Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte

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Summary We investigated hydraulic constraints on water uptake by velvet mesquite (*Prosopis velutina* Woot.) at a site with sandy-loam soil and at a site with loamy-clay soil in southeastern Arizona, USA. We predicted that trees on sandy-loam soil have less negative xylem and soil water potentials during drought and a lower resistance to xylem cavitation, and reach E_{crit} (the maximum steady-state transpiration rate without hydraulic failure) at higher soil water potentials than trees on loamy-clay soil. However, minimum predawn leaf xylem water potentials measured during the height of summer drought were significantly lower at the sandy-loam site (–3.5 ± 0.1 MPa; all errors are 95% confidence limits) than at the loamy-clay site (–2.9 ± 0.1 MPa). Minimum midday xylem water potentials also were lower at the sandy-loam site (–4.5 ± 0.1 MPa) than at the loamy-clay site (–4.0 ± 0.1 MPa). Despite the differences in leaf water potentials, there were no significant differences in either root or stem xylem embolism, mean cavitation pressure or Ψ_{95} (xylem water potential causing 95% cavitation) between trees at the two sites. A soil–plant hydraulic model parameterized with the field data predicted that E_{crit} approaches zero at a substantially higher bulk soil water potential (Ψ_s) on sandy-loam soil than on loamy-clay soil, because of limiting rhizosphere conductance. The model predicted that transpiration at the sandy-loam site is limited by E_{crit} and is tightly coupled to Ψ_s over much of the growing season, suggesting that seasonal transpiration fluxes at the sandy-loam site are strongly linked to intra-annual precipitation pulses. Conversely, the model predicted that trees on loamy-clay soil operate below E_{crit} throughout the growing season, suggesting that fluxes on fine-textured soils are closely coupled to inter-annual changes in precipitation. Information on the combined importance of xylem and rhizosphere constraints to leaf water supply across soil texture gradients provides insight into processes controlling plant water balance and larger scale hydrologic processes.

Introduction

Plants play a critical role in the hydrologic cycle because transpiration transfers large amounts of water from the soil to the atmosphere (Huxman et al. 2005, Seyfried et al. 2005). The influence of plant form on hydrologic processes may differ because of variation in factors such as vertical root distribution (Schenk and Jackson 2002) and maximum rooting depth (Canadell et al. 1996). The encroachment of woody plants into grasslands can alter ecosystem water balance by increasing rooting depth and, thus, the depth from which plants extract water for transpiration. Regardless of rooting depth, hydraulic limitations to water uptake and transport play an important role in the regulation of transpiration. Limitations imposed by soil and plant hydraulic characteristics determine, in part, the magnitude and pattern of impact on hydrologic cycle processes associated with woody plant encroachment into former grasslands. We investigated these hydraulic limits in *Prosopis velutina* Woot. (velvet mesquite), which has become established in grasslands on two different geomorphic surfaces in southern Arizona, USA.

Soil texture strongly mediates plant water availability through its control on soil hydraulic characteristics (Sperry et al. 1998, Hacke et al. 2000a, Sperry and Hacke 2002), because the saturated hydraulic conductivity of soil is a function of pore size; coarser textured soils have larger pores and higher saturated conductivity than finer textured soils (Jury et al. 1991). Coarse-textured soils, however, lose more water and have lower conductivity at higher soil water potentials (Ψ_s) than fine-textured soils, to the extent that plants growing in coarse soils exhaust their water supply at higher water poten-

tials than plants growing in fine-textured soils. Plants may overcome the effects of steeply declining soil hydraulic conductivity at high Ψ_s by developing higher root to leaf area ratios ($A_r:A_l$), or by lowering the transpiration rate (E). Both features will reduce the rate of water uptake per root surface area (rhizosphere flux density), thereby minimizing the loss of hydraulic contact between the root system and the soil (Sperry et al. 1998, Hacke et al. 2000a).

Regardless of climate or soil type, xylem cavitation resistance should correlate with the range of water potentials experienced by the plant, given that excessive costs (i.e., in carbon allocation or reduced hydraulic efficiency, or both) may be associated with overly resistant xylem (Sperry 1995, Alder et al. 1996, Hacke et al. 2001). Therefore, plants occurring on coarse-textured soils typically must operate at relatively high Ψ_s and may be more vulnerable to cavitation than plants occurring on fine-textured soils (Sperry et al. 1998, 2002, Hacke et al. 2000a). This trend may be particularly apparent in roots, which are generally more vulnerable to cavitation and demonstrate a greater plasticity across moisture gradients than stems (Alder et al. 1996, Hacke et al. 2000a, Jackson et al. 2000).

Over the last 100 years, deeply rooted leguminous trees and shrubs in the genus *Prosopis* have become established in upland and floodplain grasslands throughout the southwestern United States and northern Mexico (Brown and Archer 1989, Archer 1995). The encroachment of mesquite has the potential to dramatically alter hydrologic processes in these systems, partly because they can cope with water limitations during early life stages, followed by exploitive use of stable water sources during maturity (Brown and Archer 1989). However, the patterns and consequences of mesquite water use on ecosystem hydrology may be highly variable across soil texture gradients. We assessed the relationships between xylem cavitation vulnerability, xylem anatomy and soil texture in two populations of velvet mesquite in southeastern Arizona, USA. One population was at a seasonally dry site with sandy-loam soil characterized by a relatively high saturated hydraulic con-

ductivity that declined steeply at high Ψ_s. The second population occurred at an adjacent site with loamy-clay soils with a comparatively low saturated hydraulic conductivity that declined gradually with reductions in Ψ_s. We predicted that trees on sandy-loam soils would operate at higher soil water potentials and have xylem that is less resistant to cavitation (particularly in the roots) than trees on loamy-clay soils.

Data on plant and soil hydraulic characteristics were used to parameterize a soil–plant hydraulic transport model (Sperry et al. 1998) to identify differences in the maximum steady-state E without hydraulic failure (E_{crit}) between the sites. The E_{crit} gave us an estimate of the seasonal differences in tree water uptake and use between sites. Differences in E_{crit} across soil texture gradients could have important consequences for soil water storage, carbon and water fluxes and ecosystem productivity on the landscape scale.

