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Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community

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Abstract Plants can significantly affect ecosystem water balance by hydraulic redistribution (HR) from dry to wet soil layers via roots (also called hydraulic lift, HL, when the redistribution is from deep to shallow soil). However, the information on how co-occurring species in natural habitats differ in HL ability is insufficient. In a field study, we compared HL ability of four tree species (including three congeneric oak species) and two C4 bunch grass species that co-occur in subxeric habitats of fall-line sandhills in southeastern USA. Soil water potentials (ψ_s) were recorded hourly for 3 years both in large chambers that isolated roots for each species and outside the chambers. Outside of root chambers, soil drying occurred periodically in the top 25 cm and corresponded with lack of precipitation during the summer growing season. Soil moisture was continuously available at a 1 m depth. HL activity was observed in three of the tree species, with greater frequency for *Pinus palustris* than for *Quercus laevis* and *Q. incana*. The fourth tree species *Q. margaretta* did not exhibit HL activity even though it experienced a similar ψ_s gradient. For the C4 bunch grasses, *Aristida stricta* exhibited a small amount of HL activity, but *Schizachyrium scoparium* did not. The capacity for HL activity may be linked to the species

ecological distribution. The four species that exhibited HL activity in this subxeric habitat are also dominant in adjacent xeric sandhill habitats, whereas the species that did not exhibit HL are scarcely found in the xeric areas. This is consistent with other studies that found greater fine root survival in dry soil for the four xeric species exhibiting HL activity. The differential ability of these species to redistribute water from the deep soil to the rapidly drying shallow soil likely has a strong effect on the water balance of sandhill plant communities, and is likely linked to their differential distribution across edaphic gradients.

Keywords *Aristida stricta* · Hydraulic lift · Hydraulic redistribution · *Pinus palustris* · *Quercus laevis*

Introduction

The patterns of use and redistribution of soil water by plant species have considerable impact on the hydrological cycles of terrestrial ecosystems (Jackson et al. 2000a). For example, species from a single community may differ substantially in rooting depth and water consumption so that shifts in species composition can significantly alter patterns of ecosystem water use (Jackson et al. 2000a). Another way that plants can affect hydrology is via “hydraulic redistribution” (HR), defined as the nighttime transfer of water from wet to dry soil via plant roots (Caldwell et al. 1998). HR is more specifically called “hydraulic lift” for the 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 is present in the soil moisture profile (Burgess et al. 1998; Schulze et al. 1998; Smith et al. 1999). HR can alter the water balances of single plants, stands of single species, and entire forests and regions (Williams et al. 1993; Emerman and Dawson 1996; Burgess et al. 1998; Caldwell et al. 1998; Jackson et al. 2000b; Brooks et al. 2002; Ryel et al. 2002). For example, in a sugar maple (*Acer saccharum*) forest with root access

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to groundwater, hydraulically redistributed 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. 2000b). Simulations also suggest that as sugar maple has become more abundant in northeastern USA, the region's hydrological cycle may have changed through greater transpiration (Jackson et al. 2000b). Although species differences in HR may affect ecosystem hydrology, the information available on species-specific HR patterns in the field is scarce and insufficient for predictive models of ecosystem water flux (Millikin and Bledsoe 2000; Meinzer et al. 2001; Scholz et al. 2002).

Since the first case of HR was documented for plants in the field (Richards and Caldwell 1987), more than 60 new cases have been reported (Jackson et al. 2000a; Millikin and Bledsoe 2000). The majority of reports are greenhouse studies with seedlings (Baker and van Bavel 1988; Sakuratani et al. 1999; Song et al. 2000; Wan et al. 2000) or mono-specific stands (Wan et al. 1993; Caldwell et al. 1998; Ryel et al. 2002), where diel variations in soil water potential (ψ_s) are attributed to HR of an individual species. In natural communities, species differences in HR have also been described in low density habitats where root systems from different species generally do not overlap (e.g. deserts, Yoder and Novak 1999; Donovan et al. 2003) or where co-occurring species differ in rooting depth, phenology, or access to groundwater (e.g. trees and co-occurring grass species, Dawson 1993, 1996; Millikin and Bledsoe 2000; Ludwig et al. 2003). Differences in HR among co-occurring species have been shown for *Eucalyptus* trees and trees of the Brazilian 'Cerrado' using heat pulse systems to measure root xylem sap flux (Burgess et al. 1998; Scholz et al. 2002). This technique, however, is very labor intensive and is probably not feasible for simultaneous comparisons of large number of individuals and species. In the present study we compare HR of adult plants in a complex natural community by growing roots of known species in root chambers and measuring diel ψ_s fluctuations.

