Tree Physiology 31, 604–614
doi:10.1093/treephys/tpr056

Research paper

Contrasting drought survival strategies of sympatric willows (genus: *Salix*): consequences for coexistence and habitat specialization

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Received December 5, 2010; accepted May 16, 2011; handling Editor Frederick Meinzer

Many willow species (genus: *Salix*) co-occur within habitats (α-diversity) and across the landscape (β-diversity) throughout North America. This high diversity is challenging to explain because closely related species often share similar functional traits and thus experience heightened competition and shared pest and pathogen susceptibility. To investigate whether traits related to drought survival are important in maintaining diversity, we conducted an experimental dry-down on six willow species in a greenhouse. We compared species' growth rates, stem and leaf hydraulics, leaf function and dieback and examined potential associations between their drought responses and habitat affinities. Habitat affinities were characterized based on species occurrence in randomly established field plots in central Minnesota. Overall, species that occur in drier, more seasonally variable habitats tended to have higher water-use efficiency, and faster growth rates than species from wetter habitats. However, the greatest difference in drought survival strategies was found between two species with similar habitat affinities. We conclude that differences in willow species could be important in both driving habitat differentiation and permitting temporal differentiation in resource utilization within habitats. Therefore, species' water-use strategies could be important in maintaining both α- and β-diversity across the landscape.

Keywords: co-occurrence, dieback, drought, hydraulics, willow.

Introduction

Within and across plant lineages, there is a strong correlation between species' hydraulic architecture and their distribution along soil moisture and larger-scale precipitation gradients (Cavender-Bares and Holbrook 2001, Pockman and Sperry 2000, Maherali et al. 2004). Functional trade-offs associated with drought tolerance largely account for this correlation and are likely important in facilitating niche separation and maintaining species diversity across the landscape (β-diversity) (Silvertown et al. 1999, Cavender-Bares et al. 2004, Choat et al. 2007). However, functional divergence can also be important in facilitating co-occurrence within habitats, especially if it leads to differential resource partitioning (Elton 1946, Tilman 1982). For example, in habitats experiencing periods of limited water availability, functionally distinct species that partition water use spatially or temporally may be more likely to co-occur. Under these conditions, traits related to water use, such as hydraulic architecture, could play a critical role in promoting β-diversity (between habitats) across the landscape.

In many plant lineages, habitat specialization along a water availability gradient is attributed to a functional trade-off between drought tolerance and plant productivity (Hacke and Sperry 2001, Cochard et al. 2007). Under drought conditions, plants experience increased tension in their xylem, which can lead to cavitation, reduced hydraulic conductance and even hydraulic failure (Tyree et al. 1993, Rice et al. 2004). Plants with a high wood density are generally more resistant to cavitation (Hacke et al. 2001) because denser wood contains smaller conduits that are less likely to have large pits that can allow the spread of emboli (Wheeler et al. 2005, Hacke et al. 2006). Smaller conduits also have a lower hydraulic efficiency, which may lead to lower levels of productivity (Zimmerman 1983, Cochard et al. 2007). This trade-off between xylem safety and efficiency is often used to explain the strong associations observed between species' vulnerability to cavitation and their distribution along water availability gradients (Pockman and Sperry 2000, Maherali et al. 2004). While high cavitation resistance is common in plants from drier habitats, plants can use multiple strategies to survive drought conditions (Hacke et al. 2000, Martinez-Vilalta et al. 2003). For example, plants can be hydraulically segmented in a manner that limits the spread of runaway cavitation under drought conditions (Zimmerman 1983, Tyree and Ewers 1991). This segmentation can occur either because of hydraulic separation between parts of the plant (e.g., leaves and shoots) or because expendable organs have a higher vulnerability to cavitation. Either way, segmentation of distal leaves and branches can reduce water loss and lower xylem tension in critical organs allowing species to survive short-term drought (Tyree et al. 1993, Munné-Bosch and Alegre 2004). Therefore, species that occur in the same habitats can differ in their branch vulnerability to cavitation depending on their drought survival strategy (Martinez-Vilalta et al. 2003, Vilagrosa et al. 2003).

Throughout North America, species of the genus *Salix* (willows) occur in sympatry and have high α- and β-diversity. Since willows are closely related to each other and share a recent common ancestor, they are likely to be functionally similar and thus compete more heavily for the same resources than more distantly related species (Darwin 1859, Elton 1946). As a result, willows should demonstrate limited co-occurrence within habitats unless there has been significant divergence in functional traits related to resource use (Losos et al. 2003, Cavender-Bares et al. 2004, Fine et al. 2005). While willow species tend to occur in wetter habitats because of their relative drought intolerance (Tyree et al. 1994, Pockman and Sperry 2000, Karrenberg et al. 2002, Rood et al. 2003), there has been limited research investigating the mechanisms important in determining their habitat specialization and patterns of co-occurrence (except see Splunder et al. 1996, Woods and Cooper 2005, Dawson 1990). Several recent studies have also found that hydraulic architecture is phylogenetically conserved in some plant lineages (Choat et al. 2007, Hao et al. 2008, Willson et al. 2008), which could limit the diversity of drought survival strategies found among congeners.

To better understand the mechanisms that promote the observed diversity in Minnesota willow communities, we compared the drought survival strategies of three willow species that specialize in perennially wet habitats and three that occur in more seasonally variable habitats. We examined whether there was evidence for habitat specialization based on species' physiological traits and the extent that species co-occurring within the same habitats demonstrated physiological divergence. If drought survival strategies are primarily important in habitat specialization, the greatest divergence should occur between species in different habitats. However, if different drought survival strategies are important for reducing competitive interactions between closely related species when water is limited, then co-occurring species in dry habitats should demonstrate greater physiological divergence.

Materials and methods

Species selection

The six willow species (*Salix bebbiana* Sarg., *Salix candida* Flueggé ex Willd., *Salix discolor* Muhl., *Salix pedicellaris* Pursh, *Salix petiolaris* Sm. and *Salix pyrifolia* Andersson) in this study are native to North America and are common in the northern USA and Canada. Three of these species (*S. candida, S. pedicellaris* and *S. pyrifolia*) occur primarily in fens, bogs, marshes and wet meadows, while the remaining three species (*S. bebbiana, S. discolor* and *S. petiolaris*) occur in a larger variety of habitats that tend to be drier and more seasonally variable in water availability (Gleason and Cronquist 1991, Smith 2008). We refer to these species as wetland specialists and habitat generalists, respectively. These categorizations are consistent with wetland indicator status as determined by the United States Department of Agriculture (USDA), which categorizes species as obligate wetland (OBL) and facultative wetland (FACW) species. The one exception is *S. pyrifolia*, which is classified as a FACW but we have classified it as a wetland specialist based on its regional distribution. Species treatments and wetland indicator status were determined based on the USDA online database (http://plants.usda.gov). Seven other willow species occur locally in central Minnesota, but were not included in the present study.

