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ORIGINAL ARTICLE

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Contrasting hydraulic strategies in *Salix psammophila* and *Caragana korshinskii* in the southern Mu Us Desert, China

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Abstract *Salix psammophila* and *Caragana korshinskii* are two common shrubs in the southern Mu Us Desert, China. Their hydraulic strategies for adapting to this harsh, dry desert environment are not yet clear. This study examined the hydraulic transport efficiency, vulnerability to cavitation, and daily embolism refilling in the leaves and stems of these two shrubs during the dry season. In order to gain insight into water use strategies of whole plants, other related traits were also considered, including daily changes in stomatal conductance, leaf mass per area, leaf pressure–volume parameters, wood density and the Huber value. The leaves and stems of *S. psammophila* had greater hydraulic efficiency, but were more vulnerable to drought-induced hydraulic dysfunction than *C. korshinskii*. The difference between leaf and stem water potential at 50 % loss of conductivity was 0.12 MPa for *S. psammophila* and 0.81 MPa for *C. korshinskii*. Midday stomatal conductance decreased by 74 % compared to that at 8:30 in *S. psammophila*, whereas no change occurred in C. *korshinskii*. Daily embolism and refilling occurred in the stems of *S. psammophila* and leaves of *C. korshinskii*. These results suggest that a stricter stomatal regulation, daily embolism repair in stems, and a higher stem water capacitance could be partially compensating for the greater susceptibility to xylem embolism in *S. psammophila*, whereas higher leaf elastic modulus, greater embolism resistance in stems, larger difference between leaf and stem hydraulic safety, and drought-induced leaf shedding in *C. korshinskii* were largely responsible for its more extensive distribution in arid and desert steppes.

Keyword Cavitation · Daily embolism and refilling · Hydraulic conductivity · Safety margin · Shrubs

Introduction

The capacity of the water transport system between the soil and the leaves imposes a fundamental limitation to the ability of plants to survive and grow under water-limited conditions. When xylem water potential exceeds a certain threshold during drought, cavitation occurs with air introduced into the tracheids or the vessels, causing the formation of embolisms and the loss of hydraulic conductivity (Tyree and Sperry 1989). Reduced hydraulic conductivity can decrease stomatal conductance and photosynthetic capacity (Brodribb and Field 2000), resulting in reduced growth and primary production, and even whole-plant mortality (Hartmann et al. 2013). Hydraulic vulnerability to xylem embolism has been well studied in trees, but relatively few studies have been conducted on shrubs. Even if the length of the hydraulic pathway is relatively short in shrubs, xylem embolism and reduced water transport capacity still occur as a result of high transpiration or low soil water availability, causing shoot dieback during prolonged drought (Davis et al. 2002; Vilagrosa et al. 2003; Bucci et al. 2009).

Vulnerability to drought-induced cavitation in woody plants is usually estimated as the water potential at 50 % loss of conductivity, Ψ_{50}. It is a highly species-specific trait, where the Ψ_{50} in stems can vary across species from −0. 04 MPa in *Celastrus orbiculatus* to −14.1 MPa in *Juniperus pinchotii* (Choat et al. 2012) and the Ψ_{50} in leaves can range from −0.1 MPa in *Platanus racemosa* to −4.3 MPa in *Eucalyptus pulchella* (summarized in

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Nolf et al. 2015). The majority of previous studies have focused on either stem or leaf hydraulic traits individually (e.g. Blackman et al. 2010; Choat et al. 2012; Scoffoni et al. 2012; Nardini and Luglio 2014), and little is known about the difference in vulnerability of stems and leaves to drought-induced dysfunction within the plant hydraulic continuum. Stems are generally less vulnerable to embolism than leaves (Choat et al. 2005; Hao et al. 2008; Bucci et al. 2012), resulting in varying degree of hydraulic segmentation within the plant (Tyree and Ewers 1991). This pattern of hydraulic architecture may help woody stems to avoid a substantial loss of hydraulic function with their high construction costs. However, leaves were found to be slightly more resistant to embolism than stems in the Euphorbiaceae tree *Macaranga denticulata* (Chen et al. 2009), and leaf mid-ribs were as vulnerable as stems in *Populus euphratica* (Hukin et al. 2005) or more resistant to embolism than stems in rubber clones (Sangsing et al. 2004). The manner in which stem and leaf hydraulic properties are coordinated within the plant hydraulic continuum among different species is important for understanding the hydraulic strategies these species use to adapt to drought.

There are several important mechanisms which can alleviate the threat of cavitation: stomatal regulation, structural reinforcement of the xylem, leaf shedding, water storage, and embolism repair. Stomatal regulation helps to maintain the xylem tension above a particular threshold which severe embolism does not occur. The structural reinforcement of the xylem can contribute to avoid vessel implosion or increase the resistance to xylem embolism (Mayr et al. 2006; Meinzer et al. 2009). The hydraulic safety margin is typically defined as the difference between the minimum leaf or stem xylem water potential ($\Psi_{\min}$) experienced by a species in the field and the water potential at which hydraulic failure occurs (usually Ψ_{50}). The safety margin is used to evaluate the degree of conservatism in plant hydraulic strategies, and is closely associated with drought adaptation and global drought-induced mortality (Choat et al. 2012; Nardini et al. 2013; Delzon and Cochard 2014). Moreover, the difference between leaf Ψ_{50} and stem Ψ_{50} informs the magnitude of the difference between leaf hydraulic safety and stem hydraulic safety, where a highly positive value may imply that leaves embolize before stem xylem, close their stomata and effectively stop transpiration; thereby preventing upstream stems from reaching embolism-inducing xylem pressures (Johnson et al. 2012). Choat et al. (2012) recently reported that the stems of 70 % of 226 forest species from 81 sites worldwide operated with narrow hydraulic safety margins (< 1 MPa) against catastrophic xylem dysfunction, suggesting that unless they have a high capacity for embolism repair, they could experience reductions in productivity and survival. Klein et al. (2014) have implied little importance of the hydraulic safety margin in the vulnerability of forests to drought, and pointed out the important role played by other mechanisms such as the ability of trees to repair embolisms.

