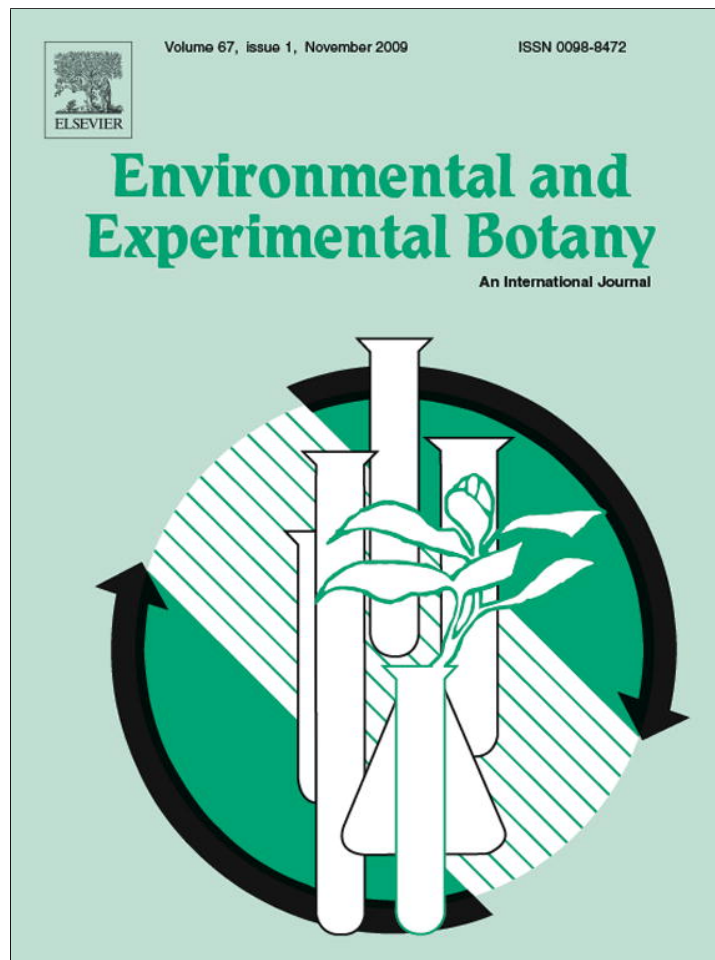


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## Environmental and Experimental Botany

journal homepage: [www.elsevier.com/locate/envexpbot](http://www.elsevier.com/locate/envexpbot)Soil salinity and drought alter wood density and vulnerability to xylem cavitation of baldcypress (*Taxodium distichum* (L.) Rich.) seedlings

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## ABSTRACT

We investigated the role of hydraulic conductivity, wood density, and xylem cavitation in the response of baldcypress (*Taxodium distichum*) seedlings to increased soil salinity and drought. One-year-old, greenhouse-grown seedlings were irrigated daily with a 100 mM ( $\approx 6\%$ ) salt solution or once per week with fresh water (drought). Controls were irrigated daily with fresh water. Gas exchange rates of stressed plants were reduced by approximately 50% (salt) and 70% (drought), resulting in a 50–60% reduction in diameter growth for both treatments. Stem-specific hydraulic conductivity ( $K_{S \text{ native}}$ ) of stressed plants was 33% (salt) and 66% (drought) lower than controls and we observed a strong positive correlation between  $K_{S \text{ native}}$  and gas exchange. In addition, we found a strong relationship between  $\text{CO}_2$  assimilation rate ( $A$ ) and the soil-to-leaf hydraulic conductance ( $k_l$ ). The relationship was identical for all treatments, suggesting that our moderate salt stress (as well as drought) did not affect the photosynthetic biochemistry of leaves, but rather reduced  $A$  via stomatal closure. Lower  $K_{S \text{ native}}$  of stressed plants was associated with increased wood density and greater resistance to xylem cavitation. Xylem pressures causing 50% loss of hydraulic conductivity ( $P_{50}$ ) were  $-2.88 \pm 0.07$  MPa (drought),  $-2.50 \pm 0.08$  MPa (salt) and  $-2.01 \pm 0.04$  MPa (controls).  $P_{50}$ s were strongly correlated with wood density ( $r = -0.71, P < 0.01$ ) and  $K_{S \text{ native}}$  ( $r = 0.74, P < 0.01$ ). These findings support the hypothesis that there is a significant trade-off between a plant's cavitation resistance and its hydraulic efficiency. The results of the present study indicate that stressed plants partitioned their biomass in a way that strengthened their xylem and reduced vulnerability to xylem cavitation. Hence, these seedlings could be better suited to be planted in environments with elevated soil salinity. For most parameters (especially  $P_{50}$ ), drought had an even more pronounced effect than salinity. This is important as nurseries could produce "stress-acclimated" seedlings simply by reducing irrigation amounts and would not have to contaminate the soils in their nursery beds with salt applications.

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## 1. Introduction

It is a well-established fact that plant survival and growth is highly dependent on water availability and unimpeded water transport (i.e. water availability to the leaves) in order to maintain photosynthesis and growth. According to the cohesion-tension theory (Dixon, 1914; Tyree, 1997; Steudle, 2001), plants transport water under negative pressure, which makes this mechanism inherently susceptible to cavitation and xylem dysfunction (Tyree and Sperry, 1989; Sperry et al., 1993). Numerous studies have shown cavitation to occur in roots (Alder et al., 1996; Linton and Nobel, 1999; Sperry and Hacke, 2002; Sperry et al., 2002; Domec et al., 2006), stems (Sperry and Tyree, 1988; Cochard, 1992; Hargrave et al., 1994; Hacke and Sauter, 1995; Jarbeau et al., 1995), and leaves (Salleo et al., 2001; Stiller et al., 2003; Nardini et al., 2003). While,

comparative studies show that, within species and/or individual plants, roots are generally more vulnerable to water stress induced cavitation than stems (Sperry and Saliendra, 1994; Jackson et al., 2000; Matzner et al., 2001), the overall degree of cavitation resistance is generally correlated with the species' habitat (Davis et al., 1998, 1999; Hacke et al., 2000; Pockman and Sperry, 2000; Jacobsen et al., 2007a,b). However, large differences in cavitation resistance in co-occurring species have been reported (Kolb and Davis, 1994).

