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Do invasive trees have a hydraulic advantage over native trees?

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Abstract

The hypothesis was tested that invasive trees have hydraulic traits that contribute to their invasive nature. Five pairs of co-occurring invasive and native trees, in mesic habitats, were selected: (1) *Tamarix ramosissima* and *Salix amygdaloides*; (2) *Robinia pseudoacacia* and *Alnus rhombifolia* (3) *Schinus terebinthifolius* and *Myrica cerifera*; (4) *Ligustrum sinense* and *Acer negundo*; and (5) *Sapium sebiferum* and *Diospyros virginiana*, respectively. Resistance to cavitation (the water potential [Ψ_x] at 75% loss of hydraulic conductivity [Ψ_{75}]) was not consistently greater for invasive compared to native species ($\Psi_{75} = -1.91$ and -1.67 MPa, respectively). Xylem specific conductivity (K_s), a measure of xylem efficiency, was not different between native and invasive species ($K_s = 3.50$ and 3.70 kg s^{-1} MPa^{-1} m^{-1}, respectively). The lack of difference for resistance to cavitation among invasive and native species suggests that the sampled invaders are not more tolerant to water stress than co-occurring native species. Apparently the spread and invasive nature of the sampled species cannot be explained by hydraulic traits alone.

Introduction

Invasive species are those that establish beyond their native range, subsequently spread, and cause harm in their new ecosystems (Mack et al. 2000). Humans have transported organisms beyond their native ranges and in this new territory most organisms perish, few become naturalized, and fewer still become invasive (Williamson and Fitter 1996). Why species invade is of great interest to ecologists and policy makers to assist in the control of currently invasive species and to aid prediction of future invaders (Mack 1996; Rejmànek and Richardson 1996).

Hypotheses concerning biotic invasions can be separated into two broad categories: (1) those focused on the community being invaded, and (2) those focused on the invading species. Hypotheses focused on attributes of communities include Elton's (1958) suggestion that communities more rich in species are more resistant to invasion. Another hypothesis predicts that in their new ranges invaders do not face as many specialist competitors, herbivores, or parasites compared to their native ranges and this release from enemies facilitates their spread (Elton 1958). Natural and human caused disturbance in communities may aid establishment for would be invaders adapted to disturbance (Davis et al. 2000). In general, alien invasions occur more frequently in certain communities and a research goal is to identify the factors making communities more or less susceptible to invasion.

Hypotheses focusing on invading species consider how attributes or functional traits of species contribute to their invasive nature (Rejmànek and Richardson 1996; Goodwin et al. 1998; Mack 2003; Callaway and Ridenour 2004; Rejànek et al. 2005). As most species perish upon introduction to a new range, it is against great odds that some species have invaded widely separated continents suggesting that they have a knack for invading (Mack et al. 2000). Knowing traits common among invading species enhances our ability to predict future invaders and better manage ongoing invasions (Daehler 2003).

One important trait for tolerating a broad range of environmental gradients related to the availability of water among woody plants is cavitation resistance. Cavitation resistance is a functional trait representing how tolerant a woody plant is to water stress (Davis et al. 2002). Cavitation is the entry of gas into water-filled xylem cells resulting in their becoming embolized and unable to transport water (Jarbeau et al. 1995). This process occurs during water stress as xylem water potentials (Ψ_x) become increasingly negative or when the xylem sap freezes and thaws (Pratt et al. 2005). Woody plants adapted to mesic environments exhibit a narrower range and lower resistance to cavitation than plants adapted to more arid upland habitats. This pattern is general and can be found across microsites within a habitat (Pockman and Sperry 2000) and across biomes (Maherali et al. 2004). Woody species with moderate to high resistances to cavitation would be more likely to invade a broader range of microsites compared to plants with lower resistance to cavitation (Baker 1974; Pockman and Sperry 2000).

In this study we compare resistance to cavitation of five invasive tree species to co-occurring native tree species in North America. The five species selected are aggressive invaders in North America and also have invaded numerous other continents and islands suggesting a knack for invading (Table 1). In addition to cavitation resistance, we assess tradeoffs among cavitation resistance, hydraulic efficiency, and xylem density. This is important because developing high resistance to cavitation may come at a cost of decreased hydraulic efficiency and increased xylem density (Hacke and Sperry 2001). We hypothesize that greater cavitation resistance may partially explain the reason for invasion by some alien species.