Species-specific HR information is not only important for understanding ecosystem hydrology, but also relevant to understanding its potential value as an adaptive trait. It has been proposed that hydraulic redistribution (in particular, hydraulic lift, HL) 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 et al. 2000a). The present study compares HL ability among four tree species and two grass species that coexist in a subxeric sandhill habitat of southeastern USA, but exhibit differential ability to colonize neighboring xeric sandhills (Weaver 1969; Jacquemain et al. 1999). The fall-line sandhills consist of deep sandy soils with poor water and nutrient retention capacity (Peet and Allard 1993; Christensen 2000; Goebel et al. 2001) and variation in topography produces an edaphic gradient of subxeric hill slopes to xeric sand ridges (Christensen 2000; Goebel et al. 2001). At the subxeric study site, the tree community consists of *Pinus*

palustris L. (longleaf pine), *Quercus laevis* Walt. (turkey oak), *Q. incana* Bartr (bluejack oak), and *Q. margaretta* Ashe (sand post oak). The understory vegetation is sparse and composed mainly of two C4 bunchgrasses, *Aristida stricta* Minchx. (wiregrass) and to a lesser extent *Schizachyrium scoparium* Minchx. (little bluestem). Root systems of tree species are highly interwoven, whereas grass species tend to occur in patches and their root systems are more easily isolated (personal observation). Among these species, only *Q. margaretta* and *S. scoparium* fail to dominate adjacent xeric sandhill ridges (Wells and Shunk 1931; West 2002). Differential species distribution across the edaphic gradient may be linked to belowground resource use and fine root demography (Mavity 1986; Donovan et al. 2000; Espeleta and Donovan 2002; West 2002; West et al. 2003a, 2003b).

The objectives of this study were to determine the extent to which HL occurred in this subxeric sandhill habitat and whether HL activity differed among the co-occurring tree and grass species. In addition, we examined whether the capacity for HL in this subxeric habitat was associated with the differential ability of the study species to colonize adjacent xeric habitats.

Materials and methods

Study site

The investigation was conducted at the Carolina Sandhills National Wildlife Refuge located in McBee, South Carolina at approximately 100 m above sea level. This site has a mean annual temperature of 16°C and a mean annual precipitation of 1,234 mm. During our study, total precipitation and summer growing season precipitation for 1999 and 2000 were below average. The study plot was located in a subxeric community, intermediate along the topographic slope, where all tree and grass species co-occurred. The soil, Typic quartzizamment (USDA 1995), consisted of a top layer of approximately 1 m of very coarse white sands, followed by a deep layer of yellow sands with little clay content. A layer of compacted and hydrophobic red clay appears at approximately 4 m. Observations of a big soil pit in the vicinity (about 100 m 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, as previously observed in soils of this region by Oliver (1978).

Experimental design and methods

Our study plot (20 m × 50 m) contained adult individuals of all of the study species: *P. palustris*, *Q. laevis*, *Q. incana*, *Q. margaretta*, *A. stricta* and *S. scoparium*. In order to collect species-specific HL activity in the field, roots of the study species were grown for 3 years in species-specific root chambers (one chamber per plant, four to six plants per species). Each root chamber was a PVC half-cylinder (diameter = 60 cm, depth = 60 cm, volume = 89 l) installed so that the sides prevented lateral colonization of any roots besides those transplanted into them, and the open top (flush with soil level) and bottom permitted precipitation input and flow-through. Each chamber had a perpendicular Plexiglass window on the side (50 × 50 cm) for observing root colonization and measuring root demography (concurrent study, Espeleta 2002). The observation windows and associated access pits were insulated except for monthly tracings of roots.