Species' habitat affinities

To document differences in species distribution along a water availability gradient, we established 50 randomly located 10 m × 30 m plots at Cedar Creek Ecosystem Science Reserve LTER (45.41°N, −93.19°W), Helen Allison Savannah Scientific (45.38°N, −93.18°W) and Natural Area (SNA) and Boot Lake SNA (45.34°N, −93.12°W) in central Minnesota in the summer of 2007. Plot locations were determined using a random number generator and a coordinate grid; plots were established only when willows were present on the ground. Of 50 total plots, there were 43 plots that contained species in this study. We measured the approximate depth to the water table in a well in the center of each plot, monthly for a year. The wells were installed the previous summer and consisted of an unmodified 1–1.5 m long PVC pipe (3.8 cm diameter) placed in the ground. The holes for the wells were made using an auger with a diameter of 15 cm. Depth to the water table was measured using a tape measure. We also measured the height of water above the soil when sites were flooded and considered plots that were saturated or on floating sphagnum mats to have a water table depth of zero. We averaged the monthly depth to the water table in all plots where each species occurred to document species' habitat affinities.

Greenhouse conditions

All the plants used in this study were propagated from seeds collected from multiple populations at Cedar Creek LTER in the spring of 2004. Plants were grown in a greenhouse (44.98°N, –93.17°W) with an average daily temperature of 20 °C and kept well watered. Watering was adjusted seasonally based on plant water use (every 2 days in summer on sunny days and every 5 days in winter on cloudy days). Supplemental light was used to maintain a day length of 12 h in the autumn and winter to prevent dormancy. In hot summer days, the temperature within the greenhouse achieved a maximum of 27 °C. Plants were fertilized using Osmocote slow release fertilizer every 4 months. We grew the plants for 2 years before the drought treatment, at which point the plants were ~0.8–1 m tall. Two weeks prior to the treatment, we transplanted all the plants into 6.25 l treepots to guarantee that they were not root bound. For the drought treatment, plants were allowed to dry out and were not subsequently watered for 2.5 months (June–August 2006). Prior to the drought, plants were watered to field capacity. Some plants were set aside for destructive measurements and some were only used for non-destructive measurements. This experiment was conducted concurrently with another study on species' photoprotective responses to drought (Savage et al. 2009). In 2008, we conducted a follow-up experiment on nine individuals of *S. bebbiana* and *S. petiolaris* to gather further data on differences in these species' leaf specific conductivity. These measurements were made on plants propagated from seeds in spring 2007 and grown under similar conditions to the first set of plants.

Pre-drought hydraulics and growth

We estimated leaf (K_{leaf}) and leaf specific whole plant (K_{plant}) hydraulic conductance on six plants per species (except *S. pyrifolia*, $n = 5$) once before the beginning of the drought. First, we measured predawn water potential (Ψ_{PD}) on one leaf per plant using a Scholander pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). Second, we selected a pair of terminal, fully expanded leaves and covered one with parafilm and aluminum foil so that it could equilibrate with the stem (Brodribb and Holbrook 2003). In the afternoon following the predawn measurements, we measured gas exchange on the transpiring leaf (uncovered leaf) using a portable photosynthesis system (LICOR 6400-40, Licor, Inc., Lincoln, NE, USA) to determine transpiration (E) per unit leaf area. Specifications regarding these measurements are described below. We then immediately measured leaf water potential (Ψ_{leaf}) on both the transpiring and non-transpiring leaves to estimate leaf (Ψ_{leaf}) and stem water potential (Ψ_{stem}). All of these measurements were taken between noon and two. We calculated K_{leaf} and K_{plant} using the following equations: $K_{\text{leaf}} = E/(\Psi_{\text{leaf}} - \Psi_{\text{stem}})$ and $K_{\text{plant}} = E/(\Psi_{\text{leaf}} - \Psi_{\text{soil}})$. These calculations are based on an Ohm's Law analogy and assume steady-state transpiration (Nardini and Salleo 2000, Cavender-Bares et al. 2007). We also assumed that the plant canopy was in equilibrium with the soil and Ψ_{PD} was equal to soil water potential (Ψ_{soil}).

Before the drought, we harvested a total of eight plants per species to determine their root (RMF), stem (SMF) and leaf (LMF) mass fractions, and their average growth rate (GR) over the 2-year period. For these measurements, we cleaned the roots with a sieve and rinsed them in water to collect as much fine root material as possible. We separated leaf, stem and root material and dried the plants in an oven at 70 °C for 5 days. We also measured the total leaf area of each plant (reported in Savage et al. 2009) and calculated specific leaf area (SLA) based on four fully expanded leaves per individual. Leaves were scanned on a flatbed scanner, and leaf area was measured digitally using ImageJ.

The progression of the drought

During the dry-down, we monitored Ψ_{PD} on seven individuals per species. We also estimated soil moisture by weighing the pots and calculating the percent of water in the soil after factoring out dry plant weight, pot weight and soil dry weight (which were measured after completion of the experiment). We measured Ψ_{PD} and estimated soil moisture when the plants were at field capacity (pre-drought conditions) and then every 2–3 days from Day 6 to Day 30 (for a total of nine measurements). Our final measurements were on Day 36 and Day 57. For our analyses, we assumed that Ψ_{PD} did not decline after the plants dropped all their leaves. Since species dried down and lost leaves at different rates, the number of Ψ_{PD} and soil moisture measurements varied among species (*S. bebbiana* $n = 64$, *S. candida* $n = 71$, *S. discolor* $n = 54$, S. *pedicellaris* $n = 66$, *S. petiolaris* $n = 64$, *S. pyrifolia* $n = 72$).

Stomatal conductance and leaf water status

On the same set of plants, we measured leaf gas exchange on the same days as the Ψ_{PD} measurements both pre-drought and during the drought. The gas exchange measurements were taken on each plant's first, fully expanded, living leaf between 800 and 1100 hours, using ambient CO_2 levels (~380 μmol mol^{-1}) and maintaining an average VPD similar to ambient. Measurements were taken at a light intensity of 1200 μmol m^{-2} s^{-1} (known to saturate photosynthesis in willows (Robinson et al. 2004)). Variation in rates of leaf dieback during the drought resulted in unequal numbers of measurements for each species (*S. bebbiana* $n = 57$, *S. candida* $n = 63$, *S. discolor* $n = 48$, *S. pedicellaris* $n = 59$, *S. petiolaris* $n = 54$, *S. pyrifolia* $n = 63$).

Five times after measuring gas exchange, we measured the relative water content (RWC) of one fully expanded leaf on the same plants. Leaves were collected, placed in a plastic bag and put in a cooler. Four leaf discs per plant (total of 1.5 cm^2) were cut using a #4 cork borer. We avoided taking tissue samples that included the midvein whenever possible. The samples were weighed, put in tubes with 1 ml of ddH_2O and left for 4 h. Afterwards, the samples were blotted dry and their turgid weight recorded. The leaf discs were then dried (70 °C for a day) to determine their dry weight. Relative water content was calculated as (wet weight – dry weight)/(turgid weight – dry weight).

