Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah

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Abstract

Shrubs of the Great Basin desert in Utah are subjected to a prolonged summer drought. One potential consequence of drought is a reduced water transport capability of the xylem. This is due to drought-induced cavitation. We used the centrifuge method to measure the vulnerability of root and stem xylem to cavitation in six native shrub species. The shrubs fall into three categories with regards to rooting depth, vegetative phenology and plant water status during drought. The "summer green" group (*Chrysothamnus viscidiflorus, Atriplex canescens, Atriplex confertifolia*) sustains summer drought with a relatively shallow root system (<2.5 m), but maintains leaf area. A "drought deciduous" group (*Grayia spinosa*, *Tetradymia glabrata*) has shallow roots but responds to drought by dropping leaves. A "phreatophytic" group (e.g. *Chrysothamnus nauseosus*) avoids low water potentials by developing a deep root system that gives them access to deeper soil moisture. We hypothesized that cavitation resistance across these groups was adjusted to the amount of drought stress a species experienced. Drought experience was quantified by measuring plant water potentials over two growing seasons. As expected, we found a significant relationship between the cavitation resistance of roots and stems of a species and the minimum seasonal water potential. Shallow rooted, drought deciduous species showed the lowest water potentials prior to leaf shedding and they had the most resistant xylem. The phreatophytic shrub *Chrysothamnus nauseosus* always maintained favourable water potentials and had the most susceptible xylem, and summer green species were intermediate. This correlation between cavitation resistance and water potential suggests that a safe xylem is associated with some "cost" for the plant. We could identify two costs or trade-offs. The first trade-off was between safety and transport efficiency as reflected by vessel diameter. In 5 out of 7 species, there was an *intra*specific relationship between vessel diameter and cavitation resistance. Roots, having larger vessels than branches, were also more vulnerable to xylem dysfunction. There was also an *inter*specific correlation between vessel diameter and cavitation resistance, but only for combined root and stem data. A second trade-off was found between safety and construction cost. Resistant xylem was strongly correlated with high wood densities, suggesting that thicker cell walls and/or narrower conduits translate into lower air permeability. Air entry into the conduit is known to be the cause of cavitation.

Sträucher der Great Basin Wüste in Utah sind einer langen Sommertrockenheit ausgesetzt. Eine Folge von Tockenstress ist eine reduzierte Wasserleitfähigkeit des Xylems, die durch Cavitationen verursacht wird. Wir benutzten die Zentrifugen-Methode, um die Cavitationsresistenz des Wurzel-

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und Sprossxylems von sechs heimischen Straucharten zu messen. Die untersuchten Pflanzen fallen in drei Gruppen hinsichtlich Wurzeltiefe, vegetativer Phänologie und Wasserstatus. Während eine Gruppe (*Chrysothamnus viscidiflorus, Atriplex canescens, Atriplex confertifolia*) die Sommertrockenheit mit einem relativ flachen Wurzelsystem (<2.5 m) überdauert, vermeiden andere (*Chrysothamnus nauseosus*) niedrige Wasserpotentiale durch tiefreichende Wurzeln, die diesen Pflanzen Zugang zu Wasser in tieferen Bodenschichten verschaffen. Eine dritte Gruppe (*Grayia spinosa, Tetradymia glabrata*) hat flache Wurzeln, verliert aber die Blätter zur Zeit der größten Sommertrockenheit. Wir testeten die Hypothese, dass die Cavitationsresistenz auf den Grad von Tockenstress abgestimmt ist, den eine Art erfährt. Wir quantifizierten Trockenstress durch das Messen der Pflanzen-Wasserpotentiale über einen Zeitraum von zwei Vegetationsperioden. Wie vermutet, fanden wir eine signifikante Beziehung zwischen der Cavitationsresistenz von Wurzeln und Sprossen einer Art und dem niedrigsten saisonalen Wasserpotential. Flachwurzelnde, blattabwerfende Arten zeigten die niedrigsten Wasserpotentiale vor dem Verlust der Blätter, während sie auch das resistenteste Xylem aufwiesen. Die tiefwurzelnde Art *Chrysothamnus nauseosus* hielt immer einen vorteilhaften Wasserstatus aufrecht und hatte das empfindlichste Xylem. Diese Korrelation zwischen Cavitationsresistenz und Wasserpotential deutet darauf hin, dass ein sicheres Xylem mit bestimmten „Kosten" für die Pflanze verbunden ist. Wir konnten zwei „Kosten" oder „trade-offs" identifizieren. Der erste „trade-off" bestand zwischen Sicherheit und Transporteffizienz hinsichtlich Gefäßdurchmesser. In 5 von 7 Arten existierte eine *intra*spezifische Beziehung zwischen Gefäßdurchmesser und Cavitationsresistenz. Wurzeln, die weitere Gefäße als Sprosse hatten, waren auch empfindlicher gegenüber dem Funktionsverlust des Xylems. Ferner gab es eine *inter*spezifische Korrelation zwischen Gefäßdurchmesser und Cavitationsresistenz, allerdings nur für kombinierte Daten von Wurzeln und Sprossen. Wir fanden einen zweiten „trade-off", und zwar zwischen Sicherheit und Konstruktionskosten. Resistentes Xylem zeigte hohe Holzdichten, was darauf hindeutet, dass dickere Zellwände mit einer geringeren Luftdurchlässigkeit verbunden sind.