Materials and methods

Plant species and study sites

Five invasive and native species pairs were selected from five sites in the northwestern and southeastern United States (see Table 1). Sites in Washington, Idaho, and Georgia were located adjacent to rivers. The site in Florida was located adjacent to a canal and a fifth site, in South Carolina, was located in a seasonal swamp. All 10 species selected for study were from different families to increase the degree of independence of data points in regression analyses aimed at evaluating tradeoffs among hydraulic traits (Ackerly 2000; Table 1). In addition, the five invasive species were selected because they represent some of the globe's most widespread and invasive tree species. The native species were chosen to represent species commonly occurring with each

Table 1. North American location of study site, species names, family, habitat, and growth habit shown for sampled tree species.

City, State of Study Site	Species	Invasive or Native	Family	Growth Habit
Weiser, Idaho	*Salix amygdaloides*	Native	Salicaceae	Deciduous
	Tamarix ramosissima	Invasive	Tamaricaceae	Deciduous
Dayton, Washington	*Alnus rhombifolia*	Native	Betulaceae	Deciduous
	Robinia pseudoacacia	Invasive	Fabaceae	Deciduous
Lakeport, Florida	*Myrica cerifera*	Native	Myricaceae	Evergreen
	Schinus terebinthifolius	Invasive	Anacardiaceae	Evergreen
Athens, Georgia	*Acer negundo*	Native	Aceraceae	Deciduous
	Ligustrum sinense	Invasive	Oleaceae	Deciduous
Georgetown, South Carolina	*Diospyros virginiana*	Native	Ebenaceae	Deciduous
	Sapium sebiferunm	Invasive	Euphorbiaceae	Deciduous

invader from our sampled list. Within a site, natives and invasives were selected that were of comparable size classes, and that were found within 1–5 m from one another.

Hydraulic conductivity and vulnerability to xylem cavitation

Hydraulic conductivity (K_h; kg m MPa^{-1} s^{-1}) was measured by pushing de-gassed acid solution through stems at low pressure (~5 kPa; Sperry et al. 1988). The solution used was of low pH (pH 2 HCl) and ultra-filtered (0.1 μm pore filter) to prevent clogging of stems (Sperry et al. 1988). Stems were mounted on a tubing apparatus connected to a low-pressure head at the basal end and an analytical balance at the distal end. The solution passing through the stem was collected on the balance connected to a laptop computer to log flux of the solution. The pressure head, stem length, and flux through the stem were used to calculate K_h after fluxes were corrected by measuring and subtracting the background flow in the tubing before and after stem flux was measured (Stiller and Sperry 2001).

Vulnerability to cavitation was estimated as the loss of K_h for lateral stems over a range of water potentials (Ψ_x). Stems were removed from trees at field sites, bagged, placed on ice, and refrigerated until sampled in the laboratory in ≤7 days. In the field, stems, approximately 35 cm long were cut. Stems were recut under water to 27 cm in the laboratory. Following trimming, stems were mounted on the tubing apparatus to measure K_h and then repeatedly flushed at about 80 kPa with acid solution until K_h did not increase between flushes. The post-flushing K_h represented maximum K_h (K_{max}), i.e. K_h with no emboli in the xylem. Stems were subjected to predetermined water potentials using the centrifuge technique (for nine species; Alder et al. 1997) and by pressurizing stems (*T. ramosissima* only) with N_2 gas (Salleo et al. 1992). We pressurized *T. ramosissima* to collect comparable data to Pockman and Sperry (2000). For the centrifuge technique, three stems were mounted onto a custom centrifuge rotor and spun to generate tensions within the stems (technique reviewed in Alder et al. 1997). For the pressure technique, stems were mounted into a metal collar and pressurized to force air into the xylem (technique reviewed in Salleo et al. 1992). Hydraulic conductivity was measured after each centrifuge or pressure treatment and percentage loss of hydraulic conductivity (PLC) was calculated as 100× $(1 - K_h/K_{max})$ for each sampled stem.

The Ψ_x at 75% loss in hydraulic conductivity (Ψ_{75}) was used as an estimate of cavitation resistance for comparisons among the 10 species. This value was chosen over the more commonly used Ψ_x at 50% loss of hydraulic conductivity because Ψ_{75} provides a better measure of cavitation resistance for plants displaying cavitation fatigue (Hacke and Sperry 2001; Hacke et al. 2001b). An additional correction for cavitation fatigue was done by calculating PLC using the K_h measured following the initial centrifuge spin at ≥−0.26 MPa in place of K_{max}. Resistance to cavitation calculated this way is more accurate because xylem that cavitates at $\Psi_x \geq -0.26$ MPa is unlikely to be functional *in situ*.