Stem hydraulics

We calculated stem hydraulic conductivity and percent loss in conductivity (PLC) on 8 plants per species under pre-drought conditions (-0.22 ± 0.1 (s.e.) MPa) and 8–10 plants per species under drought conditions. Each plant was only sampled once during the experiment and not used in any subsequent analyses because of the destructive nature of the measurements. We measured hydraulic conductance gravimetrically by running 10 mmol KCl solution (dissolved in degassed Millipore filtered water) through stem segments with a pressure head of <2 kPa. We measured the flow rate on an analytical balance (Sperry and Tyree 1988) and made cross-sections of the stem segments to measure their distal xylem area with a microscope. We calculated specific hydraulic conductivity based on the equation K_s = (stem length × hydraulic conductance)/ xylem area, and measured the area of all the leaves above the stem segment to calculate leaf specific conductivity, LSC = (stem length × hydraulic conductance)/leaf area. We also calculated the Huber value (HV) of each stem segment by dividing the xylem area by the total leaf area.

We measured hydraulic conductance on stem segments that were 22 cm long. The stem segments were cut under water with a razor blade, and the leaf scars were sealed with Loctite Super Glue 409 (Henkel, Düsseldorf, Germany) (Cavender-Bares and Holbrook 2001). The appropriate length was determined from a preliminary experiment where we incrementally cut shorter sections and monitored changes in specific conductivity (modified from Brodribb and Holbrook (2003)). We found that specific conductivity increased when willow stem segments were shorter than 20 cm, indicating that a significant number of end-walls had been removed (data not shown).

After measuring plants' native hydraulic conductivity, we recut the stems to 5 cm to determine PLC. We measured stem hydraulic conductance and flushed the stems with a syringe at a pressure of ~100 kPa for 2 min following the methods of Cavender-Bares et al. (2005). Based on a preliminary analysis, this amount of pressure and time proved sufficient to remove all the emboli in the stem segments (data not shown). After flushing the stems, we measured hydraulic conductance and calculated PLC. By measuring PLC during the dry-down, we were able to generate vulnerability curves for each species and calculate the water potential at which they experienced a 50% decline in stem conductivity (PLC_{50}). We fitted vulnerability curves using the equation: $PLC = 100/(1 + e^{a(\Psi - b)})$, where Ψ is water potential, a is a constant and b is the water potential for PLC_{50} (Pammenter and Vander Willigen 1998). We were unable to determine PLC in *S. candida* because of difficulties with measuring hydraulic conductance after flushing.

Leaf senescence and dieback

We monitored leaf dieback on a fourth set of plants consisting of 10 individuals per species. These plants were not destructively sampled at any point during the experiment. We marked 20 leaves, evenly spaced along the main stem and one side branch of each plant. On 10 days during the drought, we estimated the percent of each leaf that was living with no visible necrosis (0, 25, 50, 75 and 100%). We completed a regression analysis of leaf area on leaf length (data not shown, $P > 0.0001$) using four leaves from 15 individuals per species (Cavender-Bares et al. 2007) from leaves collected for pre-drought growth, pre-drought plant hydraulic and predawn water potential measurements (see above). We used these linear regressions to estimate the area of each monitored leaf. Since leaf areas are inflated in smaller leaves (immature willow leaves tend to be narrower than fully expanded leaves), we did a separate set of regression analyses for leaves smaller than 3 cm^2. We fitted a curve to the relationship between leaf area and Ψ_{PD} during the drought using the equation from Pammenter and Vander Willigen (1998) and estimated the Ψ_{PD} where each species experienced 50% dieback.

On the same plants used for monitoring leaf dieback, we measured relative leaf chlorophyll content using a Minolta SPAD-502 (Spectrum Technologies, Inc., Plainfield, IL, USA). We measured relative chlorophyll content on two fully expanded leaves per plant eight times during the dry-down and averaged the readings of four locations per leaf. We calibrated the SPAD meter by measuring leaf chlorophyll content in two leaves of four individuals per species from plants that were destructively sampled during the drought (see above). These leaves were frozen in liquid nitrogen immediately after collection. We used high-pressure liquid chromatography to determine leaf chlorophyll content on a leaf area basis (data not shown) (see Savage et al. 2009 for methods). SPAD readings were linearly related to leaf chlorophyll content as described by the following equation: total leaf chlorophyll = $-1.92 + 0.358 \times$ SPAD reading ($F = 12.38$, df = 47, $P < 0.0001$, $R^2 = 0.76$). There were no species or species × SPAD units effects ($\alpha = 0.01$) in the regression analysis.

Resprouting after the drought

We rewatered 18 individuals per species (except for *S. pyrifolia*, $n = 15$) after they had lost all of their leaves and monitored them for resprouting. Since they lost their leaves at different points during the drought, the timing of rewatering varied for each species. This allowed us to determine which species could resprout. However, since species lost leaves at different water potentials, these results do not relate to the ability of species to survive droughts of the same severity. For this analysis we only used plants that did not have branches removed during the experiment.

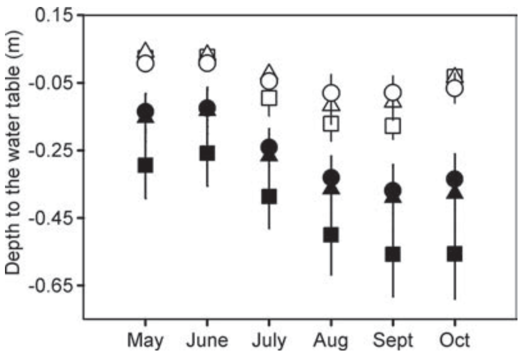

Figure 1. Habitat generalists (closed symbols) occur in drier and more seasonally variable plots than wetland specialists (open symbols). The figure shows the average depth to the water table (m) in all plots where each species occurs. Species are represented by the following symbols: filled square, *S. bebbiana*; filled triangle, *S. discolor*; filled circle, *S. petiolaris*; open square, *S. candida*; open triangle, *S. pedicellaris* and open circle, *S. pyrifolia*. Error bars are ±one standard error.

Statistics

We compared species' rates of stomatal closure by conducting a multiple regression analysis on the initial linear portion of the relationship between Ψ_{PD} and stomatal conductance (g_s), when Ψ_{PD} was greater than – 0.05 MPa. We considered stomatal closure to occur at 0.03 mol H_2O m^{-2} s^{-1} (90% reduction in g_s from pre-drought measurement). After stomatal closure, we compared species' minimal stomatal conductance (g_{min}) with an analysis of variance (ANOVA). We also completed a multiple regression analysis of photosynthetic capacity (A_{1200}) on g_s and estimated water-use efficiency (WUE) as the slope of the regression line.