Key words: Desert shrubs – vessel diameter – wood density – xylem – water transport – drought tolerance

Introduction

In the Great Basin desert of the western USA, the main seasonal moisture input is from winter precipitation (Dobrowolski et al. 1990). Summer is characterized by a prolonged drought with only minor rain events, which represents a serious challenge for the shrub flora characteristic of this habitat. During summer, the soil dries from the top down to deeper soil layers. There are often steep water potential (Ψ) gradients in the soil, with low (more negative) water potentials in upper layers and high water potentials in lower layers. Plants with deeper roots can utilize the deeper soil moisture remaining from winter recharge, and should be able to maintain favourable water potentials throughout the season. Smaller plants with shallow roots rely more on infrequent soil moisture in upper layers and are therefore subjected to lower water potentials (Dobrowolski et al. 1990).

Native shrubs have developed different strategies of coping with the challenge of drought stress and show a great deal of variation regarding seasonal drought stress, rooting depth and vegetative phenology. Based on these differences, species can be divided into three functional groups. While a "summer green" group

has a relatively shallow root system (<2.5 m) but maintains leaf area despite summer drought, drought deciduous species are also shallow-rooted but respond to drought by dropping leaves. A third "phreatophyte" group avoids low water potentials by developing a deep root system (>2.5 m).

These different strategies result in different levels of drought stress, which should also be reflected by the physiological tolerance of a plant to drought stress. Drought tolerance is a complex property, which is defined by several traits including stomatal behaviour, turgor loss point of leaf cells, and water transport capability of the xylem. In this study, we focused on the latter trait. The water transport capability of the xylem decreases as a result of drought. This is due to xylem cavitation, which is the breaking of a water column under negative xylem pressure. Once a conduit cavitates, it becomes air-filled (embolized), and is no longer available for water transport (Zimmermann 1983). Cavitation resistance is an important trait, because cavitation decreases hydraulic conductance (k), which in return will reduce a plant's potential for gas exchange (Sperry et al. 1998, Hacke et al. in press). Plants cannot supply their leaves with water if their xylem conduits are cavitated.

Previous work has shown that plants differ widely in their susceptibility to cavitation (Tyree et al. 1994). Often, there are also large differences within a plant. Roots are usually more vulnerable to cavitation than stems (Sperry & Saliendra 1994, Hacke & Sauter 1996, Mencuccini & Comstock 1997). "Air seeding" (Zimmermann 1983) or drought-induced cavitation occurs when air is sucked from an embolized into a water-filled, functional conduit. Air enters the functional conduit through the largest pore of an intervessel pit membrane (Tyree et al. 1994, Jarbeau et al. 1995). According to the capillary equation, drought-induced cavitation is a function of the pore diameter and of the pressure difference between embolized and functional conduits. The pressure in embolized conduits is atmospheric. In functional conduits, xylem pressure can be as low as –5 MPa or even lower (Pockman et al. 1995).

Our main hypothesis was that a species' cavitation resistance would vary according to the degree of drought the species experienced. Generally, riparian species show a susceptible xylem whereas desert shrubs are more cavitation resistant (e.g., Pockman et al. 1995). We expected to see an adjustment of cavitation resistance even within co-occurring species that differ in their water status as a result of variation in rooting depth and vegetative phenology. Drought stress in each species was quantified by measuring plant Ψ over two growing seasons (1998 and 1999).

If the hypothesis is right and cavitation resistance varies with drought experience, then this would indicate that a safe xylem is in some way costly for the plant. If a resistant xylem was not associated with some cost for the plant, then all plants should show an equally resistant xylem and should simply avoid cavitation. The nature of this potential penalty is not clear yet. One possible trade-off could be between cavitation resistance and hydraulic conductance ("efficiency versus safety", Zimmermann 1983). It follows from the Hagen-Poiseuille equation that wide vessels are much more efficient than smaller ones (Zimmermann 1983), but wide vessels may also be more prone to dysfunction than small conduits (e.g.,

Larcher 1994). To test this, we measured vessel diameters in roots and stems of all species and compared conduit width with cavitation resistance. A second trade-off could arise between safety and construction cost. A good indicator of construction cost is wood density. If thicker vessel walls and more robust pit membranes translate into less air permeability, then cavitation resistance should be associated with higher wood densities. There are also potential interactions between conduit diameter and wood density: a xylem with small (more resistant?) conduits may tend to show a higher wood density than a xylem with wide (and more susceptible?) conduits. However, this relationship is complicated by the contribution of non-conducting xylem fibers and other cell types to wood density.

Materials and methods

Plant material and study site

During the growing seasons of 1998 and 1999 (May through September) studies were conducted on six native Great Basin shrubs, that were representative of the three functional groups mentioned in the introduction. Based on literature data (Table 1), *Chrysothamnus nauseosus* was expected to be a deep rooted phreatophyte, *Chrysothamnus viscidiflorus* and *Atriplex confertifolia* are summer-green with reportedly shallow roots (<2.5 m), while *Grayia spinosa* and *Tetradymia glabrata* are shallow rooted and drought deciduous. The rooting depth of summer green *Atriplex canescens* was ambiguous from the literature, but appears to be shallow rooted at our site (see Results). Both *Atriplex* species show C4 photosynthesis, the other species are C3 plants. The study was conducted near Dugway, Utah, USA (Lat. 40 12 N : Long. 112 56 W). The site is at an elevation of 1326 m above sea level. Mean annual temperature is 11.1 °C, mean annual precipitation is 200 mm (weather station at Dugway). Our study site was located in an intermountain valley, had undisturbed shrub vegetation and was characterized by a coarse soil (loamy sand with a sand fraction of 81%; tested by the Utah State

Table 1. Characteristics of the Great Basin shrubs investigated in this study.

