Adjustments in hydraulic architecture of *Pinus palustris* maintain similar stomatal conductance in xeric and mesic habitats


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**ABSTRACT**

We investigated relationships between whole-tree hydraulic architecture and stomatal conductance in *Pinus palustris* Mill. (longleaf pine) across habitats that differed in soil properties and habitat structure. Trees occupying a xeric habitat (characterized by sandy, well-drained soils, higher nitrogen availability and lower overstory tree density) were shorter in stature and had lower sapwood-to-leaf area ratio ($A_{s}/A_{l}$) than trees in a mesic habitat. The soil-leaf water potential gradient ($\Psi_{s}-\Psi_{l}$) and leaf-specific hydraulic conductance ($k_{l}$) were similar between sites, as was tissue-specific hydraulic conductivity ($K_{s}$) of roots. Leaf and canopy stomatal conductance ($g_{s}$ and $G_{c}$, respectively) were also similar between sites, and they tended to be somewhat higher at the xeric site during morning hours when vapor pressure deficit ($D$) was low. A hydraulic model incorporating tree height, $A_{s}/A_{l}$, and $\Psi_{s}-\Psi_{l}$ accurately described the observed variation in individual tree $G_{net}$ ($G_{s}$ at $D = 1$ kPa) across sites and indicated that tree height was an important determinant of $G_{net}$ across sites. This, combined with a 42% higher root-to-leaf area ratio ($A_{r}/A_{l}$) at the xeric site, suggests that xeric site trees are hydraulically well equipped to realize equal and – sometimes higher – potential for conductance compared with trees on mesic sites. However, a slightly more sensitive stomatal closure response to increasing $D$ observed in xeric site trees suggests that this potential for higher conductance may only be reached when $D$ is low and when the capacity of the hydraulic system to supply water to foliage is not greatly challenged.

**Key-words:** habitat structure; hydraulic conductance; leaf water potential; longleaf pine; stand density; tree height; water relations.

**INTRODUCTION**

Stomatal conductance is well-correlated with hydraulic conductance along the soil to leaf pathway (Sperry, Alder & Eastlack 1993; Saliendra, Sperry & Comstock 1995; Bond & Kavanagh 1999; Meinzer et al. 1999; Hubbard et al. 2001). Hydraulic conductance (leaf-specific: $k_{l}$), in turn, is closely linked to plant hydraulic architecture, including sapwood-to-leaf area ratio ($A_{s}/A_{l}$), root-to-leaf area ratio ($A_{r}/A_{l}$), tissue-specific hydraulic conductivity ($K_{s}$) and plant stature or height ($h$) (Andrade et al. 1998; Ewers, Oren & Sperry 2000; Hacke et al. 2000; Schäfer, Oren & Tenhunen 2000; Maherali & DeLucia 2001; Mencuccini 2000). Increases in $k_{l}$ are correlated with increases in $A_{s}/A_{l}$, $A_{r}/A_{l}$ and $K_{s}$. Furthermore, $k_{l}$ has been shown to decrease with increasing tree height. Such adjustments in hydraulic architecture are influenced by environment and occur to balance $k_{l}$ and leaf gas exchange with avoidance of xylem dysfunction and hydraulic failure (Sperry et al. 2002; Katul, Leuning & Oren 2003).

A host of environmental variables have been shown to influence hydraulic architecture. Soil water limitation, for example, promotes biomass allocation below ground, thereby increasing standing root crop and $A_{r}/A_{l}$ (Comeau & Kimmins 1989; Gower et al. 1994; Albaugh et al. 1998; Hacke et al. 2000). Plants occupying more arid habitats maintain higher $A_{s}/A_{l}$ than plants growing in areas where atmospheric moisture is not as limiting (Callaway, DeLucia & Schlesinger 1994; Mencuccini & Grace 1995). Nitrogen fertilization has been shown to encourage leaf area production (Albaugh et al. 1998), thereby decreasing both $A_{r}/A_{l}$ and $A_{s}/A_{l}$. Soil moisture, aridity and nitrogen availability have all been shown to influence $K_{s}$ and vulnerability to xylem cavitation in various ways (Alder, Sperry & Pockman 1998; Ewers et al. 2000; Hacke et al. 2000; Maherali & DeLucia 2000). In addition to resource-related influences, hydraulic architecture has also been shown to vary according to habitat structural influences such as stand density (Whitehead, Jarvis & Waring 1984). Individual tree leaf area ($A_{l}$), canopy structure, tree height–diameter relation-
ships and biomass allocation among roots, shoots and leaves have all been shown to be influenced by stand density (Pearson, Fahey & Knight 1984; Dean & Long 1986, 1992; Oren et al. 1987). These findings in total indicate that adjustments in tree form and hydraulic architecture are made at a variety of scales, from tissues to whole trees to stands. Furthermore, these studies illustrate that the factors influencing hydraulic architecture are complex, and understanding them and their effects on stomatal conductance requires consideration of several habitat components, including resource availability and feedbacks between resource availability and habitat structure. Few studies, however, have evaluated hydraulic architecture and its consequence on stomatal conductance in this entire context.

We investigated factors influencing hydraulic architecture, hydraulic conductance and stomatal conductance for Pinus palustris (Mill.) at extreme ends of a resource availability and community composition gradient within the coastal plain region of the south-eastern United States. P. palustris has a wide ecological distribution within this region, occupying coarse-textured soils that can be extremely droughty during summer, as well as finer-textured soils often underlain by clay pans. Changes in stand structure are concomitant with changes in soil texture along this gradient. In more mesic habitats, P. palustris is the dominant overstory species, forming almost monotypic stands where fire is maintained. Some hardwood species, Quercus virginiana (Mill.), for example, are also typical in the midstory (Abrhamson & Hartnett 1990), but their density is generally low depending on the frequency and intensity of fire. In more xeric habitats, P. palustris still dominates the overstory, but the density of drought-adapted Quercus spp., primarily Q. laevis (Walt.), Q. margaretta (Ash) and Q. geminata (Small), increases dramatically in the midstory (Jacquin, Jones & Mitchell 1999). Overstory density and leaf area indices in these xeric habitats are still much lower relative to mesic habitats (Mitchell et al. 1990) and trees in xeric habitats are also shorter in stature. Per cent soil moisture in the upper soil profile is consistently lower at the xeric end of the gradient, yet soil nitrogen mineralization is higher due to higher soil temperature (Wilson et al. 1999, 2002).

