

Desert shrub water relations with respect to soil characteristics and plant functional type

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Summary

1. Soil characteristics influence plant communities in part through water relations. Hypothetically, finer textured soils in arid climates should be associated with more negative plant and soil water potentials during drought, greater resistance of xylem to cavitation, and shallower root systems than coarse soils.

2. These hypotheses were tested by comparing the water relations of Great Basin shrubs growing in sand versus loam soils. The eight study species (*Chrysothamnus nauseosus*, *Chrysothamnus viscidiflorus*, *Chrysothamnus parryi*, *Tetradymia glabrata*, *Atriplex canescens*, *Atriplex confertifolia*, *Grayia spinosa* and *Sarcobatus vermiculatus*) varied in typical rooting depth and vegetative phenology.

3. Xylem pressures for a species were, on average, 1.1 MPa more negative in the loam versus the sand site, despite greater precipitation at the loam site. Root xylem at the loam site was, on average, 0.9 MPa more resistant to cavitation than at the sand site for the same species. There was a strong trend for shallower rooting depths at the loam versus the sand site. Within a species, roots were consistently more vulnerable to cavitation than stems, and experienced more cavitation during the growing season.

4. Over most of the summer there was much more cavitation at the loam site than at the sand site. More than 80% loss of xylem conductivity (PLC) was estimated in shallow roots of three species at the loam site by the end of July, with two of the three showing extensive leaf drop and branch mortality. Transpiration rate was negatively correlated with PLC, with a tendency for lower gas-exchange rates in loam versus sand.

5. At the sand site, cavitation resistance was negatively correlated with estimated rooting depth. Drought-deciduous species had the shallowest root systems and greatest resistance to cavitation. In contrast, two species with phreatophytic tendencies were summer-active and were the most vulnerable to cavitation.

6. The cavitation resistance of roots determines the minimum water potential permitting hydraulic contact with soil. Differences in cavitation resistance of roots between desert species may contribute to differences in sensitivity of gas exchange to soil drought, ability to perform hydraulic lift, and response to late summer rain pulses.

Key-words: desert shrub communities, plant water relations, xylem cavitation, plant–soil interactions, soil texture

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Introduction

Superimposed on the influence of climate on plant productivity and diversity is the effect of soil characteristics. A basic soil property is texture, which influences infiltration and moisture retention (Jury, Gardner & Gardner 1991), and thus the availability of water and nutrients to the plant. There can be dramatic shifts in vegetation across changes in soil texture. In wetter climates, sandy soils often support a relat-

ively limited productivity and putatively xerophytic vegetation, attributed in part to poor moisture retention and the leaching of nutrients from the rooting zone (Christensen 1988). Conversely, in drier climates sandy soils can be associated with more extensive vegetation cover and an apparently more mesophytic species composition which can result from a greater availability of water in these soils (Alizai & Hulbert 1970; Kinraide 1984; Smith, Monson & Anderson 1997).

In this paper we focus on the dry end of the climate spectrum, and test several hypotheses for how soil texture influences plant water relations in a comparative study of eight shrub species of the Great Basin desert

of North America (Table 1). The arid valleys of the Great Basin include soils of dramatically differing texture, ranging from clay to dune sand. In contrast, the precipitation regime across the region is predictable: wetting of the soil profile by winter precipitation followed by midsummer drought. Differences in water availability between sites of similar topography will be dominated by soil characteristics and their influence on hydrology (Dobrowolski, Caldwell & Richards 1990).

The first hypothesis is that a shrub species in coarse-textured, sandy soils will have higher water potentials (Ψ) than the same species in loam or finer soils during drought under a similar precipitation regime (Hacke *et al.* 2000a; Sperry *et al.* 1998). There are several reasons to expect this. Most fundamentally, the larger pore spaces in sand hold water only at relatively high Ψ . In contrast, the greater abundance of small pore spaces in a finer soil hold more water to lower Ψ . In addition, the high saturated hydraulic conductivity of coarse soil causes more precipitation to soak into the soil, as opposed to running off or ponding. This should result in deeper wetting and potentially higher water tables in deep sand soils. Finally, during hot and dry weather, dry zones tend to form at the surface of sandy soils because of the large pore spaces. Dry zones inhibit the migration of deep water to the surface, minimizing evaporative loss from the surface and allowing the soil to retain more of its stored water (Campbell & Norman 1998). All these factors combined should tend to increase the soil and plant Ψ in habitats with deep, coarse soils.

To the extent that the first hypothesis is true, it follows that shrubs on deep, sandy soils should be adapted to a higher Ψ regime than the same shrub species on finer soils. There is a tendency for the cavitation resistance of the xylem to parallel the physiological Ψ range such that the xylem is no safer than necessary for its circumstances, because of costs associated with cavitation resistance (Tyree & Ewers 1991; Tyree, Davis & Cochard 1994). This seems to be particularly true of root xylem (Hacke, Sperry & Pittermann 2000b; Linton, Sperry & Williams 1998). It follows that plants in sandy soils should tend to be more vulnerable to cavitation than those on finer soils. The vulnerability

curve of the xylem, which shows how its unsaturated conductivity declines with negative pressure, should reflect the moisture characteristics of the soil from which the plant is extracting water.

The differences in moisture retention across soil texture may also have implications for plant rooting depth (Jackson, Sperry & Dawson 2000). The narrow Ψ range for plant water uptake from sand requires that the roots be in relatively wet soil, and hence grow deep. Deep root growth may also be promoted by the ease of root penetration through sand and greater oxygen availability at depth. Conversely, the broader Ψ range for plant water uptake in a finer soil may create less demand for deeper roots, especially when this is coupled with more cavitation-resistant xylem for extracting water to lower Ψ . Additional factors limiting root growth in finer soils may be the mechanical difficulty of penetrating the soil, and a possibly shallower wetting depth even during the relatively moist winters characteristic of this region. These considerations suggest a tendency for deeper root systems in a species in a sandy soil versus the same species in finer soil, particularly in a climate with a dry growing season, such as that of the Great Basin.

For practical purposes, we limited our investigation of these hypotheses to eight species across just two sites having similar drainage and climate, but with a deep sandy soil versus a deep loamy soil (Table 1). For cross-site comparisons we focused on intraspecific differences in six of the study species that were present at both sites. In addition, we compared water use between plant functional types within a site. The study species were chosen to reflect a continuum of water-use strategies from shallow-rooted, drought-deciduous shrubs to deep-rooted phreatophytes. We quantified cavitation resistance, drought experience, and relative rooting depth for all species and sites. The present study builds on previous work with six of the study species at the sand site, where it was shown that cavitation in the roots of these species is more limiting to water uptake than cavitation in stems (Hacke *et al.* 2000b). For this reason, our cavitation measurements focused on root xylem.

