

Water transport properties of seven woody species from the semi-arid Mu Us Sandy Land, China

Y. Murakami¹ · N. H. Miki² · L. Yang² · G. Zhang³ · L. H. Wang³ · K. Yoshikawa²

Received: 31 May 2014/Revised: 3 October 2015/Accepted: 30 December 2015
© International Consortium of Landscape and Ecological Engineering and Springer Japan 2016

Abstract Maintenance of water transport is very important for plant growth and survival. We studied seven woody species that inhabit the semi-arid Mu Us Sandy Land, China, to understand their strategies for maintaining hydraulic function. We evaluated water transport properties, including cavitation resistance, hydraulic recovery, and water loss regulation by stomatal control, which are associated with xylem structural and leaf physiological traits. We also discussed the water-use characteristics of these species by comparing them with those of species in other regions. Species with tracheids had higher levels of xylem resistance to cavitation and a smaller midday transpiration rate than the other species studied. Although species with vessels were less resistant to cavitation, some recovered hydraulic conductivity within 12 h of rehydration. Species with xylem tracheids could maintain their hydraulic function through resistance to cavitation and by relaxing xylem tension. Although species with vessels had less resistant xylem, they could maintain hydraulic function through hydraulic recovery even when xylem dysfunction occurred. Additionally, the species studied here were less resistant to cavitation than species in semi-arid environments, and equally or less resistant than species in humid

environments. Rather than allow hydraulic dysfunction due to drought-induced dehydration, they may develop water absorption systems to avoid or recover quickly from hydraulic dysfunction. Thus, not only stem cavitation resistance to drought but also stem–root coordination should be considered when selecting plants for the revegetation of arid regions.

Keywords Cavitation resistance · Hydraulic conductivity · Xylem cavitation · Hydraulic recovery

Introduction

In arid regions, precipitation is one factor that influences water availability to plants (Sala and Lauenroth 1982). Because rainfall is very sparse and annual amounts fluctuate greatly in arid regions, plants often experience very low water availability. Therefore, plants in arid regions have physiological and morphological responses to compensate for water deficits caused by water loss from leaves through water absorption and water transport. They restrict transpiration by performing rapid stomatal closure (Vilagrosa et al. 2003) and leaf shedding (Savage and Cavender-Bares 2011), and have an extensive collection of shallow and deep roots near groundwater to acquire water efficiently (Tokuoka and Wang 1994; Ohte et al. 2003; Bucci et al. 2009). Transpiration causes tension for water transport through the xylem over the long distance from the roots to leaves. Because water transport in the xylem has an influence on plant growth, physiological traits, productivity, and plant survival (Brodrribb and Field 2000; Cochard et al. 2007; Jacobsen et al. 2007a), the maintenance of hydraulic function is very important for plants.

✉ Y. Murakami
gev422212@s.okayama-u.ac.jp

¹ Graduate School of Environmental Science, Okayama University, 1-1-1 Tsushima-naka, Kita-ku, Okayama 700-8530, Japan

² Graduate School of Environmental and Life Science, Okayama University, 1-1-1 Tsushima-naka, Kita-ku, Okayama 700-8530, Japan

³ College of Forestry, Inner Mongolia Agricultural University, Hohhot, Inner Mongolia 010019, China

When drought occurs, the soil water potential drops and tension increases in the xylem. Cavitation induced by water stress occurs through air seeding, when air bubbles are aspirated into water-filled conduits under tension (Sperry and Tyree 1988). Embolisms caused by cavitation reduce xylem hydraulic conductivity. Consequently, xylem dysfunction caused by embolisms presents a severe problem for plant productivity and development.

Many previous studies have analyzed the maintenance of hydraulic function: xylem resistance, avoidance of hydraulic dysfunction, and hydraulic recovery. Xylem resistance to cavitation influenced plant distributions; species that inhabited drier sites had xylem that was more resistant to cavitation than other species (Pockman and Sperry 2000). Additionally, xylem resistance is related to leaf physiological (Maherali et al. 2006) and xylem structural (Hacke et al. 2001; Jansen et al. 2009) traits. The avoidance of hydraulic dysfunction may be related to stomatal control (Vilagrosa et al. 2003) and water storage (Stratton et al. 2000); water loss is regulated by stomatal control and water is stored to avoid inducing xylem embolisms and hydraulic failure due to an extremely low water potential. For hydraulic recovery, Ogasa et al. (2010) and Ogasa et al. (2013) reported that after releasing water stress, both the hydraulic conductivity and the xylem water potential of cavitation-vulnerable species were recovered rapidly in angiosperms. In addition, previous studies reported that hydraulic recovery might be associated with photosynthetic capacity (Salleo et al. 2009; Nardini et al. 2011) and water storage (Barnard et al. 2011).

Here, we studied seven coexisting woody species that are often used in afforestation to fix moving sands in the semi-arid Mu Us Sandy Land, China (UNEP 1997). Previous studies of these woody species examined leaf physiological characteristics, root system properties, and the restriction of water loss through decreases in leaf area and stomatal closure under drought conditions (Xiao et al. 2005; Yamamoto et al. 2007), as well as the efficient use of rain pulses and groundwater (Ohte et al. 2003; Yang et al. 2014). However, few of the previous studies on these woody species distributed in the Mu Us Sandy Land have focused on xylem hydraulic properties, which play important roles in water transport from root to leaf and, especially, the maintenance of hydraulic function during drought conditions. The results of such a study should enhance our understanding of the efficacy of these species in the revegetation of the Mu Us Sandy Land in a semi-arid region. Therefore, in the study reported in the present paper, we aimed to reveal the strategies used by these species to maintain hydraulic function. We evaluated the water transport properties of xylem, including cavitation resistance (Ψ_{50}), hydraulic recovery, and the regulation of water loss by stomatal control, which are associated with

xylem structural and leaf physiological traits. We also explored the water-use characteristics of the seven woody species in the Mu Us Sandy Land, which has moving sands and a water-limited environment, by comparing them with the water-use characteristics of species in other regions.

Materials and methods

Plant materials

We studied the seven most common woody species—*Artemisia sphaerocephala* Krasch, *Artemisia ordosica* Krasch, *Caragana microphylla* Lam., *Salix matsudana* Koidz., *Salix psammophila* C. Wang et C. Y. Yang, *Salix cheilophila* Schneid and *Juniperus sabina* L. (nomenclature follows the Flora of China; Flora of China Project 1999)—in the semi-arid environment of the Mu Us Sandy Land, China, an area that is characterized by a low amount of precipitation, relatively abundant groundwater, moving sands, and problems with desertification (Kobayashi 1994; Zha and Gao 1997; Wang et al. 2010). Six of these species are deciduous diffuse-porous species, while *J. sabina* is an evergreen conifer. Potted saplings of the three *Salix* species and *J. sabina* were propagated from 20- to 30-cm-long freshly rooted cuttings. The other species were 2-year-old potted seedlings. The plants were transplanted to plastic pots filled with river sand. All plants were grown in an experimental field at Okayama University, Okayama, Japan and were well watered and fertilized monthly (N:P:K = 6:10:5) until the experiments were conducted.

All measurements were conducted on potted current-year-old saplings of *S. psammophila* and *S. matsudana*, 2-year-old plants of *A. ordosica*, *A. sphaerocephala*, and *C. microphylla*, as well as 2-year-old saplings of *J. sabina* and 3-year-old saplings of *S. cheilophila* from July to October in 2010 and 2011. Plant size information is given in Table 1.