We used an ANOVA and Tukey's honestly significant difference (HSD) comparisons to examine species' pre-drought traits (RMF, LMF, SMF, A_{1200}, g_s, SLA, GR, K_s, LSC, HV, K_{plant}, K_{leaf} and soil moisture). To compare species dry-down rates, we conducted a repeated-measures multivariate analysis of variance on species' pot soil moisture over time. We tested the significance of a species by time interaction with the Wilks' lambda statistic to see whether species exhibited different responses to soil moisture. Since many plants lost their leaves, we only conducted this analysis on data from the first 30 days of the drought when we still had a full set of plants. We also examined the relationship between the log of Ψ_{PD} and the log of soil moisture using a multiple regression analysis. We examined the effects of soil moisture, species and the interaction of soil moisture and species on Ψ_{PD} in this analysis. We conducted all the statistical analyses with the program JMP 7 (SAS Institute, Inc.) except the non-linear

Table 1. Functional differences between willow habitat generalists and wetland specialists.

	Habitat generalists			Wetland specialists		
Traits[1]	*S. bebbiana*	*S. discolor*	*S. petiolaris*	*S. candida*	*S. pedicellaris*	*S. pyrifolia*
RMF	0.62 ± 0.03	0.59 ± 0.02	0.56 ± 0.03	0.54 ± 0.03	0.51 ± 0.03	0.61 ± 0.05
SMF	0.22 ± 0.02	0.21 ± 0.01	0.26 ± 0.02	0.22 ± 0.02	0.19 ± 0.01	0.27 ± 0.05
LMF**	**0.16 ± 0.02^{a,b}**	**0.20 ± 0.02^{a}**	**0.18 ± 0.02^{a,b}**	**0.24 ± 0.02^{a}**	**0.30 ± 0.03^{a,b}**	**0.12 ± 0.02^{b}**
GR***	**1.40 ± 0.24^{a,b}**	**1.85 ± 0.18^{a}**	**1.09 ± 0.19^{b}**	**0.85 ± 0.10^{b}**	**0.84 ± 0.10^{b}**	**0.79 ± 0.06^{b}**
SLA***	**1.6 ± 0.25^{c}**	**2.4 ± 0.18^{a,b,c}**	**1.4 ± 0.34^{b,c}**	**2.2 ± 0.36^{a}**	**2.0 ± 0.28^{a,b}**	**1.5 ± 0.16^{c}**
A_{1200}**	**19 ± 1.93^{a,b}**	**19 ± 1.23^{a,b}**	**22 ± 0.55^{a}**	**16 ± 1.29^{b,c}**	**18 ± 0.94^{a,b,c}**	**13 ± 1.38^{c}**
g_s	0.32 ± 0.04	0.27 ± 0.02	0.32 ± 0.03	0.32 ± 0.02	0.31 ± 0.03	0.23 ± 0.03
g_{min}***	**0.02 ± 0.00^{a}**	**0.01 ± 0.00^{a}**	**0.02 ± 0.0^{a,b}**	**0.02 ± 0.01^{a,b}**	**0.04 ± 0.01^{b}**	**0.03 ± 0.01^{b}**
HV*	**5.73 ± 0.02^{a,b}**	**3.82 ± 0.05^{b}**	**4.53 ± 0.09^{a,b}**	**6.10 ± 0.10^{a,b}**	**8.48 ± 0.10^{a}**	**4.50 ± 0.10^{a,b}**
K_s**	**1.96 ± 0.40^{b}**	**3.56 ± 0.48^{a}**	**2.64 ± 0.37^{a,b}**	**2.19 ± 0.26^{a,b}**	**1.99 ± 0.20^{b}**	**2.84 ± 0.24^{a,b}**
LSC	0.26 ± 0.07	0.45 ± 0.09	0.33 ± 0.03	0.40 ± 0.9	0.53 ± 0.06	0.40 ± 0.09
K_{plant}	0.66 ± 0.08	0.89 ± 0.09	0.56 ± 0.11	0.79 ± 0.15	0.79 ± 0.14	0.68 ± 0.22
K_{leaf}*	**0.89 ± 0.11^{b}**	**1.60 ± 0.15^{a}**	**0.88 ± 0.11^{b}**	**1.20 ± 0.10^{a,b}**	**1.30 ± 0.07^{a,b}**	**1.4 ± 0.31^{a,b}**

[1] Traits are root, stem and leaf mass fraction (RMF, SMF and LMF, g g^{-1}), growth rate (GR, g $month^{-1}$), specific leaf area (SLA, 10^2 * cm^3 g^{-1}), photosynthetic capacity (A_{1200}, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}), minimum stomatal conductance (g_{min}, mol H_2O m^{-2} s^{-1}), Huber value (HV, ×10^{-4}), branch hydraulic conductivity (K_s, kg MPa^{-1} s^{-1} m^{-1}), leaf specific hydraulic conductivity (LSC, g MPa^{-1} s^{-1} m^{-1}), leaf and leaf specific whole plant conductance (K_{leaf} and K_{plant}, mmol MPa^{-1} s^{-1} m^{-2}). The averages are reported ±one standard error. All traits besides g_{min} were measured under pre-drought conditions. Bolded traits are significantly different among species at the following significance levels: *0.05, **0.01 and *** < 0.001. The results of the Tukey HSD multiple comparisons are indicated by superscript letters ($\alpha = 0.05$).

regression analyses which were completed in Sigmaplot 9.0 (Systat Software, Inc.).

Results

Species' habitat affinities

As predicted, the three wetland specialists (*S. candida, S. pedicellaris* and *S. pyrifolia*) occurred in plots that remained wet year round, and the three habitat generalists (*S. bebbiana, S. discolor* and *S. petiolaris*) occurred in drier plots that varied more seasonally in water availability (Figure 1). These plot differences are consistent with our classifications of habitat affinity.

Pre-drought physiology and growth

Some of the differences observed in pre-drought physiology were associated with species' habitat affinities (Table 1). For example, the habitat generalists (*S. bebbiana, S. discolor* and *S. petiolaris*) tended to have higher photosynthetic capacity (A_{1200}) and higher GRs than the wetland specialists (*S. candida, S. pedicellaris* and *S. pyrifolia*) (Table 1), although these differences were not significant for all species. There was also divergence in traits that did not correspond with habitat affinity including branch specific hydraulic conductivity (K_s), leaf conductance (K_{leaf}), HV, SLA and LMF (Table 1). There were no significant differences in species' RMF and SMF, species' pre-drought LSC, leaf specific whole plant conductance (K_{plant}) and stomatal conductance (g_s) (Table 1).