Table 1. Study species and families, sites (S, sand site; L, loam site), and symbols; taxonomy follows Cronquist *et al.* (1994)

Species	Site	Family	Symbol
<i>Chrysothamnus nauseosus</i> (Pall.) Britton		Asteraceae	CN
var. <i>turbinatus</i> (M.E. Jones) S.F. Blake	S		
var. <i>oreophilus</i> (A. Nelson) H.M. Hall.	L		
<i>Chrysothamnus viscidiflorus</i> (Hook.) Nutt.		Asteraceae	CV
var. <i>viscidiflorus</i>	S		
var. <i>puberulus</i> (C.C. Eaton) Jeps. (Cronquist)	L		
<i>Chrysothamnus parryi</i> (A. Gray) Greene var. <i>affinis</i> (A. Nelson) Cronquist	L	Asteraceae	CP
<i>Tetradymia glabrata</i> T. & G.	S, L	Asteraceae	TG
<i>Atriplex canescens</i> (Pursh) Nutt.	S, L	Chenopodiaceae	ACA
<i>Atriplex confertifolia</i> (Torr. & Frem.) Wats.	S, L	Chenopodiaceae	ACO
<i>Grayia spinosa</i> (Hook.) Moq.	S, L	Chenopodiaceae	GS
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	S, L	Chenopodiaceae	SV

Table 2. Study sites in central Utah, USA (texture percentages are means of $n \geq 6$ samples)

Parameter	Sand site (Skull Valley)	Loam site (Rush Valley)
Location	40°15' N, 112°44' W	40°12' N, 112°19' W
Elevation	1463 m	1547 m
Mean annual precipitation	194 mm	273 mm
Soil type	Sand (87% sand, 6% silt, 7% clay)	Sandy loam (59% sand, 29% silt, 12% clay)

Materials and methods

STUDY SITES

The sand site was located 5 km south-west of Dugway in central Utah at the southern end of Skull Valley (Table 2). It consisted of low dunes with intervening flats. A weather station located at Dugway records a 50-years' average annual precipitation of 194 mm. The site supported a diverse shrub flora including the study species (Table 1). Soil samples at 0.3 m depth were taken at 10 locations equally distributed on dune and flats locations for texture analysis. Several pits of over 1.2 m depth were dug in the flat areas to assess any obvious layering or changes in texture with depth, as well as for obtaining soil water potential data.

The loam site was located in Rush Valley, 53 km east of the sand site. A weather station at Vernon, UT (15 km south-west of the study site) records a 47-years' average annual precipitation of 273 mm. The site consisted of slightly undulating flats on the valley floor and supported six of the study species from the sand site (Table 1). Three of these species were sparse (*C. nauseosus*, *T. glabrata* and *S. vermiculatus*). The two *Chrysothamnus* species were represented by different varieties at the two sites. In addition, we added a third *Chrysothamnus* species at midsummer that was not present at the sand site: *C. parryi*. Overall, the height and cover of the shrubs was less at the loam site than at the sand site. Six soil samples were taken at 0.3 m depth throughout the site for texture analysis, and several pits over 1.2 m were dug to assess any layering.

Voucher specimens were collected, which are especially important for plants of the highly polymorphic *Chrysothamnus* species. The taxonomy of these subspecific taxa is in considerable flux, and our taxonomy follows Cronquist *et al.* (1994). Soil texture was measured by the Utah State Analytical Laboratory (Logan, UT) using the hydrometer method.

PLANT AND SOIL WATER POTENTIALS

Plant and soil water potentials were measured for each species and site on four dates between June 20 and August 24, 2000. The two sites were visited usually within a week of each other to obtain paired observations for intersite comparison. In addition, for six of the study species (except *S. vermiculatus* and *C. parryi*) we had measured predawn (Ψ_{PD}) and midday (Ψ_{MD}) shoot water potentials at the sand site during the summers of 1998 and 1999, as reported partially by Hacke *et al.* (2000b).

The Ψ_{PD} and Ψ_{MD} were measured on shoot tips using a Scholander pressure chamber (PMS Instruments, Corvallis, OR). To minimize the influence of nocturnal transpiration on predawn measurements (Donovan *et al.* 1999), we chose basal shoots and enclosed them in aluminium foil the night before the measurement. For each measurement date and time, means of three plants were determined. The same plants were used for the predawn and midday measurement for a given date, but different plants were sampled between dates.

Within a few hours of measuring Ψ_{PD} , we also measured the soil Ψ depth profile beneath a subsample of the Ψ_{PD} plants. We dug 1.2 m deep soil pits adjacent to the plants (within 1.5 m). Soil samples were taken from the sides of these pits at 0.2, 0.4, 0.7 and 1.2 m, scraping deep into the undisturbed soil immediately before sealing the sample in a vial with parafilm to avoid drying. Soil samples were taken to the laboratory, where their water potential was measured with an isopiestic thermocouple system (Boyer 1995). Unlike conventional thermocouple psychrometry, this method is not limited to Ψ above approximately -8 MPa (Brown & Chambers 1987), and it is the most accurate method for measuring Ψ because each measurement is effectively calibrated against solutions of known Ψ . This methodology was adopted after much frustration in obtaining reliable soil Ψ data from the sand site using conventional soil psychrometers.

For each soil profile we calculated the depth-averaged soil Ψ . We divided the profile into depth intervals centred on the measurement depth, starting from 0.1 m (e.g. 0.1–0.3, 0.3–0.55, 0.55–0.95, 0.95–1.55 m). We assumed equal Ψ within each interval, summed the product of Ψ and interval size for the profile, and divided by the profile distance (1.45 m) to obtain the depth-averaged Ψ , termed Ψ_{155} for the depth of the deepest interval.

ESTIMATES OF ROOTING DEPTH

We estimated the functional rooting depth for each species and date by comparing Ψ_{PD} to the depth-averaged Ψ_{155} obtained from soil profiles. In the Great Basin climate, deeper soils are generally wetter soils (Dobrowolski *et al.* 1990). Thus the greater (more positive) the difference between Ψ_{PD} and its corresponding Ψ_{155} , the deeper the root system should be. For plants with root systems extending into the wettest soils below 1.55 m, the $(\Psi_{155} - \Psi_{PD})$ difference will also vary with the absolute dryness of the top 1.55 m of soil, independent of the rooting depth. The quotient $(\Psi_{155} - \Psi_{PD}) / \Psi_{155}$ normalizes for this effect, and was used as

an index of the relative functional rooting depth. This 'root-depth index' has a maximum of 1 for the deepest of root systems ($\Psi_{PD} = 0$), dropping to approximately 0 for root systems of 1.55 m deep (to the extent that Ψ_{PD} equals the depth-averaged soil Ψ), and becomes negative for root systems shallower than 1.55 m.

The root-depth index assumes that Ψ_{PD} will reflect the soil Ψ of the functional rooting zone. Three factors can cause a predawn disequilibrium between soil and plant Ψ : nocturnal transpiration; saline soils; and heterogeneous soil moisture (Donovan *et al.* 1999). Bagging of shoots minimized nocturnal transpiration, and saline soils were not a factor. Our soil moisture profiles were extremely heterogeneous (see Results), and certainly would cause a disequilibrium between Ψ_{PD} and the Ψ of the wettest soil layer. By comparing Ψ_{PD} with the depth-averaged Ψ of the profile, we accounted directly for the influence of soil moisture heterogeneity.

XYLEM VULNERABILITY CURVES AND NATIVE PLC MEASUREMENTS

Vulnerability curves show the percentage loss in xylem conductivity (PLC) as a function of decreasing xylem pressure. Curves for stems and roots of the sand site species were already available from a previous study of measurements made in June–August 1998 and 1999 (Hacke *et al.* 2000b). After finding no year-to-year or seasonal variation in curves that might require additional sand site measurements, we used these curves from the previous study. New curves were made for root xylem of all species at the loam site, and root and stem xylem of *S. vermiculatus* at the sand site. New curves were measured in June–August of 2000.