Materials and methods

Research sites

The study was conducted at two sites within the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA (Fravolini et al. 2003). One site was on a young Holocene (4,000 to 8,000 ybp) geomorphic surface and one site was on a mid-Pleistocene (200,000 to 300,000 ybp) geomorphic surface. The site on the Holocene surface was characterized by deep alluvial sandy-loam soils with relatively high saturated hydraulic conductivity (K_s) (Table 1). The vegetation overstory at this site was dominated by a mixed-aged stand of *Prosopis velutina*. The understory was dominated by the perennial C_4 grass *Eragrostis lehmanniana* Nees. intermixed with other herbaceous taxa. Mean annual precipitation is about 394 mm with approximately 56% falling during the summer monsoon (July–September). The site on the mid-Pleistocene surface was located 5 km from the Holocene (sandy loam) site and was characterized by deep loamy-clay soils with a comparatively

Table 1. Mean annual precipitation, location, elevation, stand density and selected soil parameters at the Santa Rita Experimental Range in southeast Arizona, USA, during the 2003 growing season. Precipitation values in parentheses represent mean annual precipitation during the summer months (July–September). Texture fraction and bulk densities were used to calculate a soil fitting parameter (b), the air entry potential (Φ_e) and saturated hydraulic conductivity (K_s).

Parameter	Sandy loam	Loamy clay
Annual precipitation (mm)	394 (220)	430 (241)
Location	31°47′N, 110°50′W	31°47′N, 110°54′W
Elevation (m)	1190	1090
Stand density (stems ha^{-1})	540	60
Soil properties (30–60 cm):		
Sand (%)	79	54
Silt (%)	11	14
Clay (%)	9	32
Bulk density (Mg m^{-3})	1.6	1.3
b	3.48	9.87
Φ_e	–1.36	–2.53
K_s (mol s^{-1} MPa^{-1} m^{-1})	29.7	8.7

low K_s (Table 1). The overstory was dominated by a mixed-age stand of *P. velutina*, however, the number of stems per hectare was substantially lower at the Pleistocene (loamy clay) site than at the sandy-loam site (Table 1). The understory vegetation at the loamy-clay site was much more sparse than at the sandy-loam site and was also dominated by *E. lehmaniana*. Mean annual precipitation at the loamy-clay site was about 430 mm with 56% falling during the summer monsoon. Mean annual air temperature on the SRER was 16 °C.

Xylem water potential

Six mature mesquite trees were randomly selected at each site for water potential measurements. Leaf xylem water potential (Ψ_x) was measured with a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR) during the 2003 growing season in June, before the onset of the monsoon, and once in mid-August at the peak of the monsoon. A single shoot tip from each of the six trees was cut with a sharp razor blade and measured at predawn (Ψ_{pd}) between 0200 and 0400 h and at midday (Ψ_{min}) between 1100 and 1300 h.

Vulnerability curves

Vulnerability curves were estimated in root and stem segments by the air-injection, or air-seeding method (Sperry and Saliendra 1994). According to air-seeding theory (Zimmermann 1983), the negative Ψ_x required to pull air into a xylem conduit (i.e, the air-entry potential) and cause cavitation is equal to the opposite positive pressure required to push air into the conduit when Ψ_x is equal to atmospheric pressure. The air-injection method produces results that are comparable with other methods to generate vulnerability curves, including dehydration (Alder et al. 1996, Pockman and Sperry 2000) and centrifugation (Pockman et al. 1995).

Vulnerability curves were measured on 5–6 trees per site during the 2003 growing season. Roots occurring between 20- and 50-cm depths were carefully excavated near the base of the tree and stems were harvested from sunlit locations near the top of the canopy. Stems and roots were cut under water and transported to the laboratory in sealed plastic bags containing moist paper towels. Sample stems and roots had an inside bark diameter of about 5 mm and were cut longer than the estimated maximum vessel lengths to prevent air from being artificially introduced into the xylem vessels. Maximum vessel lengths were measured on roots (175 cm ± 23.5, $n = 6$) and stems (66.7 cm ± 3.6, $n = 20$) as described by Zimmermann and Jeje (1981). In the laboratory, segments were re-cut underwater to prevent the introduction of additional emboli. The segment ends were trimmed with a sharp razor blade to eliminate flow restrictions introduced when the stem and root segments were cut in the field. Before determining the vulnerability curve, the segments were flushed with deionized water at 100 kPa to insure that the curve included water transport through all potentially functional xylem conduits. Flushed segments were inserted through a double-ended pressure sleeve previously described by Pockman and Sperry (2000). One end of the segment was fitted with rubber gaskets and in-

stalled in a tubing manifold filled with filtered, deionized water. Each segment was measured individually by applying gravity-induced pressure of 10 to 20 kPa depending on the length of the segment. Xylem hydraulic conductivity (K_x = mass flow rate per pressure gradient) was determined by collecting the flow from the segment in tared vials filled with cotton. After flushing, pressure inside the chamber was raised to 0.1 MPa and maintained for 20 min to allow air to fill all open vessels (if present), excluding them from subsequent K_x measurements. The pressure was then returned to atmospheric pressure and the segment was allowed to equilibrate for 10 min before making initial measurements of K_x. Previous studies have measured K_x with pressure in the pressure sleeve held at 0.1 MPa to avoid xylem leakage inside the chamber. However, we found that measurements were less variable after the pressure inside the chamber was returned to atmospheric levels. After the initial measurement, the process was repeated at progressively higher pressures in 1.0 MPa increments until embolism reached 95% or greater. The percentage loss of K_x (PLC) was plotted as the conductivity at each pressure ($K_{x,P}$) against the initial measure of conductivity at 0.1 MPa ($K_{x,0.1}$): PLC = $100(1 - K_{x,P}/K_{x,0.1})$.

The vulnerability curves were used to calculate mean cavitation pressure (Ψ_{mean}) and the Ψ_x required to eliminate 95% of xylem conductivity (Ψ_{95}). We determined Ψ_{mean} by first considering the vulnerability curve as a cumulative distribution of loss of conductance with pressure, then replotting the curve as a frequency distribution over the same pressures or "pressure classes" (Sperry and Saliendra 1994). The Ψ_{mean} for the distribution was calculated based on the mid-points of each pressure class. Mean cavitation pressure was determined for the entire vulnerability curve for comparison with conduit diameter and maximum K_x. Where Ψ_{mean} represents the entire vulnerability curve, Ψ_{95} approximates the minimum Ψ for water transport and thus for meaningful gas exchange. We estimated Ψ_{95} as Ψ_x at 95% cavitation using a Weibull function fitted to each vulnerability curve (see details below). The Weibull function was fitted with the software package JMP 5.1 (SAS Institute Inc, Cary, NC)

Specific conductivity, leaf specific conductivity and sapwood area/leaf area ratio

Specific conductivity yields a direct measure of hydraulic efficiency independent of conducting area. The specific conductivity (kg s^{-1} m^{-1} MPa^{-1}) was calculated by dividing maximum K_x by the mean cross-sectional conducting area of each root (K_r) and stem (K_{st}) segment. The cross-sectional conducting area was assumed to equal all the area beneath the root cortex or bark, unless heartwood was evident on visual examination, in which case the cross-sectional area of heartwood was subtracted. Cross-sectional area was measured with digital calipers.