Recently, studies have suggested that cavitation resistance is determined by wood anatomical and biomechanical parameters, such as wood density, modulus of rupture, and the resistance to conduit implosion  $(t/b)_h^2$  (Hacke et al., 2001a; Jacobsen et al., 2007b,c; Pratt et al., 2007). While the evolutionary and functional links between xylem properties, cavitation resistance, water use, and plant distribution are currently debated (Maherali et al., 2004, 2006; Jacobsen et al., 2007a), it is generally accepted that plants from xeric habitats have denser wood and are less vulnerable to xylem cavitation than plants from mesic habitats (Tyree et al., 1991;

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Kolb and Davis, 1994; Sperry, 1995; Pockman and Sperry, 2000; Hacke et al., 2001a; Maherali et al., 2004).

Large baldcypress tupelo swamps characterize the natural coastal wetlands of the southeastern United States, many of which are threatened by increases in flooding and salinity as a result of both natural processes and man-induced hydrologic alterations (Penland and Ramsey, 1990; Day et al., 2000; Morton et al., 2003). In addition, large areas have been clear-cut in the early 20th century (Mancil, 1980; Keddy et al., 2007). In the past, great efforts have been undertaken to restore these degraded areas. In the wetlands near Pass Manchac in southeastern Louisiana (30°17'N, 90°21'W) alone, almost 100,000 baldcypress seedlings have been planted during the past 10 years by various conservation groups (Michael Green, Southeastern Louisiana University, personal communication), however restoration success was very limited. One often-cited reason for this limited success is increased soil salinity due to salt-water intrusion from the Gulf of Mexico via Lakes Borgne and Pontchartrain (DeLaune et al., 1987; Gornitz et al., 1982; Turner, 1991, 1997). Although considerable intraspecific variation exists, baldcypress is known to be sensitive to relatively low levels of salinity (Allen et al., 1994, 1997; Krauss et al., 2000). Studies found reduced germination rates (Krauss et al., 1998), gas exchange (Pezeshki, 1990; Pezeshki et al., 1995; McLeod et al., 1996), root and shoot biomass production (Allen et al., 1997; Krauss et al., 1999), height growth (Conner et al., 1997; Krauss et al., 2000) and increased tree mortality (Krauss et al., 2000). Salinity effects are generally exacerbated by flooding (McLeod et al., 1996; Conner and Inabinette, 2003), drought (Elcan and Pezeshki, 2002; Wang and Cao, 2004), anaerobic soil conditions (Pezeshki, 1990), and insect attack (Effler and Goyer, 2006). However, it is not fully understood whether this salt sensitivity is due to (long-term) toxicity of salt ions (sodicity) or due to the effects of reduced soil water potential on plant water status. Munns (2002) reports that the short-term effects (minutes to days) of increased soil salinity are identical to those of drought. The author continues to argue that this indicates that short-term salinity effects are probably due to factors associated with water stress rather than a salt-specific effect and that the observed growth reduction is presumably regulated by hormonal signals coming from the roots (Munns, 2002, and references therein).

We conducted a preliminary greenhouse study and found 8-week-old apical shoots of baldcypress seedlings highly vulnerable to xylem cavitation ( $P_{50} = -1.23$  MPa, see Section 2 for details on  $P_{50}$ ). Hence, if the soil water potential is lowered sufficiently by salt water, young shoots of seedlings planted in saline environments would suffer greatly from xylem cavitation and seedlings could die back. The objective of the present study was to evaluate vulnerability to xylem cavitation of baldcypress seedlings grown under elevated soil salinity and under drought conditions. In particular, we wanted to answer the questions whether (a) our treatments would increase the plants' wood density, which could be associated with more cavitation resistant plants and (b) whether drought and salinity trigger a comparable response. The results of this study could aid efforts to produce more cavitation resistant baldcypress seedlings that are better suited to be planted in environments with elevated soil salinity.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

One-year-old, bare-rooted baldcypress seedlings were obtained from the Louisiana Department of Agriculture & Forestry (Baton Rouge, LA, USA) and grown in 15-L pots under ambient conditions (approximately 34/24 °C, 50/80% relative humidity, day/night)

in a greenhouse at Southeastern Louisiana University. Soil was fritted clay (Balcones Mineral Corporation, Flatonia, TX, USA) supplemented with Osmocote 13-13-13 slow release fertilizer (The Scotts Company LLC, Marysville, OH, USA).

During the first 8 weeks of seedling establishment, all plants were irrigated frequently to avoid drought stress. After plants were established they were divided into 3 groups. Control plants were watered twice daily, drought plants were watered once per week, and plants subjected to a salinity treatment were irrigated twice daily with salt solution. The concentration of the salt solution was gradually raised over a 4-week period from 35 to 100 mM ( $\approx 2\text{--}6\%$ , measured with YSI 30/10FT; YSI Incorporated, Yellow Springs, OH, USA) and was then kept constant at approximately 100 mM for the remainder of the experiment. To avoid salt build-up in the soil, plants of the salinity treatment were heavily watered with fresh water once per week.

Basal stem diameters were measured at the beginning of the treatments (May), in the middle of the growing season (August), and at the end of the growing season when plants were harvested for hydraulic measurements (November). Relative diameter growth rates were calculated for the first and second half of the growing season ( $RGR_{\text{May--August}}$  and  $RGR_{\text{August--November}}$ , respectively), as well as for the entire season ( $RGR_{\text{May--November}}$ ).