Roots for vulnerability curves were taken from the top 40 cm of soil. Segments of usually lateral roots were cut longer than 14 cm and stored in tightly closed plastic bags. In the laboratory, 14 cm segments free of major side branches were cut under water and attached to a tubing system where they were flushed for ≥ 30 min at 100 kPa with deionized, filtered (0.2 μm) water to reverse any native embolism and refill any additional embolism caused during excavation and harvesting. Segments were between 1.1 and 8.3 mm in diameter (mean 3.4 ± 0.1 mm, $n = 131$). These 14 cm root segments were then used to measure vulnerability curves by the centrifuge method (Alder *et al.* 1997; Pockman, Sperry & O'Leary 1995). In this method, the segment conductivity is repeatedly measured between spinning the segment to progressively more negative pressures in a custom centrifuge rotor. Great care and significant improvements in the hydraulic conductivity measurements were required to obtain repeatable vulnerability curves from shrub root material, owing to relatively low maximum hydraulic conductivities combined with relatively high resistance to cavitation. Details of the methodology are given by Hacke *et al.* (2000b).

Vulnerability curves were plotted as PLC versus xylem pressure, for $n \geq 6$ root segments per species.

As in previous work on desert species (Hacke *et al.* 2000b; Kolb & Sperry 1999a; Kolb & Sperry 1999b), we calculated the PLC relative to conductivity after the segments were spun to -0.5 MPa, which embolized a portion of the older xylem that was extremely vulnerable, presumably as a result of exposure to previous water stress and cavitation. Cavitation can dramatically weaken the xylem so that it is much more vulnerable if refilled (Hacke *et al.* 2001). For this reason the high pressure (less negative) end of the vulnerability curve can change dramatically as a result of previous stress exposure, confounding attempts to compare the true cavitation resistance between species. Thus, rather than using the pressure at 50 PLC as an index of cavitation resistance for comparing species, we chose the pressure at 75 PLC (P_{75}). The P_{75} for each segment was estimated from a Weibull function fit to the vulnerability curve. Prior to making intersite comparisons in vulnerability curves, we determined whether there was any dependence of P_{75} on root diameter. In cases where diameter trends were observed, we made P_{75} comparisons for equivalent diameter classes.

We also measured the *in situ*, or native, PLC on root segments. Care had to be taken to avoid cutting the roots in air, thus embolizing the relatively long vessels in these shrubs during the harvest (Kolb & Sperry 1999b). We exposed lengths of lateral roots without cutting them, and manipulated plastic bags filled with water so that the roots could be cut from the plant under water. The roots were sealed in water in these plastic bags and transported to the laboratory. The hydraulic conductivity of the segment was measured before the segments were flushed to reverse embolism, and the maximum conductivity was measured for the calculation of native PLC.

TRANSPIRATION MEASUREMENTS

Midday transpiration (E) rates per leaf area were measured on each study species in late July 2000 using a porometer (Licor 1600M, Licor Inc., Lincoln, NE). The porometer was used only to determine stomatal conductance (McDermitt 1990). The corresponding E was calculated from stomatal conductance, and the mole fraction difference in water vapour between leaf and air was determined from independent measurements of leaf temperature (portable infrared pyrometer OS-630, Omega Inc., Stamford, CT); humidity (measured with the porometer sensor); and air temperature. Boundary layer conductance was assumed to make a negligible contribution to total leaf conductance in these small-leaved plants. One shoot per plant was measured on three plants per species per site.

STATISTICS

Site and species means were compared with t -tests at a significance level of $P = 0.05$. Correlation coefficients (also tested at $P = 0.05$) and t -tests were computed

using spss 8.0 (SPSS Inc., Chicago, IL). Means \pm SE are cited in the text.

Results

SOILS, PRECIPITATION AND XYLEM PRESSURE

Soil samples at 0.3 m depth showed large differences in texture between sites (Table 2). Deeper pits (> 1.2 m) showed no obvious change in soil composition with depth; however, limited texture data at the sand site

showed a lower sand fraction (59%) and higher silt (26%) and clay (15%) fractions at 2 m than for the 30 cm samples. The texture differences between sites were likely to cause large differences in soil hydraulic properties. Using standard relationships (Campbell 1985), saturated hydraulic conductivity at the loam site was estimated to be over three times less than at the sand site, but moisture retention at -1 MPa was over three times greater.

Precipitation recorded near both sites before and during the study summer of 2000 was below normal. During the June–August measurement period (Fig. 1a,b),