Daily embolism formation and refilling have been observed in certain plants like *Vitis* (Brodersen et al. 2010), *Acer* and *Fraxinus* (Zwieniecki and Holbrook 1998), *Quercus* (Taneda and Sperry 2008), and *Laurus* (Salleo et al. 1996). The validity of the evidence for refilling in many species has been questioned due to methodological problems, the so-called cutting-induced artifacts (Sperry 2013; Wheeler et al. 2013). However, even after this cutting-induced artifact is eliminated by progressively cutting the stem multiple times under water, daily cycles of embolism formation and recovery were still observed in 5 of 9 dry forest species (Trifilò et al. 2015), suggesting that some plants do indeed lose and regain hydraulic function on a daily basis (McCulloh and Meinzer 2015). The daily cycle of embolism formation followed by refilling is considered to play an important role in the regulation of gas exchange (Lo Gullo et al. 2003). Additionally, embolism refilling is regarded as a finely regulated vital process that is essential for maintaining the integrity of the xylem water transport system and ultimately for helping the plant to cope with short-term drought stress (Clearwater and Goldstein 2005; Brodersen and McElrone 2013). It has been observed that embolism formation and repair occur in some species, but not in others (Trifilò et al., 2015). Therefore, the importance of embolism repair in regulating xylem water transport needs to be tested in more plant species in order to gain a better understanding of species-specific hydraulic responses to drought.

Salix psammophila (Salicaceae) and *Caragana korshinskii* (Fabaceae) are two dominant deciduous shrubs in the southern Mu Us desert in China. Both species play important roles in soil and water conservation, sand fixation and wind barrier. However, due to the limited annual precipitation of approximately 400 mm and the decreased groundwater levels caused by disturbances from coal mining and oil exploitation, some of the local vegetation including *S. psammophila* has shown symptoms of decline; whereas, others such as *C. korshinskii* appear to be unaffected. Previous studies which have examined the strategies used by *S. psammophila* and *C. korshinskii* to cope with drought have focused primarily on root distributions (Zhang et al. 2010), leaf anatomy, leaf water relations, photosynthetic and transpirational traits (Dong and Zhang 2001; Xu and Shan 2004), leaf osmoregulatory abilities, cellular membrane stability (Ma et al. 2008), and sources of water uptake (Wang et al. 2013); however, the hydraulic traits of these two species have received little attention. Limited researches on the hydraulic properties of these two shrubs indicated that stems of *S. psammophila* are highly vulnerable to cavitation (Ogasa et al. 2013), and that a progressive loss of stem hydraulic conductivity with age in *C. korshinskii* has been shown to partially induce a decline in the photosynthetic rate of resprouts (Fang et al. 2013). In another recent study, the stem

Table 1 Morphological parameters of the sampled *Salix psammophila* and *Caragana korshinskii* plants

Species	Basal branch diameter (cm)	Crown diameter (m)	Height (m)	Branching (no plant^{-1})
Salix psammophila	12.7 ± 0.4	3.7 ± 0.5	3.0 ± 0.1	35 ± 7
Caragana korshinskii	10.3 ± 0.6	2.2 ± 0.3	1.7 ± 0.3	21 ± 5

Tabulated valuse are the mean ± SE, n = 12

hydraulic vulnerability of these two shrubs were compared and it was found that *S. psammophila* is more vulnerable to embolism than C. *korshinskii* (Li et al. 2016). Nevertheless, neither leaf hydraulic traits and their coordination with stem hydraulic traits within the same plant continuum nor the daily embolism repair in the two species have been involved. Therefore, a study was designed to address some of these important questions. The objectives of this study were: (1) to assess the vulnerability of leaves and stems to drought-induced cavitation in 2 to 3-year-old regenerated shoots of *S. psammophila* and *C. korshinskii*, (2) to evaluate and compare the hydraulic safety margins of leaves and stems, and the magnitude of the difference between leaf hydraulic safety and stem hydraulic safety, and (3) to examine if daily embolism refilling occurs in these two species. We hypothesized that the leaves and stems of *S. psammophila* were more vulnerable to embolism than those of *C. korshinskii,* and that the leaves were more vulnerable to drought-induced hydraulic decline than stems in both species. Daily embolism formation and refilling may also occur in the more vulnerable of the shrubs, *S. psammophila*. The results of this study will contribute to our understanding of the survival, growth, and functional behavior of these common shrubs in the Mu Us Desert.

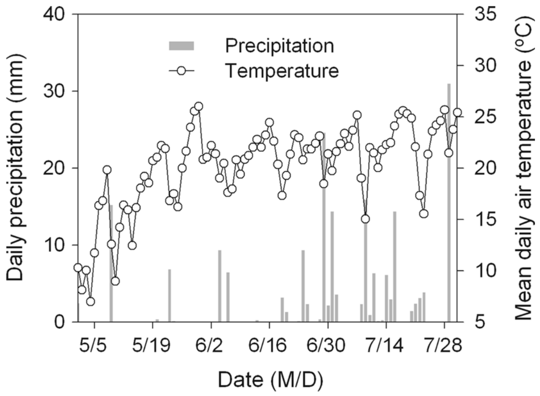

Fig. 1 Daily precipitation and mean daily air temperature from May to July, 2014, at the experimental study site

Materials and methods

Study site and plant species

The study site is located in the Liudaogou watershed of Shenmu County, Shaanxi Province, China (38°46′–38°51′N, 110°21′–110°23′E, 1274 m a.s.l.), and belongs to the transitional zone between the Loess Plateau and the Mu Us Desert. It has a temperate semi-arid climate with a mean annual air temperature of 8.4 °C and mean annual precipitation (1952–2013) of 437 mm, more than 70 % of which falls between July and September. The soils are coarse-textured sands and loess. Two adjacent stands of *S. psammophila* and *C. korshinskii* that were planted in the 1970s on relatively flat sand dunes were selected for the study. The stand density was 355 ha^{-1} for *S. psammophila* and 3240 ha^{-1} for *C. korshinskii*. The understory vegetation was mainly grasses and forbs such as *Artemisia desertorum*, *Hedysarum scoparium*, *Setaria viridis*, *Oxytropis gracillima*, *Heteropappus hispidus*, *Astragalus melilotoides*, *Cynanchum auriculatum*, and *Ixeris denticulata*.