Species	Phenology	Rooting depth	Literature source
Grayia spinosa (Chenopodiaceae)	drought deciduous	shallow (<2.5 m)	Manning & Groeneveld (1989), Branson et al. (1976)
Tetradymia glabrata (Asteraceae)	drought deciduous	shallow	This study
Chrysothamnus viscidiflorus (Asteraceae)	summer green	shallow	Klepper et al. (1985), Abbott et al. (1991), Dobrowolski et al. (1990)
Atriplex confertifolia (Chenopodiaceae)	summer green	shallow	Groeneveld (1989), Branson et al. (1976), Dobrowolski et al. (1990)
Atriplex canescens (Chenopodiacea)	summer green	probably shallow	This study
Chrysothamnus nauseosus (Asteraceae)	summer green	deep (>2.5 m)	Dobrowolski et al. (1990), Donovan et al. (1996), Lin et al. (1996)

Analytical Laboratories). Although some of the species studied are salt tolerant (e.g. *Atriplex confertifolia, Atriplex canescens*) the soil was not saline.

Water potential (Ψ) measurements

Predawn (Ψ_{PD}) and midday water potentials (Ψ_{MD}) were measured with a pressure chamber (PMS Instruments, Corvallis, OR, USA) at 5:30–6:00 and 12:00–14:00 hours, respectively, on clear days throughout the two growing seasons. Leafy shoot tips of 7–10 plants per species were used for the determination of mean Ψ.

Vulnerability to cavitation

To measure the vulnerability of xylem to cavitation we used the centrifuge technique (Pockman et al. 1995), which was described in detail by Alder et al. (1997). Stem and root segments were spun to negative xylem pressure, which resulted in a certain loss of hydraulic conductivity (k_h). The loss of k_h was then plotted versus the corresponding xylem pressure.

Stems segments 30–75 cm long were cut from the plants, were immediately wrapped in plastic bags and brought back to laboratory. Root segments 20–30 cm long were cut from roots of different diameter classes in 20–50 cm depth. Root segments were also tightly wrapped in plastic bags to minimize dehydration. In the laboratory, all segments were cut under water to a standard length of 14 cm. The cut ends were trimmed with a razor blade. Segments were then flushed with deionized and filtered (0.2 μm) water at a pressure of 50–70 kPa for 30 min to remove residual embolism. After flushing, the saturated, initial k_h (k_{h-i}) of a segment was measured using a balance with an accurracy to 0.00001 g (Sartorius BP 211 D, Sartorius AG, Göttingen, Germany) connected with a computer. Hydraulic conductivity was calculated as the mass flow rate of water (kg s^{-1}) through a segment divided by the pressure gradient along the segment (MPa m^{-1}). Segments were then spun in a Sorvall RC 5C centrifuge (Sorvall, Newton, CT, USA) for ≥3 min at target pressure. The ends of the samples were held in "L" shaped plexiglass reservoirs and were immersed in water while spinning. Immediately after centrifuging, k_h was remeasured. The percentage that k_h was below k_{h-i} gave the percent embolism induced while spinning. By plotting minimum xylem pressure vs. the corresponding embolism level, we obtained a "vulnerability curve". Root curves were based on 8–15 segments per species, stem curves were based on 6–9 segments.

Low flow rates required us to simplify the original conductivity apparatus as described by Sperry et al. (1988), so that it held only one segment. This was done to minimize the volume and complexity of the tubing system and thus to minimize weight changes that were unrelated to actual pressure-driven flow through the segment. We also replaced portions of the vinyl tubing with rigid Teflon tubing to minimize tubing volume changes. We measured a background flow rate for the segment before and after measuring the pressurized flow rate. The background rate represents any osmotic and capillary uptake of water by the segment in the absence of an applied pressure difference. Average background flow was subtracted from pressurized flow to determine the net flow for computing the conductivity of the segment. Water flow through stems was measured at a vacuum pressure of 7–10 kPa. This pressure did not cause refilling in stems, and the k_h value remained stable. Many vessels in roots were considerably longer than the segments used, and were thus cut open on both ends. The water pressure for measuring k_h in roots was ≤3 kPa, because higher water pressure caused refilling of embolized vessels that were continuous through the segment. Another characteristic of the plant material was that older growth rings contained many senescent, embolized vessels. This is similar to sagebrush, another native shrub species, where only the outermost growth ring is conducting water (Kolb & Sperry 1999). Thus, the flushing procedure refilled conduits in older growth rings that had been embolized but not otherwise occluded (similar to ring-porous trees, e.g. Cochard & Tyree 1990). These older conduits were found to be excessively vulnerable to re-cavitation, probably because of pit membrane degradation (Hacke et al., in review). In order to determine xylem vulnerability of the functional, current year xylem, all segments were spun to –0.5 MPa after flushing. This pressure was sufficient to embolize most senescent conduits that were refilled by flushing, but was too high to induce embolism in current year conduits. The k_h value obtained after spinning a segment to –0.5 MPa was therefore taken as a reference, meant to approximate 0% embolism of current year conduits.