For P. palustris occupying xeric and mesic habitats, we measured the following architectural and physiological variables: A_{G,A1}, A_{G,A1}, tree height, leaf water potential (Psi), k, leaf stomatal conductance (g_{s}) and sap-flux-scaled canopy stomatal conductance (G). Stomatal conductance across sites was evaluated in the context of hydraulic architecture using the hydraulic model of Schäfer et al. (2000). The goal of the study was to characterize hydraulic and stomatal behaviour under favourable soil moisture conditions in both habitats. We also provide some discussion and speculation about the potential role of drought and soil moisture decline across habitats. We predicted that xeric site trees would exhibit shifts in hydraulic architecture aimed at improving leaf water status, but that stomatal conductance would still be lower in trees occupying xeric versus mesic habitats.

MATERIALS AND METHODS

Study sites

Sites for this study were established in representative xeric and mesic P. palustris habitats at the Joseph W. Jones Ecological Research Center in south-west GA, USA (31°N, 84°W). Regional mean daily temperatures range from 21 to 34 °C in summer to 5–17 °C in winter, and mean annual precipitation is 1310 mm (Goebel et al. 2001). The two sites are located 5 km from one another and they experience similar climate. The sites were defined as xeric and mesic based on the drainage characteristics of their soils and on the composition of the woody plant community. The xeric site occurred on an upland sand ridge and had deep, sandy soils classified as Typic Quartzipsamments, with relatively low water holding capacity (WHC) (18 cm water per m soil in the upper 3 m) and no argillic horizon (i.e. no significant accumulation of clay) within 3 m (Goebel et al. 2001). This site measured 1.32 ha and contained 71 pine trees and 494 oak trees, the majority of which were Q. laevis. The mesic site occurred on an upland terrace and had soils classified as Aquic Arenic Kandiudults, with higher WHC (40 cm water per m soil in the upper 3 m) and an argillic horizon within 0.5 m of the soil surface (Goebel et al. 2001). These soils were sandy loam over sandy clay loam or clay. The site established in this habitat contained 121 pine trees and no oaks over an area of 0.53 ha. Soil texture fractions (per cent sand, silt, clay) for both sites for the upper 1 m soil are reported in Goebel et al. (2001) and are shown in Table 1. Saturated soil hydraulic conductivity (K_s) was measured at three depth intervals (0–40, 41–100 and 101–200 cm) at three locations per site using a compact constant head permeameter (Amoozemeter, Ksat, Inc., Raleigh, NC, USA). Stand inventory measurements, including stand density, basal area, mean tree diameter at breast height (DBH), mean tree height and mean age were made for both sites prior to the study (Mitchell et al. 1999) and are also presented in Table 1. Stands at both sites are multi-aged. Scaffolds towers were constructed prior to the study, permitting canopy access to three P. palustris trees on each site. Both sites were managed using prescribed fire and were burned in winter 2000 prior to sampling.

A_{c}

Tree A_{c} (m²) was estimated for each site using site-specific allometric equations developed at the beginning of the 2000 growing season. Branch harvests were conducted during January–February 2000 on 15 and 17 xeric and mesic site trees, respectively. Trees representing the full range of sizes present on each site were randomly selected along transects adjacent to each site. The diameter of every branch in each tree was measured by climbing the trees, and six branches per tree (two per crown third) were randomly selected and cut. Needles from cut branches were collected and dried in the laboratory to constant mass (g) at 70 °C. Projected A_{c} (cm²) was measured on a subsample of fresh needles from each branch using a leaf area meter (LI-3100, Li-Cor

Table 1. Soil and stand characteristics for xeric and mesic habitats. Soil texture fraction (per cent sand, silt, clay) and WHC represent means (n = 3 measurement locations per site; ±1 SE) taken from Goubel et al. (2001).

<table>
<thead>
<tr>
<th>Soil characteristics</th>
<th>Xeric</th>
<th>Mesic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand fraction (%)</td>
<td>89.3 (0.8)</td>
<td>63.4 (1.5)</td>
</tr>
<tr>
<td>Silt fraction (%)</td>
<td>7.1 (1.1)</td>
<td>24.3 (3.1)</td>
</tr>
<tr>
<td>Clay fraction (%)</td>
<td>3.7 (0.3)</td>
<td>12.4 (4.6)</td>
</tr>
<tr>
<td>WHC (cm m⁻¹)</td>
<td>18.0</td>
<td>40.0</td>
</tr>
<tr>
<td>Kₗₑₑ (cm h⁻¹)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–40 cm</td>
<td>49.8 (8.8)</td>
<td>5.3 (0.9)</td>
</tr>
<tr>
<td>41–100 cm</td>
<td>48.7 (13.7)</td>
<td>3.2 (1.2)</td>
</tr>
<tr>
<td>101–200 cm</td>
<td>43.1 (2.2)</td>
<td>0.2 (0.04)</td>
</tr>
</tbody>
</table>

Stand characteristics for *Pinus palustris*

| Density (trees ha⁻¹) | 54          | 230        |
| Basal area (m² ha⁻¹) | 2.7         | 10.7       |
| Mean DBH (cm)        | 24.7 (8.6–49.1) | 21.8 (7.5–52.9) |
| Mean age (years)     | 57 (7–198)  | 44 (19–166) |
| Mean height (m)      | 13.7 (6.3–20.8) | 17.7 (8.3–24.2) |
| SAI (cm² m⁻²)        | 2.18        | 7.93       |
| RA₁ (m² m⁻⁴)         | 0.67        | 1.31       |
| LA₁ (m² m⁻³) (min–max) | 0.22–0.39  | 0.65–1.11  |
| Aₓ₁/A₁ (cm² m⁻³)     | 5.6         | 7.1        |
| Aₑₑ₁/Aₑₑ (m² m⁻³)   | 1.7         | 1.2        |

Saturated soil hydraulic conductivity (*Kₗₑₑ*) was measured at three soil depth intervals at *n* = 3 measurement locations per site. Stand characteristics are for *P. palustris* only on each site (*Quercus* spp. codominant xeric site). Values in parentheses for soil characteristics are ±1 SE. Values in parentheses for the stand characteristics are ranges. Calculation of *Aₓ₁/A₁* and *Aₑₑ₁/Aₑₑ* used estimates of *Aₑₑ* averaged for November–December 2000, corresponding to the period when roots were collected.