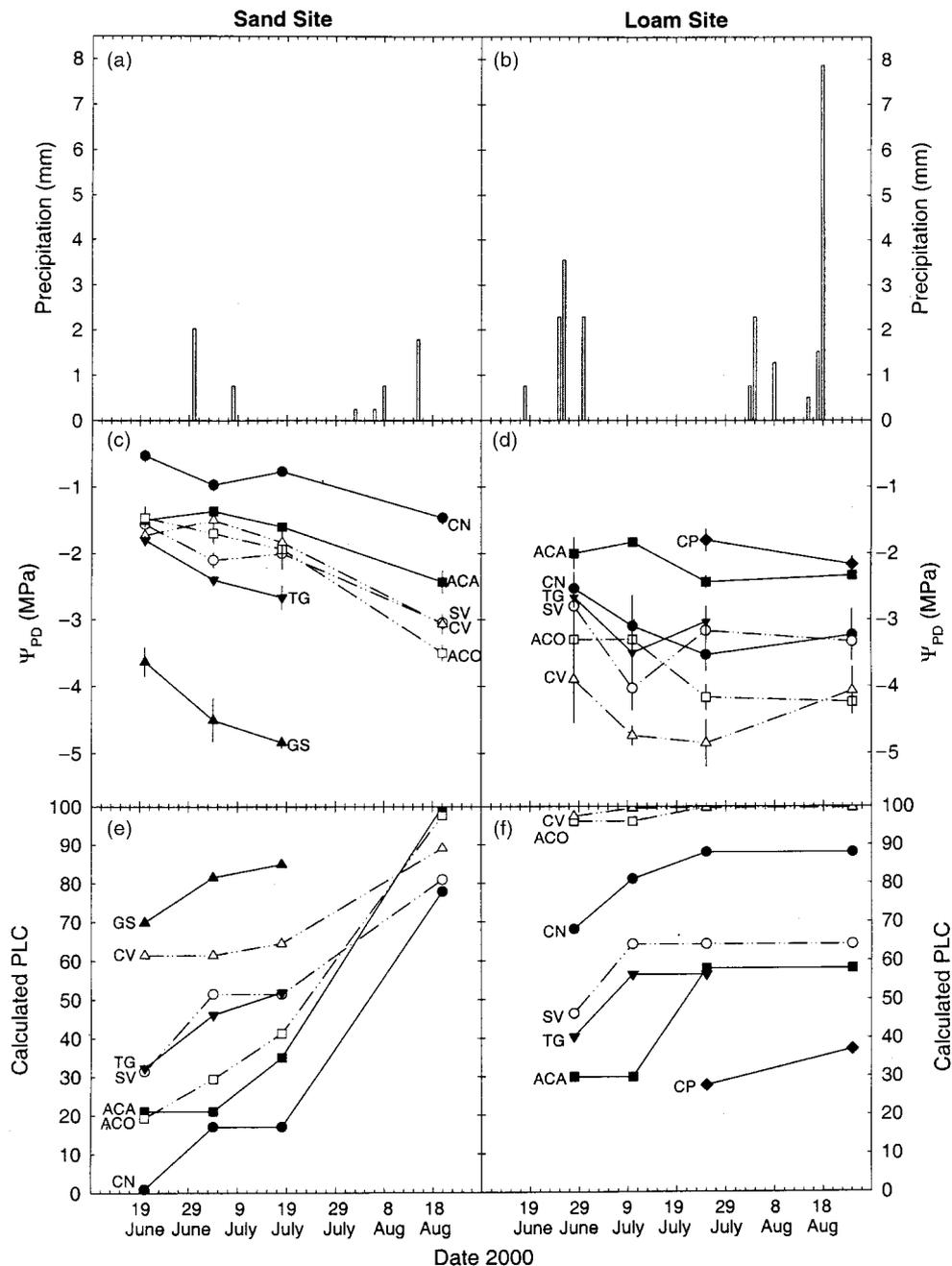


Fig. 1. Species abbreviations as in Table 1. (a,b) Precipitation near the sand site (a) at Dugway, Utah; and near the loam site (b) at Vernon, Utah. (c,d) Seasonal course of predawn xylem pressure (Ψ_{PD}) at the sand site (c) and loam site (d). Means \pm SE, $n = 3$ plants. (e,f) Calculated native percentage loss of hydraulic conductivity (PLC) in shallow lateral roots at the sand site (e) and loam site (f). Calculations based on Ψ_{PD} and vulnerability curves from these roots (Fig. 3), assuming the PLC goes up as Ψ becomes more negative, but does not decrease with rising Ψ . Means \pm SE, $n = 3$ plants.

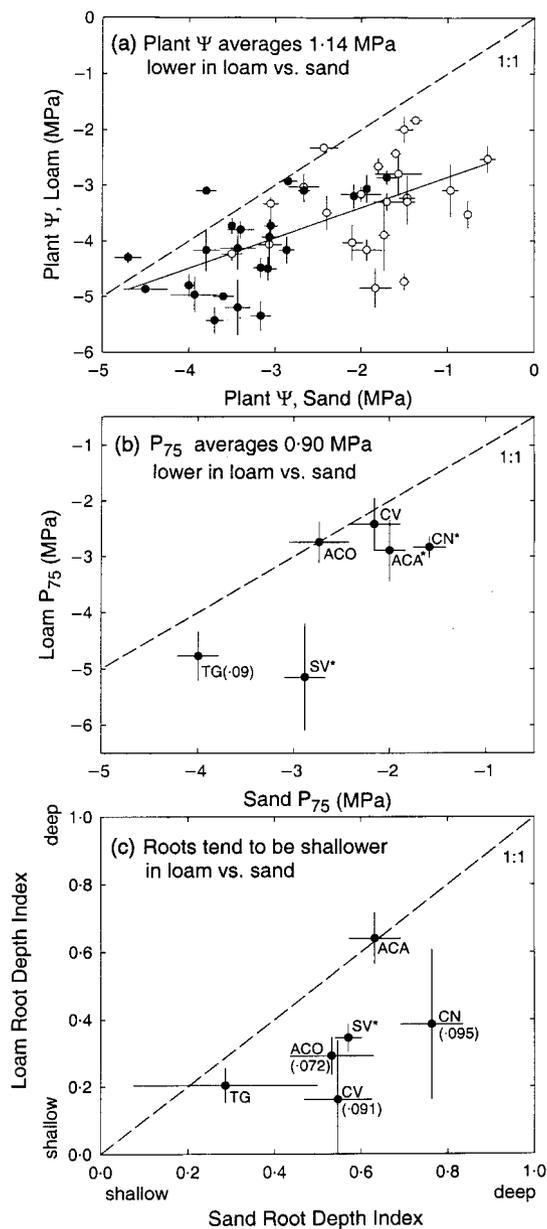


Fig. 2. Comparisons between loam versus sand sites. Species abbreviations as in Table 1. (a) Predawn (Ψ_{PD} , \circ) and midday (Ψ_{MD} , \bullet) xylem pressures for the same species at both sites for paired measurement dates in Fig. 1(c,d). Correlation is significant ($r^2 = 0.37$). Means \pm SE, $n = 3$ plants. (b) Xylem pressure causing 75 PLC in vulnerability curves (P_{75}) for the same species at the loam versus sand sites. Means \pm SE, $n \geq 6$ roots. Asterisks indicate $P < 0.05$ for site means compared by t -test, P values between 0.05 and 0.1 in parentheses. (c) Root-depth index $[(\Psi_{155} - \Psi_{PD})/\Psi_{155}]$ for the same species at the loam versus sand sites. Means \pm SE, $n = 4$. Asterisks indicate $P < 0.05$ for site means compared by t -test, parentheses indicate P values between 0.1 and 0.05.

precipitation was greater at the loam site (22.3 mm, -13% of normal) than the sand site (5.8 mm, -69% of normal). Adding the previous winter and spring precipitation (October–August), the loam site was also wetter (210 mm, -15% of normal) than the sand site (142 mm, -23% of normal).

Despite the greater precipitation indicated for the loam site, xylem pressures were considerably lower there

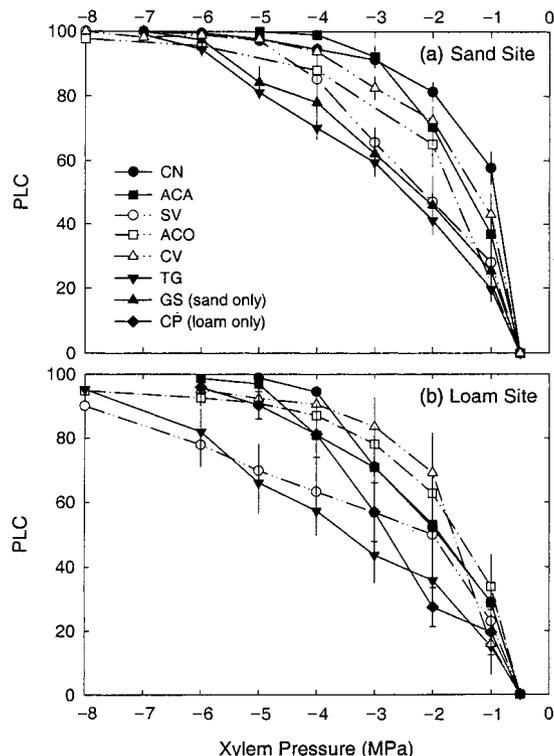


Fig. 3. Vulnerability curves showing the PLC as a function of xylem pressure. Curves are for the xylem of shallow lateral roots (from top 0.4 m of soil) for the eight study species at the sand (a) and loam (b) sites. Roots averaged 3.4 ± 0.1 mm in diameter ($n = 131$). Species abbreviations as in Table 1. Means \pm SE, $n \geq 6$.

than for the same species at the sand site, especially in June and July (Fig. 1c,d). When all species, sampling dates and measurements (Ψ_{PD} and Ψ_{MD}) were compared, species xylem pressure averaged 1.1 MPa more negative at the loam versus the sand site (Fig. 2a). The only exceptions were during the last sampling period in August, when some species were slightly drier at the sand site. This exception was associated with a significant (8 mm) rain event that occurred only at the loam site a few days before the measurement (Fig. 1b). The correlation between loam and sand Ψ for a given species (Fig. 2a) resulted from a loose tendency for species to maintain the same pressure ranking within both sites.