Leaf-specific conductivity (K_l) was calculated by dividing maximum K_x by the projected leaf area supplied by the stem segment. The ratio between mean cross-sectional sapwood area and projected leaf area (A_s:A_l) was also determined. Pro-

jected leaf area was measured by analyzing computer scans of individual leaflets with the public domain NIH Image Analysis program (available at http://rsb.info.nih.gov/nih-image/).

Model application

We used a hydraulic transport model (previously described by Sperry et al. 1998 and Hacke et al. 2000*a*) to estimate E_{crit}, the transpiration rate above which the soil–plant hydraulic conductance goes to zero and hydraulic failure occurs. From the hydraulic properties of soil and xylem, the model calculates how the total hydraulic conductance (flow rate per driving force) of the soil–plant continuum declines with increasing E and hence with declining water potential of the continuum. We parameterized the model to give hydraulic conductances and transpiration rates of the *Prosopis* stands on a ground area rather than leaf area basis to avoid complications of changing leaf area through the season. Maximum stand conductance (k_g) was set to:

$$k_g = E / (\Psi_s - \Psi_{min}) \tag{1}$$

where Ψ_s is soil water potential (assumed to equal Ψ_{pd}), Ψ_{min} is mean midday xylem water potential and E is transpiration rate, with all values determined for the wettest period during the growing season (August). We estimated E from eddy covariance data measured in 2003 at a well-watered mesquite forest located 30 km from the SRER (Scott et al. 2004). The soil at this site comprised sandy loams interspersed with layers of gravels and clays. Values of E were adjusted for relative differences in total sapwood area per ground area among the three sites in August (unpublished data). This gave a maximum $E = 1.01$ and 0.11 mmol s^{-1} m^{-2} ground area for the sandy-loam and loamy-clay sites respectively, yielding a maximum k_g of 0.76 and 0.17 mmol s^{-1} m^{-2} MPa^{-1}, respectively.

Predawn disequilibrium between leaf and soil water potential in the rhizosphere has been demonstrated in some woody plant species, resulting in underestimations of soil water available for root uptake (Donovan et al. 1999, Bucci et al. 2004). In the present study, predawn disequilibrium between Ψ_s and Ψ_{pd} would result in overestimation of k_g by Equation 1. To resolve this difficulty, we performed a sensitivity analysis of the E_{crit}: ($E/(\Psi_s - \Psi_{min})$) relationship by incrementally increasing Ψ_s from -1.3 to -0.1 MPa. The model was then parameterized with the various disequilibrium scenarios for both soil types.

The model partitioned maximum k_g equally between shoot and soil–root conductances (Hacke et al. 2000*a*). Root and shoot systems were further divided into lateral and axial components. For the root systems, axial and lateral root components were divided into five soil layers centered on five depths from 0.05 to 2 m (0.4 m increments). Root axial lengths were estimated based on presence at the midpoint of each soil layer. Relative change in root surface area with depth was estimated from mesquite root distribution patterns reported from the La Copita Research Area in southern Texas, USA (Watts and Archer, unpublished data). Maximum rhizosphere conductance was calculated from K_s (mmol s^{-1} MPa^{-1} m^{-1}), assuming a cylindrical rhizosphere sheath of 5-mm thickness from bulk soil to root surface. We determined K_s from measured soil texture fractions according to Campbell (1985), assuming K_s was constant throughout the soil profile. To convert rhizosphere conductance to a ground area basis we needed an estimate of the root area per ground area (A_r:A_g), which was unavailable for these sites. Instead, we ran the model over a range of A_r:A_g values from 0.5 to 30 to assess sensitivity to this parameter.

The water-potential-dependent decrease in k_g for xylem components was calculated from a Weibull function fit to the root or stem vulnerability curve data:

$$k_g \text{xylem} = k_g * e^{-(\Psi / d)^c} \tag{2}$$

where d and c are curve fitting parameters and k_g^* is the maximum k_g for the component determined from the partitioning of maximum whole-plant k_g (Equation 1). We used the same fitting parameters for axial and lateral components within the root and shoot systems. The Ψ_s-dependent decrease in rhizosphere conductance was calculated as:

$$k_g \text{rhizosphere} = K_s X(\Psi_e / \Psi_s)^{(2+3/b)} \tag{3}$$

where X is a factor converting soil conductivity to a ground area basis (Sperry et al. 1998), Ψ_e is air entry potential and b is a soil fitting parameter (Campbell 1985).

To run the model, bulk Ψ_s of each of the five soil layers was set to the same value and held constant. Transpiration rate was incremented until the soil–plant conductance declined to zero, yielding the maximum steady-state E_{crit} for that particular bulk Ψ_s. This was repeated for a range of Ψ_s from near zero to -10 MPa to obtain the relative sensitivity of E_{crit} to Ψ_s at each site.

Xylem anatomy and wood density

Conduit diameters were measured on a minimum of four roots and stems per site to establish vulnerability curves. Transverse sections were cut with a rotary microtome (Model 820, American Optical, Buffalo, NY). The sections were stained with toluidine blue (0.05%) to improve contrast, and mounted in glycerol. The slides were photographed at 100× with a digital camera (Nikon Coolpix, Nikon, Tokyo, Japan) mounted on a Nikon compound microscope (Nikon Eclipse E400, Nikon). Two to six randomly selected radial sections were photographed on each root and stem segment. The lumen of all xylem conduits were analyzed using NIH image program software. A minimum of 203 conduits were analyzed from stem and root segments per site. Mean conduit diameter (d) was calculated from the cross-sectional area of each conduit measured by the imaging software. We also calculated the mean hydraulic diameter (d_h), which yields the estimated percentage of total conductance contributed by each conduit. The mean of the hydraulically weighted distribution is given by: $\Sigma d^5 / \Sigma d^4$ (Sperry et al. 1994).