### 2.2. Soil-to-leaf hydraulic conductance ( $k_L$ )

In the middle of the growing season and at the height of the weekly drought stress,  $\text{CO}_2$  assimilation rate ( $A$ ), transpiration rate ( $E$ ), and stomatal conductance ( $g_s$ ) of young, fully expanded leaves of 11 representative plants from each treatment was measured using a LI-6400 photosynthesis system (LI-COR Inc., Lincoln, NE, USA). Afterwards, the leaf area inside the cuvette was measured with a LI-3100 Area Meter in order to correct the gas exchange data for leaf area. Midday leaf water potential was measured with a Scholander type pressure chamber (PMS Instrument Company, Albany, OR, USA) on comparable leaves of the same plants. Soil was sampled directly from the root zones through vertical slits in 3 representative pots for each treatment. Soil samples were pooled and soil water potentials were measured after a 15 min temperature equilibration period using a WP4-T Dewpoint Potential Meter (Decagon Devices, Pullman, WA, USA). Soil-to-leaf hydraulic conductance of the plants ( $k_L$ ) was calculated as

$$k_L = \frac{E}{\psi_{\text{soil}} - \psi_{\text{leaf}}}$$

where  $E$  is the transpiration rate of the plants and  $\psi$  is the water potential of the soil or the leaves.

### 2.3. Xylem cavitation vulnerability curves

At the end of the growing season, all treatments were irrigated with fresh water twice daily for one week to allow stressed plants to recover and to minimize native embolism. Ten representative plants from each treatment were harvested and their vulnerability to xylem cavitation was measured. Vulnerability curves show the relationship between xylem pressure and the percentage loss of hydraulic conductivity (PLC) associated with this pressure. The vulnerability curves were measured using the centrifugal force method (Alder et al., 1997) on 0.14 m stem segments cut under water from current-year growth. Before stems were flushed at 70 kPa for 30 min with deionized and filtered (0.2  $\mu\text{m}$ ) water to remove any native embolism, native hydraulic conductivity ( $K_{\text{native}}$ ) was measured and stem-specific native conductivity ( $K_{\text{S native}}$ ) was calculated based on the segments cross-section area. After flushing the maximum hydraulic conductivity ( $K_{\text{max}}$ ) was measured. The percentage that  $K_{\text{native}}$  was below  $K_{\text{max}}$  gave the segment's native PLC (=native

embolism).  $K_{\max}$  values of several stems were between 1% and 3% below  $K_{\text{native}}$ , indicating not only a lack of native embolism, but also that flushing caused minor torus aspiration. We, therefore, used the unadulterated  $K_{\text{S native}}$  in Figs. 2 and 4, as it reflects the true hydraulic conductivity better than  $K_{\max}$ . The flushed stem segments were exposed to progressively more negative pressures by spinning them in a custom-built centrifuge rotor in a Sorval RC5B centrifuge. Segments were spun for 4 min at each pressure to saturate the embolism response. The  $K$  was remeasured between each pressure and the PLC (relative to  $K_{\max}$ ) associated with each pressure was recorded in a vulnerability curve. Generally, 6–7  $K$  values were measured per stem. To estimate the pressure causing 50 PLC ( $P_{50}$ ), a Weibull function (Neufeld et al., 1992) was fitted to each segment's vulnerability curve and solved for  $P_{50}$ . After hydraulic measurements were complete, stem segments were stored in a freezer until wood density measurements could be made.

#### 2.4. Wood density and specific leaf area

Stems used for hydraulic measurements were thawed and 2 cm segments were cut from the basal end. The bark of these short segments was removed and the segments were hydrated over night in deionized water. The next day, the fresh volume ( $V_F$ ) of the segments was measured by carefully submerging them in a beaker of water (placed on an electronic balance, Sartorius LE225D, Sartorius AG, Göttingen, Germany) and noting the weight of the displaced water. This procedure was repeated 3 times and the volume was calculated from the mean of the 3 measurements. Segments were oven-dried at 85 °C for 48 h and dry mass ( $m_D$ ) was measured. To ensure weight consistency, segments were dried for an additional 24 h and the mass remeasured. Wood density ( $\rho_w$ ) of the segments was calculated as

$$\rho_w = \frac{m_D}{V_F}$$

Multiple leaves were sampled from 13 salt and 21 drought and control plants prior to harvesting stems for hydraulic measurements. Leaf area ( $A_L$ ) was measured with a LI-3100 Area Meter (LI-COR Inc., Lincoln, NE, USA) and leaves were oven-dried as described above for stem segments. Mass of the dried leaves ( $m_L$ ) was measured and specific leaf area (SLA) was calculated as

$$\text{SLA} = \frac{A_L}{m_L}$$

#### 2.5. Statistics

Data were analyzed with the SPSS 8.0 statistics package (SPSS Inc., Chicago, IL, USA) using the 0.05 and 0.01 significance levels. Comparisons were made with a one-way ANOVA and Tukey's HSD test for *a posteriori* comparisons between means of all treatments. Significance of relationships between means that were measured

on different plants and at different times (Fig. 2) were tested via contrast analysis following a one-way ANOVA.

### 3. Results

After the initial seedling establishment phase, basal diameters of the plants were similar (Table 1). During the first 3 months of growth, relative growth rates of control plants were approximately twice the rates of salt and drought treatments, resulting in significantly larger controls. During the second half of the growing season, growth rates of plants irrigated with salt solution were greatly reduced. Growth rates of controls were only slightly lower compared to the first half and drought plants did not alter their growth rates significantly. The pronounced growth reduction of salt plants was reflected in an early onset of senescence in mid-October, while drought and control plants did not senesce. (Surplus control and drought plants did not enter dormancy during the winter in the greenhouse.) Plant growth during the first half of the growing season was significantly correlated with the plants'  $\text{CO}_2$  assimilation rate ( $A$ , Table 2). However, as the timing of the gas-exchange measurements was designed to maximize the effects of drought (2 h after salt and control plants were irrigated and 1 h before the weekly irrigation of drought plants), the correlation of the two parameters was relatively weak ( $r=0.36$ ,  $P<0.05$ , data not shown).