The hydraulic traits of the two shrubs were measured during the period from June 1 to July 25, 2014 in twelve randomly selected plants, including ten plants per species in the past studies (Li et al. 2016). The morphological parameters of the sampled shrubs are given in Table 1. The climate for this period is relatively dry due to low precipitation and high mean daily air temperatures (Fig. 1). We mainly measured leaf hydraulic traits and daily changes of leaf and stem hydraulic traits in this study. For the stem hydraulic traits, including the stem vulnerability curves and wood density, the data from Li et al. (2016) were used as it was assumed that these values did not change across plants within the same field site.

Leaf and stem xylem water potential

Leaf and stem xylem water potentials (Ψ_l and Ψ_x, respectively) before dawn and at midday were measured by a pressure chamber (PMS 1000, PMS Instruments, Corvallis, USA) in six plants of each species on three sunny days in June and early July, 2014. Ψ_x was determined by sealing a leaf in a Ziploc bag inside an aluminum-foil bag to prevent transpiration from the bagged leaf. The predawn and midday samples were collected between 05:00–05:30 and 13:00–14:00, respectively on sunny days. Three uncovered and three covered leaves per plant were collected at each sampling time from the south-facing parts of the crowns, bagged, and immediately measured.

Leaf pressure–volume curves

Pressure–volume (PV) curves were constructed for four individual mature leaves from four plants of each species. Shoots with leaves were cut in the field at predawn, re-cut immediately under water, and placed in black plastic bags with the cut end in water for approximately 2 h until measurements. Then, the samples were dehydrated on the laboratory bench, leaf water potential and mass were determined periodically using a pressure chamber and an analytical balance. After all balancing pressure (water potential) and corresponding mass measurements were completed, the leaves were oven-dried at 70 °C to a constant mass and weighed. The PV curves were analyzed using a modelling program from Schulte and Hinckley (1985), which allows the estimation of saturated osmotic potential (Ψ_{sat}), osmotic potential at the turgor loss point (Ψ_{tlp}), and maximum elastic modulus ($\varepsilon_{\max}$).

Leaf vulnerability curves

The leaf vulnerability curves (VCs) for the shrubs were determined by measuring the leaf hydraulic conductance (K_{leaf}) using the rehydration kinetics method (Brodribb and Holbrook 2003). Shoots with leaves were sampled, transported, and rehydrated in the same period as those for the PV curves. A range of leaf water potentials were attained through the slow bench-drying of leafy branches. Initial leaf water potentials (Ψ_0) were then measured after a 0.5–1 h equilibration inside black plastic bags containing moist paper towels. Two adjacent leaves were cut under water and allowed to absorb water for different periods of time ranging from 15 to 60 s. Based on the analogy between the rehydration of desiccated leaves and the charging of a capacitor through a resistor, K_{leaf} (mmol $\text{m}^{-2}\ \text{s}^{-1}\ \text{MPa}^{-1}$) was calculated as follows:

$$K_{\text{leaf}} = C \ln(\Psi_0/\Psi_f)/t \tag{1}$$

where C is the leaf capacitance (mol $\text{m}^{-2}\ \text{MPa}^{-1}$), Ψ_0 is the leaf water potential before rehydration (MPa), and Ψ_f is the leaf water potential after rehydration for t seconds (MPa). The leaf vulnerability curves were plotted as K_{leaf} against Ψ_0. Capacitance values both before and after the turgor loss point were calculated from the leaf pressure–volume relationship using the following equation:

$$C_{\text{leaf}} = \Delta RWC/\Delta\Psi_1 \times (DM/LA) \times (WM/DM)/M \tag{2}$$

where RWC is the leaf relative water content (%), DM is the leaf dry mass (g), LA is the projected leaf area (m^2), WM is the mass of leaf water (g) at 100 % RWC (WM = fresh mass − dry mass), and M is the molar mass of water (g mol^{-1}).

In-situ stomatal response to leaf water potential

The response of stomatal conductance (g_s) to leaf water potential was measured between the hours of 8:30 and 13:00 on two sunny days, June 26 and July 6, 2014. The g_s for six plants per species (two leaves per plant) were determined using a portable LI-6400 photosynthetic system (LI-COR Inc., Lincoln, NE, USA). The g_s was measured at ambient photosynthetic photon flux density (550–1050 μmol $\text{m}^{-2}\ \text{s}^{-1}$), temperature (19–28 °C), relative humidity (55–30 %), and CO_2 concentration (~400 μmol mol^{-1}). The leaves were then excised and sealed immediately inside plastic bags containing moist paper towels for a 0.5 h equilibration, after which the leaf water potentials were determined using a pressure chamber.

Predawn stem specific hydraulic conductivity, leaf specific hydraulic conductivity, and the Huber value

Samples for the measurement of predawn hydraulic conductivity (K_h) were collected at the same time as those for predawn Ψ_l. The K_h was measured in six 2 to 3-year-old regenerated shoots from each of six plants per species from June 15 to July 25, 2014. Shoots greater than 1.4 m in length (maximum vessel length was 108 cm for *S. psammophila* and 70 cm for *C. korshinskii* based on air-injection experiments) were cut under water in the early morning, wrapped into black plastic bags with the cut basal ends of the branches under water, and transported to the laboratory within 30 min after excision. In the laboratory, stem segments greater than 1.3 m in length for *S. psammophila* and 1 m for *C. korshinskii* were excised from the collected shoots under water. The stem segments were debarked approximately 10 mm on each of their cut ends and the ends were trimmed with a razor blade. The samples were then mounted on the XYL'EM apparatus (Bronkhorst, Montigny-les-Cormeilles, France) for measuring K_h. The K_h values were determined at a hydrostatic pressure gradient of approximately 3 kPa using a degassed and filtered (0.22 μm) solution of 20 mM KCl and 1 mM $CaCl_2$. The K_h was converted to stem specific hydraulic conductivity (K_s, kg $\text{m}^{-1}\ \text{s}^{-1}\ \text{MPa}^{-1}$) by dividing by the xylem cross-sectional area (m^2) and also converted to leaf specific hydraulic conductivity (K_l, kg $\text{m}^{-1}\ \text{s}^{-1}$ MPa^{-1}) by dividing by the leaf area (m^2). The Huber value, which is the ratio of the stem cross-sectional area to the leaf area, was also determined. In addition, the leaves of the samples from the predawn hydraulic trait test, as well as those used to develop the PV curves, were oven-dried at 70 °C to a constant mass. The ratio of the leaf dry mass to leaf area (LMA) was then determined.