CAVITATION RESISTANCE, NATIVE PLC AND TRANSPIRATION

Roots at both sites had convex shapes to their vulnerability curves with considerable embolism at modest pressures (Fig. 3), as opposed to the concave or sigmoidal shape with a more-or-less defined cavitation threshold seen in most stem xylem of the same species (Hacke *et al.* 2000b). On average, the P_{75} of a species was 0.9 MPa more resistant in loam as compared to sand (Fig. 2b). The greatest difference was in *S. vermiculatus*, while *A. confertifolia* and *C. viscidiflorus* showed little or no adjustment, and *T. glabrata* differed only at a P value of 0.091 (Fig. 2b). There was a tendency

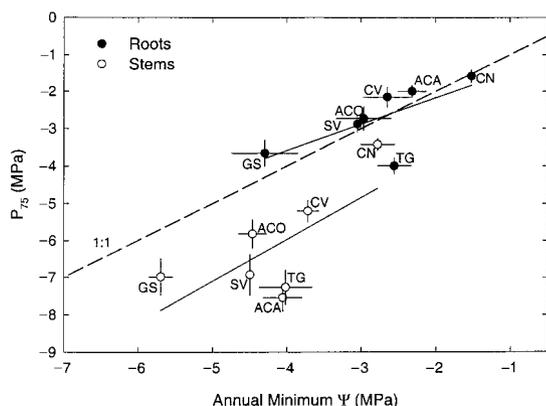


Fig. 4. Xylem pressure causing 75% loss in hydraulic conductivity (P_{75}) versus the minimum plant Ψ averaged over three summers. Data for root (●) and stem (○) xylem at the sand site. Root P_{75} is plotted versus the average minimum Ψ_{PD} , stem P_{75} is plotted versus the average minimum Ψ_{MD} . Trends are evident, but not significant, within each organ for lower Ψ to correspond with lower P_{75} . Means \pm SE, $n = 3$ for Ψ data, $n \geq 6$ for P_{75} data. Species abbreviations as in Table 1.

for the species to retain their relative resistance to cavitation across sites. For example, *T. glabrata* was among the most resistant, and *C. nauseosus* the most vulnerable species at both sites (Figs 2b and 3). Only one species showed a trend in cavitation resistance with root diameter: in *A. confertifolia* larger lateral roots were more resistant than smaller ones (data shown for smaller roots only). Hacke *et al.* (2000b) found that the tap roots of *C. nauseosus* were significantly more resistant to cavitation than the lateral roots measured for this study.

Root P_{75} averaged 3.45 MPa less negative (more vulnerable) than stem P_{75} where these organs were compared for sand site species (Fig. 4; see also Hacke *et al.* 2000b). Roots were also expected to experience much more native PLC during the summer than stems (Fig. 4). Based on the average minimum Ψ_{PD} over three summers of measurement, roots of most species at the sand site (*T. glabrata* excepted) were expected to reach a maximum near 75 PLC *in situ*, as indicated by the data ranging along the 1 : 1 line (Fig. 4). Corresponding data for stems and minimum Ψ_{MD} were well under this line, indicating much less native PLC than in roots. There was a trend for species with the lowest Ψ values also to have the lowest P_{75} . Direct measurements of native PLC for xylem of roots in the top 0.4 m of soil were consistent with predictions based on Ψ_{PD} and the vulnerability curves for similarly sized roots from the same top soil layer (Fig. 5). This correspondence allowed the estimation of seasonal native PLC in shallow roots (top 0.4 m) from vulnerability curves and native Ψ_{PD} (Fig. 1e,f). The estimated PLC in Figs 5 and 1(e,f) assumed no refilling of the xylem if Ψ_{PD} rose above a previous seasonal minimum. In fact, Ψ_{PD} generally declined monotonically through the season, with relatively minor exceptions (Fig. 1c,d).

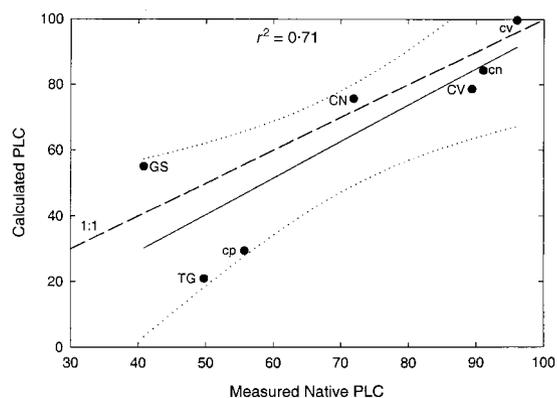


Fig. 5. Native PLC in shallow lateral roots calculated from xylem pressure and vulnerability curves versus measured native PLC in similar roots. Calculations assumed the PLC increased with seasonal declines in Ψ , but did not decrease if Ψ subsequently rose. $r^2 = 0.71$ and 95% confidence limits enclose the 1 : 1 line. Species abbreviations as in Table 1. Lower case abbreviations are species from the loam site.

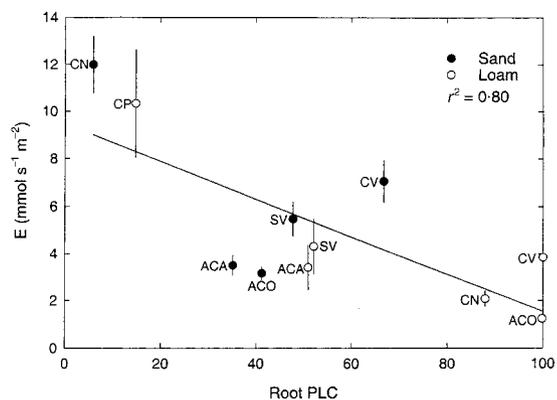


Fig. 6. Transpiration rate (E) versus calculated native PLC in shallow roots on the same day in late July 2000. ●, Sand site data; ○, loam site data. Means \pm SE, $n = 3$ plants per species. The significant trend has $r^2 = 0.80$.

The seasonal course of native PLC in shallow roots showed greater PLC at the loam versus sand sites during June and July (Fig. 1e,f). Over the first three pairs of measurements, loam site PLC averaged 35% greater than at the sand site for the same species. Three species, *A. confertifolia*, *C. viscidiflorus* and *C. nauseosus*, developed over 80 PLC by the end of July at the loam site; the first two reached nearly 100 PLC. At the sand site, only the drought-deciduous *G. spinosa* exceeded 80 PLC during this same period before dropping its leaves. Greater PLC in the shallow roots was associated with lower transpiration rates across both sites when this was measured in late July (Fig. 6, $r^2 = 0.80$). Importantly, the presence of 100 PLC in shallow roots does not necessarily mean no water supply to the canopy if roots below 0.4 m were still conducting.

Although the June and July PLC was relatively low at the sand site, by the August measurement the continued drop in Ψ (Fig. 1c) caused the estimated PLC to rise above 75 in all species, reaching near 100

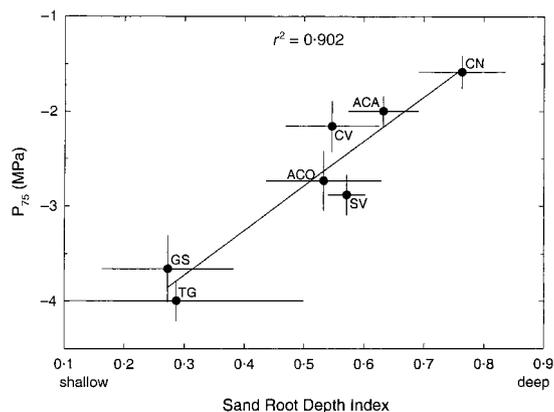


Fig. 7. Xylem pressure causing 75% loss in hydraulic conductivity (P_{75}) in shallow roots versus the root-depth index $[(\Psi_{155} - \Psi_{PD}) / \Psi_{155}]$ for species at the sand site. The trend was significant with $r^2 = 0.90$. Means \pm SE, $n \geq 6$ for P_{75} , $n = 3-4$ for depth index. Species abbreviations as in Table 1.

in *A. canescens* and *A. confertifolia*. Thus, at the end of the season, PLC estimates were comparable at both sites, exceptions being *S. vermiculatus* and *A. canescens* which had lower PLC at the loam versus the sand site at the end of the season (Fig. 1e,f).