Gas-exchange of salt and drought plants was significantly reduced when compared to controls (Table 2). While this reduction seemed most pronounced in drought plants, drought and salt treatments were not different at the  $P=0.05$  level. However,  $A$  was different at the  $P=0.06$  level (indicated by italicized letters in Table 2). Midday leaf water potentials ( $\psi_{\text{leaf}}$ ) of all three treatments were significantly different, with drought plants having the most negative and controls having the least negative  $\psi_{\text{leaf}}$ . Soil water potential ( $\psi_{\text{soil}}$ ) of salt and control plants were  $-0.93$  and  $-0.34$  MPa, respectively. The osmotic potential of the salt solution used for irrigation was approximately 0.5 MPa. Interestingly, after 7 days without irrigation,  $\psi_{\text{soil}}$  of drought plants was less negative than expected ( $-0.64$  MPa). Still, this water potential was sufficiently low to result in an almost 5-fold reduction of soil-to-leaf hydraulic conductance ( $k_L$ ) for drought plants compared to controls and salt plants. As native embolism was not measured at the time of gas-exchange measurements, we were unable to establish xylem cavitation as the cause for the  $k_L$  reduction in drought plants. However, there was no native embolism in any treatment at the end of the growing season when hydraulic measurements were made. Stomatal conductance ( $g_s$ ) as well as transpiration rate ( $E$ ) and  $k_L$  are auto-correlated. Therefore, only the relationship between  $A$  and  $k_L$ , which were measured independently is shown in Fig. 1. Absolute values of  $A$  and  $k_L$  were closely related in all treatments ( $r^2=0.79$ ,  $r^2=0.76$ , and  $r^2=0.73$ ,  $P<0.01$ , for drought, salt, and control plants, respectively; Fig. 1 solid lines). When the pooled data of all three treatments was examined, the relationship between  $A$  and  $k_L$  seemed to follow a saturation curve, with a linearly increasing lower region (mainly drought plants) followed

**Table 1**  
Basal stem diameters of one-year-old baldcypress seedlings at the beginning of treatments ( $D_{\text{May}}$ ), in the middle of the growing season ( $D_{\text{August}}$ ) and at harvest time ( $D_{\text{November}}$ ). Relative daily diameter growth rates were calculated for the first and second half of the growing season ( $RGR_{\text{May-August}}$  and  $RGR_{\text{August-November}}$ , respectively), as well as for the entire season ( $RGR_{\text{May-November}}$ ). All diameter means and all growth rates were compared with each other. Different letters indicate homogeneous sets of means determined with a Tukey's HSD test after a one-way ANOVA tested significant at the 0.05 level. Sample sizes were  $n=19$  for salt treatment and  $n=25$  for drought and control plants.

	Salt	Drought	Control
Stem diameter May ( $D_{\text{May}}$ ), mm	12.0 ± 0.45a b	11.5 ± 0.29a	11.2 ± 0.38a
Stem diameter August ( $D_{\text{August}}$ ), mm	15.5 ± 0.47c d	14.1 ± 0.39b c	17.3 ± 0.58d
Stem diameter November ( $D_{\text{November}}$ ), mm	16.3 ± 0.55c d	17.2 ± 0.48d	25.6 ± 0.72e
Relative diameter growth rate ( $RGR_{\text{May-August}}$ ), mm mm <sup>-1</sup> d <sup>-1</sup>	(3.5 ± 0.3) × 10 <sup>-3</sup> a	(2.6 ± 0.3) × 10 <sup>-3</sup> a b	(6.6 ± 0.5) × 10 <sup>-3</sup> c
Relative diameter growth rate ( $RGR_{\text{August-November}}$ ), mm mm <sup>-1</sup> d <sup>-1</sup>	(0.6 ± 0.1) × 10 <sup>-3</sup> e	(2.3 ± 0.1) × 10 <sup>-3</sup> a b	(5.1 ± 0.2) × 10 <sup>-3</sup> d
Relative diameter growth rate ( $RGR_{\text{May-November}}$ ), mm mm <sup>-1</sup> d <sup>-1</sup>	(2.0 ± 0.1) × 10 <sup>-3</sup> b	(2.8 ± 0.2) × 10 <sup>-3</sup> a b	(7.3 ± 0.4) × 10 <sup>-3</sup> c

**Table 2**

Gas exchange parameter ( $A$ ,  $E$ ,  $g_s$ ), water potential ( $\psi_{\text{leaf}}$ ,  $\psi_{\text{soil}}$ ), soil-to-leaf hydraulic conductance ( $k_L$ ), and average and specific leaf area ( $A_L$ , SLA) of bald cypress seedlings. Stem-specific hydraulic conductivity ( $K_{S \text{ native}}$ ), wood density ( $\rho_w$ ), and  $P_{50}$  of present-year stem segments used in hydraulic measurements. The timing of the gas-exchange measurements was designed to maximize the effects of drought on  $k_L$ . Values are mean  $\pm$  SE. Sample sizes for  $A$ ,  $E$ ,  $g_s$ ,  $\psi_{\text{leaf}}$  and  $k_L$  were  $n = 11$  for all three treatments. Sample sizes for  $\rho_w$ ,  $D_s$ ,  $K_{S \text{ native}}$ , and  $P_{50}$  were  $n = 10$  for salt and drought treatments and  $n = 9$  for control plants.  $A_L$  and SLA sample sizes were  $n = 13$ , 21 and 21 for salt, drought and control plants, respectively. As  $\psi_{\text{soil}}$  was measured on pooled soil samples, no statistics are given for this parameter. Different letters (in a row) indicate means are significantly different at the 0.05 level, Tukey's HSD following one-way ANOVA. Italics indicate significant differences at the 0.06 level.