Predawn and midday native embolism

Shoots were collected during the same time as those for the leaf water potential test. Six to eight shoots from six to eight plants per species were collected during each sampling time. The sampling and transport procedures were identical to those used for the hydraulic conductivity test. Once in the laboratory, the shoots were maintained with the cut end immersed in water for approximately 30 min to release tension, after which the leaves were excised under water to further release the tension (Wang et al. 2014). Then, approximately six 3.0 cm-long stems segments with diameter ca. 4.5 mm per shoot were excised under water. All stem segments were collected at a distance from the initial cut at the base of the branch ≥120 % of the maximum vessel length according to Melcher et al. (2012), and mounted on the XYL'EM apparatus. The native K_h were determined in the same manner as the predawn hydraulic conductivity measurements. Maximum K_h was measured in a similar manner after removing the embolisms from the segments by flushing them with the same solution at a pressure of 0.15 MPa for 3 min. Results of the preliminary experiments showed that this pressure and time were sufficient to remove the embolisms. The percentage loss of conductivities (PLCs) were calculated by expressing the native K_h as a percentage of maximum K_h (Sperry et al. 1988):

$$\mathrm{PLC} = 100 \times (1 - \text{native } K_h/\text{maximum } K_h) \quad (3)$$

In order to elimate the refilling during the rehydration process, girdling was also performed on another set of samples for midday embolism measurements according to the method used by Trifilò et al. (2014). Six to eight branches per species with lengths ≥120 % of the maximum vessel length were girdled in situ at the field site 1 h prior to collection. The bark was removed in 3–5 mm strips at 15 cm intervals along the entire length of the branch. The exposed wood was immediately covered with a thin layer of silicone grease to prevent desiccation. The girdled branches were collected at midday under water and the PLC was determined by the same method as the ungirdled samples.

Stem vulnerability curves and wood density

The data set containing stem vulnerability curves (VC) and wood density used in this study were obtained from Li et al. (2016). Briefly, the bench-dehydration method was used to determine the stem VCs. This method was chosen in order to avoid the open vessel artifact which is common in other methods according to Cochard et al. (2013). The samples were collected under water on July 17, 2014 after a 14 mm rainfall event and then allowed to gradually dehydrate in the laboratory. The branches were sealed in plastic bags containing moist paper towel for a minimum of 2 h in order to allow Ψ_l and Ψ_x to equilibrate before performing the Ψ_x measurements. The Ψ_x was then determined in two leaves per branch using a pressure chamber. The mean PLCs were determined at different values of Ψ_x during dehydration using the XYL'EM apparatus in six 3 cm-long shoot segments per branch. These branches were cut from the base by multiple times under water in order to relieve xylem tension. The initial and maximum values of K_h were measured in the same manner as the native PLC measurement, and the PLC values were calculated according to Eq. (3).

The PLC data were then binned for each Ψ_x and curve-fitted to the binned data. To explore the stem VCs, the relationship between Ψ_x and PLC (from which the predawn native PLC was subtracted) (Wang et al. 2014) were plotted, and fitted to the following sigmoidal function from Pammenter and Vander Willigen (1998):

$$\mathrm{PLC} = \frac{100}{1 + e^{a(\Psi_x - \Psi_{50})}} \quad (4)$$

where a is a constant related to the curve slope, and Ψ_{50} corresponds to Ψ_x at 50 % loss of conductivity.

The wood density was measured using the method of Hacke et al. (2001a) on the same samples used to determine the stem VCs. For this method, stem segments ca. 2 cm in length were soaked in distilled water for approximately 1 week, the fresh volume was then determined using a digital balance with a precision of 0.0001 g based on Archimedes' principle. Later the samples were oven-dried at 80 °C for 48 h, and their dry masses were measured. The ratio of dry mass to volume is the wood density.

Safety margin

The safety margin was used to describe the conservation degree of the integrity of the hydraulic pathway for both species. The leaf and stem safety margins were defined as the difference between minimum Ψ_l and Ψ_x during the dry season and leaf and stem Ψ_{50}, respectively. The minimum Ψ_l and Ψ_x were the lowest of three measurements performed in June and July of the study. Besides, the difference between the water potential at 50 % loss of leaf hydraulic conductance and the water potential at 50 % loss of stem hydraulic conductivity (leaf Ψ_{50} − stem Ψ_{50}) was used in order to evaluate whether the leaves were vulnerable enough to protect the stems from hydraulic dysfunction (Johnson et al. 2012).

Results

Hydraulic efficiency and vulnerability

LMA, Ψ_{sat}, Ψ_{tlp}, and C_{leaf} did not differ between the leaves of the two species, but the leaves of *S. psammophila* had a significantly lower ε_{max} than those of *C. korshinskii* (independent t test, $P < 0.01$, n = 4). The maximum K_{leaf} was 72.8 % higher for *S. psammophila* than for *C. korshinskii* (Table 2), and the leaf Ψ_{50} in *S. psammophila* was higher than that in *C. korshinskii*, with values of −1.51 and −1.83 MPa, respectively (Fig. 2; Table 3). These results indicate that the leaves of *S. psammophila* had a greater water transport efficiency and a weaker resistance to drought-induced embolism than those of *C. korshinskii*.