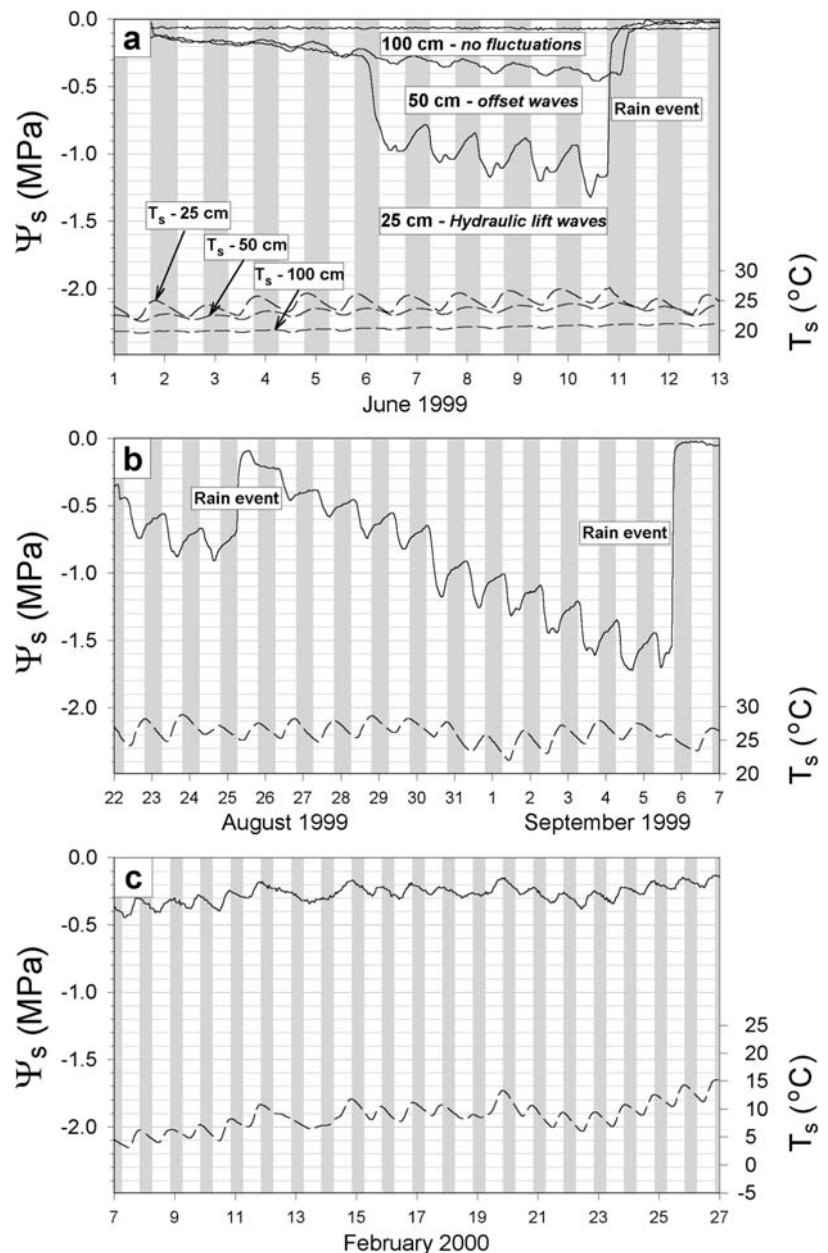
For each tree (dbh: 20–70 cm, six trees per species, four species), two intact lateral roots (1–2 m length, 0.5–1.0 cm diameter) were excavated from the soil and inserted through lateral holes into a root chamber on 19 February 1999. The roots were found generally at 25–50 cm depth in the soil but were placed at the same depth (25 cm) inside the chamber. The root chamber was then buried 1–2 m from the bole of the tree and refilled with the original soil, maintaining the original stratification. Soil water potential (ψ_s) was measured with two thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, Utah, USA) (see details below). Two psychrometers were placed in the center of each tree root chamber at 25-cm depth, approximately 5 cm from each lateral root, and 20 cm from each other. Observations through the Plexiglass window confirmed that new roots re-colonized the soil inside of all 24 tree root chambers before the end of the 1999 growing season. Other than the excavated laterals, the tree root systems were undisturbed.

For the bunch grasses (adult plants, four plants per species, two species), each plant was carefully excavated as a semi-cylindrical soil monolith (diameter =60 cm, depth =20 cm) containing the majority of the root system, on 19 February 1999. We did not

observe grass roots growing deeper than ca. 50–60 cm below the bunchgrasses. The soil just below the monolith was excavated to a depth of 60 cm and a root chamber was placed in the pit. The chamber was refilled with the original soil to a depth of 25 cm, maintaining the original stratification. One 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 (depth: 20 cm) were then placed on top. One *S. scoparium* plant died after transplant and was not replaced. This single chamber without roots was used afterward as a control chamber. In the remaining seven chambers, observations through the Plexiglass window confirmed that new roots re-colonized the soil by the spring of 1999 and reached depths of ca. 50 cm that same year.