In order to investigate if there was a relationship between xylem vulnerability and other parameters like minimum seasonal xylem pressure (Fig. 4) and vessel diameter (Fig. 6), it was useful to represent vulnerability curves by a single cavitation pressure. The mean cavitation pressure is approximately equivalent to the xylem pressure inducing 50% embolism. It was calculated from the vulnerability curve, which represented the cumulative distribution of loss of conductivity with decreasing negative pressure. The curve was converted to a non-cumulative frequency distribution of loss of conductivity vs. negative pressure. The mean of this distribution was calculated using the mid-point of each pressure increment.

Acoustic vulnerability curves

Hydraulic vulnerability curves of *C. viscidiflorus* and *C. nauseosus* stems were compared to the acoustic method (Milburn 1973, Tyree et al. 1984). As described previously (Hacke & Sauter 1995, 1996), an ultrasound sensor (model I15I, Physical Acoustics, Princeton, NJ, USA) was attached to 2-year old stems. Stems had been flushed previously to reverse any embolism. While the stems were drying on the laboratory bench, acoustic emissions (AEs) were monitored using a 4615 Drought Stress Monitor (Physical Acoustics). The total amplifier gain was set to 55 dB. Water potential was measured periodically with a pressure chamber and was plotted versus the corresponding sum of AEs.

Anatomical measurements

For a general microscopical analysis, cross sections of stems and roots were prepared. Phloem (specifically callose) was stained with aniline blue, and lignified cell walls in the xylem were stained with safranin. Vessel diameters were then measured in segments that were previously used for conductivity measurements. In stems, inner diameters of all vessels were measured in three radial sectors at 120° intervals. Sectors covered the two outermost growth rings. In small roots, all vessels in a cross section were measured. We used a light microscope interfaced with a bit pad (Donsanto Microplan II, Natick, MA, USA) to determine conduit diameter. In late May of 1999, dye perfusions were made to determine which vessels are functional at the beginning of a growing season. Long stems of *Chrysothamnus viscidiflorus* and *Chrysothamnus nauseosus* were cut, wrapped in plastic bags and brought back to the laboratory. Stems were successively cut back under water from both ends, leaving 15 cm long segments, that contained no vessels that were embolized during collection. Air injection showed that vessels in stems were much shorter that in roots. Segments were then perfused with 0.1% aqueous safranin under a pressure of 3 kPa to identify functional vessels.

Wood density

Stems and roots that were used for measuring wood density were of comparable age and dimension to those used for measuring xylem vulnerability. Segments 2.5 cm long were cut out of stems and roots. A longitudinal cut was then made in the middle of the segment, and the pith as well as the bark were removed with a razor blade. Fresh volume of the wood sample was determined by Archimedes' principle. The sample was immersed in a water-filled tray, which was placed on a balance. Displacement weight was converted to sample volume by the formula: displacement weight (g) / 0.998 (g cm^{-3}), where 0.998 g cm^{-3} is the density of water at 20 °C. Samples were then stored at 75 °C for 48 hrs, and their dry weight was measured. Wood density was calculated as the ratio of dry weight to fresh volume. A sample size of 5–10 wood segments per plant organ was analyzed.

Results

General xylem anatomy

In Asteraceae species (*Chrysothamnus, Tetradymia*), vessel groups were embedded in a matrix of relatively thick-walled fibers. Chenopodiaceae species (*Atriplex, Grayia*) had circular phloem bands (roots) or discrete phloem "islands" (stems). The "anomalous" secondary thickening in Chenopodiaceae species is caused by multiple cambiums (Heklau 1992). Often, vessels and sieve tubes were in close proximity. A possible advantage of this is that released phloem water can easily be taken up by vessels, i.e. that phloem water can be recycled efficiently (Milburn 1996). Dye perfusions conducted in May on *Chrysothamnus* showed that only earlywood vessels from the most recent growth ring and a few latewood vessels from last year's growth were water-filled, probably because of the combined effects of drought- and freezing-induced embolism. New leaves were almost exclusively supported by newly produced earlywood vessels (similar to ring-porous trees). The dye pattern suggests that most vessels of the two *Chrysothamnus* species embolize in the harsh environment of the Great Basin, and that embolism reversal is not an important factor in these plants at seasonal time scales. Like ring-porous trees, *Chrysothamnus* seems to rely on the production of new xylem to reestablish a sufficient water supply to leaves. Dye perfusions were not conducted on other species.