	Salt	Drought	Control
CO <sub>2</sub> assimilation rate ( $A$ ), $\mu\text{mol s}^{-1} \text{m}^{-2}$	4.6 $\pm$ 0.76 a	2.5 $\pm$ 0.52 a	9.2 $\pm$ 0.46 b
Transpiration rate ( $E$ ), $\text{mmol s}^{-1} \text{m}^{-2}$	3.9 $\pm$ 0.42 a	2.5 $\pm$ 0.23 a	8.7 $\pm$ 0.73 b
Stomatal conductance ( $g_s$ ), $\text{mmol s}^{-1} \text{m}^{-2}$	84 $\pm$ 9.4 a	54 $\pm$ 5.2 a	191 $\pm$ 22.9 b
Midday leaf water potential ( $\psi_{\text{leaf}}$ ), MPa	-1.8 $\pm$ 0.05 a	-2.0 $\pm$ 0.05 b	-1.3 $\pm$ 0.03 c
Soil water potential, pooled ( $\psi_{\text{soil}}$ ), MPa	-0.93	-0.64	-0.34
Soil-to-leaf hydraulic conductance ( $k_L$ ), $\text{mmol s}^{-1} \text{m}^{-2} \text{MPa}^{-1}$	4.9 $\pm$ 0.69 a	1.9 $\pm$ 0.20 b	8.8 $\pm$ 0.84 c
Average leaf area per leaf ( $A_L$ ), $\text{cm}^2$	12.0 $\pm$ 1.6 a	6.4 $\pm$ 0.5 b	14.7 $\pm$ 0.9 a
Specific leaf area (SLA), $\text{m}^2 \text{kg}^{-1}$	13.3 $\pm$ 0.4 a	11.3 $\pm$ 0.3 b	14.0 $\pm$ 0.3 a
Stem-specific hydraulic conductivity ( $K_{S \text{ native}}$ ), $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$	1.01 $\pm$ 0.10 a	0.49 $\pm$ 0.06 b	1.51 $\pm$ 0.08 c
Wood density ( $\rho_w$ ), $\text{g cm}^{-3}$	0.31 $\pm$ 0.01 a	0.34 $\pm$ 0.003 b	0.27 $\pm$ 0.01 c
$P_{50}$ , MPa	-2.50 $\pm$ 0.08 a	-2.88 $\pm$ 0.07 b	-2.01 $\pm$ 0.04 c

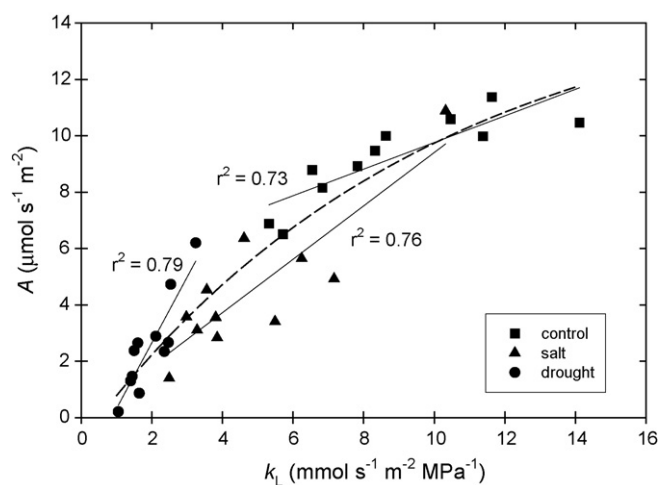
by a less steep, plateau-like region (mainly controls). We fitted an exponential rise to a maximum function (Fig. 1 dashed line) to the pooled data of all treatments [ $y = -0.82 + 16.46 \cdot (1 - \exp(-0.103x))$ ,  $r^2 = 0.87$ ]. Forcing the curve through the origin did not change the goodness of fit, however, fitting a function solely to the pooled data of drought and control plants improved the  $r^2$  to 0.96 (curve not shown).

The low  $k_L$  of drought plants was reflected in the lower stem-specific native hydraulic conductivity ( $K_{S \text{ native}}$ ) of the stem segments used for the hydraulic measurements (Table 2). Although diameters of drought and control segments were almost identical,  $K_{S \text{ native}}$  of drought plants was only one third of the controls'  $K_{S \text{ native}}$ . The relationships between  $K_{S \text{ native}}$  and gas-exchange parameters ( $A$ ,  $g_s$ ,  $E$ , mean values from Table 2) are shown in Fig. 2. Gas-exchange and  $K_{S \text{ native}}$  were measured independently on different plants and at different times during the study, yet contrast analysis confirmed a highly significant relationship between the parameters ( $P < 0.001$ ).

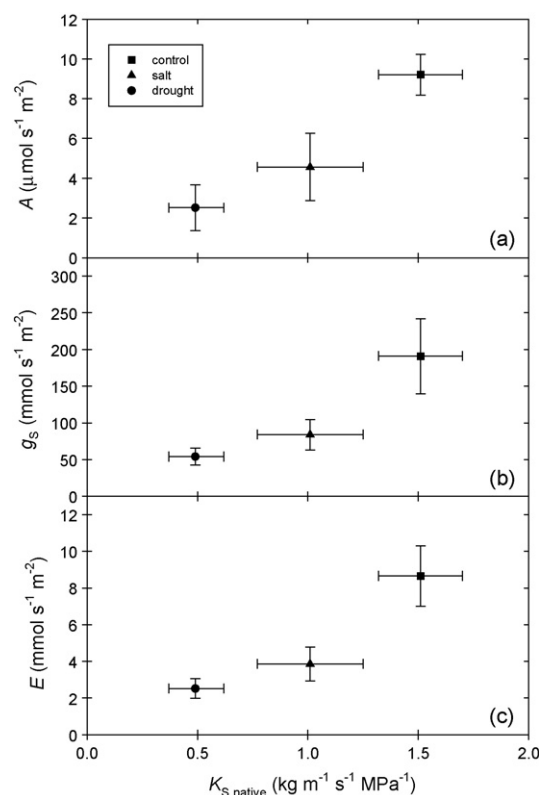
Leaf size of drought plants was significantly reduced (Table 2). Average leaf area per leaf ( $A_L$ ) of drought plants was approximately half of that of salt or control plants. In addition, specific leaf area (SLA) of drought plants was significantly lower compared to salt and control plants. The tendency in drought plants to