Wood density (D_t) was measured on stems and roots as described by Hacke et al. (2000*b*). Five to 13 root and stem segments were measured per site, including the roots and stems

measured for vulnerability to cavitation. Segments of 2.5 to 3 cm in length were cut from roots and stems and the cortex and bark were removed from each organ, respectively. Wood volume was determined by Archimedes' principle. The segments were immersed in water in a beaker that was placed on a balance. Displacement mass was measured to the nearest 0.01 g and was converted to sample volume by the formula: displacement mass/0.998 (g cm^{-3}), where 0.998 g cm^{-3} is the density of water at 20 °C. Segments were then oven-dried at 90 °C for 48 h and their dry mass determined. Wood density was calculated as the ratio of dry mass to volume.

Results

During the 2003 growing season, minimum values of Ψ_{pd} and Ψ_{min} occurred in June at both sites. In June, Ψ_{pd} was significantly lower in trees at the sandy-loam site than at the loamy-clay site (Table 2), averaging –3.5 MPa ± 0.1, $n = 6$ and –2.9 MPa ± 0.1, $n = 6$, respectively ($P = 0.0079$). The Ψ_{min} was also lower in trees on sandy-loam soils than on loamy-clay soils, averaging –4.5 MPa ± 0.1, $n = 6$ and –4.0 ± 0.1 MPa, $n = 6$, respectively ($P = 0.0029$). Apparently, mesquite trees on sandy-loam soils experienced more water stress than trees on loamy-clay soils before the onset of the monsoon. After the onset of the monsoon, Ψ_{pd} of trees at both sites converged near –1.3 MPa, whereas Ψ_{min} values were –2.6 and –2.0 MPa for trees on sandy-loam and loamy-clay soils, respectively (data not shown). There were no significant site differences in either root or stem maximum specific hydraulic conductivity (Table 2); however, leaf specific conductivity and sapwood to leaf area ratios (A_s:A_l) were higher at the sandy-loam site than at the loamy-clay site (Table 2).

Roots were only slightly more vulnerable to cavitation than stems. At both sites, roots became completely embolized at pressures only 1 to 2 MPa higher than observed for stems. Down to –7.0 MPa, mesquite stems at the sandy-loam site were slightly more vulnerable to cavitation than stems at the loamy-clay site (Figure 1), particularly at –2.0 MPa; however, Ψ_{mean} and Ψ_{95} in stems did not differ significantly between sites (Table 3). Stem Ψ_{mean} ranged from –5.5 MPa on sandy loam to –6.3 MPa on loamy clay, whereas stem Ψ_{95} ranged from –11.6 MPa on sandy loam to –11.0 MPa on loamy clay. In roots, Ψ_{mean} and Ψ_{95} were similar between sites: root Ψ_{mean}
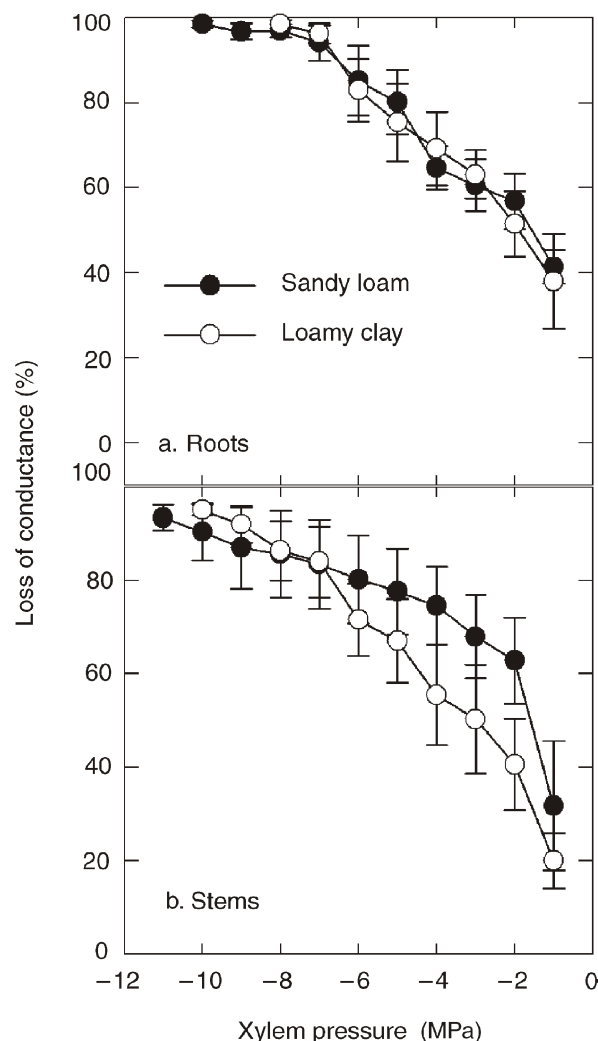

Figure 1. Xylem vulnerability curves for (a) roots and (b) stems of *Prosopis velutina* trees occurring on sandy-loam and loamy-clay soils in southeastern Arizona, USA, as measured by the air-injection technique. Vulnerability curves are shown as mean percentage loss in maximum hydraulic conductance at each pressure applied. Error bars are the standard errors of the means ($n = 5$ or 6).

ranged from –5.5 MPa on sandy-loam soils to –5.7 MPa on loamy-clay soils and root Ψ_{95} ranged from –9.6 MPa on sandy loam to –9.3 MPa on loamy clay.

Table 2. Minimum predawn (PD) and midday (MD) leaf water potentials, root (K_r), stem (K_{st}) and leaf (K_l) specific conductivities and sapwood to leaf area ratios (A_s:A_l) of *Prosopis velutina* trees on sandy-loam and loamy-clay soils at the Santa Rita Experimental Range in southeast Arizona, USA, during the 2003 growing season. P values were calculated by Student's t tests.