Water potentials

In both years, species showed a similar seasonal pattern of water potentials, but with generally lower minimum values in 1999. As expected, phreatophytic *C. nauseosus* always exhibited the highest water potentials (Fig. 1, open circles). This species uses water from deep soil layers and shows little if any water uptake from shallow soil layers (Lin et al. 1996). As a result of that, predawn and midday water potentials hardly showed any seasonal variation. In contrast, the other summer-green species (*A. canescens, A. conferti-*
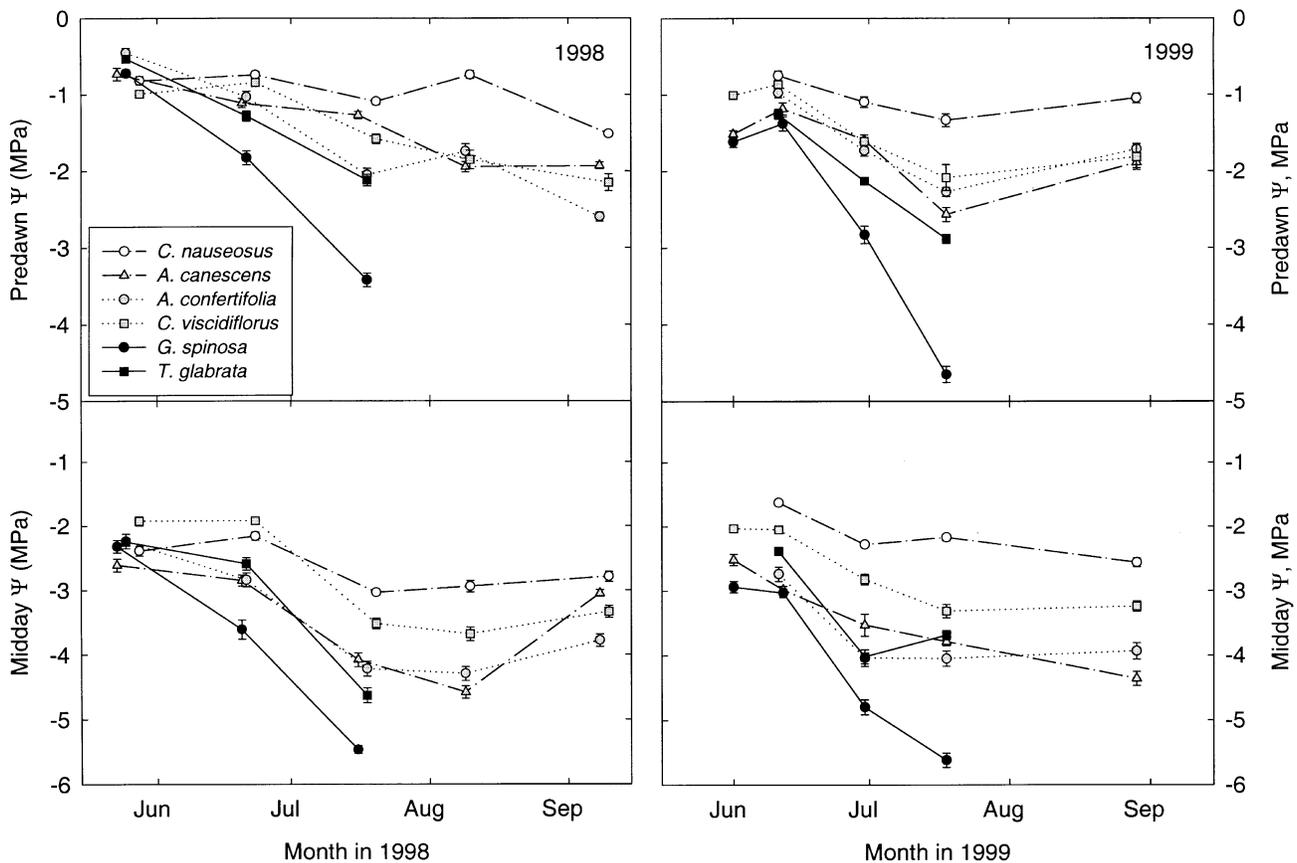
Fig. 1. Seasonal courses of predawn and midday water potentials of six Great Basin shrubs in 1998 and 1999. Plants were growing near Dugway, Utah on coarse soil. Open symbols show deep-rooted species, gray symbols mark shallow-rooted summer-green species, closed symbols represent shallow-rooted drought deciduous shrubs. In drought deciduous shrubs, water potentials could only be measured until leaves were dropped in July. Means ± SE (n = 7–10).

folia, and *C. viscidiflorus*) showed progressively more negative water potentials during the summer drought (Fig. 1), suggesting similarly shallow root distributions within this group.

The two drought-deciduous species showed the greatest decline in water potentials during the summer drought (Fig. 1, closed symbols). In both years, the predawn and midday values of *G. spinosa* and *T. glabrata* decreased progressively from May through July, until leaves were dropped (Fig. 1, closed circles). For example, by July, Ψ_{PD} in *G. spinosa* had fallen to –3.4 MPa in 1998 and to –4.7 MPa in 1999. The decline in Ψ_{PD} in these species paralleled the general seasonal decline of Ψ in upper soil layers suggesting that these two species had the shallowest root systems of all the shrubs studied. An alternative explanation is that the decline in Ψ_{PD} could reflect a progressive loss of hydraulic contact between the coarse soil and the root system as well as increasing root cavitation. According to the vulnerability curve (Fig. 2A, closed circles), roots show about 80% embolism at a Ψ of –4

MPa. If embolism in *G. spinosa* roots increased throughout the season, then plants could not fully equilibrate with the soil Ψ, and Ψ_{PD} would drop. This in return would lead to more root embolism and/or loss of rhizosphere k. This viscous cycle could result in an inadequate water supply of leaves and could trigger leaf shedding in *G. spinosa*.