Table 1 Plant materials used in this study

Species	Length or height (m)		Basal diameter (mm)	
	Mean	SE	Mean	SE
<i>A. sphaerocephala</i>	0.53	(0.06)	6.6	(0.5)
<i>A. ordosica</i>	0.49	(0.04)	7.0	(0.8)
<i>C. microphylla</i>	0.53	(0.06)	5.7	(0.4)
<i>S. matsudana</i>	1.17	(0.04)	7.6	(0.3)
<i>S. psammophila</i>	1.22	(0.06)	6.8	(0.3)
<i>S. cheilophila</i>	1.17	(0.05)	8.1	(0.3)
<i>J. sabina</i>	0.35	(0.02)	6.7	(0.4)

Values are the means and SEs for the plants used in the experiments ($n = 13$ – 25). Values for *Salix* species are the lengths of shoots that sprouted from rooted cuttings, and those for the other species are the heights of seedlings

Hydraulic conductivity measurement and vulnerability curves (VCs)

For six species with vessels (excluding *J. sabina*), vulnerability curves (VCs) were obtained from stem segments using the dehydration method of Sperry et al. (1988) and Sperry and Tyree (1990). To construct VCs, 10–16 plants of each species were used. Irrigation was withheld from potted plants for several days to a week, which resulted in natural dehydration until the xylem water potential (Ψ_{xylem}) was close to a target value. We measured Ψ_{xylem} in the distal current-year shoots of *Salix* and *Artemisia* species and in the current-year leaves of *C. microphylla* using a pressure chamber (model 600; PMS Instrument Co., Corvallis, OR, USA). Before performing Ψ_{xylem} measurements, one to three shoots (for *Salix* and *Artemisia* species) or three leaves (for *C. microphylla*) were enclosed for at least 12 h in black plastic bags and aluminum foil to remove the water potential gradient between the xylem and leaf. Additionally, the entire plant was enclosed in a black plastic bag for at least 2 h to limit transpiration and to stabilize the xylem tension prior to measuring the hydraulic conductivity (K_h) (Hacke and Sauter 1995).

Following the Ψ_{xylem} measurements, the K_h of the stem was measured at various values of stem Ψ_{xylem} . The segments used to measure K_h were cut under water from the middle of a 4.0- to 7.0-cm-long current-year stem for the three *Salix* species and from the middle of a 1-year-old main stem for the other species. After cutting the segments, the initial hydraulic conductivity (K_{init}) was measured immediately by perfusion with 0.1 μm of a filtered 20 mM KCl solution. Measurements were performed using a conductivity apparatus based on Sperry et al. (1988) under a pressure head of 4–8 kPa. The segments were flushed at 75–100 kPa for 5–15 min to remove cavitated gasses before determining the maximum hydraulic conductivity (K_{max}).

For *J. sabina*, we adopted the centrifuge technique (Alder et al. 1997). Measurements were conducted on five plants. After transporting plants to the laboratory, we cut 13.5- to 14.0-cm-long stem segments from potted plants underwater. We did not flush the segments because the plants were fully watered until the experiments were conducted, and the flushing of conifer stems has been reported to be ineffective (Sperry and Tyree 1990). After cutting the segments, K_h was measured under well-watered conditions (K_{native}) under a pressure head of 8 kPa. Segments were then spun using a centrifuge and horizontal rotor (CR21G II and R21HY; Hitachi Koki Co. Ltd., Tokyo, Japan) for 5 min at the target pressure. The xylem pressure was set to gradually become more negative. After centrifugation, K_{init} was immediately re-measured. This procedure was repeated until the percent loss of hydraulic conductivity (PLC) exceeded 80 %.

K_h was calculated as the flow rate of solution per pressure gradient (Tyree and Sperry 1988). We accounted for the background flow rate of the segment by measuring the flow rate under zero pressure before and after measuring the pressure-induced flow rate. Background flows were negative values, indicating any osmotic and capillary uptake of water by the segment in the absence of an applied pressure difference (Hacke et al. 2000). This background flow rate was averaged and then subtracted from the flow under pressure to obtain the net flow rate caused by pressure. PLC was calculated using the formula given by Sperry et al. (1988):

$$\text{PLC} = ((K_{\text{max}} - K_{\text{init}})/K_{\text{max}}) \times 100.$$

In *J. sabina*, we calculated PLC by presuming that the highest measured K_h equals K_{max} , because the highest K_h was consistently measured after low-speed centrifugation. Paired PLC measurements and mean xylem water potentials were plotted to determine VCs for the seven species. A Weibull function (Neufeld et al. 1992),

$$\text{PLC} = 100 \times (1 - \exp(-(-\Psi_{\text{xylem}}/b)^c)),$$

where Ψ_{xylem} is the xylem water potential, b is the absolute value of the xylem water potential at a 63 % loss of hydraulic conductivity, and c is a curve-fitting parameter that influences the slope of the VC (Li et al. 2009), was fitted. Curve parameters b and c were estimated with a Kaleida Graph 3.6 (Hulinks Inc., Tokyo, Japan). We obtained the xylem water potential at a 50 % loss of hydraulic conductivity (Ψ_{50}), indicating cavitation resistance (Tyree and Zimmermann 2002).

Rehydration experiments

We conducted rehydration experiments for three *Salix* species to assess the extent of hydraulic conductivity recovery, in accordance with Ogasa et al. (2010). After ceasing irrigation, potted plants were dehydrated to approximately Ψ_{50} , which was estimated using VCs. These water-stressed potted plants were then re-watered to field capacity. They were kept in the laboratory for 12 h after re-watering to simulate an overnight rehydration period (Ogasa et al. 2010). At the end of each rehydration period, Ψ_{xylem} was measured using one to three current-year shoots that had been enclosed for 12 h. Immediately after measuring Ψ_{xylem} , the K_{init} of a 4.0- to 7.0-cm-long stem segment cut from the plant was measured under the same hydrostatic pressure with the same apparatus used to measure the vulnerability to cavitation. Next, we flushed the segments and re-measured K_{max} . Rehydration experiments were conducted in three species using three to five plants during the 12-h rehydration period. Additionally, three pre-dehydration datasets and three to five post-dehydration datasets (PLC \approx 50 %) were selected from those

used for VC measurements. These data were collected under the same dehydrating conditions before re-watering and were used to compare values of hydraulic conductivity and xylem water potential at different water statuses.

Xylem-specific hydraulic conductivity

To calculate the maximum specific hydraulic conductivity ($K_{s \text{ max}}$), we determined the xylem area from thin cross-sections excised from the segments used for K_h measurements. Xylem area was determined using a light microscope (ECLIPSE 80i; Nikon, Tokyo, Japan) for *J. sabina*, a stereomicroscope (SZX-ILLB100; Olympus, Tokyo, Japan) for other six species with vessels, image processing software (GIMP 2.6; GIMP Development Team), and an image analyzer (Image J 1.44p; National Institutes of Health, Bethesda, MD, USA). $K_{s \text{ max}}$ was calculated by dividing $K_{h \text{ max}}$ by the xylem cross-sectional area for each segment, and was averaged for each species ($n = 5$). In the species studied, the xylem cross-sectional area for each segment corresponded to the functional xylem area.

Leaf physiological traits and minimum xylem water potential

The maximum photosynthetic rate (A_{area}), transpiration rate ($T_{r \text{ area}}$), and stomatal conductance ($g_{s \text{ area}}$) per unit leaf area were measured with a portable photosynthesis system (LI-6400; Li-Cor Inc., Lincoln, NE, USA) between 06:30 and 12:30. We selected five individuals per species, and one fully expanded and illuminated leaf per individual. Fixed measurement conditions in the apparatus leaf chamber were 370 ppm CO_2 , 25 °C air temperature, and < 2.0 kPa vapor pressure deficit. Measurements were conducted at saturating photosynthetic photon flux density (PPFD): 2,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the two *Artemisia* species, 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *C. microphylla*, *S. psammophila*, *S. cheilophila*, and *J. sabina*, and 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *S. matsudana*.