We prevented root invasions by removing foreign roots outside of the root entrance holes (tree chambers) and the open bottoms of chambers (tree and grass chambers). As the tree roots grew in diameter, the gaps of the entrance holes were filled by the end of the first year. To control invasions in the bottom of chambers, roots could be detected through the 1-m deep soil pit and observed via the Plexiglass windows. However, roots were not detected/observed in

Fig. 1a–c Patterns of soil water potential (ψ_s , solid line) and soil temperature (T_s , dashed line) indicative of hydraulic lift (HL) and “offset fluctuations” (Millikin and Bledsoe 2000). Gray bars indicate nighttime: **a** Depth-specific ψ_s and T_s during drying of the soil outside of root chambers from 1 June to 10 June 1999. The ψ_s pattern at 25 cm shows gradual and abrupt soil drying (June 1–5 and June 6, respectively), HR (June 6–9) and soil moisture recharge due to precipitation (June 10). Note that for HR, ψ_s becomes less negative overnight and declines sharply at sunrise. In contrast, the 50 cm depth showed only “offset waves” where ψ_s closely tracked the fluctuations in T_s and did not conform to the diurnal pattern associated with HR. The soil at 100 cm was uniformly wet and showed little fluctuation in T_s . In the afternoons of June 6–10, smaller waves preceded nighttime HR (June 2, 4–10). Their nature is uncertain, but could be a consequence of daytime HR, due to afternoon stomatal closure (see Discussion). Similar waves were observed simultaneously in psychrometers placed at 25 cm in different locations; **b** HL and **c** “offset” fluctuations, inside root chambers. Contrary to HL, offset fluctuations closely tracked T_s . Data for **b** and **c** were obtained from the same psychrometer placed at 25-cm depth inside a root chamber with roots of *Quercus laevis*, during: **b** 22 August to 6 September 1999, and **c** 7–26 February 2000



any of the chambers during the study, probably because the bottoms of chambers reached down to 60-cm depth and root densities in the soil outside the chambers were very low below 50 cm.

In March 2000 a prescribed burn crossed a fire line and burned the study plot. The fast moving fire did not damage the root chambers and was not detected as an increased temperature by any of the psychrometers at 25 cm. The trees in the study plot did not burn, but grass plants in five of the seven chambers were burned, leaving one of each species untouched. However, only overwintering aboveground tissue burned and all plants produced normal spring leaf flushes in April 2000. Post-fire ψ_s for unburned and burned grasses did not differ, so we include all chambers in the analysis and make the assumption that the fire did not substantially alter our results with the grasses.