WHC, water holding capacity; DBH, diameter at breast height; SAI, sapwood area index; LA₁, leaf area index; RA₁, root area index for roots < 5 mm in diameter; *Aₓ₁/A₁*, sapwood area to leaf area ratio; *Aₑₑ₁/Aₑₑ*, root area to leaf area ratio.

Instruments, Lincoln, NE, USA). Specific *Aₑₑ* (cm² g⁻¹) was then calculated and used to convert bulk needle dry weight to leaf area for each harvested branch. Log-log relationships between branch diameter and branch leaf area were developed from harvested branches at each site and used to predict entire tree *Aₑₑ* via branch summation. Log-log relationships between DBH and *Aₑₑ* were then developed for each site. Site differences in the relationship between DBH and *Aₑₑ* were tested using analysis of covariance (ANCOVA) to determine if the models could be reduced across sites. The slope of the DBH–*Aₑₑ* relationship was significantly different between sites (*P* < 0.001), indicating that separate models were appropriate. These models are shown in Table 2 and were used to estimate *Aₑₑ* of all other trees on each site. Leaf area index (LA₁, m² projected leaf surface m⁻² ground) was determined as the sum of *Aₑₑ* for each site divided by ground area. Regular measurements of needle elongation and senescence in the tower-accessible trees on each site by Shefield et al. (2003) were used to estimate seasonal changes in *Aₑₑ* and LA₁ as described in Addington et al. (2004).

Sapwood area (*Aₓ₁*)

*Aₓ₁* (cm²) was estimated for each site from increment cores collected from 16 trees on the xeric site and 18 on the mesic site during October 2000. Sapwood length was determined by visual inspection of the core and converted to area based on the area of a circle, subtracting the area represented by the heartwood and bark. Log-log relationships between DBH and *Aₓ₁* were developed for each site separately and tested as above to determine if the models could be reduced across sites. In this case, there was no significant difference between the sites regarding the relationship of DBH to *Aₓ₁* (*P* = 0.534), indicating that a single model was appropriate as follows:

\[ \log Aₓ₁ = 1.929 \cdot \log \text{DBH} - 0.1281 \]

\[ r^2 = 0.97, P < 0.001. \]  \( (1) \)

Table 2. Leaf area (*Aₑₑ*, m²) predictions from DBH (cm) for xeric and mesic site trees determined from pre-growing season branch harvests

<table>
<thead>
<tr>
<th>Site</th>
<th>Y</th>
<th>X</th>
<th>a</th>
<th>b</th>
<th>r²</th>
<th>P (&lt;)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xeric</td>
<td>log<em>Aₑₑ</em></td>
<td>logDBH</td>
<td>-0.908</td>
<td>1.854</td>
<td>0.99</td>
<td>0.001</td>
<td>15</td>
</tr>
<tr>
<td>Mesic</td>
<td>log<em>Aₑₑ</em></td>
<td>logDBH</td>
<td>-1.192</td>
<td>1.944</td>
<td>0.98</td>
<td>0.001</td>
<td>17</td>
</tr>
</tbody>
</table>

Equations are in the form: \( Y = a + b \cdot X \).

DBH, diameter at breast height.

At both sites, $A_s$ for all *P. palustris* trees was estimated and summed to sapwood area index (SAI, cm$^2$ sapwood area m$^{-2}$ ground) (Table 1). The $A_L$/$A_s$ presented in Table 1 was calculated by dividing SAI by LAI, using LAI averaged for November–December corresponding to the period when roots were collected.

**Root area and $K_s$**

Root area index (RAI, m$^2$ root surface area m$^{-2}$ ground) and root depth distribution were determined in November–December 2000, by excavating 2-m-deep, $2 \times 0.5$ m$^2$ pits adjacent to each site (n = 5 pits per site). Roots were collected at 20 cm depth intervals, separated from non-pine species and sorted into four diameter classes: $< 1$, 1–2, 2–5 and 5–12 mm. The diameter and length of each root $> 2$ mm (i.e. 2–5- and 5–12-mm-diameter classes) were measured and the area was calculated based on the area of cylinder. For finer roots ($< 1$- and 1–2-mm-diameter classes), total root length was estimated using ratios of root length per unit dry mass (specific root length, cm g$^{-1}$) determined for subsamples in each depth class on each site. Area was then calculated based on the area of a cylinder using the mid-point of each diameter class. Scaling from the pit to the stand level was then achieved as follows: a geographic information system (GIS) calculated the total number of $2 \times 0.5$ m$^2$ polygons that could be drawn within each stand and then measured the distance from the centre of each polygon to the nearest *P. palustris* tree. ‘Distance to nearest tree’ classes were then derived based on a frequency distribution, and pit locations were chosen to represent each of these classes. To estimate RAI, total root area from each pit was weighted by the proportion of total polygons represented by each class (i.e. number of polygons in each class relative to the total number of polygons). Only roots $< 5$ mm were used to estimate RAI (Ewers et al. 2000; Hacke et al. 2000). Estimates in Table 1 represent the root area summed over the 2 m depth profile per unit ground area. The $A_L$/$A_s$ was calculated by dividing RAI by LAI, again using LAI averaged for November–December.