The progression of the drought

In the beginning of the experiment, soil in the pots was at field capacity, and there were no significant differences in average pot soil moisture between species (Figure 2a). However, during the dry-down, the habitat generalists (*S. bebbiana, S. discolor* and *S. petiolaris*) lost water more rapidly than the wetland specialists (*S. candida, S. pedicellaris* and *S. pyrifolia*, Figure 2a). A concurrent study found that this decline in soil moisture was related to total leaf area (Savage et al. 2009). Species also varied in their predawn water potentials (Ψ_{PD}) at any given soil moisture ($F = 5.66$, df = 5/384, $P < 0.0001$) based on the regression analysis of the log(Ψ_{PD}) and log(soil moisture) (Figure 2a). However, the species effect was small, with the most divergent species (*S. pedicellaris* and *S. discolor*) having intercepts (when soil moisture = 100%) that only differed by 0.04 MPa. Since this difference is below the resolution of the pressure chamber, it is difficult to determine whether it is notable. It is possible that this difference is the result of the method we used to estimate soil water content. In our estimation, we made the assumption that root water content was constant throughout the drought. This assumption could have led to more inaccuracy in the estimation of soil moisture in species with greater root biomass (including *S. discolor*).

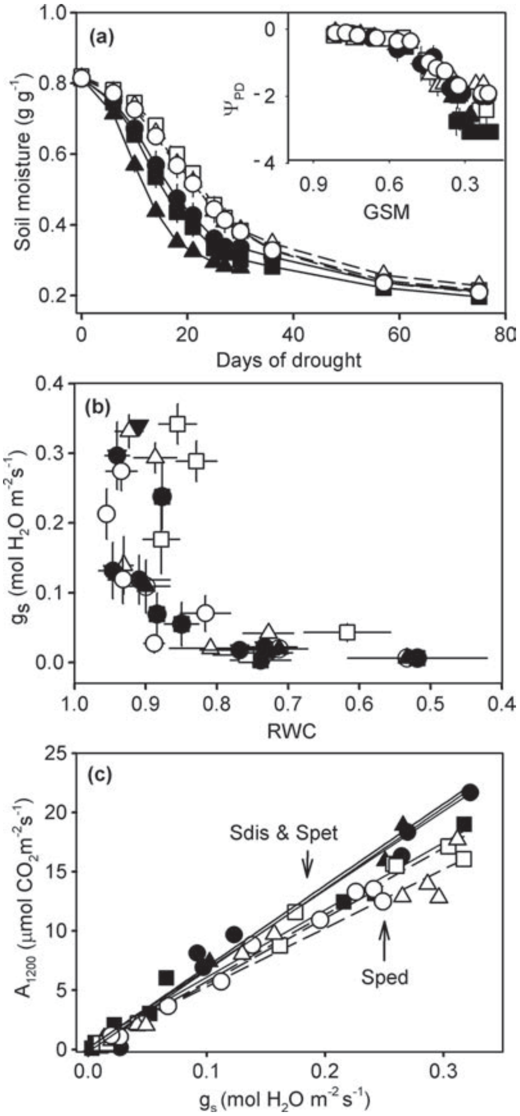

Figure 2. (a) Habitat generalists (closed symbols) demonstrated faster dry-down rates than wetland specialists (open circles). The inset shows the relationship between predawn water potential (Ψ_{PD}, MPa) and gravimetric soil moisture (GSM, g g^{-1}). (b) Stomatal conductance (g_s) declined with relative water content (RWC) similarly in all species. (c) Species differed in their ability to maintain photosynthetic capacity (A_{1200}) with declining stomatal conductance (g_s), indicating they differed in their WUE. Data points represent average values for species on each day of measurement. The symbols for each species are the same as in Figure 1, and the error bars are ±one standard error. *Salix discolor* (Sdis), *S. petiolaris* (Spet) and *S. pedicellaris* (Sped).

Stomatal conductance and leaf water status

There were consistent differences in species stomatal conductance (g_s) during the drought ($F = 4.52$, df = 5/218, $P = 0.001$) but these differences did not correspond to species' habitat affinities, and there was no significant species by Ψ_{PD} effect on g_s. There was also no association between habitat affinity and the timing of species' stomatal closure ($\Psi_{g=o}$, Table 2). All the

Table 2. Species level drought response traits.

	Habitat generalists			Wetland specialists		
Traits[1]	*S. bebbiana*	*S. discolor*	*S. petiolaris*	*S. candida*	*S. pedicellaris*	*S. pyrifolia*
$\Psi_{g=o}$	−0.66	−0.59	−0.66	−0.63	−0.71	−0.64
DB_{50}	−2.4 ± 0.2	−1.6 ± 0.1	−1.8 ± 0.1	−1.4 ± 0.1	−1.4 ± 0.1	−1.7 ± 0.1
PLC_{50}	−1.7 ± 0.1	−0.9 ± 0.1	−1.1 ± 0.1		−1.3 ± 0.1	−1.0 ± 0.1
WUE	56.6	69.5	66.5	55.8	49.2	55.3
Resprouting, %	38.9	61.6	61.6	44.4	77.8	66.7

[1] Traits reported are water potential (MPa) at stomatal closure ($\Psi_{g=o}$), 50% dieback (DB_{50}) and 50% loss in hydraulic conductivity (PLC_{50}), average water-use efficiency (WUE, µmol CO_2 mol H_2O^{-1}) and percent of plants that resprouted after the drought. Water-use efficiency was defined as the slope of the regression line of A_{1200} on g_s, and stomatal closure was estimated as the intercept of the regression line of g_s on Ψ_{PD}. DB_{50} and PLC_{50} were calculated based on fitted sigmoidal curves. Coefficients for DB_{50} and PLC_{50} are given ±one standard error.

species closed their stomata before their RWC dropped below 80% (Figure 2b). However, habitat generalists did demonstrate lower minimum stomatal conductance (g_{min}, Table 1) and greater WUE (as defined by A_{1200}/g_s, Figure 2c and Table 2) than the wetland specialists.

Leaf senescence and dieback

All six species experienced drought-induced leaf senescence during the dry-down (Figure 3). This dieback occurred sequentially with the oldest leaves exhibiting chlorosis and necrosis before the younger leaves. There was significant variation in the rate of dieback among species with similar habitat affinity (Figure 3c and d). *Salix discolor* and *S. petiolaris*, two habitat generalists, demonstrated the fastest and slowest rates of chlorophyll loss, respectively (Figure 3a). These rates were consistent with their overall divergence in leaf dieback rate (Figure 3c and Table 2).

Stem hydraulics

Differences in species' vulnerability to cavitation did not appear to relate to their habitat affinity, and the species with the highest and one of the species with the lowest vulnerability to cavitation were both habitat generalists (Figure 4a and b and Table 2). As the drought progressed, three species maintained a constant LSC (*S. bebbiana, S. candida* and *S. pedicellaris*) and three species demonstrated an increase in LSC (*S. discolor, S. petiolaris* and *S. pyrifolia*, Figure 5). PLC_{50} correlated with branch K_s across all species (Figure 4c).