Table 2 Leaf and stem hydraulic traits in *Salix psammophila* and *Caragana korshinskii*, including leaf dry mass per leaf area (LMA), saturated osmotic potential (Ψ_{sat}), osmotic potential at turgor loss point (Ψ_{tlp}), maximum elastic modulus (ε_{max}), leaf hydraulic capacitance (C_{leaf}), maximum leaf hydraulic conductance ($K_{leaf–max}$, leaf hydraulic conductance at $\Psi_l = -0.2$ MPa), wood density (ρ_{wood}), stem specific hydraulic conductivity (K_s), leaf specific hydraulic conductivity (K_l) and the Huber value (HV)

Organ	Hydraulic trait	*Salix psammophila*	*Caragana korshinskii*	Significance (n)
Leaf	LMA (mg cm^{-2})	13.87 ± 1.12	13.41 ± 0.59	$P > 0.05$ (n = 10)
	Ψ_{sat} (MPa)	−1.69 ± 0.11	−1.84 ± 0.09	$P > 0.05$ (n = 4)
	Ψ_{tlp} (MPa)	−2.19 ± 0.13	−2.22 ± 0.10	$P > 0.05$ (n = 4)
	ε_{max} (MPa)	9.15 ± 0.45	13.31 ± 0.65	$P < 0.01$ (n = 4)
	C_{leaf} (mol m^{-2} MPa^{-1})	1.27 ± 0.11	1.04 ± 0.07	$P > 0.05$ (n = 4)
	$K_{leaf\text{-}max}$ (mmol m^{-2} s^{-1} MPa^{-1})	30.96	17.92	
Stem	ρ_{wood} (g cm^{-3})	0.46 ± 0.01	0.63 ± 0.03	$P < 0.01$ (n = 9)
	K_s (kg m^{-1} s^{-1} MPa^{-1})	10.17 ± 0.17	4.32 ± 1.13	$P < 0.05$ (n = 6)
	K_l (×10^{-3} kg m^{-1} s^{-1} MPa^{-1})	1.49 ± 0.30	0.78 ± 0.17	$P < 0.05$ (n = 6)
	HV (×10^{-4} cm^2 cm^{-2})	1.51 ± 0.26	1.32 ± 0.07	$P > 0.05$ (n = 6)

The significance between species was tested using an independent *t* test. Tabulated values are the mean ± SE and n is the sample size

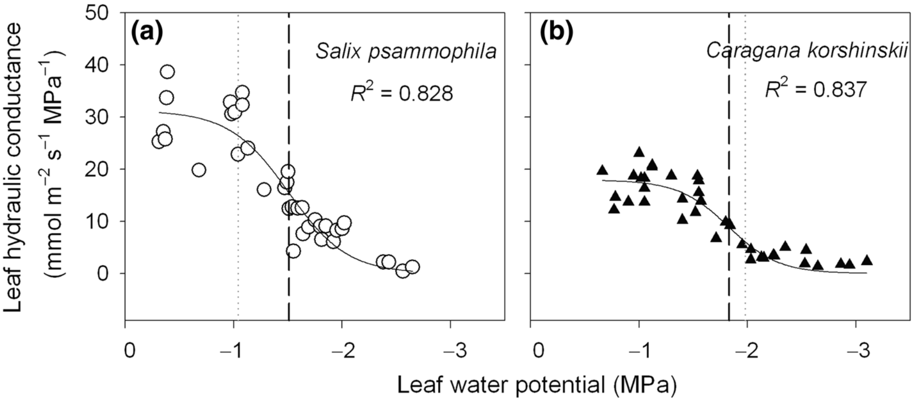

Fig. 2 Changes in leaf hydraulic conductance with leaf water potential in *Salix psammophila* (**a**) and *Caragana korshinskii* (**b**). The *curves* were modeled using the sigmoidal function $f = a/(1 + \exp(-(x - x_0)/b))$. The *dotted* and *dashed vertical lines* correspond to minimum leaf water potential (Ψ_{min}) during the dry season and leaf water potential at 50 % loss of leaf maximum hydraulic conductance Ψ_{50}, respectively. The difference between Ψ_{min} and Ψ_{50} is the hydraulic safety margin of leaves

Table 3 Hydraulic safety margins of leaves and stems and difference between leaf and stem hydraulic safety in *Salix psammophila* and *Caragana korshinskii*

Shrubs	Leaf Ψ_{min} (MPa)	Stem Ψ_{min} (MPa)	Leaf Ψ_{50} (MPa)	Stem Ψ_{50} (MPa)	Hydraulic safety margin (MPa)		Leaf Ψ_{50} − Stem Ψ_{50} (MPa)
					Leaf Ψ_{min} − Leaf Ψ_{50}	Stem Ψ_{min} − Stem Ψ_{50}	
Salix psammophila	−1.04	−0.77	−1.51	−1.63	0.47	0.86	0.12
Caragana korshinskii	−1.98	−1.21	−1.83	−2.64	−0.15	1.43	0.81

Ψ_{min} is the minimum leaf or stem water potential measured during the dry season, and Ψ_{50} is the leaf or stem water potential at 50 % loss of conductivity

The stem K_s and K_l values of *S. psammophila* were 1.35 and 0.91 times greater, respectively than that of *C. korshinskii*; however, the two shrubs had approximately the same Huber value (Table 2). The stem Ψ_{50} for *S. psammophila* and *C. korshinskii* were −1.63 and −2.64 MPa, respectively (Fig. 3, Table 3) and the VC for *S. psammophila* exhibited a larger slope, indicated by a larger value of the constant '*a*' in Eq. (4). The larger stem Ψ_{50} and slope indicate that the stems of *S. psammophila* were more vulnerable than those of *C. korshinskii* to drought-induced cavitation. The wood density of stems was found to be lower in *S. psammophila* than in *C. korshinskii* (Table 2).

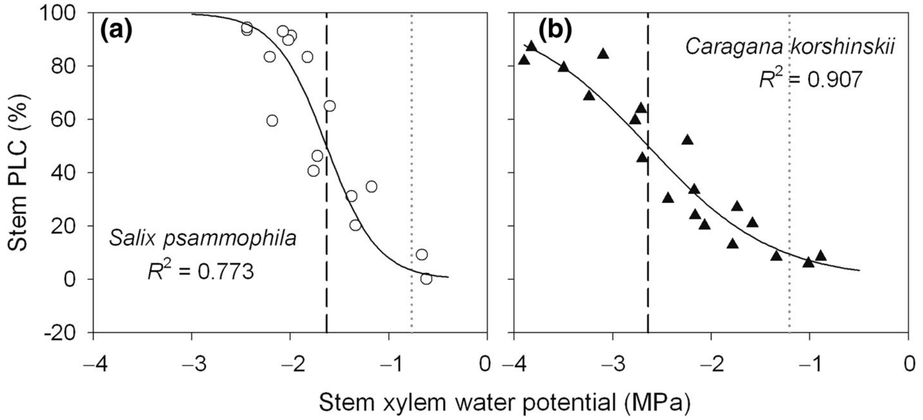

Fig. 3 Stem vulnerability curves for *Salix psammophila* (**a**) and *Caragana korshinskii* (**b**). The vulnerability curve data were taken from Li et al. (2016). The PLC is the percentage loss of conductivities. The *curves* were modeled by the sigmoidal function $f = 100/(1 + \exp(a(x - b)))$, where a is a constant related to the curve slope, b corresponds to Ψ_x at 50 % loss of conductivity. The *dotted* and *dashed vertical lines* correspond to minimum xylem water potential during the dry season ($\Psi_{\min}$) and xylem water potential at 50 % loss of conductivities (Ψ_{50}), respectively. The difference between $\Psi_{\min}$ and Ψ_{50} is hydraulic safety margin of stems