SOIL Ψ PROFILES AND ROOT-DEPTH INDEX

Average soil Ψ at 20 cm depth ranged from a high of -8.3 ± 2.0 MPa (early July at the sand site) to a low of -15.6 ± 1.2 MPa (August at the sand site). Average Ψ at 120 cm deep ranged from a high of -1.8 ± 0.6 MPa (early July at the sand site) to a low of -6.1 ± 0.5 MPa (June at the loam site).

Morning soil Ψ profiles showed a generally strong increase in Ψ (less negative Ψ) with depth. Only 10 of

32 profiles deviated more than 0.5 MPa from a monotonic rise in Ψ from layer to layer. Of these 10, six were localized to the first measurement period in June. By the August measurement, all profiles showed a progressive increase in Ψ with depth. At no time was the shallowest soil layer wetter than the deepest one. Averaging over both sites for the entire summer, the Ψ of the deepest layer (1.2 m) was 6.6 ± 0.8 MPa less negative than the Ψ of the shallowest layer (0.2 m, $n = 32$). It is possible that some of the irregular profiles in the early season were associated with more hydraulic lift of deep soil water at this time of year (Richards & Caldwell 1987).

The root-depth index $[(\Psi_{155} - \Psi_{PD}) / \Psi_{155}]$, averaged over the measurement dates] averaged 0.22 points shallower at the loam versus the sand site for the same species, suggesting a trend towards shallower functional rooting depth in the loam soil (Fig. 2c). Owing to small sample sizes ($n = 3-4$) and plant-to-plant variation, only *S. vermiculatus* was statistically significant at the 0.05 level. Three other species (*A. confertifolia*, *C. nauseosus* and *C. viscidiflorus*) were different at relatively low P values of 0.072–0.095. The depth index was positive for all species at both sites, i.e. Ψ_{PD} was less negative than Ψ_{155} , indicating that roots extended below 1.55 m at both sites and in all species.

At the sand site there was a strong relationship between root depth and cavitation resistance (Fig. 7). The shallower the root-depth index, the more resistant the xylem to cavitation ($r^2 = 0.90$). No such trend was evident at the loam site because three of the species (*C. nauseosus*, *C. viscidiflorus* and *A. confertifolia*) showed shallow root depth indices in combination with relatively vulnerable xylem. As discussed further below, two of these species (the *Chrysothamnus* species) showed considerable leaf and branch dieback by midsummer (Fig. 8).

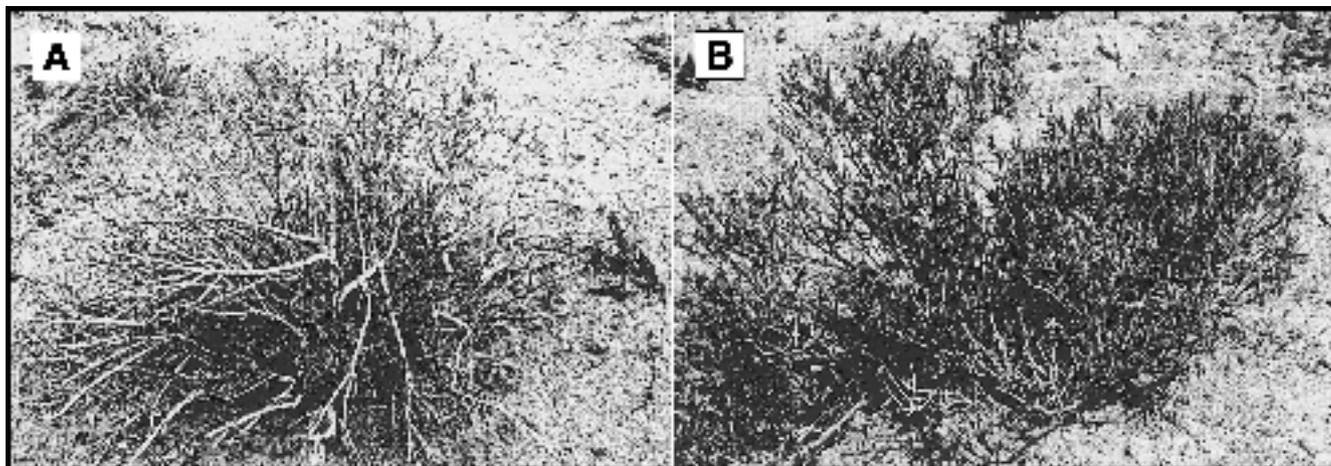


Fig. 8. (a) *Chrysothamnus viscidiflorus* at the loam site in late summer 2001, showing extensive dieback from the previous years with current year's growth resprouting from the base. This species experienced near 100 PLC in its shallow roots the previous summer (Figs 1f and 5), and had the shallowest root-depth index at the site (Fig. 2c). Considerable leaf dieback and reduced flowering was observed during the summers of 2000 and 2001. (b) *Chrysothamnus parryi* at the loam site on the same day for comparison. This species experienced less than 40 PLC the previous summer (Figs 1f and 5), and had the second deepest root index at the site (0.41 ± 0.04). It showed little or no dieback of leaves and branches.

Discussion

SOIL TEXTURE HYPOTHESES

The results were generally consistent with the expected differences in plant water relations between the sand versus loam sites. As hypothesized, species' Ψ was lower at the loam versus sand site over most of the summer, despite greater precipitation at the loam site (Figs 1 and 2a). This was associated with generally more cavitation-resistant root xylem at the loam site, with the exceptions of *C. viscidiflorus* and *A. confertifolia*, which showed little or no adjustment (Figs 2b and 3). Estimated rooting depths tended to be shallower at the loam site as expected, with the clear exceptions of *A. canescens* with its phreatophytic tendencies (Fig. 2c) and the drought-deciduous and shallow-rooted *T. glabrata*. More site and season comparisons would be necessary before generalizing these results for the region. However, the data show the large differences in plant water relations that can occur between sites of similar climate and topography, but with very different soil texture.

Similar conclusions were reached in a study of *Pinus taeda* (loblolly pine) growing on sand versus loam soils in North Carolina, USA (Hacke *et al.* 2000a). Sand trees experienced uniformly higher Ψ , had deeper roots, and these roots were more vulnerable to cavitation than loam trees. In addition, the sand trees had a much higher root-to-leaf area ratio, as expected, to minimize the development of limiting hydraulic resistances in the rhizosphere in sandy soil as well as to increase nutrient uptake in these relatively sterile soils (Haynes & Gower 1995). Sandy soils on the south-eastern coastal plain are generally considered to support vegetation with more long-lived and sclerophyllous leaves, but this trait may be more an adaptation to low nutrient availability rather than low soil Ψ (Givnish 1979; Loveless 1961).

The intraspecific variation we observed in cavitation resistance of roots (Figs 2b and 3) was apparently an adaptive response to the site's soil characteristics. Greater cavitation resistance in a finer-textured soil would enhance the water extraction capability of the root system, allowing the plant to withdraw more of the water that is retained at low Ψ in a finer soil. In this sense, the operating Ψ range of a plant and the cavitation resistance of the root xylem go hand-in-hand: plant Ψ can be lower in cavitation-resistant plants because the roots can remain in hydraulic contact with a drier soil.