Resprouting after the drought

The six willow species differed in their ability to resprout after leaf shedding. *Salix bebbiana* had the lowest resprouting ability (38.9%) compared with the other habitat generalists (*S. discolor* (61.6%) and *S. petiolaris* (61.6%)). The wetland specialists (*S. candida, S. pedicellaris* and *S. pyrifolia*) had resprouting percentages of 44.4, 77.8 and 66.7%, respectively (Table 2).

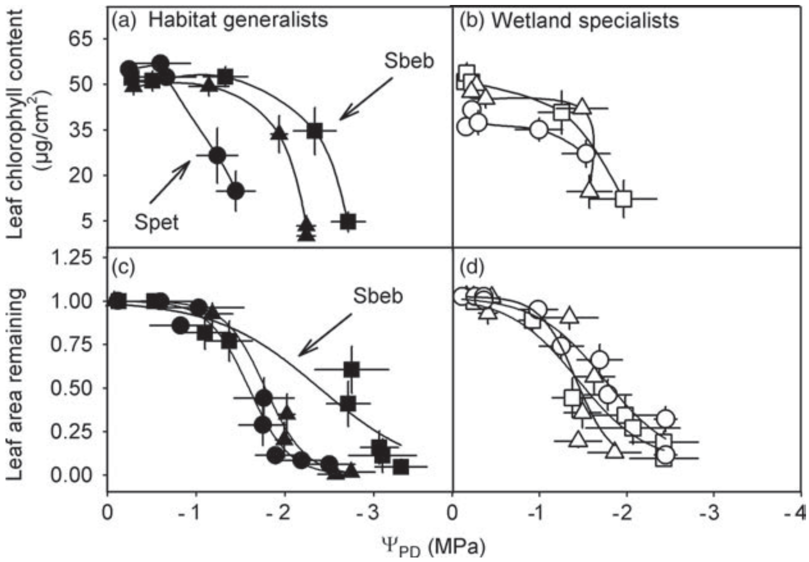

Figure 3. Habitat generalists (closed symbols) varied more in their rate of leaf chlorophyll loss (a, c) and leaf dieback (b, d) during the drought than wetland specialists (open symbols). Error bars are ±one standard error and the symbols for each species are the same as in Figure 1. Species abbreviations are given for *S. bebbiana* (Sbeb) and *S. petiolaris* (Spet)

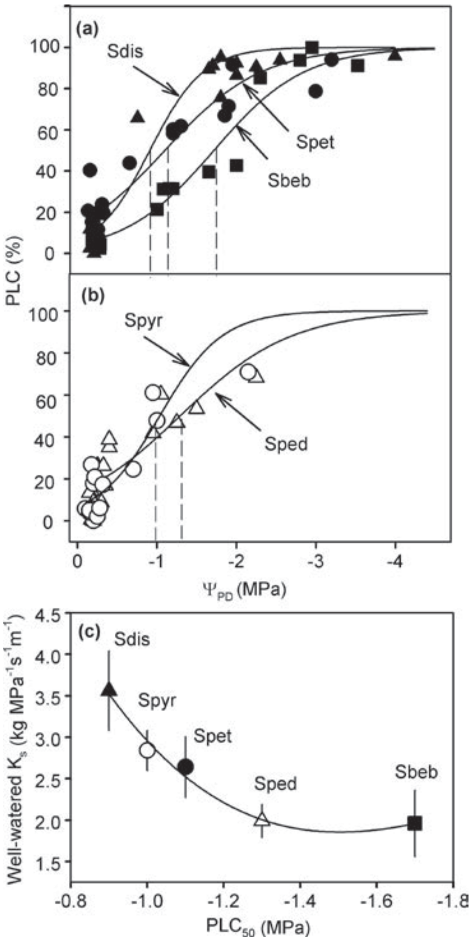

Figure 4. (a) Habitat generalists (closed symbols) and (b) wetland specialists (open symbols) varied in their vulnerability to cavitation. The most (*S. discolor*, Sdis) and the least (*S. bebbiana*, Sbeb) vulnerable species were both habitat generalists. Each point represents a different individual. (c) There was evidence for a trade-off between safety and efficiency in terms of species' vulnerability to cavitation (described by PLC_{50}) and their branch hydraulic conductivity (K_s). The symbols for each species are the same as in Figure 1, and error bars are ±one standard error.

Discussion

In this study, we investigated the extent that traits related to species' drought survival differed between species with similar and divergent habitat affinity in ways that could be influential in maintaining both β-diversity across the landscape and α-diversity within habitats. While there is evidence for some physiological divergence between species with different habitat affinity, hydraulic traits such as cavitation resistance varied more among co-occurring species than species from different habitats (Table 3). This divergence may provide an important mechanism for partitioning water use and allowing species to co-occur in seasonally dry habitats.

The wetland specialists in this study tended to have lower rates of photosynthesis (A_{1200}) and slower GRs than the habitat generalists (Table 1). While slow GRs are not necessarily adaptive, they can arise from adaptive differences in species' resource allocation (Lambers and Poorter 1992). For example, plants from nutrient-limited habitats often invest more in defense and less in growth than species from more nutrient-rich habitats (Chapin 1980, Reich 1993). Since wetland habitats are not only nutrient limited, but also frequently waterlogged, it is possible that species that survive in these habitats depend on functional traits that reduce growth. The habitat generalists and wetland specialists also differed in their response to drought conditions (Table 3). For example, the habitat generalists had higher WUE (Table 2), and two of the habitat generalists exhibited lower minimum stomatal conductance than the other species (Table 2).

Consistent with other research on willows and their closest relatives, the cottonwoods, the species in this study were highly vulnerable to cavitation (Figure 4a and b) and experienced precocious leaf shedding when exposed to a short-term drought (Figure 3) (Tyree et al. 1994, Rood et al. 2000, Amlin and Rood 2002). This is not surprising, considering that there

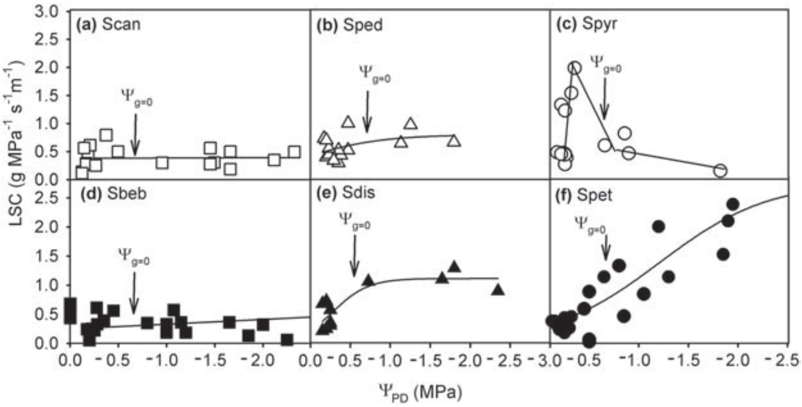

Figure 5. Two of the habitat generalists (*S. discolor*, Sdis, and *S. petiolaris*, Spet) exhibited consistent increases in their leaf specific conductivity (LSC) during the drought. This response was different than the other four species, which demonstrated either a small spike (*S. pyrifolia*, Spyr) or a constant LSC (*S. candida*, Scan, *S. pedicellaris*, Sped). On each graph, estimates of the water potential at stomatal closure are labeled for each species. The symbols for each species are the same as in Figure 1.