Xylem area of stems was measured to calculate xylem specific conductivity (K_s). The active xylem area was stained by siphoning a filtered (0.1 μm pore exclusion) solution of red food colorant (80% vol vol^{-1}; Schilling, Hunt Valley, MD) through stems for 30 min at low tensions (about -5 ± 2 kPa; Hargrave et al. 1994). After staining, stems were thin-sectioned, mounted in glycerol, digitally photographed, and xylem area was measured with Scion Image (Scion Corporation, Frederick, MD).

Water potentials

Water potential was estimated with a pressure chamber (PMS, Corvalis, OR). Measurements were made at predawn, 10:00 h, 13:00 h, and 16:00 h in the spring (May and June) and summer (August and September), 2001. Leaves were bagged on the plant for at least 2 h prior to excision to allow equilibration with the stems. Water potential measured with a pressure chamber assumes the osmotic potential of the xylem sap to be zero; however, we did not verify this assumption so, by convention, we use the term water potential, but more accurately this value is the xylem pressure potential.

Xylem density and percentage saturated water content

Xylem density was measured on stems used for hydraulic conductivity and vulnerability to cavitation measurements. Segments, 2.5 cm, long were soaked in water under vacuum until gas bubbles no longer appeared (about 24 h). Bark and pith were removed from segments and the density measured by water displacement. Samples were dried in an oven for at least 48 h and dry weight of the xylem was measured for calculation of densities. Percentage saturated water content was also calculated as an estimate of potential stem capacitance as follows: 100× (mass of water displaced – the dry mass)/dry mass (Borchert 1994).

Data analysis

Data were analyzed as a two factor nested design. We compared differences among sites (factor 1) and species (factor 2) nested within the five sites. For the Ψ_x data, the design was analyzed as a two factor nested design with repeated measures. Data were analyzed using an ANOVA followed by a Tukey's post-hoc analysis and a Fisher's LSD post-hoc analysis for the Ψ_x data (SAS, Cary, NC). Pooled analyses comparing native to invasive species were done as contrasts. Data were transformed as necessary to satisfy assumptions of statistical models.

Results

No consistent trend in cavitation resistance was found between invasive and native species, although, resistance to cavitation was different between three of the co-occurring species pairs. The invasive species S. *sebiferum* was more resistant to cavitation than the co-occurring native *D. virginiana* (Figure 1e; Table 2). In contrast, resistance to cavitation for the native species *S. amygdaloides* and *A. rhombifolia* were greater than the co-occurring invasive species *T. ramosissima* and *R. pseudoacacia* (Figure 1a and b; Table 2). *S. terebinthifolius* and *L. sinense*, both invasive species, were not different in resistance to cavitation compared to the co-occurring native species *M. cerifera* and *A. negundo* (Figure 1c and d; Table 2). A comparison of pooled averages found no difference in resistance to cavitation between invasive and native species (Table 2).

Xylem specific conductivity was not different between any of the species pairs or in a pooled analysis of K_s comparing all native to invasive species (Table 3). Xylem density was greater for the invasive species, *T. ramosissima, R. pseudoacacia*, and *L. sinense*, compared to the co-occurring native species, *S. amygdaloides, A. rhombifolia*, and *A. negundo*, respectively (Table 3). In one case, the native species *M cerifera* had greater xylem density than its co-occurring invasive counterpart, *S. terebinthifolius* (Table 3). In the final pair, the native tree *D. virginiana* and the co-occurring invasive *S. sebiferum* had xylem densities that were not different (Table 3). A pooled average comparing the xylem density of invasive to native species indicated that xylem density was greater for the invasive species (Table 3).

During May and June, the invasive species generally exhibited lower water potential (Ψ_x) compared to the native species for three of five comparisons. Water potential for *T. ramosissima* was lower compared to *S. amygdaloides* at predawn, 10:00, and 13:00 h (Figure 2a), and Ψ_x for *L. sinense* was lower compared to *A. negundo* at predawn, 10:00, and 13:00 h (Figure 2g). Water potential for *M. cerifera* was lower compared to *S. terebinthifolius* at 10:00 h, and for *S. terebinthifolius* was lower compared to *M. cerifera* at 16:00 h (Figure 2e). Water potential was not different between both the invasive and native species pairs of *R. pseudoacacia* and *A. rhombifolia*, and of *S. sebiferum* and *D. virginiana* (Figure 2c and i, respectively).