We measured Ψ_{xylem} at midday (11:00–14:30) to evaluate plant water status on a clear day (PPFD $\geq 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$). For measurements, we used three current-year shoots or three leaves (only *C. microphylla*) that had been enclosed for 12 h to allow the water potential of the leafy shoots or leaves to equilibrate with the xylem. We measured three individuals per species using a pressure chamber (model 600; PMS Instrument Co.).

Xylem structural traits

Segments that were used to measure wood density (WD) were adjacent to the segments used to measure xylem vulnerability, except for in *S. cheilophila* because the adjacent segments were too small to measure WD. Thus, in *S. cheilophila*, we

selected different individuals from those used to measure hydraulic conductivity. Segments 5.0–8.0 cm long were cut from stems, and the bark was removed with a razor blade. The sample was immersed in a distilled-water-filled vial for over 48 h. Water-saturated volume was determined by water displacement. Displacement weight was converted to sample volume by the formula: displacement weight (g)/0.997 g cm^{-3} , where 0.997 g cm^{-3} is the density of water at 25 °C (Hacke et al. 2001). Samples were stored at 80 °C for 48 h, and their dry weights were then determined. WD was calculated as the ratio of dry weight to water-saturated fresh volume using a sample size of four to six wood segments per species.

We calculated conduit area (CA) and conduit diameter (D_C) to evaluate conduit traits ($n = 3\text{--}6$). Measurements of D_C were made on sections cut from the segments adjacent to the segments used for hydraulic conductivity measurements. Wood sections were stained with 0.1 % wt /vol of 0.1- μm -filtered safranin dye (Sperry et al. 1991). After staining, 30- μm -thick cross sections were obtained from the middle part of the dye-stained segments using a sliding microtome. Transverse sections were divided into four 90° radial sectors, and one sector was randomly chosen for vessel measurement. For the tracheids of *J. sabina*, we randomly selected three radial files. D_C was then calculated as the diameter of a circle with an area that was equal to the measured lumen area (Linton et al. 1998; Davis et al. 1999). Conduits less than 10 μm in diameter for the three *Salix* species, and less than 5 μm for the two *Artemisia* species and *C. microphylla*, were not included in the calculations of conduit traits because their contribution to the flow was considered to be negligible. Additionally, we calculated conduit density (CD) as the number of conduits divided by the xylem area, and we calculated conduit fraction (F_C) as the sum of the total CA divided by the xylem area.

Statistical analyses

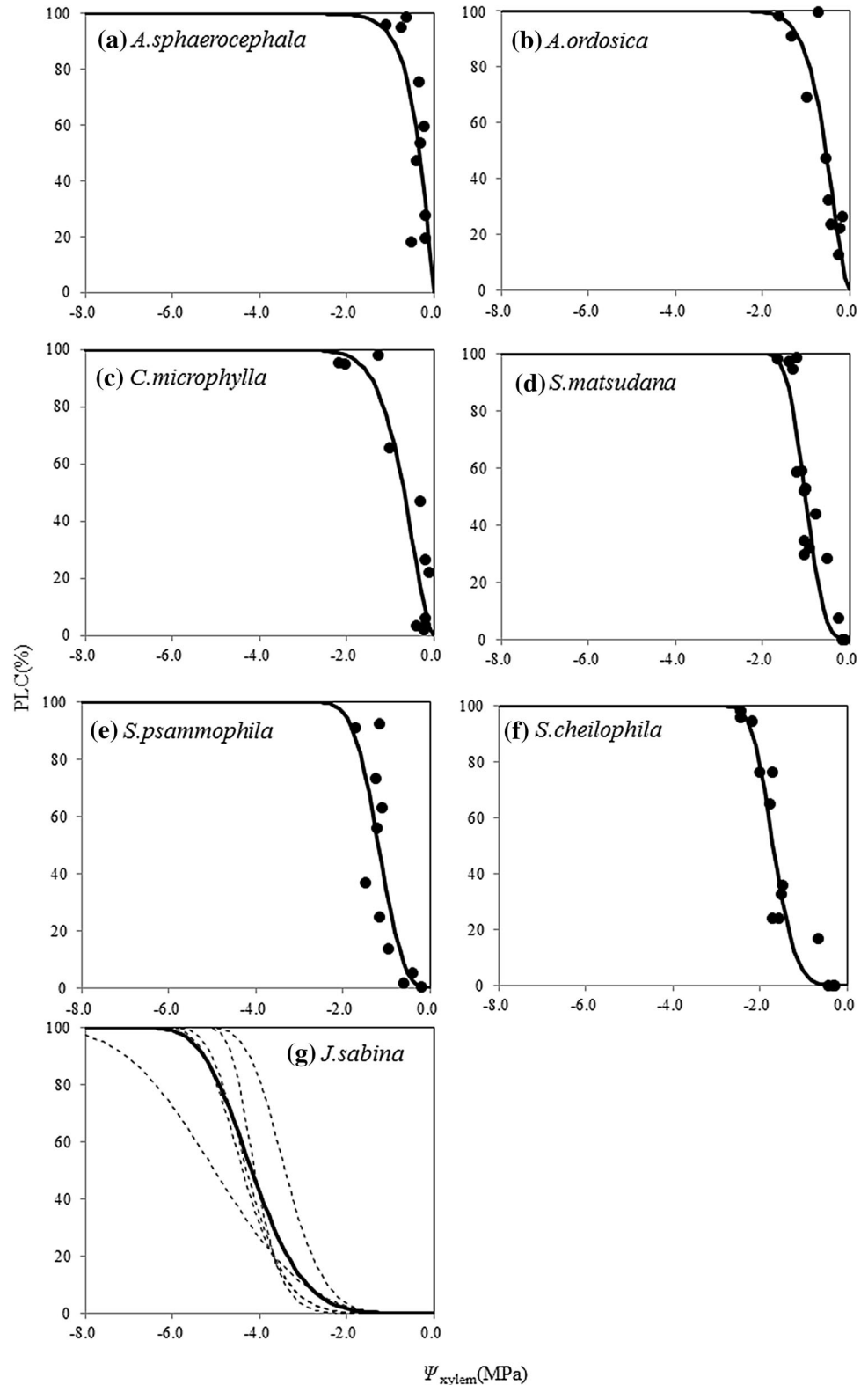
Statistical comparisons among species were conducted using one-way analysis of variance. Dunnett's test was applied for multiple comparisons among water statuses, and Statistica (StatSoft Inc., Tulsa, OK, USA) was used for the analysis. A standardized major axis regression was used to characterize the relationships between traits. Regression slopes and all other statistical parameters were calculated using the SMATR 2.0 statistical software (Warton et al. 2006).

Results

Xylem physiological traits

VCS varied substantially among species (Fig. 1). The resistance of the xylem to cavitation in the various species can be compared using the xylem water potential at a 50 %

Fig. 1a–g Curves for the vulnerability of xylem to cavitation for seven woody species (**a** *Artemisia sphaerocephala* Krasch, **b** *Artemisia ordosica* Krasch, **c** *Caragana microphylla* Lam., **d** *Salix matsudana* Koidz., **e** *Salix psammophila* C. Wang et C. Y. Yang, **f** *Salix cheilophila* Schneid, and **g** *Juniperus sabina* L.) in the Mu Us Sandy Land, China. The centrifugation technique was used for *Juniperus sabina* and the dehydration method was used for the other six species. Vulnerability curves were estimated from 5–16 samples per species. In **g**, dashed lines represent individual curves and the solid line represents the average curve for *J. sabina*



loss of hydraulic conductivity (Ψ_{50}). The xylem of *A. sphaerocephala* and *A. ordosica* was the least resistant to cavitation, with Ψ_{50} values of -0.32 and -0.54 MPa, respectively. That of *J. sabina* was by far the most resistant

to cavitation (Table 2), followed by the xylem of the three *Salix* species and *C. microphylla*.