$K_s$ (kg m$^{-3}$ s$^{-1}$ MPa$^{-1}$) was measured on six roots, $< 5$ mm in outer diameter, per site. These measurements represent root xylem axial conductivity. Roots were collected in the upper 0.2 m soil on each site and $K_s$ was measured for different xylem cavitation-inducing pressures simulated in the laboratory via the centrifugal force method described in Alder et al. (1997) and Hacke et al. (2000).

**$y_L$ and $g_s$**

$y_L$ (MPa) and $g_s$ (mmol m$^{-2}$ s$^{-1}$) were measured in the upper canopy thirds of the three tower-accessible trees on each site throughout the growing season, March–October 2000. Pre-dawn, midmorning and midday measurements of $y_L$ were made approximately every 2 weeks using a pressure chamber (Model 1062, PMS Instruments, Corvallis, OR, USA). Mid-morning and midday measurements of $g_s$ were made every 4–5 weeks using a portable infrared gas analyser (IRGA) equipped with an artificial light source (Model LI-6400, Li-Cor Instruments). To isolate the influence of hydraulic architecture on $y_L$, the influence of environmental variables on $g_s$ had to be removed. This was done by holding photon flux density at a constant 1000 μmol m$^{-2}$ s$^{-1}$ inside the chamber, and maintaining CO$\_2$ concentration at 350 μmol. Needle temperature and relative humidity (RH), however, were allowed to vary with atmospheric conditions so that data would be collected over a range of vapour pressure deficit ($D$). The $D$ range was 0.99–4.67 kPa on the xeric site (median = 2.41 kPa) and 1.18–4.45 kPa on the mesic site (median = 2.65 kPa). A boundary line analysis was done at the end of the season to depict the upper boundary of the response of $g_s$ to $D$ for each tree (Schäfer et al. 2000). This analysis removed the influence of all other environmental variables on the response of $y_L$ to $D$, including effects of a drought that occurred early in the growing season (Addington et al. 2004). A reference $g_s$ ($g_{so}$), defined as $g_s$ at 1 kPa $D$, was then generated by fitting the data to the functional form:

$$g_s = b - m \cdot \ln D,$$  \hspace{1cm} (2)

where the $y$-intercept represents $g_{so}$ at 1 kPa $D$, and the slope of the relationship between $g_s$ and $\ln D$ ($-dg/d\ln D$), represents the sensitivity of the stomatal response to $D$ (Oren et al. 1999). Measurements of $g_s$ were made on both previous- and current-year needles once new needles reached at least 50% of total elongation. This occurred in August 2000. All measurements of $g_s$ are reported on a leaf area basis, determined by measuring needle radius using digital calipers and calculating all-sided leaf area inside the chamber assuming a cylindrical needle shape (Svensson & Davies 1992).

**$G_s$ and $k_L$**

$G_s$ (mmol H$_2$O m$^{-2}$ s$^{-1}$) was calculated from measurements of sap flux density ($J_s$, mm$^{-2}$ s$^{-1}$) made in the xylem of seven trees on each site during September 2000. Trees were selected to represent the range of tree sizes present on each site and included the three tower-accessible trees on each site (Table 3). Xeric site measurements took place on 2–4, 8–14 and 29 September while mesic site measurements were conducted on 3, 9, 12–14 and 26–29 September. Thermal dissipation probes (TDPs) (Model TDP30, Dynamax, Inc., Houston, TX, USA) were used to measure $J_s$ based on the technique of Granier (1987). Probes were installed in the outer 30 mm of hydroactive xylem at a stem height of 1.3 m on the north side of all trees. Variation in $J_s$ with radial depth was evaluated for the three tower trees on each site by installing north-facing TDPs at 30–60 mm sapwood depth. These measurements were made on 28–30 August, prior to the September measurements. To scale $J_s$ across the entire radial profile, the per cent of hydroactive xylem represented by $0–30$ and $30–60$ mm sapwood depths were plotted against per cent flux measured at these depths (Ford et al. 2004a). Per cent flux beyond 60 mm sapwood depth was then determined based on per cent of hydroactive
Table 3. Response of stomatal conductance at leaf ($g_s$) and canopy ($G_A$) scales to vapour pressure deficit ($D$) in xeric and mesic site trees of various DBH, tree heights (Ht) and ages.

<table>
<thead>
<tr>
<th>Site</th>
<th>DBH (cm)</th>
<th>Ht (m)</th>
<th>Age (year)</th>
<th>$g_s$ at $D = 0$</th>
<th>$\frac{d}{dlnD}g_s$</th>
<th>$\frac{d}{dlnD}G_A$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xeric</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.0</td>
<td>11.1</td>
<td>52</td>
<td></td>
<td>86.15</td>
<td>56.19</td>
<td>0.95</td>
<td>17</td>
</tr>
<tr>
<td>20.3</td>
<td>13.6</td>
<td>53</td>
<td></td>
<td>99.40</td>
<td>61.79</td>
<td>0.95</td>
<td>20</td>
</tr>
<tr>
<td>22.3</td>
<td>14.9</td>
<td>55</td>
<td></td>
<td>61.14</td>
<td>43.77</td>
<td>0.91</td>
<td>18</td>
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<tr>
<td>27.3*</td>
<td>17.0</td>
<td>47</td>
<td></td>
<td>135.10</td>
<td>76.45</td>
<td>0.83</td>
<td>14</td>
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<tr>
<td>30.0*</td>
<td>17.9</td>
<td>44</td>
<td></td>
<td>131.21</td>
<td>69.94</td>
<td>0.78</td>
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<tr>
<td>32.6*</td>
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<td>130.29</td>
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<td>0.86</td>
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<tr>
<td>36.2</td>
<td>17.7</td>
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<td></td>
<td>74.30</td>
<td>55.92</td>
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<tr>
<td>Mesic</td>
<td></td>
<td></td>
<td></td>
<td>75.27</td>
<td>65.23</td>
<td>0.97</td>
<td>11</td>
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<tr>
<td>17.5</td>
<td>17.6</td>
<td>46</td>
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<td>66.12</td>
<td>49.42</td>
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<td>57.68</td>
<td>36.71</td>
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<tr>
<td>26.9</td>
<td>21.0</td>
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<td></td>
<td>39.05</td>
<td>33.84</td>
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<td>29.4</td>
<td>18.1</td>
<td>57</td>
<td></td>
<td>37.2*</td>
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<td>0.97</td>
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<td>37.2*</td>
<td>25.7</td>
<td>73</td>
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<td>110.27</td>
<td>53.40</td>
<td>0.80</td>
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<tr>
<td>39.6*</td>
<td>26.6</td>
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<tr>
<td>39.8*</td>
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<td>69</td>
<td></td>
<td>119.93</td>
<td>67.17</td>
<td>0.79</td>
<td>14</td>
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</tbody>
</table>