During the months of August and September, Ψ_x for invasive species compared to native species was lower for four of the five species pairs. Water potential for *T. ramosissima* was lower than that of *S. amygdaloides* at midday (Figure 2b), and for *R. pseudoacacia* was lower compared to *A. rhombifolia* at 13:00 and 16:00 h (Figure 2d). Water potential for *S. terebinthifolius* was lower compared to *M. cerifera* at predawn 13:00 and 16:00 h (Figure 2f). For *L. sinense*, Ψ_x was lower compared to *A. negundo* during all measurement periods (Figure 2h). Wa-

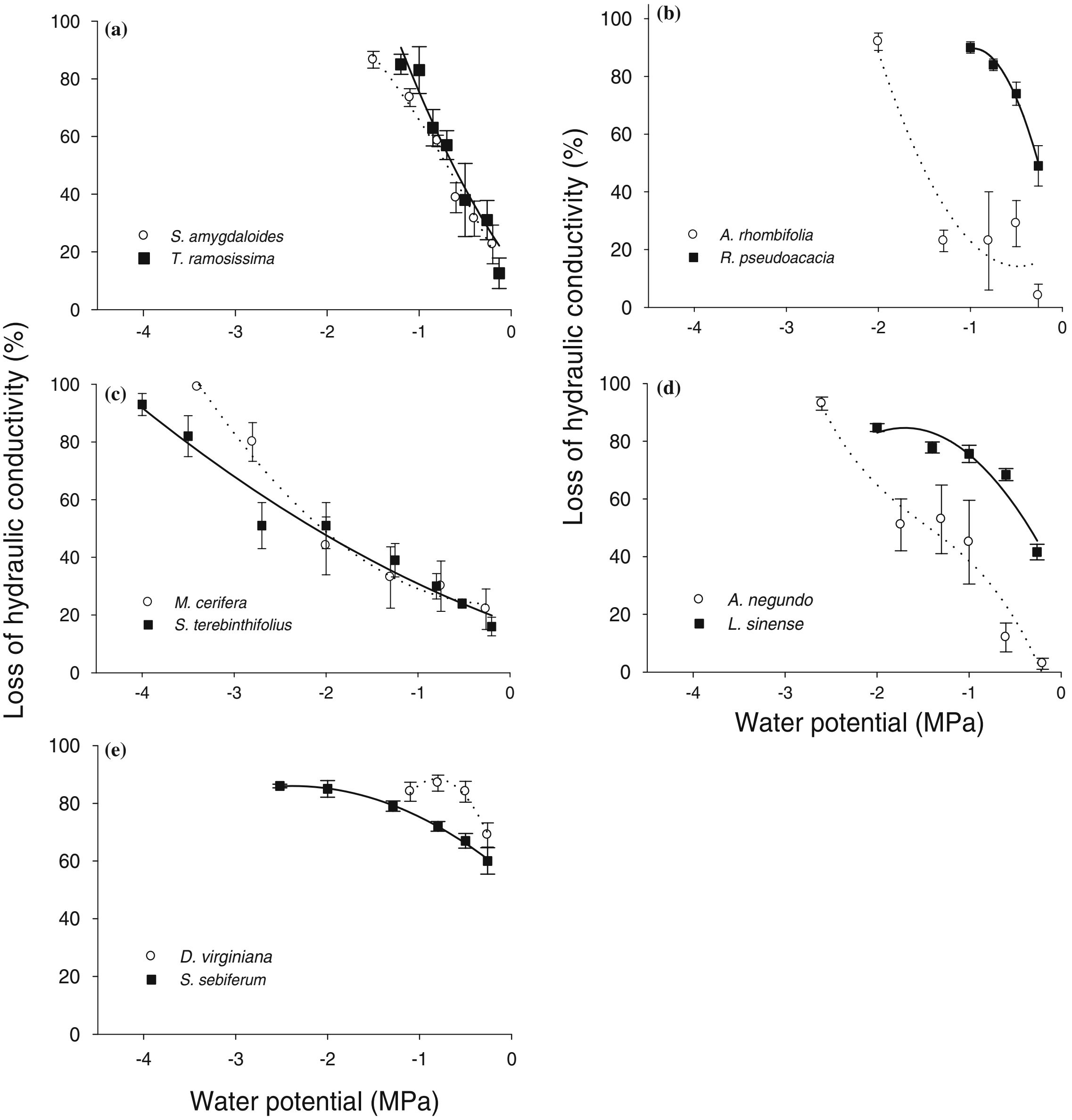

Figure 1. Percentage loss of hydraulic conductivity (PLC) of stems shown as a function of xylem water potential (Ψ_x). Panels represent vulnerability to cavitation of five native (open circles and dotted line) and five invasive species (closed square and solid line; see Table 1 for species descriptions). Each symbol represents a mean ± 1 SE for a given Ψ_x ($N = 5$–6). Data were fit with quadratic models ($r^2 > 0.93$ for all panels) and species differences are reported in Table 2. Data are not adjusted for cavitation fatigue.

ter potential for *D. virginiana* compared to *S. sebiferum* showed no difference (Figure 2j).

Xylem density was correlated with xylem saturated water content (SWC) and the seasonal change in Ψ_x for pooled analyses of invasive and native species. Species with greater xylem density tended to have lower values of SWC ($P < 0.01$; $r^2 = 0.97$; Figure 3) and a greater seasonal change in predawn $\Psi_x(\Delta\Psi_{pd})$($P < 0.01$; $r^2 = 0.69$; Figure 4a). In addition, species with greater SWC tended to exhibit lower $\Delta\Psi_{pd}$($P < 0.01$; $r^2 = 0.64$; Figure 4b).

Table 2. The vulnerability to cavitation shown for co-occurring native (n) and invasive (i) species.

State	Species	Ψ_{75} (MPa)
Idaho	*Salix amygdaloides* (n)	−1.21 ± 0.06
	Tamarix ramosissima (i)	−0.86 ± 0.14*
Washington	*Alnus rhombifolia* (n)	−1.73 ± 0.08
	Robinia pseudoacacia (i)	−0.91 ± 0.04**
Florida	*Myrica cerifera* (n)	−2.61 ± 0.23
	Schinus terebinthifolius (i)	−3.11 ± 0.30