grow smaller, denser leaves was consistent with the plants' wood properties (Table 2). Wood density ( $\rho_w$ ) of slow growing drought plants was highest,  $\rho_w$  of controls was lowest and salt plants had intermediate  $\rho_w$ . These trends in  $\rho_w$  matched the significant differences in vulnerability to xylem cavitation. Fig. 3 shows vulnerability curves for current-year stem segments. Curves for all three treatments were significantly different from each other. Stressed plants were less vulnerable to cavitation ( $P_{50} = -2.88 \pm 0.07$  and  $-2.50 \pm 0.08$  MPa for drought and salt plants, respectively) than control plants ( $P_{50} = -2.01 \pm 0.04$  MPa).

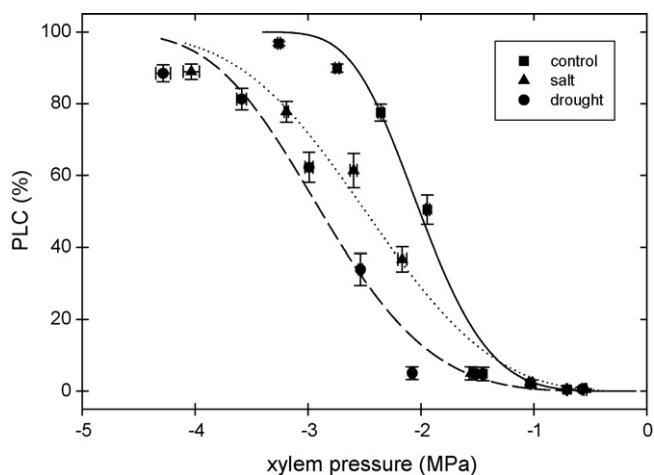
Differences in cavitation vulnerability and in wood density could be a result of the plants' growth rates. Correlation analysis



**Fig. 1.** The relationship between soil-to-leaf hydraulic conductance ( $k_L$ ) and CO<sub>2</sub> assimilation rate ( $A$ ) in *Taxodium distichum*. Correlations for all treatments were highly significant ( $P < 0.01$ ). The  $r^2$  values within the figure are for linear regressions (solid lines). In addition to the regression analysis, we fitted an exponential rise to a maximum function (dashed line) to the pooled data [ $y = -0.82 + 16.46 \cdot (1 - \exp(-0.103x))$ ,  $r^2 = 0.87$ ].

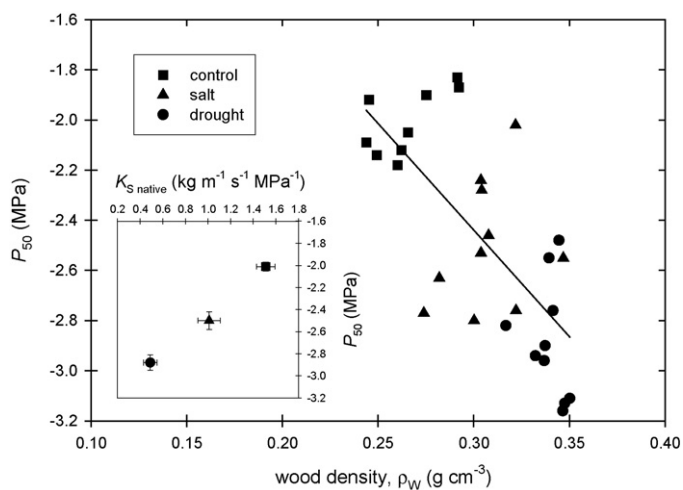


**Fig. 2.** The relationship between (a) CO<sub>2</sub> assimilation rate ( $A$ ), (b) stomatal conductance ( $g_s$ ) and (c) transpiration rate ( $E$ ) and native hydraulic conductivity ( $K_{S \text{ native}}$ ). Mean values from Table 1. Error bars show the upper and lower boundaries of the 95% confidence intervals. Sample sizes for  $A$ ,  $g_s$  and  $E$  were  $n = 11$  for all treatments. Sample sizes for  $K_{S \text{ native}}$  were  $n = 10$  for salt and drought treatments and  $n = 9$  for control plants.



**Fig. 3.** Vulnerability curves of current-year stems in *Taxodium distichum*. Curves show percentage loss of hydraulic conductivity (PLC) with decreasing xylem pressure for drought (circles,  $n = 10$ ), salt (triangles,  $n = 10$ ) and control plants (squares,  $n = 9$ ). Means and SE (error bars are partly covered by symbols) are shown for greater clarity; however, Weibull functions were fitted to the raw data of each treatment (solid line = control, dotted line = salt, and dashed line = drought).

revealed significant ( $P < 0.01$ ) correlations between  $P_{50}$ ,  $\rho_w$  and the plants' RGRs. While correlations were similar for all 3 RGRs presented in Table 1, the correlations with  $RGR_{\text{May–August}}$  was strongest. Increased RGR resulted in more vulnerable plants ( $r = 0.61$ ,  $P < 0.01$ ) and in less dense wood ( $r = -0.63$ ,  $P < 0.01$ ). Wood density has recently been linked to cavitation vulnerability (Hacke et al., 2001a). In general, denser wood seems to be more cavitation resistant than less dense wood. For baldcypress, this relationship between  $\rho_w$  and  $P_{50}$  is shown in Fig. 4 ( $r = -0.71$ ,  $P < 0.01$ ). In conifers, denser wood can be caused by thicker tracheid walls and/or reduced tracheid lumen per given cross-section area (Pittermann et al., 2006). Either would cause a reduction in hydraulic conductivity when compared to plants with less dense wood. In the present study,  $K_{S \text{ native}}$  and wood density of baldcypress were negatively correlated ( $r = -0.72$ ,  $P < 0.01$ , data not shown as the figure is almost identical to Fig. 4) and the relationship between  $K_{S \text{ native}}$  and  $P_{50}$  is shown as an insert in Fig. 4 ( $r = 0.74$ ,  $P < 0.01$ ).