Parameter	Sandy loam	Loamy clay	P
PD (MPa)	–3.52 ± 0.14	–2.94 ± 0.14	0.0079
MD (MPa)	–4.47 ± 0.12	–3.95 ± 0.09	0.0029
K_r (kg s^{-1} m^{-1} MPa^{-1})	22.47 ± 6.78	31.13 ± 11.11	0.53
K_{st} (kg s^{-1} m^{-1} MPa^{-1})	0.39 ± 0.10	0.36 ± 0.04	0.79
K_l (kg s^{-1} m^{-1} MPa^{-1})	$7.1 \times 10^{-4} \pm 2.2 \times 10^{-4}$	$2.5 \times 10^{-4} \pm 7.1 \times 10^{-5}$	0.0808
A_s:A_l (m^2 m^{-2})	$7.8 \times 10^{-4} \pm 7.5 \times 10^{-5}$	$5.8 \times 10^{-4} \pm 5.3 \times 10^{-5}$	0.0484

Table 3. Mean cavitation pressure, pressure causing 95% loss of conductance (Ψ_{95}), mean conduit diameter (d), hydraulically weighted conduit diameter (d_h) and wood density (D_t) of roots and stems of *Prosopis velutina* trees on sandy-loam and loamy-clay soils at the Santa Rita Experimental Range in southeast Arizona, USA, during the 2003 growing season. *P* values were calculated by Student's *t* tests. Numbers in brackets are equal to one standard error of the mean.

Parameter	Roots			Stems		
	Sandy loam	Loamy clay	*P*	Sandy loam	Loamy clay	*P*
Mean cavitation pressure	−5.45 (0.91)	−5.66 (0.69)	0.86	−5.51 (1.28)	−6.33 (0.95)	0.61
Ψ_{95}	−9.59 (2.09)	−9.31 (2.02)	0.93	−11.57 (2.54)	−10.97 (2.16)	0.71
d	71.5 (3.0)	86.5 (4.0)	0.0018	35.9 (1.0)	47.0 (1.2)	< 0.0001
d_h	159.0 (22.7)	177.2 (25.7)	0.56	59.0 (7.6)	78.2 (7.5)	0.0727
D_t	0.52 (0.04)	0.53 (0.04)	0.99	0.67 (0.02)	0.69 (0.02)	0.52

Despite similar vulnerabilities to cavitation, the model predicted that water uptake at the sandy-loam site was considerably more sensitive to Ψ_s than at the loamy-clay site (Figure 2). In wet soil, E_{crit} was higher at the sandy-loam site than at the loamy-clay site, paralleling the higher plant hydraulic conductance at the sandy-loam site (whole-plant $k_g = 0.76$ versus 0.17 mmol s^{-1} m^{-2} MPa^{-1}). In drier soil, however, E_{crit} fell more abruptly at the sandy-loam site than at the loamy-clay site and was more sensitive to $A_r:A_g$. At the sandy-loam site, sensitivity of E_{crit} to soil Ψ_s increased with decreasing $A_r:A_g$ (Figure 2). The E_{crit} became negligible (= 1% of its maximum) at a bulk Ψ_s as high as –2.0 MPa at the sandy-loam site compared with –9.3 MPa at the loamy-clay site (Figure 3). This "extraction limit" provides an estimate of the minimum bulk Ψ_s for meaningful stand water uptake.

According to the model, E_{crit} was more sensitive to Ψ_s at the sandy-loam site because water uptake was rhizosphere-limited rather than xylem-limited. This was evident from the higher soil Ψ extraction limit than xylem pressure near complete cavitation (Figure 3, closed symbols). Only at an $A_r:A_g$ of 20 did the extraction limit approach the Ψ_{95} for root xylem (Figure 3, closed symbols). Conversely, the loamy-clay site was xylem-limited because the extraction limit matched the xylem pressure causing near complete cavitation for all $A_r:A_g$ values tested (Figure 3 open symbols).

Because E_{crit} predicts the maximum possible water use rate of the stand, a comparison of E_{crit} with actual estimated stand water use indicates how severely water use was constrained by hydraulic limits, and how responsive it should be to soil water changes. At the sandy-loam site, E_{crit} under dry, pre-monsoonal conditions was substantially below E estimated for wet, monsoonal conditions (Figure 2a), implying that water uptake at the sandy-loam site was hydraulically limited and responsive to Ψ_s over much of the growing season. In contrast, at the loamy-clay site, E_{crit} during pre-monsoonal drought exceeded wet-season E (Figure 2b), implying that water use at the loamy-clay site is relatively unresponsive to the physiological range of Ψ_s. These results indicate that mesquite water use should be much more sensitive to seasonal inputs of precipitation at the sandy-loam site than at the loamy-clay site.

The model was parameterized with rhizosphere Ψ_s estimated from measurements of Ψ_{pd}. Because substantial disequilibrium may occur between these two parameters, a sensi-
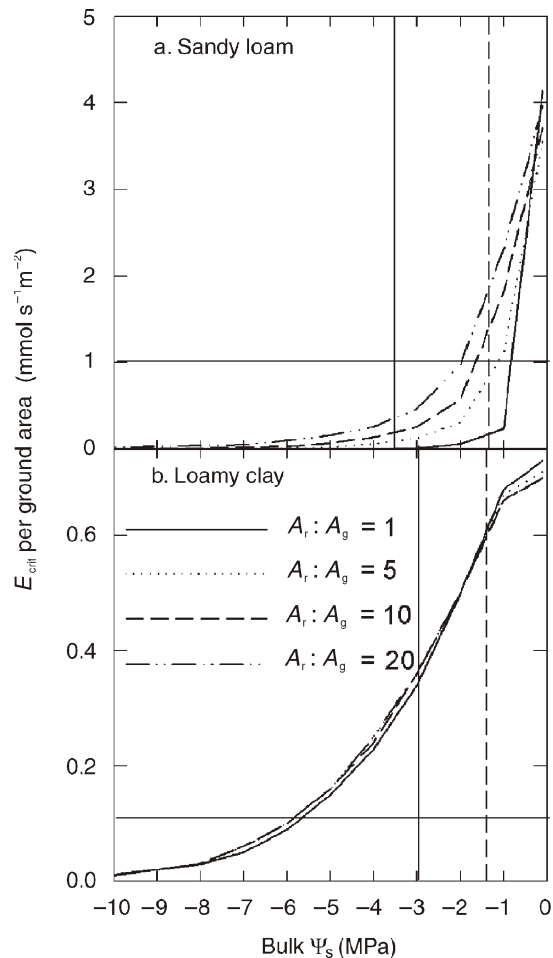