Data were evaluated by fitting the upper boundary of the $g_s$ and $G_A$ response to $D$ to the functional form: $g_s = G_0 e^{-a \cdot D}$. This analysis generates a reference stomatal conductance ($g_s$ at $D = 1$ kPa) equal to $g_s$ and $G_A$ at 1 kPa D, and a corresponding sensitivity to increasing D equal to the slope of the $g_s$ and $G_A$ response to D ($\frac{d}{dlnD}g_s$ and $\frac{d}{dlnD}G_A$ in mmol m$^{-2}$ s$^{-1}$ kPa$^{-1}$). Leaf data represent measurements made approximately monthly from March–October 2000, while canopy data on each site is for several days in September 2000. The number of points in each regression relationship is shown in the column labelled n. Trees accessible by canopy scaffold towers are denoted by an asterisk (*).

DBH, diameter at breast height.

xylem beyond 60 mm using a 3-parameter Gaussian function (Ford et al. 2004a). Radial profiles for trees on which $J_e$ was measured only in the outer 30 mm xylem were similarly obtained using the Gaussian function to predict radial decline based on per cent of hydroactive xylem measured in each tree. Because radial variation tended to change according to driving force and maximum flux, midday averages were used, corresponding to the time period when $J_e$ was relatively stable and when stored water was less likely to have a large influence on $J_e$ (Oren et al. 1998; Ewers & Oren 2000; Ford et al. 2004a,b). All probes were insulated from solar radiation using reflective shielding and $J_e$ was recorded every minute and averaged over a 30 min interval using dataloggers (Model CR-10, Campbell Scientific, Inc., Logan, UT, USA). Neither site had a continuous power source, so dataloggers were powered by battery. The measurement dates listed above appear sporadic because days in which batteries were not fully charged were removed from the analysis.

Transpiration per unit leaf area ($\frac{E_l}{A_L}$, kg m$^{-2}$ leaf s$^{-1}$) was estimated by multiplying whole-tree $E_l$ by $A_L$/$A_L$ determined for each tree. $k_l$ (kg m$^{-2}$ leaf h$^{-1}$ MPa$^{-1}$) was calculated for the three tower-accessible trees on each site on two of the measurement days (13–14 September), corresponding to days when $Y_L$ was measured. Midday $E_l$ was divided by the midday water potential gradient ($\Psi_L - \Psi_h$) using pre-dawn $\Psi_L$ as a proxy for $\Psi_L$ and correcting for gravitational effects on the water column of height $h$ and density $\rho$ ($\frac{h \rho g}{9.81}$). $G_s$ was calculated for all seven trees on each site using the following equation derived from Whitehead & Jarvis (1981):

$$G_s = (G_s, T, \rho E_l) D,$$  (3)

where $G_s$ is the universal gas constant adjusted for water vapour (0.462 m$^2$ kPa K$^{-1}$ kg$^{-1}$), $T_s$ is the air temperature in degrees K and $\rho$ is the density of water (998 kg m$^{-3}$). The Tenets formula (Murray 1967) was used to calculate C from canopy $T_A$ and RH. This calculation substituted $T_A$ for leaf temperature based on the assumption that the canopy and surrounding atmosphere are closely coupled due to the open nature and roughness of the coniferous canopy on both study sites. Both $T_A$ and RH were measured using T-A RH sensors (Model H8, HOBO Computer Corp., Bourne, MA, USA) affixed to each tower in the upper canopy third. Solar radiation was measured at a weather station located between the sites using a pyranometer (Model LI-200S, Li-Cor Instruments).

Statistical and model analysis

Analysis of covariance (ANCOVA) was employed for testing differences between sites for most variables, including the relationship between DBH and tree height, DBH and $A_L$, DBH and $A_L$, soil depth and $A_L$, $D$, and pre-dawn $\Psi_L$, $D$, and $G_s$. In cases where these relationships were non-linear, variables were log-transformed to meet the assumption of linearity in ANCOVA. Differences among slope coefficients were tested first and if there was no significant difference, tests for differences between intercepts were carried out. All analyses were conducted using individual trees (or pits in the case of root area analyses) within each site and were performed using the general linear model (GLM) procedure in SAS version 8.1 (SAS Institute, Cary, NC, USA). All linear and non-linear curve-fits were made using SigmaPlot software (SigmaPlot v5.0; SPSS, Chicago, IL, USA).