**Fig. 4.** The relationship between  $P_{50}$  and wood density ( $\rho_w$ ) of current-year stem xylem in *Taxodium distichum* ( $r^2 = 0.50$ ) and between  $P_{50}$  and stem-specific native hydraulic conductivity ( $K_{S \text{ native}}$ , insert). Error bars indicate 1SE and are partly covered by symbols ( $n = 10$  for salt and drought treatments and  $n = 9$  for control plants,  $r = 0.74$ ,  $P < 0.01$ ).

#### 4. Discussion

The objective of the present study was to evaluate growth, wood density, and vulnerability to xylem cavitation of baldcypress seedlings grown under elevated soil salinity and under drought conditions. During plant growth, care was taken to impose maximum stress on the plants without causing visible and permanent injury to the plants. In a preliminary experiment, we found that prolonged exposure to soil salinity between 135 and 170 mM (8–10‰) caused high rates of mortality, especially when the soil was not flushed with fresh water to remove excess salt. To avoid tree mortality, we kept our salt treatments at about 100 mM (6‰), which is approximately double the long-term salinity average but comparable to recent, drought-induced peak salinities near Pass Manchac (Thomson et al., 2002), an area in southeastern Louisiana where cypress restoration is of especial interest.

Soil salinity and drought had the same effect on a number of parameters. Both treatments resulted in significantly reduced diameter growth rates (RGR), gas exchange rates ( $A$ ,  $E$ ,  $g_s$ ), stem-specific native hydraulic conductivity ( $K_{S \text{ native}}$ ) and vulnerability to xylem cavitation ( $P_{50}$ ). Both treatments increased the plants' wood density ( $\rho_w$ ). With the exception of second-half and entire-season diameter growth rates ( $RGR_{\text{August–November}}$  and  $RGR_{\text{May–November}}$ , respectively), drought had an even more pronounced effect than salinity on all parameters. RGR of drought plants was reduced but constant throughout the entire growing season (Table 1). RGR of salt plants was dramatically reduced during the second half of the growing season. This led to a low RGR for the entire season in this treatment. This, and the early onset of senescence suggest that there might have been additional long-term salinity effects (Tattini et al., 2002), which could lead to a reduction of photosynthesis and growth (Munns, 2002, and references therein), but that were not investigated in this study.

While we did not measure leaf turnover, it was apparent during the second half of the growing season that older leaves began to die back. The total leaf area of salt plants was reduced compared to drought plants, and even more so compared to controls. Similar reductions in total leaf biomass as a result of exposure to salinity have been previously reported for baldcypress (Allen et al., 1997), olive (Bongi and Loreto, 1989), wheat (Munns et al., 1995), and maize (Fortmeier and Schubert, 1995). However, this salt-induced senescence was not reflected in our average leaf area per leaf ( $A_L$ ) and specific leaf area (SLA) data, as we only used fully grown, healthy looking leaves for these measurements.  $A_L$  and SLA were only reduced in drought plants, while salt and control plants did not differ. Thus, the seedlings in our study responded to their respective stress in two different ways. Drought stress resulted in smaller and denser leaves as previously reported for a variety of tree species (Abrams, 1994) and in reduced gas exchange rates. Leaves from salt treated plants remained “control like” with respect to  $A_L$  and SLA, but reduced total leaf biomass and reduced gas exchange moderately.

Drought reduced the soil-to-leaf hydraulic conductance ( $k_L$ ) by almost 5-fold compared to controls, while  $k_L$  of salt plants was reduced by less than half (Table 2). Due to the destructive nature of hydraulic measurements, we did not measure native embolism in stems at the same time as the conductance measurements. We, therefore, are unable to conclusively exclude xylem embolism as the cause for the reduced  $k_L$ . However, we found no native embolism at the end of the experiment when hydraulic measurements were made. Because all plants were irrigated twice daily with fresh water and allowed to recover for one week prior to hydraulic measurements, there is a possibility that any embolized conduits, which might have been present at the height of the drought, were refilled via bubble dissolution (Tyree and Yang, 1992) during the recovery phase. Yet, it seems unlikely that stem embolisms were responsible

for the large  $k_L$  reduction in drought plants. We used vulnerability curves (Fig. 3) to estimate embolism in stems. Midday leaf water potentials of all 3 treatments were in a range that would have caused less than 20 PLC in stems. It is, therefore, more likely that the  $k_L$  reduction was caused by stomatal closure in combination with significant reductions in  $K_{S\text{ native}}$  and possibly by embolisms in roots or leaves.