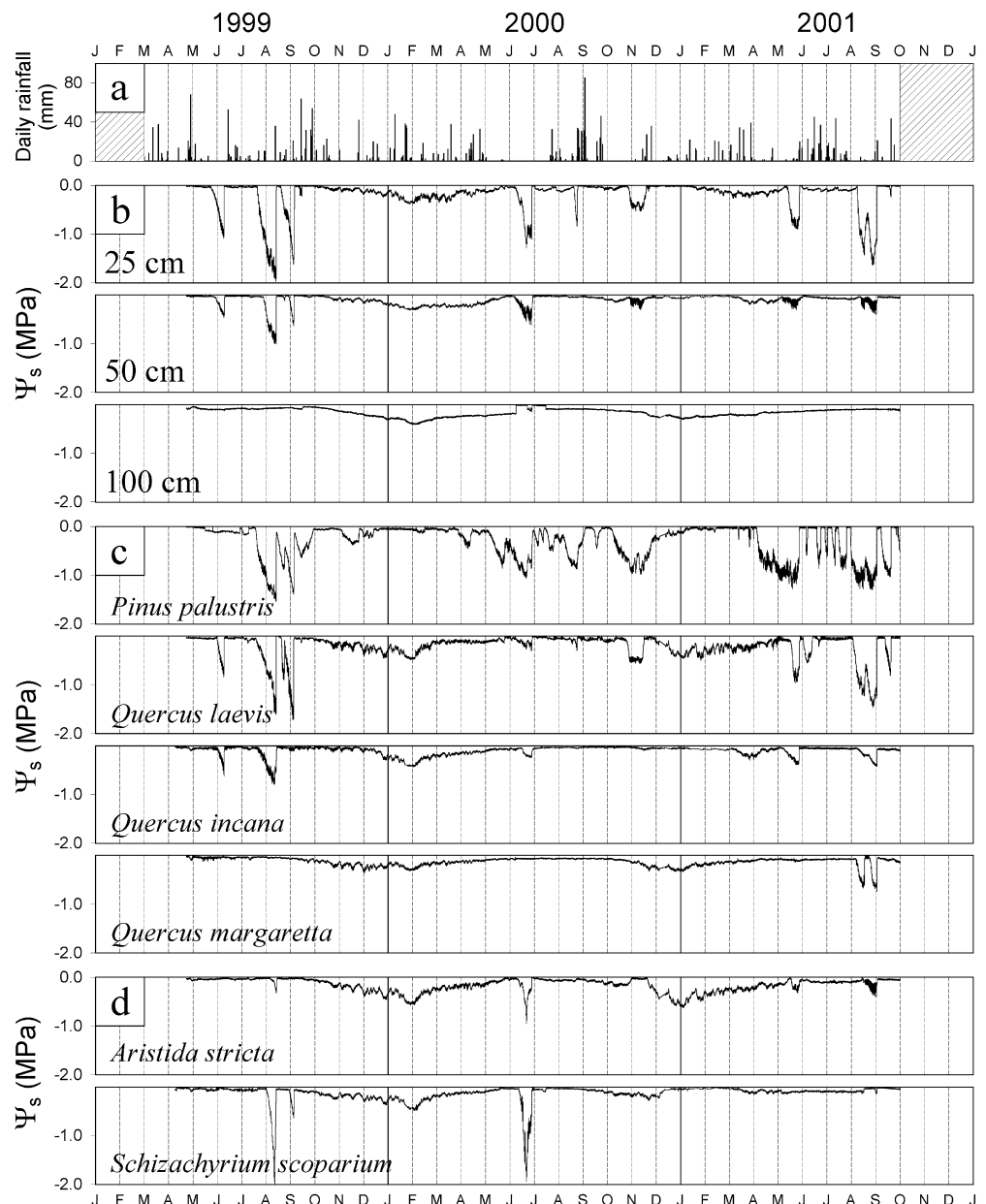
Soil water potential (ψ_s) and HL

Soil temperature and ψ_s were measured every hour for 3 years in our study plot with 80 individually calibrated psychrometers (Brown

and Bartos 1982) interfaced with two data loggers (CR7; Campbell Scientific, Logan, Utah, USA). Both data loggers were placed in two different locations inside the study area so the distance to any psychrometer tip was not greater than 10 m. To prevent excessive temperature fluctuations in the CR7 panel, each data logger was buried in the ground inside hermetic boxes that were covered by a plastic-fiberglass insulation sheet. The data logger box was unburied every 1–2 months to replace data storage modules and desiccant bags. Psychrometer offset values were generally within the range necessary for accurate readings of water potential (-5 to $+5$ μV , Brown and Bartos 1982) and data with offset values beyond that range were discarded. In addition to installation at 25 cm depth in each root chamber (see above), psychrometers were placed in the general soil matrix outside of chambers at 25, 50 and 100 cm soil depths in at six locations in the study plot. Air temperature and photosynthetic flux density (quantum sensor, LICOR, Lincoln, Neb., USA) were also recorded hourly.

Patterns of ψ_s were examined for each psychrometer and each day throughout the study to assess the presence of HR events (Caldwell et al. 1998). The criteria for the presence of HL were a diel fluctuation of at more than 0.05 MPa and a pattern of increasing ψ_s

Fig. 2a–d Rainfall (mm) and maximum soil drying recorded throughout 3 consecutive years (1999–2001). **a** Daily precipitation at the CSNWR headquarters, approximately 7 km from the study plot. Data of maximum soil drying corresponds to the psychrometer with the minimum curve of soil water potential (ψ_s) at each location: **b** hourly ψ_s outside root chambers at three different depths (25, 50 and 100 cm), **c** hourly ψ_s inside root chambers with roots of tree species (*Pinus palustris*, *Quercus laevis*, *Quercus incana* and *Quercus margaretta*), **d** hourly ψ_s inside root chambers with roots of grass species (*Aristida stricta* and *Schizachyrium scoparium*)



drying curves (e.g. Fig. 1a, curve at 25 cm depth for 6 June 1999). This was also indicated by the continuously high ψ_s recorded in the control chamber containing only soil without grass or tree roots (data not shown).

HL activity was common in the subxeric sandhill community during the 3-year study (Table 1, Figs. 2, 3). It was most prevalent at 25 cm depth, but also common at 50 cm depth outside of the root chambers (Fig. 3). Even though the soil at 100 cm depth was generally wetter than the surface soils (Tables 1, 2, Fig. 2b), HL was still recorded in a few instances at 100 cm (Fig. 3). There was a strong seasonality in the patterns of ψ_s (inside and outside the root chambers). During the winter months of December to March, all soils were continuously wet ($\psi_s > -0.2$ MPa, Fig. 2) and HL was not observed. During the rest of the year (April to November), HL was common, and could be observed for more than 100 days per year and 20 days in a single month inside the root chambers of tree species and in the soils outside of chambers (Fig. 3).

Tree species differed in the HL activity assessed as Percent Dry Days With HL ($P=0.048$) and Number of HL Days ($P=0.058$) (Tables 1, 2). Species also differed in soil drying within the chambers (Seasonal ψ_s , $P=0.049$). Among the trees, *Pinus palustris* exhibited the highest HL activity and the most soil drying, especially during 2000 and 2001. *Quercus laevis* and *Q. incana* exhibited intermediate HL activity and less negative Seasonal ψ_s . *Q. margareta* did not exhibit any HL during the 3 years of the study, but Seasonal ψ_s was similar to the other *Quercus* species.