We do not know whether the intraspecific variation in cavitation resistance was a consequence of genetic variation between the populations, or of phenotypic plasticity. Studies of subspecies of *Artemisia tridentata* (sagebrush) have shown that considerable intraspecific variation in cavitation resistance in stems of this species is maintained in a common garden, suggesting genetic differentiation in the trait (Kolb & Sperry

1999a). Conversely, in the *P. taeda* study mentioned above, sand and loam trees were related at the half-sib level, suggesting that phenotypic plasticity was responsible for the adjustment in hydraulic traits. Two of our study species were represented by different taxonomic varieties at each site (*C. nauseosus* and *C. viscidiflorus*, Table 1); however, this did not necessarily correspond with differences in cavitation resistance, as both *C. viscidiflorus* subspecies had similar P_{75} values (Fig. 2b). In addition, species with no obvious morphological differentiation between sites had large differences in cavitation resistance (e.g. *S. vermiculatus* and *A. canescens*).

IMPORTANCE OF CAVITATION IN ROOT XYLEM

Our study of root hydraulics was necessarily limited in this comparative project, but is suggestive of the importance of root cavitation for plant performance under water stress. In these desert shrubs, roots were much more vulnerable than stems and experienced more cavitation during soil drought (Fig. 4). This suggests that, in terms of xylem transport, the root system is the more limiting component. The same conclusion was reached in a study of another Great Basin shrub, *A. tridentata* (Kolb & Sperry 1999b). However, our studies have estimated PLC and cavitation resistance only in shallow lateral roots of limited diameter range, which leaves the vast majority of the underground conducting system uncharacterized. There will undoubtedly be variation in cavitation resistance within the root system. For example, we observed that large roots of *A. confertifolia* were more resistant than small ones, and tap roots of *C. nauseosus* were more resistant than shallow lateral roots (Hacke *et al.* 2000b). Similar differences were found in *P. taeda* roots (Hacke *et al.* 2000a), and roots of *Psuedostuga menziesii* (Sperry & Ikeda 1997). Roots can also vary their cavitation resistance with depth, as recent studies with *Juniperus asheii* have shown (W.T. Pockman *et al.*, unpublished results). Perhaps the most important roots are the fine roots, which have the greatest surface area and hence the greatest potential for water uptake. We do not know how the cavitation resistance of these roots compares to that of larger roots that have been measured.

Cavitation in shallow roots may influence the ability of desert shrubs to utilize summer rain. The higher the PLC of shallow roots prior to the rain event, the less uptake would be expected following the event, unless the cavitation was rapidly reversible. Interestingly, *C. nauseosus*, *A. canescens*, and *A. confertifolia* are all relatively unresponsive to simulated rain events after significant drought (Hodgkinson, Johnson & Norton 1978; Lin, Phillips & Ehleringer 1996). Each of these species in our study had very high PLC in shallow roots by mid-August (Fig. 1e,f).

Root cavitation also has implications for the operation of hydraulic redistribution of water by deep root

systems (Caldwell, Dawson & Richards 1998). Deep-rooted species with vulnerable shallow roots will lift less water over a prolonged summer drought than a deep-rooted species with resistant shallow roots. Using this information, we can tentatively rank the lifting capability of our three deep-rooted species: *C. nauseosus* would be the poorest lifter, followed closely by *A. canescens*, and *S. vermiculatus* should be the best lifter. Although these three species have not been compared systematically, *C. nauseosus* shows comparatively less hydraulic lifting capability over the summer than *S. vermiculatus* (L.A. Donovan, personal communication; Caldwell *et al.* 1998). Good lifters like *S. vermiculatus* should tend to have broader functional rooting depths over the season (hence also a shallower root index) because more of the root system remains in hydraulic contact with the shallower soil by virtue of its greater cavitation resistance.

Root cavitation should influence how Ψ_{PD} 'equilibrates' with a heterogeneous soil moisture profile. The Ψ_{PD} represents a complex average of hydraulic conductances linking different layers of the rooting zone with their soil. As shallow roots cavitate and lose hydraulic contact with the drying topsoil, the functional rooting depth will shift deeper. It is theoretically possible that the shift to deeper layers would be associated with an increase in Ψ_{PD} , even in the absence of any rainfall. This could even happen on a daily basis if shallow roots lose contact with dry soil during the day (via hydraulic failure at the rhizosphere, for example), but regain it at night. This could perhaps cause Ψ_{MD} to be less negative than Ψ_{PD} , as has been occasionally observed in *Larrea tridentata* (Syvertsen, Cunningham & Feather 1975).

IMPLICATIONS FOR SHRUB FUNCTIONAL TYPES AND FITNESS

Species at the sand site exhibited a continuum of water-use strategies based on correspondence between root-depth index, cavitation resistance, vegetative phenology and seasonal regimes in Ψ . At one extreme were the drought-deciduous species (*G. spinosa* and *T. glabrata*) with the shallowest root indices (Fig. 7), most cavitation-resistant root xylem (Fig. 3), and the lowest midsummer Ψ (Fig. 1c). These traits would maximize water extraction from the shallow soil during the first half of the growing season prior to leaf drop and drought dormancy. At the other extreme were two species with the most phreatophytic tendencies (*C. nauseosus* and *A. canescens*). These summer-active species had the deepest root indices (Fig. 7), most vulnerable root xylem (Fig. 3), and uniformly highest Ψ throughout the summer (Fig. 1c). All these traits suggest preferential use of more stable deep soil water supplies. Intermediate between these extremes were three summer-active species with moderate root-depth indices, cavitation resistance and Ψ regimes (*C. viscidiflorus*, *A. confertifolia* and *S. vermiculatus*). These

species were apparently exploiting both deep and shallow soil water. *Sarcobatus vermiculatus* is often regarded as a phreatophyte (Nichols 1994), and it had the deepest root index of these three intermediate species.

The same species at the loam site did not all conform to the clear trends observed at the sand site. Three of the seven species at this site showed a potentially deadly combination of relatively shallow root indices and relatively vulnerable xylem, resulting in high native PLC: *C. viscidiflorus*, *C. nauseosus* and *A. confertifolia* (Fig. 1f). These were the same species showing some of the lower transpiration rates (Fig. 6). If the only roots present were shallow roots with nearly 100 PLC, the leaves of these species should face a restricted water supply.

Two of these species (*C. nauseosus* and *C. viscidiflorus*) did exhibit considerable leaf dieback during July and August. This was apparently coupled with branch dieback – the following year (2001) the shoots of many *C. viscidiflorus* plants were completely dead, with new growth emerging from the root collar (Fig. 8a). In contrast, neighbouring *C. parryi* plants with less than 40 PLC and high transpiration rates in 2000 were in good condition, showing relatively little branch dieback (Fig. 8b). The low PLC in *C. parryi* was a result of its more cavitation-resistant xylem and deeper roots. Leaf and branch dieback in *C. viscidiflorus* and *C. nauseosus* has direct consequences for at least the current year's fitness, because both are autumn-flowering species. In contrast to this 'accidental' drought-deciduousness, the normal type seen in spring-flowering *T. glabrata* and *G. spinosa* was not associated with pronounced branch dieback or the development of near 100 PLC prior to leaf drop, owing to the relatively cavitation-resistant xylem in these species. Although *C. viscidiflorus* and *C. nauseosus* were able to persist through the following year (Fig. 8a), it seems possible that multiple years of subnormal precipitation could result in substantial whole-plant mortality for these species at the loam site, as has been observed for *C. nauseosus* in other studies (Toft 1995).