The midday xylem water potential ($\Psi_{\text{x min}}$) differed among species and ranged from -0.27 ± 0.02 MPa in *A.*

Table 2 Summary of physiological characteristics of the xylem and leaves, and structural characteristics of the xylem (mean \pm SE), for seven woody species in the Mu Us Sandy Land, China

	<i>A. sphaerocephala</i>		<i>A. ordosica</i>		<i>C. microphylla</i>		<i>S. matsudana</i>		<i>S. psammophila</i>		<i>S. cheilophila</i>		<i>J. sabina</i>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Xylem physiological traits														
Ψ_{50}	-0.32	(0.03)	-0.54	(0.02)	-0.68	(0.02)	-1.01	(0.08)	-1.18	(0.06)	-1.70	(0.09)	-4.25	(0.26)
$\Psi_{x \text{ min}}$	-0.38 ^b	(0.03)	-0.27 ^a	(0.02)	-0.53 ^{bc}	(0.02)	-0.65 ^c	(0.08)	-1.00 ^{de}	(0.06)	-1.12 ^e	(0.09)	-0.77 ^{cd}	(0.04)
$K_s \text{ max}$	2.78 ^b	(0.41)	1.43 ^{abcd}	(0.35)	2.01 ^{bc}	(0.41)	3.62 ^a	(0.46)	1.38 ^{bcd}	(0.30)	1.05 ^{cd}	(0.27)	0.24 ^d	(0.04)
Xylem structural traits														
WD	0.53 ^{abc}	(0.03)	0.66 ^a	(0.04)	0.65 ^a	(0.05)	0.40 ^c	(0.02)	0.43 ^c	(0.02)	0.49 ^{bc}	(0.00)	0.57 ^b	(0.01)
CA	297.01 ^b	(37.84)	143.38 ^{cd}	(27.86)	198.36 ^{bc}	(15.41)	462.37 ^a	(15.78)	275.26 ^b	(23.16)	206.48 ^{bc}	(36.85)	40.61 ^d	(8.32)
D_C	17.79 ^b	(1.12)	12.57 ^c	(1.20)	14.82 ^{bc}	(0.61)	23.46 ^a	(0.38)	18.13 ^b	(0.76)	15.71 ^{bc}	(1.36)	6.82 ^d	(0.69)
CD	264.53 ^b	(30.24)	322.47 ^b	(85.99)	205.31 ^b	(48.28)	229.78 ^b	(13.32)	271.67 ^b	(23.03)	313.72 ^b	(23.50)	6693.99 ^a	(510.27)
F_C	0.08 ^b	(0.01)	0.04 ^b	(0.00)	0.04 ^b	(0.01)	0.11 ^b	(0.01)	0.07 ^b	(0.01)	0.06 ^b	(0.01)	0.28 ^a	(0.08)
Leaf physiological traits														
A_{area}	28.53 ^b	(2.39)	21.00 ^{bc}	(1.32)	19.25 ^{bc}	(3.38)	19.13 ^{bc}	(2.40)	33.01 ^a	(3.13)	23.26 ^b	(2.04)	11.64 ^c	(0.63)
T_{area}	6.40 ^b	(1.10)	3.56 ^{bc}	(0.53)	3.58 ^{bc}	(0.85)	4.17 ^{bc}	(0.66)	8.21 ^a	(0.89)	4.70 ^{bc}	(0.74)	2.17 ^c	(0.32)
g_{area}	0.61 ^b	(0.12)	0.31 ^b	(0.05)	0.33 ^b	(0.10)	0.53 ^b	(0.13)	1.24 ^a	(0.20)	0.51 ^b	(0.17)	0.17 ^b	(0.02)

Values for different species that are labeled with *different letters* are significantly different ($P < 0.05$, one-way analysis of variance)

Symbols/abbreviations and units are: Ψ_{50} (MPa), xylem water potential at a 50 % loss of hydraulic conductivity; $\Psi_{x \text{ min}}$ (MPa), daily minimum xylem water potential; $K_{s \text{ max}}$ ($\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$), maximum specific hydraulic conductivity; WD (g cm^{-3}), density of wood; CA (μm^2), conduit area; D_C (μm), conduit diameter; CD (mm^{-2}), conduit density; F_C ($\text{mm}^2 \text{mm}^{-2}$), ratio of the sum of the conduit lumen area to the xylem area; A_{area} ($\mu\text{mol m}^{-2} \text{s}^{-1}$), maximum net photosynthetic rate per unit leaf area; T_{area} ($\text{mmol m}^{-2} \text{s}^{-1}$), maximum transpiration rate per unit leaf area; g_{area} ($\text{mol m}^{-2} \text{s}^{-1}$), maximum stomatal conductance per unit leaf area

ordosica to -1.12 ± 0.09 MPa in *S. cheilophila* (Table 2). Additionally, we evaluated the safety margins of the studied species. The difference between $\Psi_{x \text{ min}}$ and Ψ_{50} represents the hydraulic safety margin for loss of hydraulic function at midday (Pockman and Sperry 2000). We found that species with greater negative Ψ_{50} values had larger safety margins than species with smaller negative Ψ_{50} values (Fig. 2). In our results, *J. sabina* had the highest margin of safety for avoiding cavitation among the species analyzed here (Fig. 2).

$K_s \text{ max}$ varied among species (Table 2), ranging from $0.24 \pm 0.04 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ in *J. sabina* to $3.62 \pm 0.46 \text{ kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ in *S. matsudana*. The value of $K_s \text{ max}$

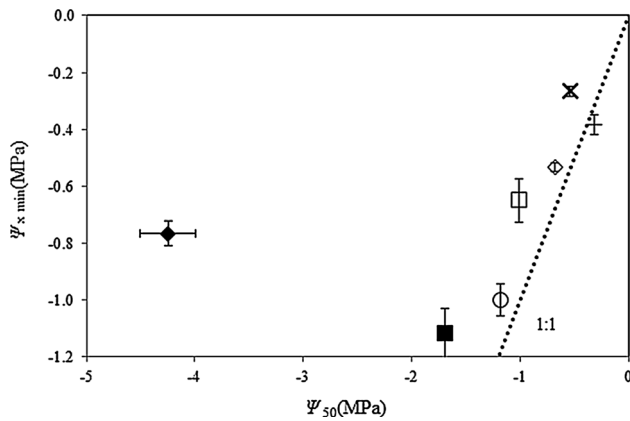


Fig. 2 Relationship between xylem water potential causing a 50 % loss in hydraulic conductivity (Ψ_{50}) and midday xylem water potential ($\Psi_{x \text{ min}}$) for seven woody species in the Mu Us Sandy Land, China. Dashed line represents a 1:1 relationship. Error bars represent SE ($y: n = 0-5$). Symbols are: crosses, *Artemisia sphaerocephala*; multiplication symbols, *Artemisia ordosica*; unfilled diamonds, *Caragana microphylla*; unfilled squares, *Salix matsudana*; unfilled circles, *Salix psammophila*; filled squares, *Salix cheilophila*; filled diamonds, *Juniperus sabina*

for *J. sabina* was much lower than those for the other species.

Xylem structural traits

Table 2 shows xylem structural traits for the seven species. The WD of the species analyzed varied from $0.40 \pm 0.02 \text{ g cm}^{-3}$ for *S. matsudana* to $0.66 \pm 0.04 \text{ g cm}^{-3}$ for *A. ordosica*. In terms of conduit size (CA and D_C), *S. matsudana* had the widest conduits ($462.37 \pm 15.78 \mu\text{m}^2$ and $23.46 \pm 0.38 \mu\text{m}$, respectively), while *J. sabina* had the narrowest conduits ($40.61 \pm 8.32 \mu\text{m}^2$ and $6.82 \pm 0.69 \mu\text{m}$, respectively). Additionally, *J. sabina* had significantly more conduits than any of the other six species ($P < 0.05$; Table 2, CD). We also calculated F_C , which varied among the seven species and was significantly higher in *J. sabina* than in the other six species ($P < 0.05$; Table 2).

