Tradeoffs between hydraulic and mechanical stress responses of mature Norway spruce trunk wood

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Summary We tested the effects of growth characteristics and basic density on hydraulic and mechanical properties of mature Norway spruce (Picea abies (L.) Karst.) wood from six 24-year-old clones, grown on two sites in southern Sweden differing in water availability. Hydraulic parameters assessed were specific hydraulic conductivity at full saturation (k_{s100}) and vulnerability to cavitation ($\Psi_{50}$), mechanical parameters included bending strength ($\sigma_b$), modulus of elasticity (MOE), compression strength ($\sigma_c$) and Young’s modulus (E). Basic density, diameter at breast height, tree height, and hydraulic and mechanical parameters varied considerably among clones. Clonal means of hydraulic and mechanical properties were strongly related to basic density and to growth parameters across sites, especially to diameter at breast height. Compared with stem wood of slower growing clones, stem wood of rapidly growing clones had significantly lower basic density, lower $\sigma_b$, MOE, $\sigma_c$ and E, was more vulnerable to cavitation, but had higher $k_{s100}$. Basic density was negatively correlated to $\Psi_{50}$ and $k_{s100}$. We therefore found a tradeoff between $\Psi_{50}$ and $k_{s100}$. Clones with high basic density had significantly lower hydraulic vulnerability, but also lower hydraulic conductivity at full saturation and thus less rapid growth than clones with low basic density. This tradeoff involved a negative relationship between $\Psi_{50}$ and $\sigma_b$, as well as MOE, and between $k_{s100}$ and $\sigma_c$, MOE and $\sigma_c$. Basic density and $\Psi_{50}$ showed no site-specific differences, but tree height, diameter at breast height, $k_{s100}$ and mechanical strength and stiffness were significantly lower at the drier site. Basic density had no influence on the site-dependent differences in hydraulic and mechanical properties, but was strongly negatively related to diameter at breast height. Selecting for growth may thus lead not only to a reduction in mechanical strength and stiffness but also to a reduction in hydraulic safety.

Keywords: biomechanics, hydraulic conductivity, Picea abies, vulnerability to cavitation.

Introduction

In conifers, such as Norway spruce (Picea abies (L.) Karst.), with growth rates inversely related to wood density (Johansson 1993, Rozenberg and Cahalan 1997, Hannrup et al. 2004), rapid growth rate is the principal criterion for tree breeding and high density is of only secondary importance (Zobel and Jett 1995). Nevertheless, in some conifers, density is strongly related to mechanical and hydraulic wood functions important for tree survival (Evans and Ilic 2001, Hacke and Sperry 2001, Hacke et al. 2001, Rosner et al. 2007). Selection for breeding, without considering the relationships between wood structure and tree survival, may result in trees with enhanced growth but lower survival prospects (Booker and Sell 1998, Domec and Gartner 2002a, Rozenberg et al. 2002). In the present study, we tested the effects of growth traits on hydraulic and mechanical properties and determined how these biological functions of wood are related in the trunk of mature Norway spruce.

Much is known about heritability of growth parameters and wood properties in spruce species (Rozenberg and Cahalan 1997, Hannrup et al. 2004). Heritabilities for growth parameters and specific gravity tend to be higher than for other traits, and both are genotypically and phenotypically negatively correlated in Norway spruce wood (Hannrup et al. 2004). There is, however, a lack of information on how growth and density are related to hydraulic and mechanical properties in the mature Norway spruce trunk. Recently, Rosner et al. (2007) investigated the structural properties influencing hydraulic and mechanical properties in the juvenile Norway spruce trunk, but the relationships found may be inapplicable to the mature trunk. Mechanical stiffness is strongly related to density in both juvenile and mature Norway spruce wood (Rozenberg and Cahalan 1997, Lundström et al. 2007); however, hydraulic conductivity and vulnerability to cavitation are unrelated to density in juvenile wood, which can be explained by the complex density structure of the first annual rings (Mayr and Cochard 2003, Mayr et al. 2003, Rosner et al. 2007). In past studies, much effort has focused on relating wood structural...

Rapid growth depends on less densely structured wood to guarantee efficient water transport. Hydraulic effectiveness and safety are conflicting wood functions: the most conductive tissues are the most vulnerable to cavitation (Cochard 1992, Piñol and Sala 2000, Domec and Gartner 2001, 2003, Tyree and Zimmermann 2002, Bouffier et al. 2003). Larger and more numerous pit membranes in earlywood facilitate water transport, but may require thicker secondary cell walls to compensate for a potential weakening of walls (Gartner 1995, Hacke and Sperry 2001, Domec and Gartner 2002b). Little is known, however, about genetic versus environmental controls on cavitation resistance and xylem conductivity (Hacke and Sperry 2001). High biomass allocation aboveground demands an increase in mechanical strength and stiffness to support the crown, and height influences the magnitude of the bending moment under conditions of dynamic wind loading (Mattheck 1998, Spatz and Bruechert 2000). Wood density is considered the best predictive trait for mechanical properties (Niklas 1992). Mechanical strength and stiffness increase with increasing wood density, therefore a tradeoff between mechanical stiffness and hydraulic efficiency (maximum sap flow rate) should be expected (Hacke and Sperry 2001, Roderick and Berry 2001, Domec and Gartner 2002a). In some conifer species, however, no such tradeoff between mechanical stiffness and hydraulic conductivity was found (Mencuccini et al. 1997, Jagels et al. 2003, Jagels and Visscher 2006), because mechanical stiffness can be modified not only by increasing whole-wood density but also by varying latewood percentage, tracheid length, microfibril angles, arrangement of cell wall layers or cell wall chemistry (Mencuccini et al. 1997, Ezquerra and Gil 2001, Gindl 2001, Jagels et al. 2003, Jagels and Visscher 2006).