The results for *A. confertifolia* at the loam site were somewhat puzzling. This species was relatively abundant at the site, and is generally regarded as successful on heavy soils (Stutz & Sanderson 1983). However, this species showed no adjustment in cavitation resistance between sites (Fig. 2b) and, like *C. nauseosus* and *C. viscidiflorus*, it experienced high shallow-root PLC early in the summer in combination with an overall shallow root-depth index and low gas-exchange rates (Fig. 6). These traits would seem to compromise its competitive ability in a loam soil. However, unlike the *Chrysothamnus* species, *A. confertifolia* did not show obvious dieback. Perhaps the higher water-use efficiency associated with C_4 photosynthesis in this species may have allowed it to survive despite low gas-exchange rates (Lin *et al.* 1996). Furthermore, its root-depth index was deeper than its suffering neighbour *C. viscidiflorus* (Fig. 2c), perhaps allowing limited access to deeper

water despite the nearly complete loss of conductivity in some of the root system for much of the summer (Fig. 1f). Considerable drought-induced mortality has been observed in *A. confertifolia* in long-term studies (Chambers & Norton 1993), and it is possible that it may take several dry years in succession before dieback would be evident.

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References

- Alder, N.N., Pockman, W.T., Sperry, J.S. & Nuismer, S. (1997) Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany* **48**, 665–674.
- Alizai, H.U. & Hulbert, L.C. (1970) Effects of soil texture on evaporative loss and available water in semi-arid climates. *Soil Science* **110**, 328–332.
- Boyer, J.S. (1995) *Measuring the Water Status of Plants and Soils*. Academic Press, San Diego, CA.
- Brown, R.W. & Chambers, J.C. (1987) Measurement of *in situ* water potential with thermocouple psychrometers: a critical evaluation. *Proceedings of International Conference on Measurement of Soil and Plant Water Status*. Utah State University, Logan, UT.
- Caldwell, M.M., Dawson, T.E. & Richards, J.H. (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* **95**, 151–161.
- Campbell, G.S. (1985) *Soil Physics with BASIC*. Elsevier, Amsterdam.
- Campbell, G.S. & Norman, J.N. (1998) *An Introduction to Environmental Biophysics*. Springer, New York.
- Chambers, J.C. & Norton, B.E. (1993) Effects of grazing and drought on population dynamics of salt desert shrub communities on the Desert Experimental Range, Utah. *Journal of Arid Environments* **24**, 261–275.
- Christensen, N.L. (1988) Vegetation of the southeastern coastal plain. *North American Terrestrial Vegetation* (eds M.G. Barbour & W.D. Billings), pp. 318–363. Cambridge University Press, Cambridge, UK.
- Cronquist, A., Holmgren, A.H., Holmgren, N.H., Reveal, J.L. & Holmgren, P.K. (1994) *Intermountain Flora*. New York Botanical Garden, Bronx, NY.
- Dobrowolski, J.P., Caldwell, M.M. & Richards, J.H. (1990) Basin hydrology and plant root systems. *Plant Biology of the Basin and Range* (eds C.B. Osmond, L.F. Pitelka & G.M. Hidy), pp. 243–292. Springer-Verlag, Berlin.
- Donovan, L.A., Grise, D.J., West, J.B., Pappert, R.A., Alder, N.N. & Richards, J.H. (1999) Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. *Oecologia* **120**, 209–217.
- Givnish, T.J. (1979) On the adaptive significance of leaf form. *Topics in Plant Population Biology* (eds O.T. Solbrig, S. Jain, G.B. Johnson & P.H. Raven), pp. 375–407. Columbia University Press, New York.
- Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schafer, K.V.R. & Oren, R. (2000a) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* **124**, 495–505.
- Hacke, U.G., Sperry, J.S. & Pittermann, J. (2000b) Drought experience and cavitation resistance in six desert shrubs of the Great Basin, Utah. *Basic and Applied Ecology* **1**, 31–41.
- Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J. & McCulloh, K.A. (2001) Cavitation fatigue: embolism and refilling cycles can weaken cavitation resistance of xylem. *Plant Physiology* **125**, 779–786.
- Haynes, B.E. & Gower, S.T. (1995) Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* **15**, 317–325.
- Hodgkinson, K.C., Johnson, P.S. & Norton, B.E. (1978) Influence of summer rainfall on root and shoot growth of a cold-winter desert shrub, *Atriplex confertifolia*. *Oecologia* **34**, 353–362.
- Jackson, R.B., Sperry, J.S. & Dawson, T.E. (2000) Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* **5**, 482–488.
- Jury, W.A., Gardner, W.R. & Gardner, W.H. (1991) *Soil Physics*. John Wiley, New York.
- Kinraide, T.B. (1984) The influence of soil texture on the vegetation of a grazed, short-grass prairie in Colorado. *Southwestern Naturalist* **29**, 277–287.
- Kolb, K.J. & Sperry, J.S. (1999a) Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* **80**, 2373–2384.
- Kolb, K.J. & Sperry, J.S. (1999b) Transport constraints on water use by the Great Basin shrub, *Artemisia tridentata*. *Plant, Cell and Environment* **22**, 925–935.
- Lin, G., Phillips, S.L. & Ehleringer, J.R. (1996) Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* **106**, 8–17.
- Linton, M.J., Sperry, J.S. & Williams, D.G. (1998) Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Functional Ecology* **12**, 906–911.
- Loveless, A.R. (1961) A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and meophytis leaves. *Annals of Botany (London)* **25**, 168–184.
- McDermitt, D.K. (1990) Sources of error in the estimation of stomatal conductance and transpiration from porometer data. *Hortscience* **25**, 1538–1548.
- Nichols, W.D. (1994) Groundwater discharge by phreatophyte shrubs in the Great Basin as related to depth to groundwater. *Water Resources Research* **30**, 3265–3274.
- Pockman, W.T., Sperry, J.S. & O'Leary, W.J. (1995) Sustained and significant negative water pressure in xylem. *Nature* **378**, 715–716.
- Richards, J.H. & Caldwell, M.M. (1987) Hydraulic lift: substantial nocturnal transport of water between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**, 486–489.
- Smith, S.D., Monson, R.K. & Anderson, J.E. (1997) *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin.
- Sperry, J.S. & Ikeda, T. (1997) Xylem cavitation in roots and stems of Douglas fir and white fir. *Tree Physiology* **17**, 275–280.
- Sperry, J.S., Adler, F.R., Campbell, G.S. & Comstock, J.P. (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**, 347–359.
- Stutz, H.C. & Sanderson, S.C. (1983) Evolutionary studies of *Atriplex*: chromosome races of *A. confertifolia* (shadscale). *American Journal of Botany* **70**, 1536–1547.
- Syvetsen, J.P., Cunningham, G.L. & Feather, T.V. (1975) Anomalous diurnal patterns of stem xylem water potentials in *Larrea tridentata*. *Ecology* **56**, 1423–1428.

- Toft, C.A. (1995) A 10-year demographic study of rabbitbrush (*Chrysothamnus nauseosus*): growth, survival and water limitation. *Oecologia* **101**, 1–12.
- Tyree, M.T. & Ewers, F.W. (1991) The hydraulic architecture of trees and other woody plants (Tansley Review No. 34). *New Phytologist* **119**, 345–360.

- Tyree, M., Davis, S. & Cochard, H. (1994) Biophysical perspectives of xylem evolution – is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *International Organization of Wood Anatomists Journal* **15**, 335–360.

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