To facilitate comparison of $G_s$ between sites, a boundary line analysis that incorporated solar radiation and $D$ was performed and a reference $G_s$ ($G_{xer}$) was determined for each tree, as described for leaf-level $g_s$ measurements. Data where $D < 0.60$ kPa were removed from this analysis to minimize any errors associated with calculating $G_s$ at low $D$ (Ewers & Oren 2000). The range of $D$ over which data was collected and used in this analysis was $0.60-2.51$ kPa on the xeric site (median = 1.26 kPa) and 0.80-2.30 kPa on the mesic site (median = 1.07 kPa). The influence of hydraulic architecture on stomatal conductance across sites was then evaluated using $G_{xer}$ and the hydraulic model of Schäfer et al. (2000):

$$G_{xer} = E_{c} = (1/h) \cdot (A_s/A_t) \cdot (\Psi_s - \Psi_L - hpg).$$

(4)

The model assumes that $k_s$ is proportional to the term $(1/h) \cdot (A_s/A_t)$, that is, $k_s$ is inversely proportional to $h$ or the path length over which water must travel and is directly proportional to $A_s$ or the conducting area. The proportionality to $A_t$ implicitly assumes that the sapwood-area-specific conductivity of the plant trunk does not vary between sites or with age. The bases for these assumptions are described more comprehensively by Schäfer et al. (2000). Although we measured $K_s$ in roots and found similarity between sites (see below), these estimates were not included in the model because they represent only the root portion of soil-leaf conductivity. For modelling purposes, $A_s/A_t$ was estimated from $h$ using the relationship between $A_s/A_t$ and $h$ presented in Fig. 2. The pooled average $\Psi_s - \Psi_L$ across sites was used for the term $\Psi_s - \Psi_L - hpg$, and this term was allowed to vary with changes in $hpg$. The model predicted a relative change in $G_{xer}$ expected across trees based on relative changes in each of the input variables. Each input variable was normalized by its average across trees to derive this relative change. The relative variation in $G_{xer}$ predicted by the model for each tree was then multiplied by the average actual $G_{xer}$ across trees to generate the dashed line in Fig. 8.

**RESULTS**

Maximum pine LAI occurred in September for both sites and was nearly a third at the xeric relative to the mesic site, reflecting the lower density of pine at the xeric site (Table I). Leaf area per tree at a given DBH was significantly higher at the xeric site ($P < 0.001$), but sapwood area per DBH was similar ($P = 0.534$), leading to lower $A_s/A_t$ for xeric site trees compared to those on the mesic site (Table I). Tree height for a given DBH was significantly lower on the xeric site ($P < 0.001$; Fig. 1), and the increase in $A_s/A_t$ from the xeric to the mesic site was positively, though weakly, correlated with the increase in tree height across stands ($r^2 = 0.26$, $P < 0.01$; Fig. 2). The relationship between $A_s/A_t$ and tree height was more obvious within the xeric stand than within the mesic stand (Fig. 2).

Pine RAI was lower on the xeric site, again reflecting the lower pine density on this site, but this is likewise compensated for by a higher amount of mean root area per individual tree (Table I). The analysis revealed no site by soil depth interaction ($P = 0.187$), indicating that the stands had similar root distribution with depth (Fig. 3). Although both total root and leaf areas were lower at the xeric site, $A_s/A_t$ was 42% higher on this site relative to the mesic site (Table I). There was no significant difference between sites in the response of $K_s$ of roots to xylem pressure ($P = 0.771$), and no significant difference in maximum $K_s$ at a given xylem pressure ($P = 0.324$), though mean maximum $K_s$ was slightly higher on the xeric site (Fig. 4).

$\Psi_s$ varied with $D$, but no site differences were observed in the relationship between $\Psi_s$ and $D$ ($P = 0.441$). $\Psi_s$ at a given $D$ was similar at both sites ($P = 0.231$), though $\Psi_s$ tended to be slightly less negative on the xeric site, particularly before dawn when $D$ was low (Fig. 5). Mean predawn $\Psi_s$ over the course of the measurement period was $-0.49$ and $-0.58$ MPa for the xeric and mesic sites, respectively. Mean mid-morning $\Psi_s$ was $-1.06$ and $-1.12$ MPa, and mean midday $\Psi_s$ was $-1.58$ and $-1.67$ MPa for xeric and mesic, respectively. The soil-leaf water potential gradient ($\Psi_s - \Psi_L$) was likewise similar between the sites (1.08 and
Figure 3. Root area index (RAI) of *Pinus palustris* roots < 5 mm diameter at 0.2 m depth intervals for xeric and mesic sites. Values represent the mean of *n* = 5 excavation pits per site (± 1 SE).

1.09 MPa for xeric and mesic, respectively). Incorporating the effect of gravity on the $\Psi_s - \Psi_p - h_p g$ (using 0.01 MPa per m tree height), however, showed that xeric site trees had a slightly higher average driving force for water flow owing to their shorter stature (0.90 and 0.84 MPa for xeric and mesic, respectively), $k_l$, was similar between the sites ($t$-test, $P = 0.232$; Fig. 6).

The response of $g_s$ to $D$ was also similar between sites (slopes comparison, $P = 0.239$), and there was no significant difference in $g_s$ at a given $D$ (intercepts comparison, $P = 0.015$; Fig. 7). Again, however, $g_s$ tended to be higher at low $D$ on the xeric site and showed a somewhat more sensitive stomatal response to increasing $D$. At the reference $D$ ($D = 1$ kPa), $g_s$ averaged 13% higher on the xeric site compared to the mesic site (132.20 versus 117.67), and the average slope of the $g_s$ to ln$D$ response ($-dG_s/dlnD$) was 73.97 and 63.42 for the xeric and mesic sites, respectively (Table 3). There was no significant difference between needle-age classes (current- versus previous-year needles) in the response of $g_s$ to $D$ for either site (minimum $P = 0.106$).

Patterns in $g_s$ and response to $D$ observed between sites at the leaf level were similar at the canopy level. $G_s$ at the xeric site showed a slightly more sensitive stomatal response to increasing $D$, though there was no significant difference in the overall response of $G_s$ to $D$ between sites ($P = 0.651$). The average slope of the $G_s$ response to ln$D$ ($-dG_s/dlnD$) was 43.03 and 34.24 for the xeric and mesic sites, respectively (Table 3). At 1 kPa $D$, $G_s$ (= $G_{max}$) was an average 30% higher on the xeric site compared to the mesic site (62.26 versus 47.75), yet there was no statistically sig-

Figure 4. Response of tissue specific hydraulic conductivity ($K_t$) of roots < 5 mm diameter to increasingly negative root xylem pressure for *n* = 6 (means ± 1 SE) xeric and mesic site roots.