Figure 2. Effect of soil texture on E_{crit} (maximum steady-state E without hydraulic failure) in *Prosopis velutina* trees occurring on sandy-loam and loamy-clay soils in southeastern Arizona, USA. Shown are E_{crit} values for (a) sandy-loam soils and (b) loamy-clay soils at root area per ground area ratios ($A_r:A_g$) of 1 (solid), 5 (dotted), 10 (dashed) and 20 (dash-dotted line). Horizontal lines represent the estimated maximum transpiration rate under wet, post-monsoonal conditions (estimated from eddy covariance measurements), solid vertical lines represent the minimum predawn water potentials measured during the 2003 growing season (–3.5 MPa on sandy loam and –2.9 on loamy clay, Table 2) and dashed vertical lines represent predawn water potentials measured in August after the onset of the monsoon. Predicted E_{crit} values are based on a constant soil water potential (Ψ_s) throughout the soil profile.
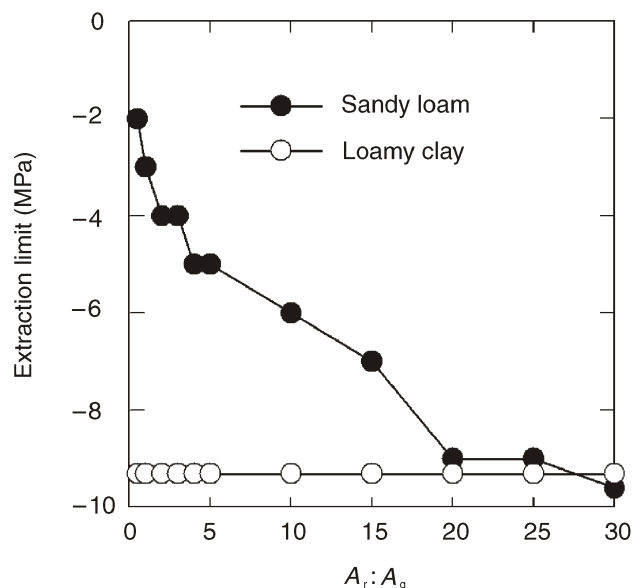
Figure 3. Modeled extraction limits (bulk soil water potential at maximum steady-state E without hydraulic failure = 1% of maximum) versus root to ground area ratios $(A_r:A_g)$. The minimum possible extraction limit is the xylem pressure causing complete xylem cavitation. Higher (less negative) extraction limits are the result of loss of conductivity in the soil–root interface caused by insufficient root surface area and steep water potential gradients in the rhizosphere.

tivity analysis was performed by incrementally increasing Ψ_s values in Equation 1 from –1.3 to –0.1 MPa. The E_{crit} of trees at the sandy-loam site was relatively insensitive to increases in Ψ_s and subsequent decreases in k_g (see Equation 1) across the range of $A_r:A_g$ values tested (see Figure 4a for an example with $A_r:A_g$ set to 5). Although E_{crit} of trees at the loamy-clay site fell sharply with increasing Ψ_s, E_{crit} never fell below wet-season E over the range of Ψ_s and $A_r:A_g$ values tested in the model (Figure 4b).

Hydraulically weighted mean conduit diameter (d_h) was larger in mesquite stems at the loamy-clay site than at the sandy-loam site (78.2 ± 7.5 and 59.0 ± 7.6 µm, respectively, $P = 0.0727$; Table 3). Likewise, d_h in roots was slightly higher at the loamy-clay site than at the sandy-loam site (177.2 ± 25.7 and 159.2 ± 22.7, respectively), however, differences were not significant ($P = 0.56$; Table 3). Despite having stems with larger conduits, mesquite trees at the loamy-clay site were no more vulnerable to cavitation than trees at the sandy-loam site, suggesting that there is no tradeoff between xylem hydraulic efficiency and cavitation vulnerability in velvet mesquite trees as reported for other species (Tyree et al. 1994, Alder et al. 1996, Pockman and Sperry 2000, Hacke et al. 2001).

Wood density (D_t) of stems and roots did not vary between sites ($P = 0.98$ for roots and $P = 0.52$ for stems, Table 3). Mean wood density of roots ranged from 0.52 g cm^{-3} on sandy loam to 0.53 g cm^{-3} on loamy clay, whereas stem wood density ranged from 0.67 g cm^{-3} on sandy loam to 0.69 g cm^{-3} on loamy clay. There was a significant linear decrease in Ψ_{mean} with increasing D_t in roots ($\Psi_{mean} = (0.77 - 9.78)D_t$; $r^2 = 0.87$, $P < 0.0001$, $n = 10$; Figure 5a), suggesting that wood density of

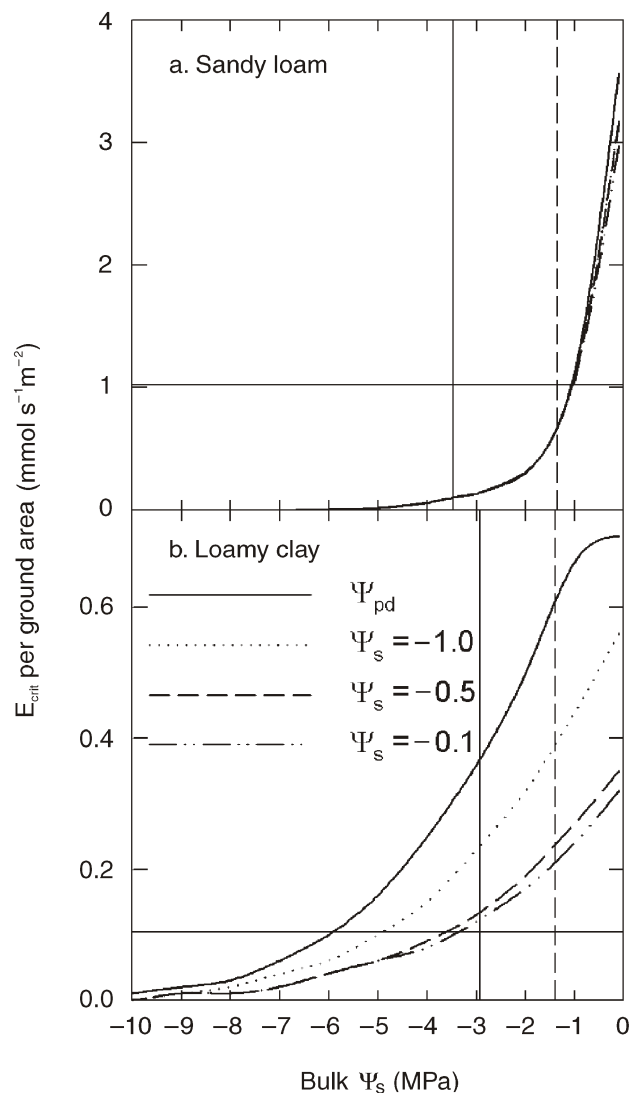Figure 4. Modeled E_{crit} (bulk soil water potential (Ψ_s) at maximum steady-state E without hydraulic failure) for *Prosopis velutina* trees occurring on sandy-loam and loamy-clay soils in southeastern Arizona, USA, with a root area to ground area ratio ($A_r:A_g$) equal to 5. Shown are E_{crit} values for (a) sandy-loam soils and (b) loamy-clay soils at Ψ_s of –1.0 MPa (dotted), –0.5 MPa (dashed) and –0.1 MPa (dash-dotted line), which were assumed to equal predawn water potentials (Ψ_{pd}; solid line) in August after the onset of the monsoon. Horizontal lines represent the estimated maximum transpiration rate under wet, post-monsoonal conditions (estimated from eddy covariance measurements), solid vertical lines represent the minimum Ψ_{pd} measured during the 2003 growing season (–3.5 MPa on sandy loam and –2.9 on loamy clay, Table 2) and dashed vertical lines represent Ψ_{pd} measured in August after the onset of the monsoon (–1.3 MPa for both sites).