Xylem vulnerability

In all species, roots (Fig. 2A) were clearly more vulnerable to cavitation than stems (Fig. 2B). Within roots, samples of the phreatophyte *C. nauseosus* were most susceptible (Fig. 2A, open circles), roots of the two drought deciduous species were most resistant (Fig. 2A, closed symbols), and roots of the summer green species were intermediate (Fig. 2A, gray symbols). In stems of most species, the vulnerability curves had a relatively shallow slope (Fig. 2B). An exception was *C. nauseosus,* where embolism in stems increased abruptly between water potentials of –2 to
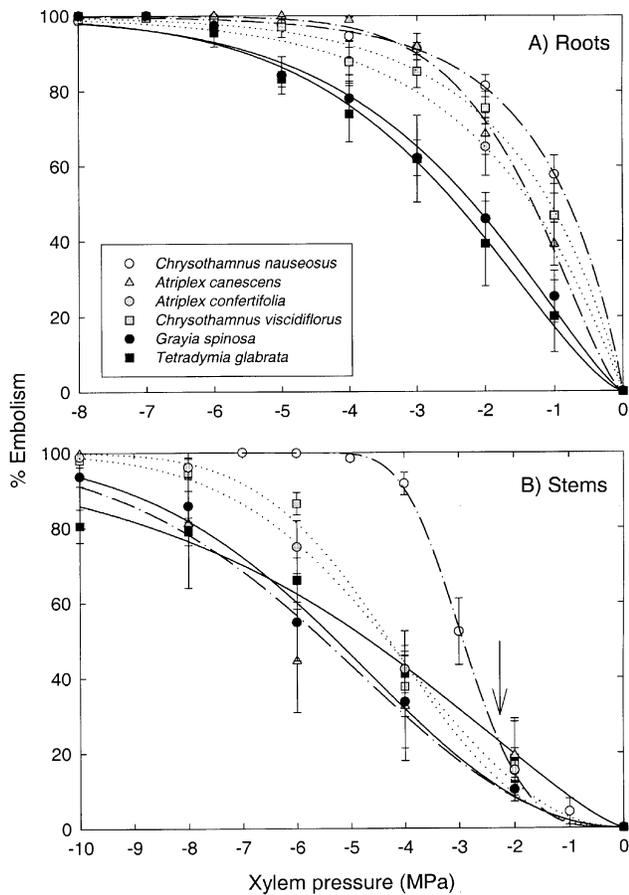
Fig. 2. Vulnerability curves of small roots (A) and 2–3 year old stems (B). Root diameter was 1.4–3.5 mm, stem diameter was 2.5–6.7 mm. Symbols like in Fig. 1. Curves were fitted by a Weibull function. Means ± SE (n = 6–15).

Fig. 3. Acoustic versus hydraulic vulnerability curves for *Chrysothamnus nauseosus* and *Chrysothamnus viscidiflorus* stems. Open circles represent results from n = 3 stems. Closed circles are means from hydraulic curves as shown in Fig. 2B.

–4 MPa (Fig. 2B, open circles). Midday leaf water potentials of this phreatophyte never fell below –3 MPa (Fig. 1). The average Ψ_{MD} from two growing seasons was –2.3 ± 0.1 (see arrow in Fig. 1B). The steep vulnerability curve of *C. nauseosus* was confirmed with an acoustic curve (Fig. 3A). Acoustic and hydraulic vulnerability curves for *C. viscidiflorus* stems were also very similar (Fig. 3).

As hypothesized, cavitation resistance agreed well with the amount of drought stress a species experienced. *C. nauseosus*, having the highest water potentials, also had the most susceptible roots and stems (Fig. 2, open circles). The shallow rooted summer green species had intermediate predawn water potentials and intermediate root vulnerability curves (Fig. 2A, gray symbols). The two drought deciduous species showed the lowest predawn water potentials and the most resistant root xylem (Fig. 2A, closed symbols). This agreement resulted in the highly significant relationship shown in Fig. 4. The graph shows

cavitation resistance (expressed as mean cavitation pressure) as a function of the minimum seasonal Ψ from two growing seasons. We used Ψ_{PD} as a measure of drought stress in roots, and plotted the minimum Ψ_{PD} vs. the mean cavitation pressure of roots (closed circles). Similarly, we plotted the minimum Ψ_{MD} of a species vs. the mean cavitation pressure of stems (gray circles). The regression line approximates the 1:1 line (dashed line). Since the mean cavitation pressure is equivalent to the Ψ at ~50% embolism, there was approximately ~50% embolism in roots and stems at the peak of the summer drought. However, closer inspection indicates that for most species, the more vulnerable root xylem became more that 50% embolized; substantially so in the drought deciduous *G. spinosa* (solid circle farthest above the 1:1 line). Conversely, the more resistant xylem was generally less than 50% embolized.

While it is obvious that data points in Fig. 4 cannot be far *above* the 1:1 line (because the xylem would be-
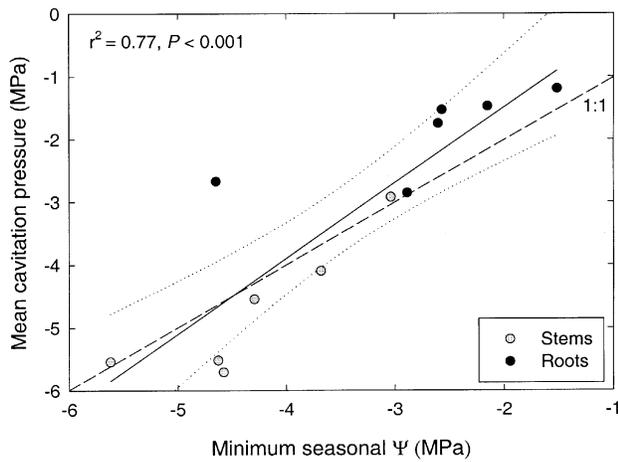
Fig. 4. Mean cavitation pressure (representing the xylem pressure at ~50% embolism) of roots and stems as a function of the minimum seasonal water potential. Mean cavitation pressure of roots was plotted vs the minimum seasonal predawn water potential (closed circles); mean cavitation pressure of stems was plotted vs the minimum seasonal midday water potential (gray circles). There was a highly significant correlation, indicating that vessels were only as cavitation-resistant as required by the specific growing conditions. Dotted lines show 95% confidence intervals, dashed line shows 1:1 relationship.