Table 3. Traits that are similar or divergent among species with the same habitat affinity.

Similar traits within habitats[1]	Divergent traits within habitats
GR	K_s
A_{1200}	K_{leaf}
WUE	$\Psi_{g=o}$
	DB_{50}
	PLC_{50}

[1] Traits are defined in Tables 1 and 2.

is evidence that closely related species share similar hydraulic architecture and cavitation resistance (Choat et al. 2007, Hao et al. 2008, Willson et al. 2008). While leaf shedding typically coincides with hydraulic failure in the leaf or petiole (Nardini et al. 2001, Cochard et al. 2002, Hukin et al. 2005), it can be beneficial under drought conditions when it leads to vascular segmentation (Zimmerman 1983, Rood et al. 2000, Munné-Bosch and Alegre 2004). One line of evidence for segmentation is an increase in LSC under drought conditions, indicating that leaf drop occurs at a faster rate than stem cavitation. If there is no barrier to the spread of emboli or if stem and leaf xylem have a similar vulnerability to cavitation, then LSC would remain constant under drought conditions. While both of these patterns have been observed in droughted plants (Shumway et al. 1991, Vilagrosa et al. 2003, Ladjal et al. 2005), their prevalence among drought deciduous species, including willows, is largely unknown.

In this study, we found that some species demonstrated an increase in LSC (*S. discolor, S. petiolaris* and *S. pyrifolia*) while some maintained a constant LSC (*S. bebbiana, S. candida* and *S. pedicellaris*) during the drought (Figure 5). This distinction appears to correspond to differences in species' cavitation resistance and may be indicative of different drought survival strategies. The three species with the lowest cavitation resistance demonstrated the greatest increase in LSC during the drought (Table 2 and Figure 5). We hypothesize that this relationship is driven by a trade-off between xylem safety (as defined by PLC_{50}) and efficiency (as defined by K_s, Figure 4c). Therefore, species with a high vulnerability to cavitation prevent extensive hydraulic failure by dropping their leaves early in the drought but can quickly compensate for this loss with rapid resprouting facilitated by their higher hydraulic efficiency. Meanwhile, species with a low vulnerability to cavitation are more drought tolerant and hold onto their leaves later into the drought but ultimately experience hydraulic failure.

The greatest functional divergence in drought survival strategy occurred between two habitat generalists (*S. discolor* and *S. bebbiana*, Tables 2 and 3). *Salix discolor* was a true drought avoider. It closed its stomata rapidly (Table 2) and quickly dropped its leaves (Figure 3c), thus preventing extensive cavitation, as indicated by an increase in LSC (Figure 5e). As a result, this species, which was the least resistant to cavitation, prevented excessively negative water potentials in its xylem and maintained a high resprouting ability (Table 2). Meanwhile, *S. bebbiana* was more of a drought tolerator. It had the lowest vulnerability to cavitation (Figure 4a), maintained a greater margin between stomatal closure and cavitation induction (Table 2) and kept its leaves later into the drought than any other species (Figure 3c). When it finally dropped its leaves, stem cavitation occurred simultaneously (Figure 5d), and it had the lowest resprouting ability of the habitat generalists (Table 2). *Salix petiolaris*, the third habitat generalist, demonstrated an intermediate response. This species had the most dramatic increase in LSC (Figure 5f) and resprouted readily, but it did not close its stomata or drop its leaves as rapidly as *S. discolor* during the dry-down (Table 2).

While these different strategies appear viable in the same habitat, they could result in differential water use under drought conditions. Drought tolerators require water throughout the drought to maintain their leaves and do not require water for resprouting if the drought is short. Meanwhile, drought avoiders drop their leaves rapidly and only require water for resprouting. We hypothesize that this divergence in the temporal use of water could play an important role in promoting species co-occurrence in habitats where water is seasonally limited. From this perspective, it is also possible to explain why the wetland specialists demonstrated limited functional variability and had more similar rates of dieback and vulnerability to cavitation (Figures 3b, d and 4b). These species occur in habitats that are rarely limited in water availability and should have limited selective pressure to diverge in their water use under drought conditions. The one wetland specialist that did increase its LSC during the drought only did it for a short period of time, and could not prevent extensive stem cavitation after stomatal closure (Figure 5c).

Conclusions

We found evidence for differentiation in water-use strategies among willow species that could be important to their habitat differentiation (β-diversity), as well as their co-occurrence within habitats (α-diversity). While many studies have documented divergence in drought survival strategy among co-occurring species (Pockman and Sperry 2000, Martinez-Vilalta et al. 2002, 2003), significant divergence has not been observed among many closely related species (but see Ladjal et al. 2005, Choat et al. 2007). However, further research is needed to better understand whether this divergence could minimize competition for water in seasonally limited habitats and to examine whether species' drought survival strategies change when plants are grown in mixed species communities. It is also possible that some of the observed species variation could contribute to differences in species microhabitat preference, but further research is needed to investigate whether there could be a more continuous gradient in species drought responses that corresponds to their habitat affinity.

Acknowledgments

We would like to thank Rebecca Montgomery, Peter Reich, Ruth Shaw, George Weiblen, Stewart Rood, Rick Meinzer, Dustin Haines and an anonymous reviewer. for their feedback on the manuscript. Thank you to Barbara Delaney and John Haarstad for help locating willow populations. All seeds were collected with permission from Cedar Creek Ecosystem Science Reserve LTER. We would also like to acknowledge the Minnesota Department of Natural Resources for permission to do field work at several Scientific and Natural Areas.

Funding

Research was funded by the University of Minnesota, Department of Plant Biology, the Bell Museum (Dayton-Wilkie Natural History Funds) and the National Science Foundation LTER grant to Cedar Creek Ecosystem Science Reserve (DEB: 0620652, JCB).

References

Amlin, N.M. and S.B. Rood. 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. Wetlands 22:338–346.

Brodribb, T.J. and N.M. Holbrook. 2003. Changes in leaf hydraulic conductance during leaf shedding in seasonally dry tropical forest. New Phytol. 158:295–303.

Cavender-Bares, J. and N.M. Holbrook. 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with, contrasting habitats. Plant, Cell Environ. 24:1243–1256.

Cavender-Bares, J., K. Kitajima and F.A. Bazzaz. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecol. Monogr. 74:635–662.

Cavender-Bares, J., P. Cortes, S. Rambal, R. Joffre, B. Miles and A. Rocheteau. 2005. Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: a comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. New Phytol. 168:597–612.

Cavender-Bares, J., L. Sack and J. Savage. 2007. Atmospheric and soil drought reduce nocturnal conductance in live oaks. Tree Physiol. 27:611–620.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11:233–260.