Gas-exchange rates were influenced by the plants' water transport capacity. Absolute values of  $A$  and  $k_L$  were closely related for drought and control plants (Fig. 1). When pooled, the relationship between  $A$  and  $k_L$  followed a saturation curve, similar to those observed in several previous studies (Meinzer and Grantz, 1990; Sperry et al., 1993; Meinzer et al., 1995; Saliendra et al., 1995; Hubbard et al., 2001; Stiller et al., 2003). Reduced  $k_L$  limits  $A$  by triggering stomatal closure in order to prevent an excessive drop in  $\psi_{\text{leaf}}$  (Fuchs and Livingston, 1996; Sperry, 2000) and avoid catastrophic runaway cavitation (Tyree and Sperry, 1988). We do not show the relationship between  $k_L$  and  $g_S$  (or  $E$ ) due to autocorrelation. However, we observed a strong relationship between  $A$  and  $g_S$  similar to those reported by Farquhar and Sharkey (1982) and Wong et al. (1985). Data points for all 3 treatments fell on the same saturation curve [ $y = 15.96(1 - \exp(-0.0044x))$ ,  $r^2 = 0.86$ ], indicating that the reduction of  $A$  was due to stomatal closure rather than toxic effects of salt ions (Munns et al., 1983; Munns and Passioura, 1984; Munns, 1988; Flowers and Yeo, 1986) or a direct effect of low  $\psi_{\text{leaf}}$  on photosynthetic biochemistry (Kaiser, 1987; Epron and Dreyer, 1990). These conclusions are corroborated by the close relationships between gas-exchange parameters and  $K_{S\text{ native}}$  (Fig. 2), which were measured independently on different plants and at different times during the study. The main objective during plant growth was to impose ample stress, but to avoid excessive stress levels. As a result, plants showed "classic" water stress symptoms like stomatal closure, reduced photosynthesis and low RGR (Turner et al., 1985; Schulze, 1986; Nobel and Valenzuela, 1987; Passioura, 1996).

Reduced growth rates had a significant effect on wood densities ( $\rho_w$ ) and the associated vulnerability to xylem cavitation. Drought ( $P_{50} = -2.88 \pm 0.07$ ) and salt plants ( $P_{50} = -2.50 \pm 0.08$  MPa) were less vulnerable to cavitation than control plants ( $P_{50} = -2.01 \pm 0.04$  MPa). The difference between  $P_{50}$ s of salt plants and controls matched the osmotic potential of our irrigation solution (0.5 MPa). To our knowledge, this is the first time that such a close (1:1) relationship between the magnitude of applied stress and the resulting shift in cavitation resistance was observed. At this time, our limited data set does not allow us to conclude whether this 1:1 relationship is merely coincidental or whether it truly reflects an intrinsic plant response.

Our results show that baldcypress has the ability to acclimate to its growing conditions and respond to stress with a reduction in cavitation vulnerability (Fig. 3). Cavitation vulnerability can vary greatly across species (Maherali et al., 2004) and  $P_{50}$ s of co-occurring species can be significantly different (Kolb and Davis, 1994). Additionally, substantial intraspecific variation has been observed (Matzner et al., 2001) and, within their physiological range, plants do acclimate to their respective growth conditions. This can either mean a long-term response – plants acclimating to the conditions of the growing season – such as baldcypress in the present study or as previously reported for sunflower (Stiller and Sperry, 2002). Or the acclimation to stress can occur rather rapidly. In our sunflower study, we observed a short-term response to drought stress. After a 14-day drought/irrigation cycle, sunflower stems were significantly less vulnerable to cavitation than before. The mechanisms for long- and short-term acclimation are presumably different. Long-term acclimation seems to be a consequence of altered wood properties (Hacke et al., 2001a; Jacobsen et al., 2007b,c; Pratt et al., 2007). In contrast, the observed short-term response was associated with the reversal of cavita-

tion fatigue (Hacke et al., 2001b, 2003; Stiller and Sperry, 2002), the mechanism of which is not fully understood at this time. Nevertheless, in order to reduce cavitation vulnerability, plants must reduce air seeding—i.e. the leakiness of the inter-conduit pits to air (Zimmermann, 1983; Sperry and Tyree, 1988; Tyree and Sperry, 1989; Jarbeau et al., 1995).

The anatomies of angiosperm and conifer pits are different. Increased cavitation resistance in angiosperms is associated with reduced porosity of the inter-conduit pit-membranes, which, in turn, can lower the hydraulic conductivity of the pits (Sperry, 2003; Sperry and Hacke, 2004). In comparison, conifers possess bordered pit membranes (Bauch et al., 1972), which have a relatively high hydraulic conductivity (due to their torus-margo configuration) and prevent air seeding through torus-aspiration (Sperry, 2003; Hacke et al., 2004). Thus, air seeding in conifers depends on the mechanical properties of the bordered pits and the surrounding tracheid walls (Sperry and Tyree, 1990). In order to increase cavitation resistance, conifers have to strengthen or thicken their conduit walls, which can result in increased wood density and reduced hydraulic conductivity (Hacke et al., 2001a, 2004).

It has, therefore, long been suggested that increased cavitation resistance should be associated with reduced hydraulic conductivity ( $K_S$ ) (Zimmermann, 1983; Tyree and Sperry, 1989). However, the relationship between  $K_S$  and  $P_{50}$  across different species is weak at best (Tyree et al., 1994; Maherali et al., 2004). The few significant correlations between the two parameters that have been observed in past studies mainly arise from the comparison of roots and stems within the same species or even within individual plants (Sperry and Saliendra, 1994; Matzner et al., 2001). In contrast, our results show a strong relationship between  $K_S$  and the  $P_{50}$  of *Taxodium* stems (Fig. 4, insert)—supporting the hypothesis of a trade-off between a plant's cavitation resistance and its hydraulic efficiency.

## 5. Conclusions

The results of this study show that baldcypress seedlings react to moderate soil salinity and drought stress similarly. Both treatments reduced the plants' gas exchange, diameter growth rates and hydraulic conductivity, and increased wood density. This indicates that stressed plants partitioned their biomass in a way that strengthened their xylem and reduced vulnerability to xylem cavitation. Hence, these seedlings could be better suited to be planted in environments with elevated soil salinity. Drought had an even more pronounced effect on cavitation vulnerability than salinity. This is important as nurseries could produce "stress-acclimated" seedlings simply by reducing irrigation amounts and would not have to contaminate the soils in their nursery beds with salt applications. Whether stress-acclimated seedlings truly have lower mortality rates in saline environments is currently under investigation.

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