Figure 5. Leaf water potential ($\Psi_L$) at a given vapour pressure deficit ($D$) for xeric and mesic sites measured biweekly, March-October 2000. Values represent mean of *n* = 3 trees per site (± 1 SE).

Figure 6. Leaf specific hydraulic conductance ($k_l$) for xeric and mesic sites. Values represent *n* = 3 trees per site (means ± 1 SE) averaged for 13–14 September 2000.
significant difference in $G_{\text{sat}}$ between sites ($P = 0.499$). The higher mean $G_{\text{sat}}$ observed on the xeric site appeared largely attributable to differences in tree height. A decline in $G_{\text{sat}}$ with increasing tree height was observed across sites ($r^2 = 0.52, P = 0.018$; Fig. 8), implying that a single $G_{\text{sat}}$-tree-height relationship explains the data well across the sites. The predicted decline in $G_{\text{sat}}$ with increasing tree height based on the hydraulic model in Eqn 4 is shown as the dashed line in Fig. 8. Model output closely follows the least square fit to the actual data.

DISCUSSION

To successfully extract and use water, plants that exist across a range of habitats must make adjustments in hydraulic architecture that maintain hydraulic compatibil-

Figure 7. Response of $g_s$ to increasing vapour pressure deficit ($D$) for previous-year needles on xeric and mesic sites measured monthly, March–October 2000. Values represent mean of $n = 3$ trees per site (± 1 SE), and regression curves represent the upper boundary of the response on both sites.

Figure 8. Decline in canopy stomatal conductance at a reference vapour pressure deficit ($G_{\text{sat}}$, $D = 1$ kPa) with increasing tree height across xeric and mesic sites measured for several days in September 2000. Solid line represents least square fit to the data ($r^2 = 0.52, P = 0.0177$), while dashed line shows the expected decline across sites based on observed architectural adjustments and the hydraulic model (Eqn 4).
In our study, differences in \( A_{\text{x}}/A_{\text{m}} \) across sites appeared to be due primarily to differences in the height distribution of trees. Consistent with other studies (Schäfer et al. 2000; McDowell et al. 2002), we observed an increase in \( A_{\text{x}}/A_{\text{m}} \) with increasing tree height across sites (Fig. 2). Our use of the hydraulic model (Eqn 4) showed that tree height and \( A_{\text{x}}/A_{\text{m}} \) influenced water transport and stomatal conductance in counteracting ways. To illustrate this, the hydraulic model can be modified to represent a predicted ratio of \( G_{\text{net}} \) between sites \((G_{\text{x}}/G_{\text{me}})\) based on ratios of input variables as follows:

\[
G_{\text{x}}/G_{\text{me}} = \left( h_{\text{x}}/h_{\text{me}} \right) \cdot \left( A_{\text{x}}/A_{\text{me}} \right) \cdot \left( \Delta \Psi_{\text{x}}/\Delta \Psi_{\text{me}} \right).
\]

where \( h_{\text{x}}/h_{\text{me}} \) is the xeric/mesic inverse height ratio, \( A_{\text{x}}/A_{\text{me}} \) is the ratio of \( A_{\text{x}}/A_{\text{me}} \) and \( \Delta \Psi_{\text{x}}/\Delta \Psi_{\text{me}} \) is the ratio \( \Psi_{\text{x}} - \Psi_{\text{c}} \) between sites, adjusted for gravity. Using the values in Table 1, \( h_{\text{x}}/h_{\text{me}} \) equals 1.29, meaning that in isolation the reduced path length afforded by shorter trees on the xeric site would translate to 29% higher conductance in xeric site trees versus those in the mesic site. The term \( A_{\text{x}}/A_{\text{me}} \) equals 0.79, which would result in a similar proportion of stomatal conductance. Combining these two factors in Eqn 5 shows that the effect on mean stomatal conductance of higher \( A_{\text{x}}/A_{\text{m}} \) in the mesic stand nearly exactly compensated for the effect of greater tree height (i.e. predicted \( G_{\text{x}}/G_{\text{me}} \) is 1.29/0.79 = 1.62). We interpret these results to mean that the site-to-site difference in soil texture and WHC did not affect \( A_{\text{x}}/A_{\text{m}} \) directly, but rather indirectly through its effect on stand structure and tree height.

Site differences in soil properties appeared to have no direct effect on \( \Psi_{\text{x}} - \Psi_{\text{c}} \) across sites either. In fact, the differences in \( \Delta \Psi_{\text{x}}/\Delta \Psi_{\text{me}} \) between the sites appeared to be mostly driven by the differences in tree height and associated effects of gravity. Applied at a stand level, there was an estimated enhancement of conductance of 3% (i.e. \( \Delta \Psi_{\text{x}}/\Delta \Psi_{\text{me}} \) = 1.03) at the xeric site. This, together with the combined effect of the differences in height and \( A_{\text{x}}/A_{\text{m}} \), would result in a xeric site conductance predicted to be 1.05 that of mesic site trees. The fact that a single relationship between \( G_{\text{net}} \) and tree height in Fig. 8 explains the data well across sites further suggests that the variation we did observe in \( G_{\text{net}} \) is largely attributable to the differences in tree height distribution across sites.