HL activity was much less ubiquitous for the grasses (Table 1, Fig. 3). HL activity was found inside one root chamber of *A. stricta* 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). HL was not recorded in the summer of 1999 for any grass species (Fig. 3). *Schizachyrium scoparium* did not exhibit any HL during the 3 years of the study.

HL also appeared to be very prevalent during drying cycles in hydraulic lifting tree species. In the soil outside of the root chambers, and in the root chambers of tree species with HL activity (*P. palustris*, *Q. incana* and *Q. laevis*), HL was present in up to 90% of all drying cycles of the soil. Similar to the sharp ψ_s decreases during a single day of soil drying (e.g. ψ_s at 25 cm, 6 June 1999, Fig. 1a) we also observed sharp increases in ψ_s after HL events. The amplitude of a HL wave in a single day reached in some instances values up to 0.3 MPa (Fig. 1b) or even 0.42 MPa (Table 1).

Discussion

The dominant species in the subxeric sandhill habitat differed in HL activity. Our technical approach of transplanting roots into field root chambers proved to be successful to study simultaneously a larger number of replicates and species in a habitat where root systems generally overlap. Like other investigations that compared

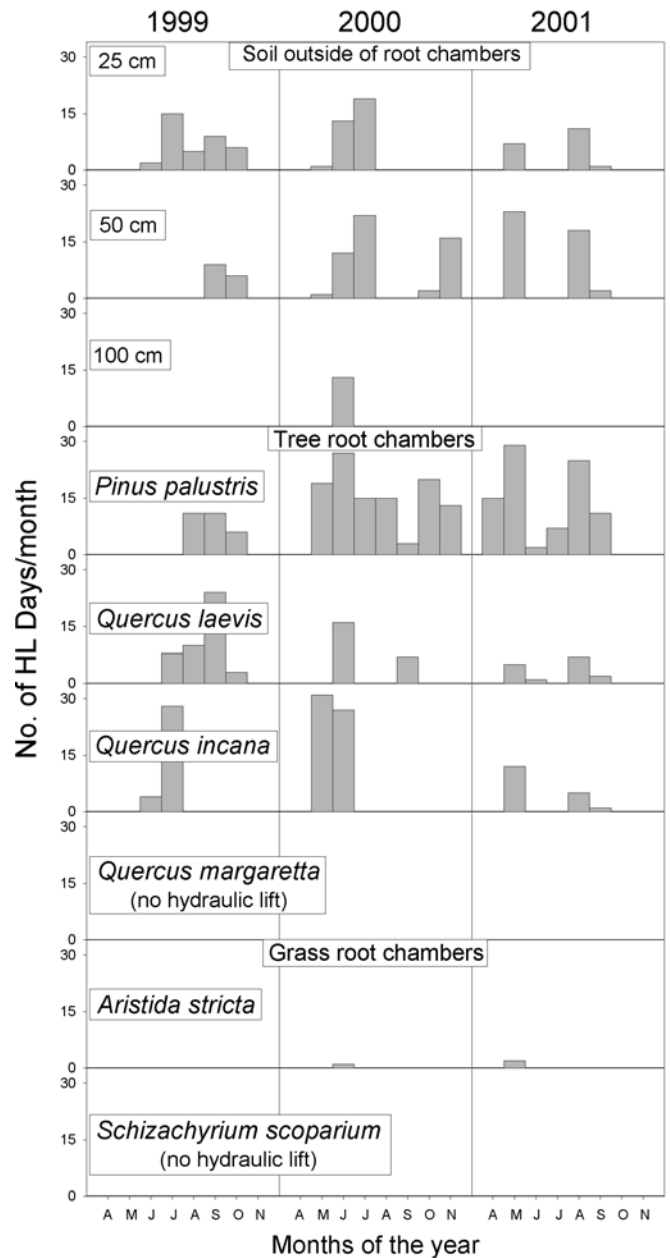


Fig. 3 Maximum number days with hydraulic lift (HL) registered each month (April to November) during 3 consecutive years (1999–2001), for 25, 50 and 100 cm outside root chambers and 25 cm soil depth inside chambers with roots of the following tree species: *Pp* (*Pinus palustris*), *Ql* (*Quercus laevis*), *Qi* (*Quercus incana*), *Qm* (*Q. margareta*), and grass species: *As* (*Aristida stricta*), *Ss* (*Schizachyrium scoparium*). For each tree species and soil depth outside of chambers, $n=6$. For each grass species, $n=3$ (*S. scoparium*) and 4 (*A. stricta*)