South Carolina	*Diospyros virginiana* (n)	−0.80 ± 0.14
	Sapium sebiferum (i)	−2.70 ± 0.06**
Georgia	*Acer nugundo* (n)	−1.85 ± 0.04
	Ligustrum sinense (i)	−2.10 ± 0.18
Pooled Average	Native trees	−1.67 ± 0.13
	Invasive trees	−1.91 ± 0.19

Table 3. Xylem specific conductivity (K_s) and xylem density shown for co-occurring native (n) and invasive (i) species.

State	Species	K_s (kg s^{-1} MPa^{-1} m^{-1})	Xylem Density (g cm^{-3})
Idaho	*S. amygdaloides*(n)	1.90 ± 0.37	0.458 ± 0.013
	T. ramosissima (i)	2.66 ± 0.58	0.702 ± 0.041***
Washington	*A. rhombifolia* (n)	7.48 ± 1.69	0.422 ± 0.017
	R. pseudoacacia (i)	9.02 ± 1.22	0.577 ± 0.016***
Florida	*M. cerifera* (n)	2.03 ± 0.32	0.539 ± 0.013
	S. terebinthifolius (i)	2.22 ± 0.16	0.411 ± 0.020***
South Carolina	*D. virginiana* (n)	4.13 ± 0.48	0.553 ± 0.015
	S. sebiferum (i)	4.17 ± 1.23	0.518 ± 0.015
Georgia	*A. negundo* (n)	1.95 ± 0.24	0.391 ± 0.015
	L. sinense (i)	1.24 ± 0.21	0.682 ± 0.015***
Pooled Average	Native trees	3.50 ± 0.53	0.473 ± 0.013
	Invasive trees	3.70 ± 0.62	0.578 ± 0.022***

Discussion

Invasive trees do not generally display greater resistance to cavitation compared to co-occurring native trees in our study. Of the five pairs of sampled species only one invasive tree, *S. sebiferum*, yielded results consistent with our initial hypothesis, i.e. *S. sebiferum* was more resistant to cavitation compared to a co-occurring native tree, *D. virginiana*. In contrast to our hypothesis, two native trees, *A. rhombifolia* and *S. amygdaloides*, were more resistant to cavitation compared to the co-occurring invasive trees *R. pseudoacacia* and *T. ramosissima*, respectively, and the other two species pairs, *S. terebinthifolius* and *M. cerifera*, and *L. sinense* and *A. negundo* were not different in their resistance to cavitation. This suggests that the invasive species in our study do not generally exhibit greater resistance to water stress compared to co-occurring native species. Contrary to our initial hypothesis the success of invasive trees does not appear to be related to their greater resistance to water stress.