roots may be related to xylem support and cavitation resistance. Conversely, mean cavitation pressure in stems was apparently unrelated to D_t ($P = 0.16$, $n = 8$; Figure 5b).

Discussion

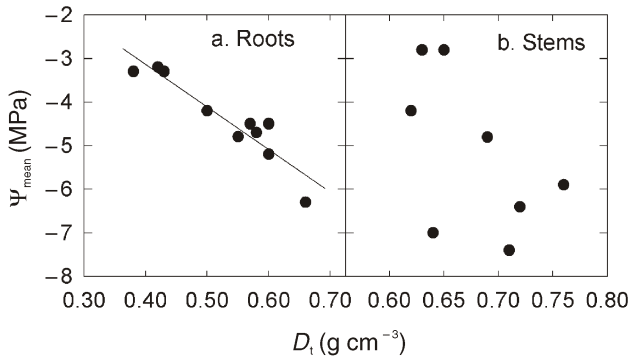Our analyses revealed significant differences in soil hydraulic

Figure 5. Relationship between mean cavitation pressure (Ψ_{mean}) and wood density (D_t) in (a) *Prosopis velutina* roots and (b) *Prosopis velutina* stems at the Santa Rita Experimental Range in southeastern Arizona, USA. There was a significant relationship between Ψ_{mean} and D_t in roots ($\Psi_{mean} = (0.77 - 9.78)D_t$, $r^2 = 0.87$, $P < 0.0001$, $n = 10$), but not in stems ($P = 0.16$, $n = 8$).

limits to water use by velvet mesquite trees growing in sandy-loam soil versus loamy-clay soil; however, these differences did not translate into substantial adjustments in xylem hydraulic properties across soil textures, as observed in some studies (Alder et al. 1996, Hacke et al. 2000*a*). Nevertheless, soil and plant hydraulic limitations on water uptake and transport play an important role in regulating seasonal patterns of mesquite transpiration in this system. Our data indicate that the influence of woody plant invasion on the hydrologic cycle of ecosystems formerly dominated by grasses may vary across landscapes as a function of soil texture. On coarse-textured soils, transpiration appears to be highly sensitive to seasonal precipitation patterns, reducing the impact of woody plant encroachment on the hydrologic cycle during periods of drought, particularly where deep soil water is unavailable or beyond rooting depth. On finer textured soils, or on coarse textured soils where trees have access to deep soil water, high rates of transpiration can be sustained without approaching transport limits.

According to the hydraulic transport model, the combined soil and xylem hydraulic limits to leaf water supply were more significant at the sandy-loam site than at the loamy-clay site throughout much of the growing season. As xylem resistances were similar between sites, differences in hydraulic limits were likely caused by the sharp contrast in rhizosphere conductance, which differed between sites for two reasons. First, pre-monsoon Ψ_s was lower at the sandy-loam site than at the loamy-clay site and second, coarse-textured soils lose more water at high Ψ_s than fine-textured soils, because of the weaker capillary forces that retain water in the larger pore spaces (Campbell 1985). Therefore, trees growing in sandy-loam soil require less negative Ψ_s to exhaust the water supply in the rhizosphere than trees growing in loamy-clay soil, resulting in greater hydraulic limits during drought. These results may explain why K_l and $A_s:A_l$ were higher at the sandy-loam site where prolonged leaf water deficits before the monsoon may have resulted in significant leaf drop. Leaf shed during drought would reduce the transpirational demand for water relative to the supply capacity of the conducting xylem.

Rhizosphere conductance varies considerably with soil texture, with much steeper declines in coarse soils as water funnels towards the absorbing roots. Trees on coarse-textured soils may reduce hydraulic limits in the rhizosphere by reducing the rate of water uptake per unit surface area (rhizosphere flux density) through the development of a large, absorbant root surface area relative to the transpiring surface area. Most studies express transpiration on a leaf area basis, rather than a ground area basis, and the relevant ratio is $A_r:A_l$. Intraspecific differences in $A_r:A_l$ have often been observed between trees on coarse and fine-textured soils (Glinski and Lipiec 1990, Hacke et al. 2000*a*). For example, $A_r:A_l$ in 15-year-old *Pinus taeda* stands in North Carolina was six times higher in sand soils than in loam soils, thereby sharply reducing the rhizosphere flux density at the sandy site (Hacke et al. 2000*a*). Trees might be expected to operate near the $A_r:A_l$ threshold where xylem becomes limiting unless nutrient limitation rather than water limitation requires a high $A_r:A_l$ ratio (Sperry et al. 1998). However, according to the model, for trees at the sandy-loam site, hydraulic failure in the rhizosphere occurred before xylem failure across a range of $A_r:A_l$ ratios that would reasonably be expected in woody plants (Rendig and Taylor 1989, Tyree et al. 1998, Hacke et al. 2000*a*), partly because of the high cavitation resistance of roots and stems at this site. Conversely, in trees at the loamy-clay site, hydraulic failure was limited to the xylem over the same range in $A_r:A_l$ (Tyree et al. 1998, Hacke et al. 2000*a*). Data describing mesquite root density and distribution would greatly improve model parameterization but are difficult to obtain because mesquite roots can extend as deep as 50 m (Phillips 1963).