Leaf physiological traits

A_{area} and $T_r \text{ area}$ were greatest for *S. psammophila* and smallest for *J. sabina*. $g_s \text{ area}$ was significantly greater in *S. psammophila* than in the other six species ($P < 0.05$; Table 2), but no significant difference was observed among the other six species ($P > 0.05$; Table 2).

Relationships among hydraulic traits for the six species with vessels

We analyzed the relationships among the hydraulic traits of six species. *J. sabina* was excluded because its tracheids have a different wood structure from the vessels of the other species. Ψ_{50} was significantly correlated with $\Psi_{x \text{ min}}$ (Table 3; $r^2 = 0.876$), and species with xylem that was more resistant to cavitation had lower $\Psi_{x \text{ min}}$ values.

Table 3 Standardized major axis regression relationships for each pair of parameters for six woody species from the Mu Us Sandy Land, China

	Ψ_{50}	$\Psi_{x \text{ min}}$	$K_s \text{ max}$	WD	CA	D_C	CD	F_C	A_{area}	$T_r \text{ area}$	$g_s \text{ area}$
Ψ_{50}		0.006	0.422	0.258	0.901	0.740	0.620	0.651	0.903	0.811	0.558
$\Psi_{x \text{ min}}$	0.876(+)		0.442	0.173	0.825	0.643	0.807	0.569	0.499	0.404	0.247
$K_s \text{ max}$	0.166	0.154		0.506	0.036	0.074	0.179	0.131	0.598	0.808	0.787
WD	0.302	0.406	0.118		0.062	0.031	0.858	0.012	0.461	0.27	0.165
CA	0.004	0.014	0.708(+)	0.622		0.000	0.316	0.003	0.999	0.71	0.597
D_C	0.031	0.059	0.591	0.728(-)	0.983(+)		0.336	0.001	0.902	0.61	0.479
CD	0.067	0.017	0.399	0.009	0.247	0.230		0.612	0.651	0.876	0.973
F_C	0.056	0.087	0.473	0.829(-)	0.912(+)	0.938(+)	0.070		0.741	0.498	0.424
A_{area}	0.004	0.121	0.076	0.142	0.000	0.004	0.056	0.030		0.001	0.022
$T_r \text{ area}$	0.016	0.179	0.017	0.29	0.038	0.071	0.007	0.122	0.951(+)		0.005
$g_s \text{ area}$	0.093	0.314	0.02	0.418	0.076	0.132	0	0.165	0.767(+)	0.887(+)	

Coefficients of determination (r^2) are given below the diagonal, and the positive (+) or negative (-) nature of the relationship is indicated. P values are given above the diagonal. Significant correlations are shown in bold type

See footnote in Table 2 for abbreviations

However, Ψ_{50} was not associated with $K_{s \max}$ (Table 3), and the previously observed trade-off between xylem safety and hydraulic efficiency (Jacobsen et al. 2005) did not exist here. Additionally, Ψ_{50} was not significantly correlated with xylem structural or leaf physiological traits (Table 3).

Although xylem structural traits were not significantly correlated with xylem resistance to cavitation and photosynthetic rate (Table 3), CA was significantly correlated with $K_{s \max}$ (Table 3). D_C and F_C were significantly correlated with WD and CA (Table 3). Further, D_C was positively associated with F_C . Species with narrower conduits have lower porosity values and higher WDs than species with wider conduits.

Hydraulic recovery by rehydration for *Salix* species

For the three *Salix* species, the Ψ_{xylem} after dehydration was significantly lower than that before dehydration (Fig. 3). Additionally, the PLC significantly increased after dehydration (Fig. 3). However, there was no significant difference between the parameter values observed before dehydration and those seen 12 h after rehydration; Ψ_{xylem} and hydraulic conductivity had recovered significantly from dehydration by 12 h after rehydration (Fig. 3).

Discussion

The xylem in *J. sabina* was by far the most resistant to cavitation among the seven species studied here, although the $K_{s \max}$ of this species was extremely low (Fig. 1, Table 2). When cavitation occurs and hydraulic function is lost, plants with tracheids cannot recover their hydraulic function because of the presence of torus–margo structures (Siau 1984; Utsumi et al. 2003). However, even if cavitation occurs in one tracheid, the functional tracheids adjacent to the embolized tracheid can stop gas from entering (Zimmermann 1983). In addition to the high resistance to cavitation, midday transpiration rates and the decrease in Ψ_{xylem} at midday, when compared with Ψ_{50} , were small (Table 2, Fig. 2). In a previous study, *J. sabina* had a low stomatal density and minimal water loss (Dong and Zhang 2000). Additionally, *J. sabina* has adventitious roots near the soil surface and deeper roots near groundwater (Ohte et al. 2003; Yang et al. 2014). Yang et al. (2014) reported that *J. sabina* had integrated water use between the main root system, which reached deeper soil depths, and adventitious roots for maximum water acquisition from the subsoil water, groundwater, and small rainfalls. These results suggest that *J. sabina* may be able to maintain hydraulic function by possessing xylem that is strongly resistant to cavitation from tracheids, by relaxing xylem

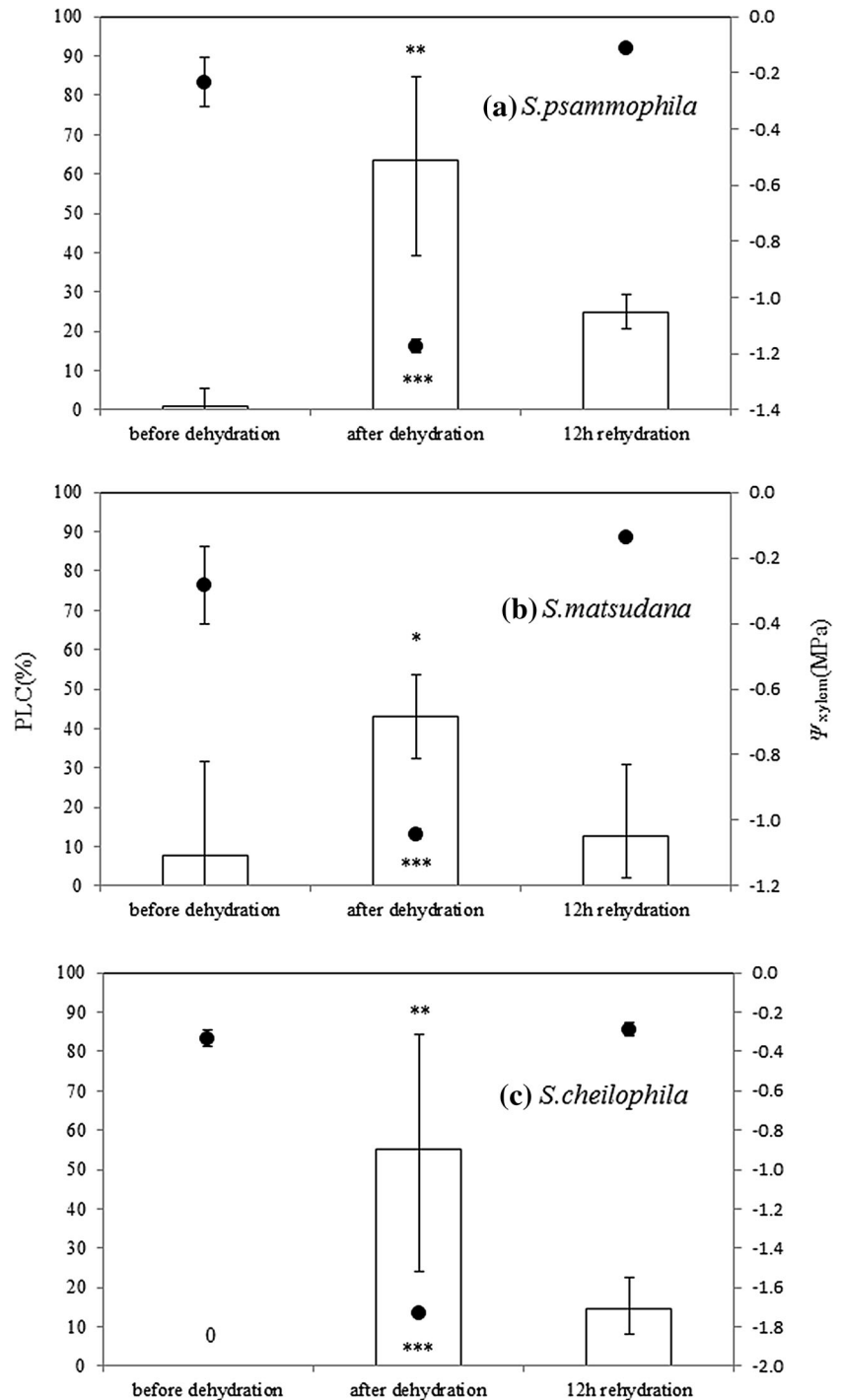
tension through limited water loss, and by absorbing water efficiently from a wide range using its roots.