Pockman and Sperry (2000) proposed that greater resistance to cavitation of *T. ramosissima* compared to co-occurring native woody species might contribute to its successful invasion in western North America by allowing *T. ramosissima* to better tolerate decreases in Ψ_x due to disturbances caused by human activity (dams, weirs, pumping, etc.), or from its own transpiration. Our results do not support the Pockman and Sperry observations for *T. ramosissima* or for other invasive species. In fact, due to their greater resistance to cavitation,

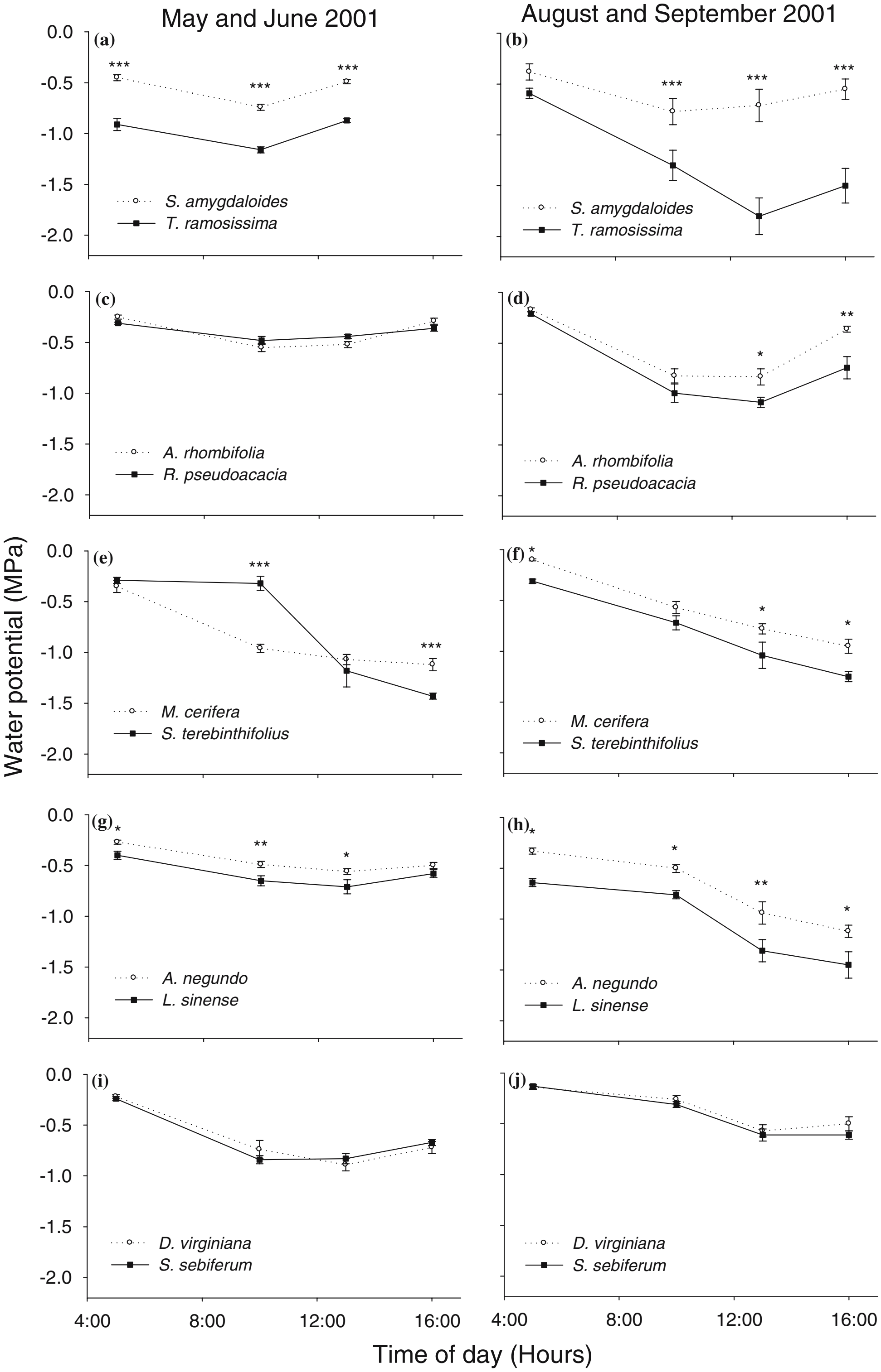

Figure 2. Water potential shown for five native (open circles and dotted lines) and five invasive species (closed squares and solid lines) sampled in 2001. Water potential was estimated with a pressure chamber on bagged branchlets. Data points represent means ± 1 SE ($N = 5$–6). Asterisks indicate a difference between a species pair ($^{*} = P < 0.05$; $^{**} = P < 0.01$; $^{***} = P < 0.001$).

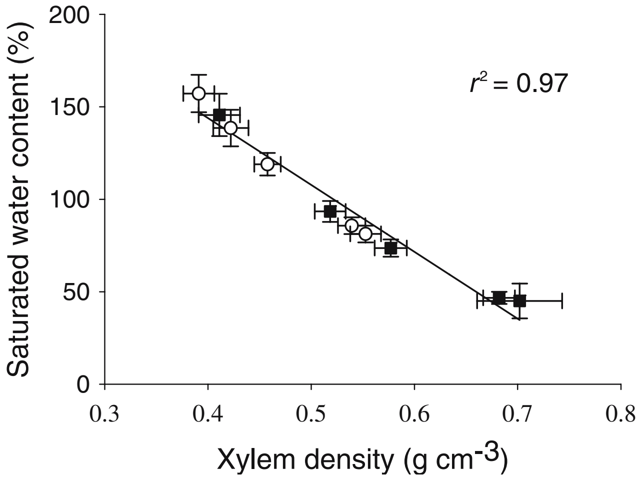