Fig. 5. Vessel diameter distribution in different organs of *Chrysothamnus nauseosus*. Means ± SE (n = 6–11).

Fig. 6. (A) *Intra*specific relationship of mean cavitation pressure versus vessel diameter of root and stem segments of *Chrysothamnus viscidiflorus*. (B) *Inter*specific relationship of mean cavitation pressure versus vessel diameter. There was a correlation for collective root and stem data. Stems usually had a lower cavitation pressure (were more resistant) and had smaller vessels than roots. There was no correlation among stems and among roots of different species (dotted lines). Abbreviations show first letters of genus and species name: *Atriplex canescens* (Aca), *Atriplex confertifolia* (Aco), *Chrysothamnus nauseosus* (Cn), *Chrysothamnus viscidiflorus* (Cv), *Grayia spinosa* (Gs), *Sarcobatus vermiculatus* (Sv), *Tetradymia glabrata* (Tg). Appendix "R" means small roots (<4mm), "LR" means "large roots" (≥4mm).

come completely embolized), this does not explain why data points should not be scattered well *under* the line. In fact, being far under the line would insure a large safety margin from high embolism rates during drought. For instance, why was the cavitation pressure in *C. nauseosus* roots and stems not as low as in other species? There must be some cost involved in having a resistant xylem.

Vessel diameters and wood density

A representative example for the vessel diameter distribution is shown in Fig. 5. In *C. nauseosus*, vessels were widest in taproots (>4 mm), intermediate in small absorbing roots (1.5–2.5 mm), and narrowest in stems. In 5 out of 7 species, there was a statistically significant *intra*specific correlation between mean vessel diameter and mean cavitation pressure. This is shown for *C. viscidiflorus* in Fig. 6A. Stems had smaller vessels than roots while stems were also more resistant to cavitation. Although the correlation was significant for collective root and stem data, there was no correlation among stems and among roots of this species. When root and stem data of all species was combined, there was a significant *inter*specific correlation (r² = 0.48) between vessel diameter and cavitation resistance (Fig. 6B, solid regression line). However, there was no correlation among stems of different species and among roots (Fig. 6B, dotted lines).

Fig. 7. Mean cavitation pressure as a function of wood density. A significant correlation was found for both combined root and stem data as well as for stems only. Cavitation-resistant species showed a higher wood density than vulnerable species. Species abbreviations as in Fig. 6.

Wood density proved to be an even better anatomical correlate of xylem vulnerability than diameter (Fig. 7, $r^2 = 0.78$). Wood density explained 78% of the variation in cavitation resistance versus only 48% explained by conduit diameter. Stems that were most susceptible to cavitation had the lowest wood density, and vice versa. Only three large roots (>4 mm in diameter) were included, but data for large roots fell reasonably well on the regression line.

Discussion

As hypothesized, differences in drought experience resulting from the different water use strategies (Fig. 1) agreed with vulnerability to cavitation (Figs. 2, 3, 4). Species that experienced low water potentials during drought had resistant xylem, species with a more favourable water status were more susceptible to cavitation. This finding emphasizes that cavitation resistance is an important trait that – among other traits – defines drought tolerance and the Ψ range a species can sustain. Cavitation resistance is likely to be associated with other parameters that determine plant Ψ, like rooting depth. *C. nauseosus*, a deep rooted species, showed the highest water potentials and the most susceptible xylem. Shallow rooted species had lower water potentials and were more resistant to cavitation. A caveat to this statement is that relative rooting depth was assessed from literature data (Table 1), and from predawn water potentials. We are planning excavations to measure root distribution at the site directly.

Table 1 indicates that the six shrubs investigated can be divided into three functional groups. Some of the study species exhibited seasonal Ψ patterns that were expected based on putative rooting depth and phenology. Others showed surprising results. As expected, the deep rooted species *C. nauseosus* consistently maintained the highest predawn and midday water potentials throughout both growing seasons (Fig. 1, open circles). This agrees with results of Lin et al. (1996), who found similar water potentials in this species. As in this study, the authors found isohydric behaviour in *C. nauseosus*, i.e. there were no significant seasonal changes in Ψ. Isohydric control of Ψ_{MD} is necessary in this species, because stems showed a sharp increase in embolism between water potentials of –2 and –4 MPa (Fig. 2B). The average Ψ_{MD} was -2.3 ± 0.1 (see arrow in Fig. 2B). The actual embolism rate in stems was probably even lower than the arrow suggests, because Ψ_{MD} (=leaf Ψ) is usually lower than the xylem pressure in stems, on which the vulnerability curve was based. Steep vulnerability curves and isohydric behaviour also occur in other species with consistent access to water like *Betula occidentalis* (Sperry & Saliendra 1994, Saliendra et al. 1995) and *Populus balsamifera* (Hacke & Sauter 1995). Nonetheless, seedlings of *C. nauseosus* are subjected to lower water potentials than adults and must rely on water uptake from shallow soil layers (Donovan & Ehleringer 1994). If xylem vulnerability of seedlings is similar to that of adults, then cavitation could be limiting seedling establishment in this species.