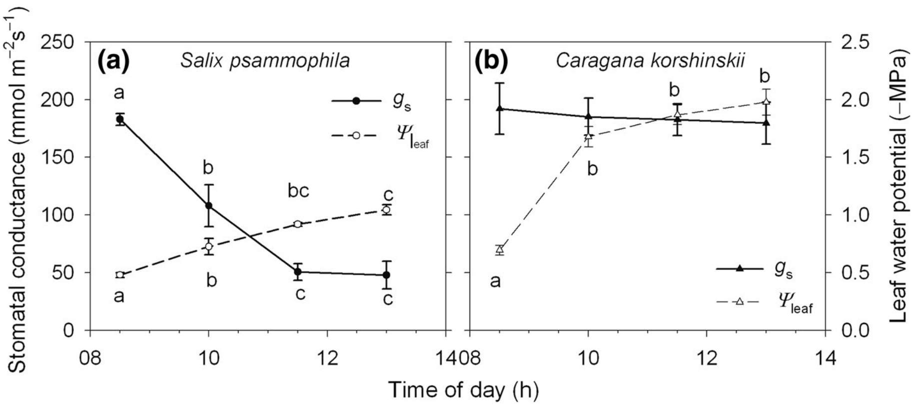

Fig. 4 Leaf water potential and stomatal conductance in two shrubs from 08:30 to 13:00 on two clear and sunny days. *Lower case letters* indicate significant differences across daily measurements at the 0.05 level

Safety margin

The leaves of *S. psammophila* had a much higher seasonal minimum water potential than those of *C. korshinskii* (Table 3; Fig. 3). Leaf stomatal conductance decreased by 74 % when the leaf water potential dropped from −0.48 MPa at 08:30 to −1.04 MPa at 13:00 (midday) in *S. psammophila*. In contrast, no decrease in stomatal conductance was found in *C. korshinskii* when the leaf water potential dropped from −0.69 MPa at 08:30 to −1.98 MPa at 13:00 (Fig. 4). The leaf hydraulic safety margins were 0.47 MPa in *S. psammophila* and −0.15 MPa in *C. korshinskii* (Table 3), suggesting that leaves of *C. korshinskii* may suffer from daily embolism and refilling.

The stem hydraulic safety margins were 0.86 MPa for *S. psammophila* and 1.43 MPa for *C. korshinskii* (Table 3); hence, the stems of *C. korshinskii* had a wider hydraulic safety margin by 0.57 MPa. The hydraulic safety margins of both shrubs were smaller in leaves than in stems (Table 3), with leaves showing greater vulnerability than stems. The role of leaves in the protection of stems, evaluated by leaf Ψ_{50} − stem Ψ_{50}, was 0.12 MPa for *S. psammophila* compared to 0.81 MPa for *C. korshinskii* (Table 3).

Daily embolism and refilling

The predawn and midday K_{leaf} were estimated by extrapolating the predawn and midday Ψ_l values into the VC functions (Fig. 2). Predawn K_{leaf} was nearly identical to the maximum values for both shrubs, and midday K_{leaf} decreased by 8.5 % in *S. psammophila* and by 35.5 % in *C. korshinskii* (Table 4). The K_{leaf} of *C. korshinskii* decreased substantially at midday, suggesting that daily embolism and refilling may occur in the leaves of this species.

Table 4 Estimated predawn and midday leaf hydraulic conductance (K_{leaf}) in *Salix psammophila* and *Caragana korshinskii*

Shrubs	Ψ_{pd} (MPa)	Ψ_{md} (MPa)	Predawn K_{leaf} (mmol $\mathrm{m^{-2}\,s^{-1}\,MPa^{-1}}$)	Midday K_{leaf} (mmol $\mathrm{m^{-2}\,s^{-1}\,MPa^{-1}}$)	Predawn loss of K_{leaf} (%)	Midday loss of K_{leaf} (%)
Salix psammophila	−0.28 ± 0.04	−0.88 ± 0.03	30.86 ± 0.05	28.33 ± 0.24	0.32	8.49
Caragana korshinskii	−0.44 ± 0.03	−1.68 ± 0.07	17.89 ± 0.01	11.55 ± 1.20	0.17	35.55

K_{leaf} was estimated from leaf vulnerability curve. Loss of K_{leaf} is: $(1 - K_{\mathrm{leaf}}/K_{\mathrm{leaf\text{-}max}}) \times 100$. Tabulated values are the mean ± SE, n = 6
Predawn and midday leaf water potential (Ψ_{pd} and Ψ_{md}, respecitively) were measured during dry season

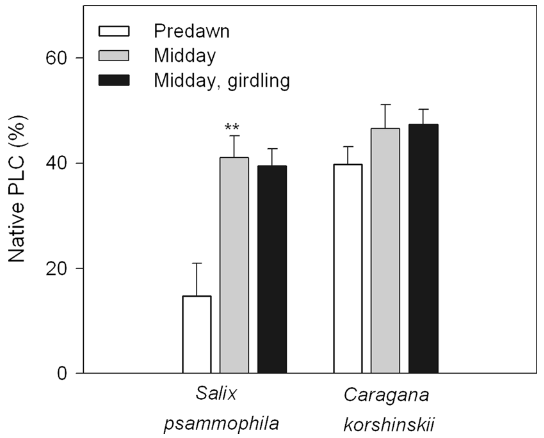

Fig. 5 Predawn and midday native percentage loss of conductivities (PLC) in stems of *Salix psammophila* and *Caragana korshinskii*. Values are the mean ± SE, n = 6–8. **denotes a significant difference between predawn and midday PLCs at $P < 0.01$ by an independent *t* test

The predawn native PLC of the stems was 14.8 % in *S. psammophila* and 39.7 % in *C. korshinskii*. The midday PLC, which reached 41.0 %, was significantly higher than the predawn PLC in *S. psammophila* (independent *t* test, $P < 0.05$, n = 6–8); however, the midday and predawn PLCs were nearly identical in *C. korshinskii* (Fig. 5). The midday PLCs did not differ between the girdled and ungirdled samples for either species, suggesting that the underestimation of the PLC values, which is caused by refilling during the rehydration process, was avoided.