HR across different functional types, such as trees and understory plants (Dawson 1993), and trees and grasses (Ludwig 2001; Ludwig et al. 2003), we found different patterns of ψ_s and different HR activity among overstory trees and grasses that dominate the understory vegetation. In our study of subxeric sandhills, trees were clearly the dominant redistributors of water to the surface soil. Nonetheless, we also found differences within the species

Table 2 Analysis of variance results for soil depth, tree species, and grass species in the dynamics of soil water potential (ψ_s) and hydraulic lift (HL) during 3 years of study in the sandhills. See Table 1 and methods for species and details on variables

Variable	Outside root chambers			Inside root chambers					
	Differences across soil depth			Differences among trees			Differences among grasses		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Seasonal ψ_s	2	0.456	0.643	3	3.200	0.049	2	1.790	0.222
Number of dry days	2	3.738	0.049	3	1.122	0.369	2	0.530	0.499
Number of HL days	2	1.299	0.304	3	3.036	0.058	2	2.087	0.208
Percent dry days with HL	2	1.132	0.348	3	3.151	0.048	2	2.125	0.205
HL ψ_s amplitude	2	1.239	0.319	3	2.179	0.1280	2	2.143	0.203

of trees and grasses studied, including significant differences between *Quercus* species. This indicates that differentiation in HL activity can occur for closely related species in the same community. Therefore, even small changes in species composition or relative dominance can potentially alter the hydraulic redistribution patterns of entire ecosystems (sensu Jackson et al. 2000a).

Differences in HL activity were also associated with the ecological distribution and apparent resource use strategies of the species, suggesting that HR may be involved in the differential ability of plants to tolerate resource limitation or compete for soil resources (sensu Grime 1977; Aerts 1999). HL activity was recorded in all species except for *Q. margaretta* and *S. scoparium*, the study species that generally do not occur in the most xeric habitats. In previous studies, *Q. laevis* and *Q. incana* were more conservative in water use than *Q. margaretta* (Donovan et al. 2000) and *Q. laevis* seedlings exhibited lower photosynthetic ability but greater water use efficiency than other mesic oak species (Vaitkus and McLeod 1995). On the other hand, *Quercus* species from more mesic sandhill habitats, including *Q. margaretta*, exhibited greater fine root growth in response to resource addition (Espeleta 2002; Espeleta and Donovan 2002). 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 generally restricted to subxeric and mesic habitats (West et al. 2003a). HL may contribute to tolerance of more frequent and severe droughts in xeric habitats. Hydraulically lifted water can prolong fine root survival in dry surface soil and increase the population of new roots, which are known to exhibit greater water efflux rates during HL events (Dawson 1998). This greater fine root survival and increased soil moisture could improve nutrient uptake in otherwise dry surface soils (Caldwell et al. 1991; Matzner and Richards 1996; Dawson 1998; De Kroon et al. 1998).

Why was HL absent in *Q. margaretta* and *S. scoparium*? Starting with *Q. margaretta*, we can eliminate some possibilities. It was not likely due to inadequate access to subsurface water during the course of the investigation. ψ_s was generally high at 1 m depth and measurements of predawn leaf water potentials (all trees > -0.5 MPa, data not shown) during periods of low ψ_s in late summer of 2001 indicated that all of the tree species

had access to wet soil layers. It was also not likely due to lack of sufficient gradient in water potential between deep and surface soil in order to drive water efflux from roots. HL activity was observed in *Q. incana*; however, chambers with roots of *Q. incana* and *Q. margaretta* exhibited a similar intensity of soil drying (although *Q. incana* had lower Number of Dry Days than *Q. margaretta*, mean and minimum Seasonal ψ_s were similar, Table 1). It was also not due to a lack of root proliferation inside the root chamber. In a concomitant study (same root chambers and time interval) that compared root demography of all tree species of this study, *Q. margaretta* was second only to *P. palustris* in fine root growth (Espeleta 2002). This suggests species differences in HL may be due to species-specific hydraulic constraints that limit the transport of water from deep wet soil and/or the efflux out of surface roots to the dry soil, such as the loss of hydraulic conductivity in the surface fine roots.