The ratio \( A_{\text{x}}/A_{\text{m}} \) also greatly affects the amount of water that can be extracted from the soil (Sperry et al. 1998). When stands reach a stage of development in which their leaf and root areas are at maximum, the ratio \( A_{\text{x}}/A_{\text{m}} \) at this quasi steady state is highly dependent on soil texture, increasing with increasing sand fraction. Consistent with its sandy texture, xeric site \( A_{\text{x}}/A_{\text{m}} \) was 42% higher than the mesic site (Table 1). While this adjustment in \( A_{\text{x}}/A_{\text{m}} \) is much less than the five-fold adjustment observed in a similar study in Pinus taeda (L) (Hacke et al. 2000), it still likely improved water uptake efficiency at the xeric site considerably. It is not possible to assess entirely the effect of higher \( A_{\text{x}}/A_{\text{m}} \) on the water economy of P. palustris without accounting for water consumption by the oak component also occupying this site. Nevertheless, our results show that at a reference \( D = 1 \) kPa, mean \( g_{\text{net}} \) and \( G_{\text{net}} \) were similar at both sites, or perhaps even higher (13 and 30% for \( g_{\text{net}} \) and \( G_{\text{net}} \), respectively; Table 3) at the xeric site. The combined above-ground hydraulic adjustments at the xeric site (1.05 that of the mesic site) may not be sufficient to explain the somewhat higher conductance on the xeric site at low \( D \), indicating that below-ground adjustments in hydraulic architecture likely contributed as well. Such below-ground adjustment is consistent with the slightly higher (16%) mean \( K_S \) of small roots at the xeric site.

We also assumed that xeric site trees would be deeper rooted than mesic site trees and that proportionately, more root biomass would be found at depth on the xeric site. We found no evidence for this in our 2 m depth pit samples. Yet P. palustris is a species known to extend a taproot deep into the soil profile, particularly on sandy sites (Heyward 1933). While we feel our sampling strategy was reasonable for quantifying fine roots within the 2 m depth profile, it was less well suited for determining the depth distribution of the entire rooting profile. Maximum rooting depth is relevant to the current study because of its consequence on hydraulic architecture and water transport; deep rooting may reach additional water resources, but it also increases the path length over which water must be transported. More information is needed to address this issue.

While it appears that P. palustris occupying xeric sites are confronted with greater challenges regarding water acquisition relative to trees occupying more mesic sites, adjustments in hydraulic architecture have enabled individual trees on xeric sites to realize equal - and sometimes higher - potential for conductance. The potential for higher conductance at xeric sites may, however, only be reached during times in which \( D \) is low and when soil moisture across sites is favourable and does not limit the capacity of the hydraulic system to supply water to foliage. Consistent with this scenario is the observation in this study that as \( D \) increased, both \( g_S \) and \( G_S \) showed a steeper decline in xeric site trees (Table 3). This pattern implies a slightly more sensitive stomatal conductance response to increasing \( D \) in xeric site trees, likely necessary to regulate \( \Psi_{\text{c}} \) and avoid xylem cavitation (Oren et al. 1998). It appears that trees on the xeric site are hydraulically best suited to taking advantage of periods when water is available, but the trade-off is that they may have smaller margins of safety from hydraulic failure during drought and are thus required to show a more sensitive stomatal closure response to increasing soil water limitation (Sperry et al. 1998). Future work should parameterize the model of Sperry et al. (1998) to evaluate response to declining soil moisture and how changes in hydraulic architecture across sites may influence site water use envelopes and predicted cavitation-inducing transpiration rates (\( E_{\text{ax}} \)). Differences in root radial resistance across sites should also be considered here. We present results only for root axial resistance, yet root radial resistance can be orders of magnitude greater than axial resistance (Studele & Peterson 1998). For large woody plants, however, the relative importance of root radial and axial resistance in
limiting transpiration is not well understood due to path length effects. The length over which water must flow radi- ally is much less than the axial length, therefore, the impor- tance of axial resistance should increase with plant size (Sperry et al. 2002). Hacke et al. (2000) also demonstrate good agreement between whole-plant water use and axial conductivity during water stress, suggesting that differences in root radial resistance across sites and during drought are either negligible or parallel the change in axial resistance.

Lastly, the influence of the oak component on pine hydraulic architecture should be investigated, as these spec- ies not only alter stand structure but also nutrient avail- ability. Higher nitrogen availability and mineralization has been reported for the xeric site, believed to be a result of higher quality leaf litter return provided by the oaks, oak root turnover, and higher soil temperatures for mineralization (Wilson et al. 2002). By altering nutrient availability relative to the mesic site, oaks on the xeric site may provide a fertilizing effect, encouraging leaf area production in the pines and therefore decreasing A/CAn. In this situation, xeric site P. palustris may in fact be more sensitive to drought, consistent with the findings of Ewers et al. (2000) in P. taeda that nitrogen-fertilized stands had smaller mar- gins of safety from predicted hydraulic failure during model- led drought compared to non-fertilized stands. The frequency of drought therefore may be greater for the xeric site relative to the mesic site in this study, meaning that trees on the xeric site may spend proportionately more time in a state of drought relative to mesic site trees. A limited data set collected on these sites during a drought that occurred earlier in the growing season suggests this pattern (Addington 2001), and may explain why longer-term water-use efficiency estimates for these sites indicate that xeric site trees are more water-use efficient compared to mesic site trees (Addington 2001; see also Ford 2004).

The patterns of stomatal behaviour observed in this study suggest that whole-plant architectural and leaf physiological adjustments are well coordinated with one another and with environment and habitat structure. Other studies have demonstrated integration among hydraulic architecture and water transport efficiency to maintain homeostasis (Whitehead et al. 1984; Meinzer, Woodruff & Shaw 2004). Our results are consistent with these studies and suggest that interactions among soil properties and stand-level fac- tors such as tree density are important determinants of individual tree form and height, and that hydraulic adjust- ments across these scales ensure similar site-to-site stomatal capability.

ACKNOWLEDGMENTS

We thank the Robert W. Woodruff Foundation and the Joseph W. Jones Ecological Research Center for supporting this research. We are grateful to Ann Addington, Michael Bell, Aaron DeLong, Barbara Fowler, Virgil Holton, Stacy Hurst, Dan McColville, Ernie Mitchell, Nancy Newberry, Mary Carol Sheffield and Dwan Williams for their help with work in the field and laboratory. We also thank Larry West for loaning equipment, and Karina Schäfer for help in developing the hydraulic model. Cheley Ford and Tim Harrington provided valuable comments on earlier versions of the manuscript, and comments from Nate McDowell and another anonymous reviewer also considerably improved the manuscript.

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*Received 5 May 2005; revised in revised form 22 July 2005; accepted for publication 6 August 2005*