Discussion

Hydraulic transport efficiency and vulnerability to cavitation

The two species did not differ in their ability to perform leaf osmotic adjustment or in their tolerance to low water potential because the PV curve parameters like Ψ_{sat}, Ψ_{tlp}, and C_{leaf} of the leaves did not differ between the two species. However, *C. korshinskii* showed a greater $\varepsilon_{\max}$. A relatively high $\varepsilon_{\max}$ allows the cells to maintain a high turgor pressure under drought (Fang et al. 2011), or to maintain a higher RWC at turgor loss point, thus, avoiding dangerous cell dehydration and shrinkage (Bartlett et al. 2012). Moreover, a greater $\varepsilon_{\max}$ may also enable a more rapid refilling of embolisms in the leaf xylems (Salleo et al. 1997), which may occur in *C. korshinskii*, because the leaves experience daily embolism and refilling.

Salix psammophila had higher leaf- and stem-level hydraulic transport efficiencies than *C. korshinskii*. It is known that *S. psammophila* is a "water-spending" species, has relatively large leaf and stem xylem conduit diameters, and usually accesses water by means of extensive rooting in the shallow soil layers (Dong and Zhang 2001), which is consistent with the higher water transport efficiencies observed in both the leaves and stems of this species in this study. These higher transport efficiencies may contribute to the higher growth rate in *S. psammophila*. It has been observed that *C. korshinskii* has a large root system, and mainly uses deep soil water (Zhang et al. 2010). The cost of this extensive root system may contribute to lower above-ground growth rates in this deeply rooted species. Two-year-old regenerated shoots of *S. psammophila* reached 1.4 ± 0.2 m in height; whereas, the *C. korshinskii* in our study grew to only 0.6 ± 0.1 m.

The mean leaf Ψ_{50} values were −1.51 MPa in *S. psammophila* and −1.83 MPa in *C. korshinskii*, which are within the range of −1 to −3 MPa that previous studies have reported in many woody angiosperms (Blackman et al. 2010). The stem Ψ_{50} was −1.63 MPa in *S. psammophila*, which is slightly more negative than the −1.18 MPa that has been reported in young potted plants of this species (Ogasa et al. 2013) and also within the range reported for other willows (Cochard et al. 2007; Wikberg and Ögren 2007). The stem Ψ_{50} for *C. korshinskii* was −2.64 MPa, which is very similar to the mean Ψ_{50} (−2.66 MPa) for winter deciduous shrubs (Maherali et al. 2004). The stem Ψ_{50} data shows that the two desert shrubs did not have greater embolism resistance than other temperate woody plants. The leaves and stems of *S. psammophila* were more conductive and more vulnerable to drought-induced cavitation than those of *C. korshinskii* (Figs. 2, 3, Table 3), suggesting a tradeoff relationship between xylem efficiency and safety as previous studies have reported (Maherali et al. 2004; Hacke et al. 2006; Pittermann et al. 2010). This difference in cavitation resistance adjusted the ranges of field stem water potential that the species experienced, therefore, midday Ψ_{x} was lower in *C. korshinskii* than in *S. psammophila*. The *C. korshinskii* had a stronger resistance to cavitation, allowing it to better adapt to dry habitats. It is possible that *C. korshinskii* developed this resistance by reinforcing its xylem structure because cavitation resistance is positively correlated with wood density (Hacke et al. 2001a). A high cavitation resistance is regarded as an important trait of drought resistance and may be closely associated with the extensive distribution of *C. korshinskii* in arid and desert steppes.

Coordination of stem and leaf hydraulic vulnerability

The difference between leaf Ψ_{50} and stem Ψ_{50} were 0.12 MPa in *S. psammophila* and 0.81 MPa in *C. korshinskii* (Table 3), which are comparable to those reported for 26 angiosperm species from temperate and tropical biomes (−0.1 to 2.4 MPa, Nolf et al. 2015); however, these values are below the observed range for cold desert shrubs in Patagonia that receive a mean annual precipitation of less than 200 mm (0.8–2.7 MPa, Bucci et al. 2013). The *S. psammophila* showed a positive leaf hydraulic safety margin as opposed to the negative safety margin in *C. korshinskii*; however, *C. korshinskii* had a wider stem hydraulic safety margin as well as a greater difference of hydraulic safety between leaves and stems than *S. psammophila*. Based on these results, it can be concluded that the two shrubs have different hydraulic systems. The negative hydraulic safety margins in the leaves of *C. korshinskii* may be an indicator of their tendency to function as hydraulic circuit breakers, which can cut off upstream portions of transpiration from the atmosphere and; thus, prevent stem xylems from experiencing dangerous pressures (Bucci et al. 2013). The greater loss of leaf hydraulic conductance at midday compared to early morning (Table 4) also verified the formation and repair of daily embolisms in *C. korshinskii*. The leaves tend to be more vulnerable to hydraulic decline than the stems in the two studied species, which is consistent with previous observations of other plant species (Hao et al. 2008; Chen et al. 2009; Bucci et al. 2012). The leaves can act as safety valves to protect carbon costly xylems from hydraulic dysfunction, the so-called “vulnerability segmentation” (Tyree and Ewers 1991). The compound leaf form has evolved to facilitate hydraulic segmentation, supported by compound leaves dieback under drought stress while stems remain intact (Malhado et al. 2010). Drought-induced leaf shedding was also frequently observed in *C. korshinskii* in the field, which was possibly caused by the afore-mentioned hydraulic vulnerability and/or hydraulic segmentation. Therefore, it can be assumed that the role of leaves in protecting stems from hydraulic dysfunction was more prevalent in *C. korshinskii*. Thus, in terms of the leaf and stem hydraulic systems, *C. korshinskii* had obvious advantages over *S. psammophila*. Firstly, negative safety margins in the leaves of *C. korshinskii* could help to maximize carbon assimilation through daily embolism formation and repair under unstressed condition. A higher midday stomatal conductance was found in *C. korshinskii* though its midday leaf hydraulic conductance was depressed. Contrarily, some studies have found that lower midday stomatal conductance was often related to decreased midday leaf hydraulic conductance (Brodribb and Holbrook 2004; Zhang et al. 2013). These contrasting results may indicate that stomatal behavior was directly related to soil water availability, the rooting depth, stem water status, and/or other various causes (Zhang et al. 2013) rather than leaf water status. Secondly, relatively large safety margin in the stems of *C. korshinskii* could decrease their risk of embolism when facing drought. Lastly, the ability of *C. korshinskii* to sacrifice its leaves in order to protect the water transport integrity in its stems could also contribute to the survival of this species under severe drought.