Water loss by transpiration and carbon gain by photosynthesis are both mediated by stomata. Thus, *J. sabina* may simultaneously regulate water loss and productivity. To obtain high xylem resistance to cavitation, plants need to have wood with a high construction cost, as shown by their high WD (Hacke et al. 2001). However, construction cost, as indicated by WD, is smaller in conifers than in angiosperms (Hacke et al. 2001; Hacke et al. 2005; Sperry et al. 2006). In this study, we found the same tendency: *J. sabina* was more resistant than other species to cavitation despite having a similar WD to that of angiosperms (Table 2). Even if productivity is regulated, *J. sabina* may be able to grow in water-resource-limited habitats because of its low construction cost and the resistance of its xylem to cavitation, which is greater than that of angiosperm xylem.

Aside from *J. sabina*, the other six species studied here have vessels that are less resistant to cavitation and have smaller safety margins than *J. sabina* (Table 2, Fig. 2). This result suggests that these six species have a higher risk of cavitation during periods of drought because regulated water loss by stomatal closure cannot be very effective and the safety margin is small. Actually, previous research showed that six shrubs distributed in an arid region lost from 53 % to 93 % of their hydraulic conductivity during daily water shortages (Miranda et al. 2010). In this study, after Ψ_{50} was induced by dehydration, three *Salix* species recovered their hydraulic conductivity within 12 h after rehydration (Fig. 3). Additionally, there was a negative correlation between xylem resistance to cavitation ($|\Psi_{50}|$) and xylem recovery, and cavitation-vulnerable species showed better xylem recovery performance (Ogasa et al. 2013). Therefore, *Artemisia* and *Caragana* species that have a low resistance to cavitation, and for which Ψ_{50} is higher than that in the *Salix* species studied here, may also be able to maintain hydraulic function through the overnight recovery of hydraulic function after hydraulic dysfunction. In addition, six species with vessels have adventitious roots (Tokuoka and Wang 1994; Tokuoka 2001; Teraminami et al. 2010; Teraminami et al. 2013). Therefore, these species may be able to gain small amounts of rainwater from a wide range of soil conditions, allowing them to use water efficiently. Furthermore, *S. matsudana* and *S. cheilophila* can extend their roots up towards groundwater (Arata et al. 2001; Ohte et al. 2003). This effective water absorption may make it possible to recover hydraulic function.

Xylem resistance to cavitation in vessels is associated with various traits, such as leaf physiological (Santiago et al. 2004; Maherli et al. 2006) and xylem structural (Hacke et al. 2001) traits. Thus, we analyzed their

Fig. 3a–c Percent loss of hydraulic conductivity (*PLC*) in shoots and xylem water potential (*closed circles*) before dehydration, after dehydration, and after a 12-h rehydration period for three *Salix* species (**a** *Salix psammophila* C. Wang et C. Y. Yang, **b** *Salix matsudana* Koidz., and **c** *Salix cheilophila* Schneid). Values are the mean \pm 95 % confidence interval for *PLC* and the mean \pm SE for xylem water potential ($n = 3–6$). Significant differences with respect to the controls are indicated as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, as determined for each parameter using Dunnett’s test



relationships among six species with vessels while excluding the conifer *J. sabina* from this part of the analysis. However, we could not find a relationship between area-based leaf physiological traits, WD, and xylem resistance to cavitation (Table 3). Previous studies reported that the photosynthetic capacity was related to leaf morphological properties such as leaf density (Fu et al. 2012) and leaf mass per area (Ishida et al. 2008). Additionally, Ψ_{50}

was associated with leaf density (Fu et al. 2012), leaf dry matter content, and leaf size (Markesteyn et al. 2011). Species with higher xylem resistance had higher leaf densities and leaf dry matter contents and smaller leaves (stem–leaf coordination in drought tolerance). Moreover, mass-based rates of photosynthesis and stomatal conductance were related to Ψ_{50} in a previous study (Ambrose et al. 2009). Therefore, leaf morphological traits may be

important indices that can be used to evaluate drought tolerance. Because we did not account for differences in leaf morphological traits such as leaf density and leaf dry matter content, we could not document the relationship between area-based leaf physiological traits and xylem resistance. In addition, because the magnitude of g_s depends on the hydraulic conductivity (Nardini and Salleo 2000), a trade-off between vulnerability to cavitation and water transport has been observed (Maherali et al. 2006); some species with high g_s area had xylem that was more vulnerable to cavitation. However, this tendency was not found in the present study. Arango-Velez et al. (2011) also reported that stomatal conductance might not always be the main factor linked to defense against stem xylem cavitation.

Species with a high photosynthetic capacity have denser wood (Santiago et al. 2004) and increased resistance of their xylem to cavitation (Hacke et al. 2001). Although previous studies have documented relationships between WD and Ψ_{50} over relatively wide WD ranges, 0.34–1.07 g cm⁻³ (Zanne et al. 2010) and 0.19–0.75 g cm⁻³ (Marksteijn et al. 2011), this relationship has not been reported for relatively narrow ranges, such as those for hybrid poplar (0.33–0.41 g cm⁻³; Fichot et al. 2010) and angiosperms in Tasmanian forests (0.54–0.83 g cm⁻³; Blackman et al. 2010). Xylem resistance to cavitation is not only associated with mechanical strength as determined by WD (Hacke et al. 2001; Jacobsen et al. 2005); it can also be governed by the pit structure of inter-vessels (Jansen et al. 2009). Therefore, differences in cavitation resistance among species that do not have large differences in WD may be associated with pit structure, which is related to air seeding, rather than mechanical strength.

