as *Q. margaretta* and *P. palustris*, showed greater ability to produce fine roots, which might allow rapid foraging for nutrients and greater competitive ability in more fertile, mesic habitats (Grime 1977; Aerts 1999; Aerts and Chapin 2000). Hydraulic lift may be important for colonization of xeric habitats (where surface drought is more frequent and intense), because it may reduce root death in dry soil and increase the length of time in which soil nutrients are available (Caldwell et al. 1991). All hydraulic-lifting species in this study were characterized by lower fine root turnover rates. Because low turnover of roots may increase root efficiency in resource-poor habitats, the coupling of hydraulic lift and surface fine root survival in xeric species may be part of a strategy to ensure conservation of resources via maintenance of fine roots in dry soil. Since fine root turnover is estimated to represent a large fraction of primary

productivity in many ecosystems (Caldwell et al. 1991), the association between HL and fine root demography deserves more attention in future of studies of plant communities under limiting resources.

Responses to resource availability were also predicted by the optimality theory (Givnish 1986). The notion that optimal fine root lifespan might be the result of maximization of tissue efficiency (Bloom et al. 1985; Eissenstat and Yanai 1997) is supported by greater root turnover rates of seedlings exposed to high resource supply, suggesting that costs of root death and reconstruction may be less critical when they are outbalanced by greater benefits in resource acquisition. Further support also comes from the observation of a tradeoff between the ability of roots to grow fast and persist alive. The *Quercus* species with greater fine root longevities and little fine root death (O. laevis and O. incana) exhibited little fine root growth, whereas the species that dominate in mesic habitats (Q. margaretta and Q. marilandica) showed the opposite response. Producing large numbers of fine roots may only be economically efficient if it results in comparatively greater benefits of resource uptake. This condition may be encountered only by species in high resource environments. On the other hand, costs of root maintenance can be sustained in infertile conditions only if root persistence prevents loss of comparatively more valuable resources in infertile conditions (Eissenstat and Yanai 1997). Therefore, the benefits of short root lifespan may be reduced in soils of low fertility, because there is little benefit of growing new roots into unexplored, but infertile soil (Eissenstat et al. 2000).

Results of the greenhouse studies with seedlings indicate that optimization in root efficiency is achieved mainly by adjustments in fine root demography rather than in fine root morphology (specific root length, fine root diameter and tissue density). In contrast to fine root demography, fine root morphology was identical across *Quercus* species from the different fertility habitats and also as a response to variation in resource availability. This suggests that at finer geographic and taxonomical scales root morphology may be less variable than root demography and that potential correlations between structure and function in roots may not be

evident unless comparisons are drawn across larger scales, as previously denoted for aboveground tissues (Reich 1993).

This study is the first to describe species-specific patterns of fine root demography and hydraulic lift ability for a group of tree species distributed along a narrow ecological gradient in a single natural community. The large degree of differentiation observed suggests that species differences at small scales must also be considered for understanding plant adaptive theory (sensu Grime et al. 1991) and plant effects on ecosystem function. In particular, it suggests that the theory on the adaptive value of belowground traits may be applicable to finer scales than previously thought (Eissenstat et al. 2000; Jackson et al. 2000), and that similar species may have potentially different effects on belowground ecosystem processes, even as divergent as those predicted across very different vegetation types and biomes (Gill and Jackson 2000; Jackson et al. 2000). In order to have a better understanding of plant adaptive traits and predictive ability of the potential effect of shifts in species composition on ecosystem resource cycling, there is a need to further investigate fine root demography and hydraulic lift in a series of environments. By selecting several global habitats, such as those already included in the Long Term Ecological Research (LTER) network, it may be possible to study whether different biomes and vegetation types differ in fine-scale variability of belowground dynamics. By this way, it will be easier to predict when species differences are more likely to be relevant. The lack of this type of information in the scientific literature reflects the enormous technical limitations of isolating species-specific processes in mixed-species communities. This study demonstrates that obtaining species-specific information of fine root demography and hydraulic lift in multi-specific natural communities is feasible when soil conditions facilitate root excavations. In the future, perhaps by combining methods to monitor root demography and hydraulic redistribution with techniques using species-specific molecular markers (sensu Linder et al. 2000), it will be more possible to study species-specific belowground processes in other habitats.

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Figure 6.1. Fine root turnover at different scales: a) Broad scale patterns across different vegetation types and terrestrial biomes as denoted by Gill and Jackson (2000), b) Small-scale patterns across different species of sandhill trees (*Quercus margaretta, Q. incana, Q. laevis* and *Pinus palustris*) and grasses (*Schizachyrium scoparium* and *Aristida stricta*). Data of sandhill trees are from this study; data of sandhill grasses are from West, Espeleta and Donovan (unpubl.). In all cases fine root turnover was calculated as the annual belowground primary productivity (BNPP) divided by the maximum belowground standing crop (see Gill and Jackson 2000 for details). For the case of sandhill tree and grass species, data included only the last year of the study, when belowground standing crops were most stable.