Greater death of *Q. margaretta* fine roots as a response to the drying surface soil can explain why HL was not observed in *Q. margaretta*. Death of surface fine roots upon drying of the topsoil can lead to the loss of root-soil contact and hydraulic conductivity, and this restricts water efflux from fine roots to dry soil and HL (Caldwell et al. 1998). This type of drought-deciduousness has been reported previously in succulent desert species in which water efflux from roots increases as ψ_s starts to decrease (Nobel 1994). Further decreases in ψ_s eventually induce root death and cause cessation of water efflux. In this context, death of surface fine roots in response to drying of the topsoil may function as a “hydraulic fuse” that prevents excessive water efflux into the soil (Jackson et al. 2000a). Fine roots in surface soil of some tree species have also shown to be susceptible to even moderate drying (fine root death in Sitka spruce can be triggered just below -0.01 MPa, Deans 1979). Evidence from concomitant studies using the sandhill tree species indicate that mesic oak species exhibit substantial root death as a response to soil drying (Espeleta 2002; Espeleta and Donovan 2002). In a greenhouse study using seedlings, fine surface roots in *Q. margaretta* and another mesic sandhill oak species (*Q. marilandica*) were more susceptible to surface drought than the more xeric species *Q. incana* and *Q. laevis* (Espeleta 2002). At our field site, *Q. margaretta* exhibited greater rates of fine root mortality in the summer than the

other tree species, and substantial death occurred at comparatively higher ψ_s than xeric species (Espeleta 2002). The association between fine root demography and HL had been previously suggested in the literature (Eissenstat and Yanai 1997; Caldwell et al. 1991; Caldwell et al. 1998) but this study with sandhill species is the first demonstration of this link in the field.

In contrast to trees, HL in grasses may be more easily limited by a shallow root system that does not access deeper wetter soil. We observed some deep roots reaching depths close to 50 cm in chambers with plants of the two grass species (West et al. 2003a) but it is less probable that many roots were present down to 1 m where water availability was essentially continuous. Analogous to *Q. margaretta*, the complete absence of HL activity in *S. scoparium* might also reflect inherent HL inability due to greater death rates of surface fine roots of that species relative to *A. stricta* (West et al. 2003a).

It is possible that differences among species in HL activity might be linked to differences in root membrane permeability to water efflux. Due to the steep drying curves and the large amplitude of HL waves observed, we think that roots from hydraulic lifters in this habitat can drive substantial changes in soil water content. High permeability to water flux by tree roots can allow high water movement in either direction (i.e. uptake or efflux), enough for changing substantially the ψ_s of the nearby soil volume. The afternoon waves observed sometimes before nighttime HL (Fig. 1a) can also be linked to high water conductance via roots. If water moves fast into and out of roots, afternoon stomatal closure can drive fast recharge of plant water potential, and, eventually, some water efflux can occur during the day. Daytime HL has also been observed for CAM species not exhibiting nighttime HL (Yoder and Novak 1999) and in taproots at the beginning of the wet season (Smith et al. 1999). Most recently, Scholz et al. (2002) recorded reverse sap flow (indicative of hydraulic redistribution) for tree species of the Brazilian cerrado. This efflux can continue up until soil and plant water potential equilibrate, leading to continuous HR (Burgess et al. 2000), or to short HR waves if stomates reopen. The possibility of these short lapses of daytime HL occurring under natural conditions in the sandhills deserves further investigation; including simultaneous studies of diel root water and stomatal conductance.

The profuse occurrence of HL and the high magnitude of HL waves in the surface soil outside of the root chambers suggests that tree roots can potentially contribute significantly to the rewetting of the topsoil. The frequency and magnitude of soil drying in the external soil resembles more the patterns observed in the root chambers of *P. palustris* and *Q. laevis* (to a lesser degree), than those of the grass chambers or the other tree species. This suggests that these tree species may determine the patterns of surface ψ_s of the subxeric community. Also, this suggests that trees and grasses directly interact in surface soils, resulting in a clear potential for either competition or facilitative interactions between them (Caldwell and Richards 1989; Dawson 1993). Our results therefore agree with previous studies (Le Roux et al. 1995; Ludwig 2001) that found no evidence of niche differentiation between roots of trees and grasses in savanna ecosystems

via differential vertical deployment of roots (the 'two-layer hypothesis', Sala et al. 1989; Scholes and Archer 1997).

Because tree and grass species are all mining the coarse sands of the top soil, hydraulically lifted water may significantly ameliorate the frequency and intensity of surface drought in these sandhill plant communities. The relative dominance of species that redistribute water from the deep soil to the rapidly drying shallow soil likely has a strong effect on ecosystem water balance. Our results also indicate that the scale of species differentiation in HR activity is finer than previously described, because large differences were observed for the first time among congeneric species that coexist in the same habitat. Therefore, potentially large changes in ecosystem hydrology and associated processes can occur as a consequence of relatively small changes in species composition. Detection of fine scale species differences in HL ability with our chamber techniques and other methods (e.g. Burgess et al. 1998; Scholz et al. 2002) will further improve the understanding of individual species' contribution to ecosystem water balance.

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