Figure 4 shows the relationship between Ψ_{50} and $\Psi_{x \text{ min}}$, and combines our data with available data from previous studies. We used data on conifers and broadleaf trees distributed in semi-arid and humid regions. Overall, we found that higher cavitation resistance corresponded to higher xylem safety. Although the Mu Us Sandy Land is classified as semi-arid (UNEP 1997), species distributed therein tend to be less resistant to hydraulic cavitation and have smaller safety margins when compared with other species distributed in semi-arid environments. However, the levels of cavitation resistance and xylem safety of the species in this study were similar to or smaller than those of species in humid environments. We also found the same tendencies when these factors were compared with those for conifers and broadleaf trees. Jacobsen et al. (2007b) suggested that aridity, which can be measured based on precipitation, does not always predict cavitation resistance in woody shrubs because some species growing in more mesic conditions are more resistant to cavitation than

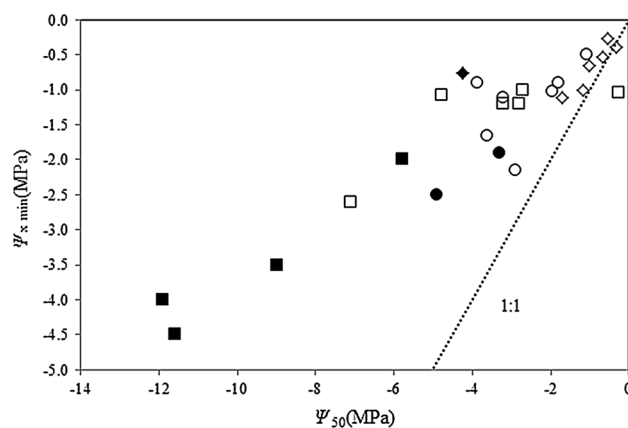


Fig. 4 Relationship between xylem water potential causing a 50 % loss in hydraulic conductivity (Ψ_{50}) and midday xylem water potential ($\Psi_{x \text{ min}}$). Dashed line represents a 1:1 relationship. Data are from this study and published values from Cochard et al. (1999), Domec et al. (2008), Eggenmeyer et al. (2006), Froend and Drake (2006), Hacke and Sauter (1995), Leffler et al. (2002), Miller et al. (1992), Ogasa et al. (2013), Pockman and Sperry (2000), Stout and Sala (2003), Taneda and Sperry (2008), Vilagrosa et al. (2003), and Willson et al. (2008). Symbols are: filled squares, conifers in a semi-arid environment; unfilled squares, broadleaf trees in a semi-arid environment; filled circles, conifers in a humid environment; unfilled circles, broadleaf trees in a humid environment; filled diamonds, conifers in the Mu Us Sandy Land; unfilled diamonds, broadleaf trees in the Mu Us Sandy Land

species growing in more arid conditions. In addition, they suggested that the difference in cavitation resistance is also affected by differences in root depth and the heterogeneity of soil moisture availability. Many of the plants distributed in the Mu Us Sandy Land have adventitious roots (Tokuoka and Wang 1994; Tokuoka 2001; Teraminami et al. 2010; Teraminami et al. 2013) and can extend their roots up towards groundwater (Ohte et al. 2003). Therefore, they can use rainfall and groundwater efficiently (Kobayashi 1994; Yang et al. 2014). This may compensate for lower xylem cavitation resistance.

In this study, we have revealed the strategies used by seven woody species from the Mu Us Sandy Land to maintain hydraulic function. The maintenance of hydraulic function may also be related to root depth and soil water availability. Rather than permit hydraulic dysfunction due to drought-induced dehydration, plants may develop water absorption systems that allow them to avoid or recover quickly from hydraulic dysfunction. This suggests stem–root coordination in drought tolerance. Therefore, these species may be able to maintain hydraulic function and concurrently ensure productivity. Although cavitation resistance is often used as an index of drought tolerance (Pockman and Sperry 2000), stem–root coordination should be considered when selecting plants for the revegetation of arid regions.

Acknowledgments The authors thank Drs. Keiji Sakamoto, Muneto Hirobe, and Mayumi Ogasa for helpful comments. This work was supported by a Grant-in-Aid for Young Scientists (B) (25850107) from the Japan Society for the Promotion of Science. This study was also conducted under the Cooperative Research Program of the Arid Land Research Center, Tottori University, Japan.

References

- Alder NN, Pockman WT, Sperry JS, Nuismer S (1997) Use of centrifugal force in the study of xylem cavitation. *J Exp Bot* 48:665–674
- Ambrose AR, Sillett SC, Dawson TE (2009) Effects of tree height on branch hydraulics, leaf structure and gas exchange in California redwoods. *Plant Cell Environ* 32:743–757
- Arango-Velez A, Zwiazek JJ, Thomas BR, Tyree MT (2011) Stomatal factors and vulnerability of stem xylem to cavitation in poplars. *Physiol Plant* 143:154–165
- Arata F, Matsuo N, Ohte N, Sugimoto A, Zhang G, Wang LH, Yoshikawa K (2001) Water source of *Sabina vulgaris* Ant. and *Salix cheilophila* Schneid.: tracing by stable isotope of water. *J Jpn Soc Reveg Technol* 27:258–260 (in Japanese with English abstract)
- Barnard DM, Meinzer FC, Lachenbruch B, McCulloh KA, Johnson DM, Woodruff DR (2011) Climate-related trends in sapwood biophysical properties in two conifers: avoidance of hydraulic dysfunction through coordinated adjustments in xylem efficiency, safety and capacitance. *Plant Cell Environ* 34:643–654
- Blackman CJ, Brodribb TJ, Jordan GJ (2010) Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytol* 188:1113–1123
- Brodribb TJ, Field TS (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rain forests. *Plant Cell Environ* 23:1381–1388
- Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Arce ME (2009) Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia* 160:631–641
- Cochard H, Lemoine D, Dreyer E (1999) The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. *Plant Cell Environ* 22:101–108
- Cochard H, Casella E, Mencuccini M (2007) Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. *Tree Physiol* 27:1761–1767
- Davis SD, Sperry JS, Hacke UG (1999) The relationship between xylem conduit diameter and cavitation caused by freezing. *Am J Bot* 86:1367–1372
- Domec J-C, Lachenbruch B, Meinzer FC, Woodruff DR, Warren JM, McCulloh KA (2008) Maximum height in a conifer is associated with conflicting requirements for xylem design. *Proc Natl Acad Sci USA* 105:12069–12074
- Dong X, Zhang X (2000) Special stomatal distribution in *Sabina vulgaris* in relation to its survival in a desert environment. *Trees* 14:369–375
- Eggenmeyer KD, Awada T, Wedin DA, Harvey FE, Zhou X (2006) Ecophysiology of two native invasive woody species and two dominant warm-season grasses in the semiarid grasslands of the Nebraska sandhills. *Int J Plant Sci* 167:991–999
- Fichot R, Barigah TS, Chamailard S, Thiec DL, Laurans F, Cochard H, Brignolas F (2010) Common trade-offs between xylem resistance to cavitation and other physiological traits do not hold among unrelated *Populus deltoides* × *Populus nigra* hybrids. *Plant Cell Environ* 33:1553–1568
- Flora of China Project (1999) Flora of China. <http://flora.huh.harvard.edu/china/>. Last accessed Feb 2012
- Froend RH, Drake PL (2006) Defining phreatophyte response to reduced water availability: preliminary investigations of the use of xylem cavitation vulnerability in *Banksia* woodland species. *Au J Bot* 54:173–179
- Fu P-L, Jiang Y-J, Wang A-Y, Brodribb TJ, Zhang J-L, Zhu S-D, Cao K-F (2012) Stem hydraulic traits and leaf water-stress tolerance are coordinated with the leaf phenology of angiosperm trees in an Asian tropical dry karst forest. *Ann Bot* 110:189–199
- Hacke UG, Sauter JJ (1995) Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. *purpurea* and *Populus balsamifera*. *J Exp Bot* 46:1177–1183
- Hacke UG, Sperry JS, Pittermann J (2000) Drought experience and cavitation resistance in six shrubs from the Great Basin. *Utah Basic Appl Ecol* 1:31–41
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461
- Hacke UG, Sperry JS, Pittermann J (2005) Efficiency versus safety tradeoffs for water conduction in angiosperm vessels versus gymnosperm tracheids. In: Holbrook NM, Zwieniecki MA (eds) *Vascular transport in plants*. Elsevier, London, pp 333–353
- Ishida A, Nakano T, Yazaki K, Matsuki S, Koike N, Lauenstein DL, Shimizu M, Yamashita N (2008) Coordination between leaf and stem traits related to leaf carbon gain and hydraulics across 32 drought-tolerant angiosperms. *Oecologia* 156:193–202
- Jacobsen AL, Ewers FW, Platt RB, Paddock WA III, Davis SD (2005) Do xylem fibers affect vessel cavitation resistance? *Plant Physiol* 139:546–556
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD (2007a) Cavitation resistance among 26 chaparral species of southern California. *Ecol Monogr* 77:99–115
- Jacobsen AL, Pratt RB, Davis SD, Ewers FW (2007b) Cavitation resistance and seasonal hydraulics differ among three arid Californian plant communities. *Plant Cell Environ* 30:1599–1609
- Jansen S, Choat B, Pletsers A (2009) Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. *Am J Bot* 96:409–419
- Kobayashi T (1994) Studies on ecology and water relations of revegetation plants in the Mu-Utsu Sandy District. *China Tech Bull Fac Hort Chiba Univ* 48:329–381 (in Japanese with English summary)
- Leffler AJ, Ryel RJ, Hipps L, Ivans S, Caldwell MM (2002) Carbon acquisition and water use in a northern Utah *Juniperus osteosperma* (Utah juniper) population. *Tree Physiol* 22:1221–1230
- Li Y, Sperry JS, Shao M (2009) Hydraulic conductance and vulnerability to cavitation in corn (*Zea mays* L.) hybrids of differing drought resistance. *Environ Exp Bot* 66:341–346
- Linton MJ, Sperry JS, Williams DG (1998) Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Funct Ecol* 12:906–911
- Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB (2006) Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant Cell Environ* 29:571–583
- Markesteyn L, Poorter L, Paz H, Sack L, Bongers F (2011) Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant Cell Environ* 34:137–148
- Miller PM, Eddleman LE, Miller JM (1992) The seasonal course of physiological processes in *Juniperus occidentalis*. *For Ecol Manag* 48:185–215