Choat, B., L. Sack and N.M. Holbrook. 2007. Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. New Phytol. 175:686–698.

Cochard, H., L. Coll, X. Le Roux and T. Ameglio. 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. Plant Physiol. 128:282–290.

Cochard, H., E. Casella and M. Mencuccini. 2007. Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. Tree Physiol. 27:1761–1767.

Darwin, C. 1859. The origin of species by means of natural selection. Murray, London.

Dawson, T.E. 1990. Spatial and physiological overlap of 3 cooccurring alpine willows. Funct. Ecol. 4:13–25.

Elton, C. 1946. Competition and the structure of ecological communities. J. Anim. Ecol. 15:54–68.

Fine, P.V.A., D.C. Daly, G.V. Munoz, I. Mesones and K.M. Cameron. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. Evolution 59:1464–1478.

Gleason, H.A. and A. Cronquist. 1991. Manual of vascular plants of Northeastern United States and Adjacent Canada, 2nd edn. New York Botanical Gardens, New York.

Hacke, U.G. and J.S. Sperry. 2001. Functional and ecological xylem anatomy. Perspect. Plant Ecol. Evol. Syst. 4:97–115.

Hacke, U.G., J.S. Sperry and J. Pittermann. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. Basic Appl. Ecol. 1:31–41.

Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. Davis and K.A. McCulloch. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126:457–461.

Hacke, U.G., J.S. Sperry, J.K. Wheeler and L. Castro. 2006. Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol. 26:689–701.

Hao, G.Y., W.A. Hoffmann, F.G. Scholz, S.J. Bucci, F.C. Meinzer, A.C. Franco, K.F. Cao and G. Goldstein. 2008. Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. Oecologia 155:405–415.

Hukin, D., H. Cochard, E. Dreyer, D.L. Thiec and M.B. Bogeat-Triboulot. 2005. Cavitation vulnerability in roots and shoots: does *Populus euphratica* Oliv., a poplar from arid areas of Central Asia, differ from other poplar species? J. Exp. Bot. 56:2003–2010.

Karrenberg, S., P.J. Edwards and J. Kollmann. 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biol. 47:733–748.

Ladjal, M., R. Huc and M. Ducrey. 2005. Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. Tree Physiol. 25:1109–1117.

Lambers, H. and H. Poorter. 1992. Inherent variation in growth-rate between higher-plants—a search for physiological causes and ecological consequences. Adv. Ecol. Res. 23:187–261.

Losos, J.B., M. Leal, R.E. Glor, K. de Queiroz, P.E. Hertz, L.R. Schettino, A.C. Lara, T.R. Jackman and A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. Nature 424:542–545.

Maherali, H., W.T. Pockman and R.B. Jackson. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85:2184–2199.

Martinez-Vilalta, J., E. Prat, I. Oliveras and J. Pinol. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133:19–29.

Martinez-Vilalta, J., M. Mangiron, R. Ogaya, M. Sauret, L. Serrano, J. Penuelas and J. Pinol. 2003. Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. Tree Physiol. 23:747–758.

Munné-Bosch, S. and L. Alegre. 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. Funct. Plant Biol. 31:203–216.

Nardini, A. and S. Salleo. 2000. Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees-Struct. Funct. 15:14–24.

Nardini, A., M.T. Tyree and S. Salleo. 2001. Xylem cavitation in the leaf of *Prunus laurocerasus* and its impact on leaf hydraulics. Plant Physiol. 125:1700–1709.

Pammenter, N.W. and C. Vander Willigen. 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. Tree Physiol. 18:589–593.

Pockman, W.T. and J.S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. Am. J. Bot. 87:1287–1299.

Reich, P. 1993. Reconciling apparent discrepancies among studies relating life span, structure and function of leaves in contrasting plant life forms and climates: 'the blind men and the elephant retold'. Funct. Ecol. 7:721–725.

Rice, K.J., S.L. Matzner, W. Byer and J.R. Brown. 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. Oecologia 139:190–198.

Robinson, K.M., A. Karp and G. Taylor. 2004. Defining leaf traits linked to yield in short-rotation coppice *Salix*. Biomass Bioenergy 26:417–431.

Rood, S.B., S. Patino, K. Coombs and M.T. Tyree. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees-Struct. Funct. 14:248–257.

Rood, S.B., J.H. Braatne and F.M.R. Hughes. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiol. 23:1113–1124.

Savage, J.A., J. Cavender-Bares and A. Verhoeven. 2009. Willow species (genus: *Salix*) with contrasting habitat affinities differ in their photoprotective responses to water stress. Funct. Plant Biol. 36:300–309.

Shumway, D.L., K.C. Steiner and M.D. Abrams. 1991. Effects of drought stress on hydraulic architecture of seedlings from 5 populations of Green Ash. Can. J. Bot. 69:2158–2164.

Silvertown, J., M.E. Dodd, D.J.G. Gowing and J.O. Mountford. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Smith, W. 2008. Trees and shrubs of Minnesota. University of Minnesota Press, Minneapolis, 640 p.

Sperry, J.S. and M.T. Tyree. 1988. Mechanism of water stress-induced xylem embolism. Plant Physiol. 88:581–587.

Splunder, I.V., L.A. Voesenek, H. Coops, X.J. De Vries and C.W. Blom. 1996. Morphological responses of seedlings of four species of Salicaceae to drought. Can. J. Bot. 74:1988–1995.

Tilman, D. 1982. Resource competition and community structure. Monographs in population biology. Princeton University Press, Princeton.

Tyree, M.T. and F.W. Ewers. 1991. Tansley Review No. 34. The hydraulic architecture of trees and other woody plants. New Phytol. 119:345–360.

Tyree, M.T., H. Cochard, P. Cruiziat, B. Sinclair and T. Ameglio. 1993. Drought-induced leaf shedding in walnut—evidence for vulnerability segmentation. Plant, Cell Environ. 16:879–882.

Tyree, M.T., K.J. Kolb, S.B. Rood and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta—a possible factor in the decline of the ecosystem. Tree Physiol. 14:455–466.

Vilagrosa, A., J. Bellot, V.R. Vallejo and E. Gil-Pelegrin. 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.

Wheeler, J.K., J.S. Sperry, U.G. Hacke and N. Hoang. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. Plant, Cell Environ. 28:800–812.

Willson, C.J., P.S. Manos and R.B. Jackson. 2008. Hydraulic traits are influenced by phylogenetic history in the drought-resistant, invasive genus Juniperus (Cupressaceae). Am. J. Bot. 95:299–314.

Woods, S.W. and D.J. Cooper. 2005. Hydrologic factors affecting initial willow seedling establishment along a subalpine stream, Colorado, USA. Arctic Antarctic Alpine Res. 37:636–643.

Zimmerman, M.H. 1983. Xylem structure and the ascent of sap. Springer, Berlin, 143 p.