Daily embolism and refilling

In comparison to *C. korshinskii*, the stems of *S. psammophila* were found to be more vulnerable to cavitation and the leaves provided little hydraulic protection to stem hydraulic integrity. Therefore, *S. psammophila* may have evolved other adaptive hydraulic strategies to cope with this harsh, dry desert habitat. It was found that the stem xylems of *S. psammophila* could embolize and refill daily; thus, helping to reduce the threat of cavitation. Although proof of the existence of daily embolism and refilling has been controversial due to experimental artifacts (Wheeler et al. 2013), newly performed control experiments (Trifilò et al. 2014, 2015; Venturas et al. 2015) and in vivo observations of formation and recovery of xylem embolisms (Brodersen et al. 2010; Zwieniecki et al. 2013; Knipfer et al. 2015) suggest that the phenomenon is not merely a technical error of sampling and hydraulic measurement techniques, but that it truly occurs in some species. Ogasa et al. (2013) found that high vulnerability to cavitation in some willow species, including *S. psammophila*, was compensated by a high recovery performace, which was evaluated using the ratio of xylem hydraulic conductivity in plants that were rewatered after soil drought to that in plants under moist conditions. Thus far, the mechanism responsible for daily embolism and refilling is not clear; however, it may be related to the generation of local positive pressures via osmotic mechanisms, which are triggered by solute and sugar release from vessel-associated parenchyma cells into the embolized conduit (Salleo et al. 1996; Johnson et al. 2012).

In addition to daily and seasonal embolism repair, other strategies may be used by *S. psammophila* to adapt to dry desert environments. Based on the stem vulnerability curve (Fig. 3) and daily changes in stomatal conductance (Fig. 4), it can be concluded that *S. psammophila* employs an isohydric control over its stomatal behavior. The midday stomatal conductance of *S. psammophila* decreased by 74 % compared to the early morning, and the slope of its stem VC curve was steeper and had a higher Ψ_{50} (−1.63 MPa) than that of *C. korshinskii*. This suggests that *S. psammophila* may regulate their stomata more strictly to protect the xylem from developing embolisms, which may account for their larger leaf hydraulic safety margin. Additionally, *S. psammophila* may have a greater water capacitance, indicated by its lower wood density (Meinzer et al. 2009). Possibly the transient release of stem-stored water may inhibit a rapid transpiration-induced decrease in xylem tension and prevent *S. psammophila* stems from xylem embolism, partially compensating for the disadvantages of their relatively more vulnerable xylems.

It is notable that the predawn native PLC in *C. korshinskii* was as high as 39.7 %, which is considerably higher than the commonly observed range of 5–20 % in most species (Tyree and Ewers 1991) and even higher than the 30 % observed in highly conservative *Robinia pseudoacacia* (Wang et al. 2014) and 34.6 % in oak trees (Taneda and Sperry 2008), but lower than for species in arid Californian plant communities which have PLC values near 50 % (Jacobsen et al. 2007). The relatively high native PLC in *C. korshinskii* may be attributed to several causes. Firstly, a higher predawn PLC may be caused by the accumulation of embolisms in shoots that are at least 1-year-old considering that daily embolism repair does not occur in stems of *C. korshinskii*. Secondly, some or all of the relatively high native PLC values may have been due to embolized vessels that later grew tyloses (Cao and Zhang 1991). Tyloses develop within a part of the vessels, so when the native PLC was measured on short stem segments, some of the vessels that were partially blocked by tyloses were flushed and removed with the testing solution; thus, resulting in an increased predawn native PLC. Lastly, it is possible that cavitation or frost fatigue (Hacke et al. 2001b; Anderegg et al. 2013; Christensen-Dalsgaard and Tyree 2014) may have also increased the vulnerability of the stems because non-current-year branches were used in our study. It has been noted that some conservative tree species frequently exhibit high native PLCs. A relatively high native PLC may be a requirement for limiting nocturnal transpiration or is potentially a constraint to the early onset of daily sap flow in dry environments. The physiological role of a high native PLC in the drought stress adaptation of these species is worthy of further study.

Conclusion

Our research has demonstrated that *S. psammophila* and *C. korshinskii* use different hydraulic strategies to adapt to the dry sandy environment. It was found that *S. psammophila* had greater leaf and stem hydraulic transport efficiencies, but that its leaves and stems were more vulnerable to drought-induced embolism than those of *C. korshinskii*. The leaves of *S. psammophila* were less vulnerable to embolism than its stems; whereas, in *C. korshinskii* the leaves were more vulnerable than stems to embolism, suggesting that the leaves of *C. korshinskii* provide more hydraulic protection to the stem hydraulic integrity. The disadvantages that arise from having a greater hydraulic vulnerability and leaves with little ability to provide protection from stem hydraulic dysfunction in *S. psammophila* can be partially compensated for by stronger stomatal regulation, daily embolism and refilling, and possibly by a higher stem water capictance in this species. Relatively high values of leaf elastic modulus, stem cavitation resistance, and the difference between leaf and stem hydraulic safety, as well as the occurrence of drought-induced leaf shedding in *C. korshinskii* may allow it to better cope with drought. The results of this study indicate that the two shrubs employ different mechanisms to adapt to the dry desert environment.

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