- Miranda J de D, Padilla FM, Martinez-Vilalta J, Pugnaire FI (2010) Woody species of a semi-arid community are only moderately resistant to cavitation. *Funct Plant Biol* 37:828–839
- Nardini A, Salleo S (2000) Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? *Trees Struct Funct* 15:14–24
- Nardini A, Lo Gullo MA, Salleo S (2011) Refilling embolized xylem conduits: is it a matter of phloem unloading? *Plant Sci* 180:604–611
- Neufeld HS, Grantz DA, Meinzer FC, Goldstein G, Crisosto GM, Crisosto C (1992) Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. *Plant Physiol* 100:1020–1028
- Ogasa M, Miki N, Yoshikawa K (2010) Changes of hydraulic conductivity during dehydration and rehydration in *Quercus serrata* Thunb. and *Betula platyphylla* var. *japonica* Hara: the effect of xylem structures. *Tree Physiol* 30:608–617
- Ogasa M, Miki HN, Murakami Y, Yoshikawa K (2013) Recovery performance in xylem hydraulic conductivity is correlated with cavitation resistance for temperate deciduous tree species. *Tree Physiol* 33:335–344
- Ohte N, Koba K, Yoshikawa K, Sugimoto A, Matsuo N, Kabeta N, Wang L (2003) Water utilization of natural and planted trees in the semiarid desert of inner Mongolia, China. *Ecol Appl* 13:337–351
- Pockman WT, Sperry JS (2000) Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *Am J Bot* 87:1287–1299
- Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53:301–304
- Salleo S, Trifilo P, Esposito S, Nardini A, Lo Gullo MA (2009) Starch-to-sugar conversion in wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for embolism repair? *Funct Plant Biol* 36:815–825
- Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140:543–550
- Savage JA, Cavender-Bares JM (2011) Contrasting drought survival strategies of sympatric willows (genus: *Salix*): consequences for coexistence and habitat specialization. *Tree Physiol* 31:604–614
- Siau JF (1984) Transport processes in wood. Springer-Verlag, New York
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ* 11:35–40
- Sperry JS, Tyree MT (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiol* 88:581–587
- Sperry JS, Tyree MT (1990) Water-stress-induced xylem embolism in three species of conifers. *Plant Cell Environ* 13:427–436
- Sperry JS, Pery AH, Sullivan JE (1991) Pit membrane degradation and air-embolism formation in ageing xylem vessels of *Populus tremuloides* Michx. *J Exp Bot* 42:1399–1406
- Sperry JS, Hacke UG, Pittermann J (2006) Size and function in conifer tracheids and angiosperm vessels. *Am J Bot* 93:1490–1500
- Stout DL, Sala A (2003) Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. *Tree Physiol* 23:43–50
- Stratton L, Goldstein G, Meinzer FC (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell Environ* 23:99–106
- Taneda H, Sperry JS (2008) A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. *Tree Physiol* 28:1641–1651
- Teraminami T, Nakashima A, Nakazato N, Ichihara S, Kurotaki M, Yamamoto M, Yamamoto M, Yoshikawa K, Zhang GS (2010) Effects of pile up of sand on growth and morphology of *Salix psammophila* in the Mu-Uss Sandy Land, Inner Mongolia, China. *J Jpn Soc Reveng Technol* 36:87–92 (in Japanese with English abstract)
- Teraminami T, Nakashima A, Ominami M, Yamamoto M, Zhang GS, Yoshikawa K (2013) Effects of sand burial depth on the root system of *Salix cheilophila* seedlings in Mu Us Sandy Land, Inner Mongolia, China. *Landscape Ecol Eng* 9:249–257
- Tokuoka M (2001) *Artemisia ordosica* in use for revegetation of semi-arid regions in China (I). *Bull Kochi Univ Forest* 28:17–22 (in Japanese with English summary)
- Tokuoka M, Wang LH (1994) A few observations on the distribution and regeneration of *Sabina vulgaris*. *J Jpn Soc Reveng Technol* 19:261–266 (in Japanese with English abstract)
- Tyree MT, Sperry JS (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol* 88:574–580
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Springer, Berlin
- UNEP (1997) World atlas of desertification, 2nd edn. Edward Arnold, London
- Utsumi Y, Sano Y, Funada R, Ohtani J, Fujikawa S (2003) Seasonal and perennial changes in the distribution of water in the sapwood of conifers in a sub-frigid zone. *Plant Physiol* 131:1826–1833
- Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrin E (2003) Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *J Exp Bot* 54:2015–2024
- Wang XM, Zhang CX, Hasi E, Dong ZB (2010) Has the Three Norths Forest Shelterbelt Program solved the desertification and dust storm problems in arid and semiarid China? *J Arid Environ* 74:13–22
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Willson CJ, Manos PS, Jackson RB (2008) Hydraulic traits are influenced by phylogenetic history in the drought-resistant, invasive genus *Juniperus* (Cupressaceae). *Am J Bot* 95:299–314
- Xiao CW, Zhou GS, Zhang XS, Zhao JZ, Wu G (2005) Responses of dominant desert species *Artemisia ordosica* and *Salix psammophila* to water stress. *Photosynthetica* 43(3):467–471
- Yamamoto M, Tamai S, Yamanaka N (2007) Ecophysiological responses to drought stress in *Salix psammophila* C. Wang et Ch.Y. Yang and *Salix matsudana* Koidz. *J Jpn Soc Reveng Technol* 32:425–431 (in Japanese with English abstract)
- Yang L, Miki HN, Matsuo N, Zhang GS, Wang L, Yoshikawa K (2014) Contribution of adventitious roots to water use strategy of *Juniperus sabina* in a semiarid area of China. *J Agric Sci Technol A* 4:251–259
- Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SEJ, Coomes DA (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215
- Zha Y, Gao J (1997) Characteristics of desertification and its rehabilitation in China. *J Arid Environ* 37:419–432
- Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer-Verlag, Berlin