The fact that drought deciduous species were more resistant to cavitation than summer green species (Fig. 2) is surprising. We had expected the drought deciduous shrubs to be more vulnerable than the summer green ones, thus developing more embolism and forcing them to drop leaves and terminate gas exchange during peak drought. Instead, what seems to be driving the drought deciduous behavior are much lower water potentials presumably associated with significantly shallower root systems. In short, these drought deciduous shrubs simply run out of extractable soil water. While greater cavitation resistance allows them to maximize water extraction from the shallow soil, ultimately the supply is exhausted by midsummer and the shrubs become leafless. Associated with the drying soil is substantial cavitation in the root xylem, at least in *G. spinosa* (Fig. 4).

In all plants, small roots were clearly more vulnerable than stems (Fig. 2). This pattern has also been found in trees (Sperry & Saliendra 1994, Hacke & Sauter 1996) and other desert shrubs (Mencuccini & Comstock 1997). Within roots of a species, small roots were more susceptible than large roots (Fig. 6B, "CNR" vs "CN LR", "AcoR" vs "Aco LR"). Similar results were found in conifers (Sperry & Ikeda 1997, Hacke et al. in press). Root cavitation occurred well

within the physiological Ψ range of our species (Figs. 1,2,4). Because of their great susceptibility, small roots may be called the "Achilles' heel" for water transport within the plant. A positive aspect of their susceptibility is that there is a clearly defined element along the flow path where hydraulic failure may occur under severe drought conditions, thus protecting or enhancing the performance of the remaining system. Confining cavitation to "cheap" organs like small roots may be advantageous compared to a random distribution of cavitation within a plant. Clearly, it would be counterproductive if organs that represent many years of carbon allocation, like stems or large taproots, would be particularly susceptible to cavitation. Reversal of cavitation triggered by rain events may also be more readily achieved in the root system given its proximity to the soil. Failure in the small roots during drought would influence the shift in water use to deeper soil layers as well as modulate the extent of nocturnal hydraulic lift from deep to shallow soil (Caldwell & Richards 1989). By controlling the point of hydraulic failure cavitation in small roots may play an analogous role to a fuse in an electrical circuit.

The close correlation between minimum xylem pressure and xylem vulnerability (Fig. 4) indicates that there is a cost involved in having an overly resistant xylem. Otherwise, all species should show an equally resistant xylem and should simply avoid any cavitation. One potential penalty associated with a safe xylem could be a lower transport efficiency. According to the Hagen-Poiseuille equation, k_h is strongly influenced by conduit diameter, and often it is speculated that there is a trade-off between vessel diameter and vulnerability (e.g. Larcher 1994). Indeed, in *C. viscidiflorus*, as in most of the other species, there was a statistically significant intraspecific correlation for combined stem and root data (Fig. 6A). An interspecific correlation was also found for combined root and stem data of all species (Fig. 6B). However, among stems and among roots of different species was no such correlation (Fig. 6B, dotted lines). As described in previous studies (Tyree et al. 1994, Jarbeau et al. 1995), drought-induced cavitation depends on two factors: xylem pressure and porosity of intervessel pit membranes. The reason why there was only a somewhat ambiguous correlation between vessel diameter and vulnerability to drought-induced cavitation is that there is no direct causal relationship between the two parameters. A trade-off between transport efficiency and cavitation resistance is more likely to become apparent in pit membrane structure. A large, porous pit membrane will facilitate flow, but it will also be prone to air seeding.

Another cost for developing a safe xylem could be a requirement to allocate more biomass to the xylem.

This is suggested by the strong relationship between wood density and cavitation resistance (Fig. 7). Smaller conduits and/or thicker conduit walls may be necessary to insure resistance to greater compressive forces associated with more negative pressures, and to minimize permeability of the walls (including pit membranes) to air seeding. Thick walls and/or narrow conduits require denser wood and higher construction costs. Growing a denser wood also requires a slower growth rate (Enquist et al. 1999), which would compromise competitive ability. An ongoing study (U.G. Hacke, J.S. Sperry, S.D. Davis, W.T. Pockman, in preparation) suggests that the density-vulnerability relationship holds among conifers as well as diffuse-porous stems of a wide variety of shrubs and trees, but that it may be influenced by the relative abundance of fibers vs. vessels in angiosperm xylem. More work is necessary to evaluate the several inter-related trade-offs that are involved in developing cavitation-resistant xylem. Such research might focus on the site of air seeding and its relationship to overall xylem structure and function.

Conclusions and perspective

As hypothesized, cavitation resistance was adjusted to the amount of drought stress a species experienced. The fact that xylem was not overly resistant, but only as resistant as required, indicates that there is a cost involved in developing safe xylem. There was a statistically significant relationship between vessel diameter and resistance to drought-induced cavitation for combined root and stem data. An even better correlation was found between cavitation resistance and wood density. This suggests that there are two trade-offs: safety versus efficiency and safety versus construction cost. Data on cavitation resistance, water potential, and root distribution will be used in a future study to evaluate hydraulic limits for gas exchange in our species.

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