Figure 3. Percentage saturated water content (water (g)/xylem (g)×100) of stem segments, an estimate of potential capacitance, plotted as a function of xylem density. Native species are represented by open circles and invasive species by closed squares. The line is fitted to the combined data for native and invasive species ($P < 0.01$). Data points represent means ± 1 SE ($N = 6$).

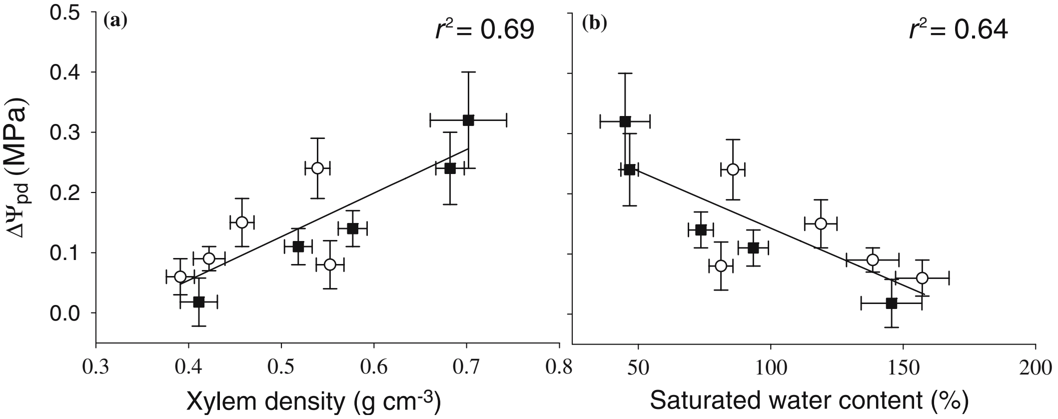

Figure 4. Seasonal change in predawn water potential ($\Delta\Psi_{\mathrm{Pd}}$) plotted as a function of xylem density (a) and percentage saturated water content (b). Data were collected during the 2001 growing season to provide a range of data values. Native species are represented by open circles and invasive species by closed squares. Lines are fitted to the combined data for native and invasive species ($P < 0.01$ for a and b). Data points represent means ± 1 SE ($N \geq 5$).

the native species *A. rhombifolia* and *S. amygdaloides* are more tolerant of decreasing Ψ_x compared to the co-occurring invaders *R. pseudoacacia* and *T. ramosissima*.