Woody plants that occur on coarse-textured soils generally experience less negative xylem pressure and have xylem that is more vulnerable to cavitation than the same species on finer soils, suggesting that resistance to cavitation parallels the range of Ψ_s in which water is physically extractable from the rhizosphere. (Sperry et al. 1998, Hacke et al. 2000*a*, Sperry and Hacke 2002). In our study, however, trees at the sandy-loam site developed lower (more negative) xylem pressures than at the loamy-clay site, but vulnerabilities to cavitation were similar. The observed combination of resistant xylem and rhizosphere-limited water uptake in trees at the sandy-loam site may have important advantages. High cavitation resistance in shallow roots may facilitate rapid uptake of summer rain that generally occurs in low-frequency intense pulses. More vulnerable root xylem would have to reverse cavitation by refilling before there could be significant uptake through existing roots. Although refilling of embolized conduits has been reported previously in diffuse-porous species, it has not been seen in ring-porous species such as velvet mesquite (Jaquish and Ewers 2001). Mesquite trees respond immediately to simulated rain after extensive drought on both sandy-loam and loamy-clay soils (Fravolini et al. 2005), strongly suggesting that the root system remains highly conductive during drought. It is unlikely that new roots could grow fast enough to explain the rapidity with which the plants take up summer rain (North and Nobel 1995).

Avoidance of cavitation may facilitate hydraulic redistribution of water by deep root systems and vice versa (Caldwell et al. 1998, Sperry and Hacke 2002, Hultine et al. 2003, Domec et al. 2004). Hydraulic lift occurs in mesquite roots during extended periods of drought and immediately reverses direction (i.e., hydraulic descent) in response to moderate rain events (Hultine et al. 2004). These patterns of hydraulic redistribution suggest that a large portion of the root system remains in hydraulic contact with the soil during drought by virtue of high cavitation resistance.

We predicted that mesquite trees occurring on sandy-loam soils would have a higher Ψ_{min} than trees on loamy-clay soils by developing deeper and more extensive root systems than trees on loamy-clay soils. We found, however, that Ψ_{min} during peak drought was lower in trees in sandy-loam soil than in loamy-clay soil. Because mesquite trees occurred at much greater densities at the sandy-loam site than on the loamy-clay site, it may be that the total extraction of bulk soil water by roots in sandy-loam soils was much greater during the previous 24 months when precipitation was below average at both sites, thereby reducing the available water for root uptake to the extent that Ψ_{min} was lower on the sandy-loam soil than on the loamy-clay soil. Patterns of pre-monsoon Ψ_{pd} and Ψ_{min} in 2003 paralleled patterns reported for other years on the SRER with below average winter and spring precipitation including 1999 and 2000 (Fravolini et al. 2003).

Traditional expectations for whole-plant water relations are based on the assumption that Ψ_{pd} is in equilibrium with Ψ_s in the rooting zone. It is now apparent that predawn disequilibrium between soil and leaf water potential occurs in at least some woody plant species (Donovan et al. 1999, Bucci et al. 2004). In our study, modeled predictions of E_{crit} were based on the assumption that Ψ_s is in equilibrium with Ψ_{pd}. Nevertheless, disequilibrium would have little or no impact on E_{crit} at the sandy-loam site because of the steep decline in rhizosphere K that occurs relative to plant K on sandy-loam soil regardless of bulk Ψ_s. On the other hand, modeled E_{crit} at the loamy-clay site fell sharply in response to predawn disequilibrium, but never fell below maximum E over the range of Ψ_s and A_r:A_g we tested.

Mesquite appears to be comparatively immune to any tradeoff between vessel diameter and safety from cavitation. Mean diameters of over 70 μm are large for a Ψ_{mean} below –5 MPa (Table 3, root data). Furthermore, despite having substantially greater maximum conductance and mean hydraulic conduit diameter, mesquite roots at both sites were only slightly more vulnerable to cavitation than stems, suggesting that there is not a strong tradeoff within individual mesquite trees between cavitation resistance and hydraulic efficiency as shown in some species (Sperry and Saliendra 1994, Tyree et al. 1994, Wagner et al. 1998), but not others (Alder et al. 1996). The ability of mesquite to be both hydraulically efficient and relatively safe from cavitation may contribute to its consistently high cavitation resistance across sites and to its success as a deep-rooted tree of arid habitats.

Xylem cavitation resistance may also be associated with wood density. The construction of progressively denser wood,

at the cost of greater carbon investment and lower rates of growth, may prevent the implosion of xylem elements from increasingly negative pressures occurring in the xylem as Ψ_s decreases or leaf water demand increases, or both (Hacke et al. 2001). Cavitation resistance increased with increasing D_t in the roots but not in the stems. One possible explanation is that stem D_t is primarily linked to the presence of fibers that are more directly related to plant structure and support than to protecting conduits from implosion. In angiosperms, fibers typically occupy a larger percentage of the cross-sectional area of aboveground woody tissues than do xylem conduits (Gartner 1995) and could therefore limit the relationship between D_t and cavitation resistance. In contrast, the primary function of woody roots is to transport water and solutes while playing only a minor role in plant structure and support. Roots may therefore have a higher proportion of their cross-sectional area occupied by xylem conduits than stems, suggesting that, relative to stems, root D_t is more closely linked to structural changes in conduit cell walls that inhibit xylem implosion.

During the growing season, precipitation pulses play a major role in ecosystem water balance in much of the southwestern United States (Huxman et al. 2004). However, rain pulses (< 10 mm) during the summer monsoon apparently do not penetrate to the rooting zone at the loamy-clay site because of the low K_s in these soils (Fravolini et al. 2005) coupled with mesquite rooting distributions that, in the SRER, rarely occur above 15 cm in the soil profile (Cable 1977). Therefore, trees on loamy-clay soil likely respond only to intense precipitation inputs that occur much less frequently than moderate events. Conversely, mesquite trees on sandy-loam soils are highly sensitive to small precipitation pulses reflected by uptake of pulse water and carbon gain (Fravolini et al. 2005). Given that mesquite transpiration at the sandy-loam site was apparently severely limited by low rhizosphere conductance before the monsoon, it is likely that carbon and water fluxes are well coupled to precipitation inputs during the summer monsoon, whereas fluxes at the loamy-clay site are likely more closely coupled to inter-annual rather than to intra-annual changes in precipitation. Climate change is expected to bring substantial variations in inter- and intra-annual summer precipitation patterns in the arid southwestern United States (Houghton et al. 1996, Weltzin et al. 2003). Changes in precipitation patterns coupled with differences in soil hydraulic limits across the landscape will likely lead to differences in plant water use that may have important consequences for future patterns of plant community structure and ecosystem water balance.

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