Minimum Ψ_x was lower for most of the sampled invaders compared to the co-occurring native species. This lower water potential for invaders suggests that they were under greater water stress than the native species. For example, the invasive species probably had greater levels of embolism at their lower Ψ_x since they do not have greater resistance to cavitation. Unless embolism among the invasive species was reversible on a daily basis, which is unlikely for distal branches of trees (Yang and Tyree 1992; however see Zwieniecki and Holbrook 1998), it would limit carbon uptake and ultimately growth (Brodribb and Feild 2000). In opposition to our initial hypothesis, our results suggest that most of the invasive species were under greater water stress than the native species.

Our results indicate that *T. ramosissima* was less resistant to cavitation than previously reported by

Pockman and Sperry (2000). Pockman and Sperry (2000) found that *T. ramossissima* in the Sonoran Desert had greater resistance to cavitation ($\Psi_{75} \cong -3$ MPa) than the population we sampled in west central Idaho ($\Psi_{75} = -0.86$ MPa). However, populations of *T. ramosissima* in the Sonoran Desert may be more resistant to cavitation than those in west central Idaho. To test this we measured cavitation resistance for a population of *T. ramosissima* growing in a seasonal wash in the Sonoran Desert near the town Palm Springs, California. Surprisingly, the Ψ_{75} for our Sonoran Desert population was −1.15 MPa (Pratt, unpublished data) and was not different from the population we sampled in Idaho ($P > 0.05$; $N = 6$). It is unclear if this population variation results from plasticity for cavitation resistance or if it is due to genetic differences among populations. Nevertheless, variation in cavitation resistance for *T. ramosissima* may partially explain why it is able to invade a broad range of habitats in the western United States.

Previous studies have found that *T. ramosissima* and *S. terebinthifolius* have at least the hydraulic efficiency (estimated as xylem specific conductivity; K_s) of co-occurring native trees (Pockman and Sperry 2000; Stratton et al. 2000). Plants with greater K_s have advantages compared to plants with lower K_s including higher Ψ_x, photosynthetic capacity (Brodribb and Feild 2000), and higher growth rates (Shumway et al. 1993; Vander Willigen and Pammenter 1998; Wang et al. 2003). We found no difference in K_s between native and invasive species suggesting no advantage in hydraulic efficiency.

Among woody plants, greater cavitation resistance is correlated with denser xylem and lower K_s, which represent costs associated with developing high cavitation resistance (Lawton 1984; Enquist et al. 1999; Hacke et al. 2001a; Sperry and Hacke 2004). We found no evidence for such correlations for native or invasive species, which is likely due to the narrow range of cavitation resistance exhibited among our sampled species (Wright et al. 2004). However, we found that despite their low resistance to cavitation, *T. ramosissima* and *L. sinense* had high-density xylem when compared to woody angiosperms and the other species (c.f. Hacke and Sperry 2001 and Alden 1995; this study). This finding suggests that woody plants in mesic habitats can have relatively dense xylem and low resistance to cavitation. In mesic habitats high xylem density may be important for reasons unrelated to cavitation resistance such as to resist mechanical damage during spring floods, and to resist pathogens and herbivores (Lucas et al. 2000).

Xylem density has been shown to correlate with water storage in stems and may have functional importance for plant water relations in our study (Stratton et al. 2000). Species with denser xylem tend to have reduced saturated xylem water content (Desch 1968), and experience a greater drop in seasonal Ψ_x (Borchert 1994; Stratton et al. 2000). Consistently higher xylem density, for native and invasive species, was associated with lower saturated water content of xylem. Apparently denser xylem has less volume to store water, leaving species with denser xylem less able to buffer seasonal and diurnal decline in Ψ_x (Desch 1968; Stratton et al. 2000). Decreased water storage capacity with increasing xylem density appears to be a tradeoff, leading to greater declines in seasonal Ψ_x for invasive and native species with denser xylem.

Our study suggests that invasive species do not exhibit hydraulic advantages including greater resistance to cavitation or K_s compared to co-occurring native species. All of our study species exhibited low cavitation resistance when compared to other woody angiosperms (Maherali et al. 2004) suggesting a low resistance to water stress. The hydraulic traits of the invasive species in our study were not different from many woody angiosperms adapted to mesic habitats (Sparks and Black 1999; Pockman and Sperry 2000) suggesting that hydraulic traits cannot explain the success of invasive species over native species in our study.

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