To test the effects of growth rate on hydraulic and mechanical properties of mature wood we investigated Norway spruce clones differing in growth rates on two sites with different water availability. Given the negative relationship between growth and wood density, we expected clonal as well as site differences in hydraulic and mechanical properties. We predicted that density is positively related to hydraulic safety but negatively related to hydraulic conductivity, because wood structure is less complex in mature tree stems than in juvenile tree stems or branches (Mayr and Cochard 2003, Mayr et al. 2003, Rosner et al. 2007). We hypothesized that a possible tradeoff between hydraulic vulnerability and conductivity (hereafter termed wood density-based tradeoff) involves a negative relationship between mechanical strength and hydraulic vulnerability as well as hydraulic conductivity.

Materials and methods

Site and trial description

Wood specimens came from 24-year-old Norway spruce trees (Picea abies (L.) Karst.) of two clonal trials in southern Sweden, Tönnersjöheden and Vissefjärda. In 1982, two-season-old rooted cuttings were randomly planted as 1.4 x 1.4 m spaced tree plots in a randomized block design. In total, 325 clones with nine replicates were planted within 0.7-ha areas at both sites. Tönnersjöheden has almost twice as much precipitation during the growth season and more than three times higher humidity (difference between precipitation and evaporation) than Vissefjärda, especially during the growth period (Table 1). Therefore, Tönnersjöheden (hereafter denoted wet site) should have higher water availability than Vissefjärda (hereafter denoted dry site). Based on a screening in 2002, we selected six clones differing in growth characteristics with five replicates per site.

Sample harvesting and storage

Trees were harvested during a wet period in mid-June 2004, when plant water stress was minimal. Tree height (H) was divided by stem diameter outside bark (D) measured at breast height (1.3 m) to determine the $H/D$ ratio. Wood bole segments, 20–30 cm in length, were taken immediately after felling at 1.3-m height from the ground. During transport, samples were kept wet in plastic bags containing some fresh water. In the laboratory, bole segments were debarked and split along

<table>
<thead>
<tr>
<th>Site type</th>
<th>Tönnersjöheden</th>
<th>Vissefjärda</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site type</td>
<td>Wet</td>
<td>Dry</td>
</tr>
<tr>
<td>Latitude (N)</td>
<td>56°57’</td>
<td>56°54’</td>
</tr>
<tr>
<td>Longitude (E)</td>
<td>13°07’</td>
<td>15°53’</td>
</tr>
<tr>
<td>Altitude (m a.s.l.)</td>
<td>60</td>
<td>120</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>&lt; 5</td>
<td>&lt; 5</td>
</tr>
<tr>
<td>Wind exposure</td>
<td>Low</td>
<td>Low</td>
</tr>
<tr>
<td>Precipitation during growth period (mm)</td>
<td>600</td>
<td>350</td>
</tr>
<tr>
<td>Available water during growth period (mm)</td>
<td>&gt; 150</td>
<td>&lt; 50</td>
</tr>
<tr>
<td>Site index ($H_{100}$)</td>
<td>G32</td>
<td>G28</td>
</tr>
<tr>
<td>Field vegetation type</td>
<td>Narrow grass</td>
<td>Bilberry (Vaccinium myrtillus)</td>
</tr>
</tbody>
</table>

1. Difference between precipitation and evaporation.
3. Height of dominant trees at age 100 years estimated according to Hägglund and Lundmark (1981).
the grain. An outer sapwood zone of 20 mm was separated from
the split samples and put in plastic zip bags together with fresh
water containing 0.01% (v/v) Micropur (Katadyn Prod-


cuts), a source of silver chloride, to prevent microbial growth.
Samples were sent within 24 h to BOKU Vienna (Austria) and
stored frozen at –18 °C until processed (Mayr et al. 2003,
Rosner et al. 2006).

Preparation of standard beams for flow experiments and
mechanical testing
Wood samples were thawed in fresh water. Outer sapwood
specimens with a transverse surface area of about 9 × 9 mm
were isolated by splitting the wood along the grain with a
chisel. Tangential and radial faces of the beams used for hy-
draulic testing were planed on a sliding microtome. Specimens
were shortened on a band saw, and specimen ends were re-cut
with a razor blade. During all these steps the specimens were
kept wet. They were then soaked in distilled water under vac-
uum for at least 48 h to refill embolized tracheids and then
stored in degassed water containing 0.01% Micropur. The fi-
nal standard dimensions of the specimens were 6 mm in the
tangential and radial planes and 110 mm in length. Standard
beams were produced from specimens taken at 1.3 m from the
ground containing annual rings 17–19. Additional wood
beams with the same final dimensions were prepared with a
saw. Specimens were kept wet during all preparation steps and
stored for three days at 4 °C in fresh tap water containing
0.01% Micropur until mechanical tests were performed.

Hydraulic method to assess hydraulic vulnerability
Hydraulic conductivity was measured under a hydraulic pres-
sure head of 5.4 kPa with distilled, filtered (0.22 μm) and
degassed water containing 0.005% Micropur. Conductivity data
were corrected to 20 °C to account for the temperature depend-
ence of fluid viscosity. Vulnerability curves were obtained as
described by Spicer and Gartner (1998) and Domec and Gart-
nr (2001). After determination of saturated mass and conduc-
tivity at full saturation (\(k_{100}\) ), air overpressure (\(P\) ) was applied
to the sides of the specimens, while the ends protruded from a
double-ended pressure chamber (PMS Instruments, Corvallis,
OR), to induce cavitation. After the pressure treatment, the
specimens were weighed and put in distilled water for about
30 min. Hydraulic conductivity (\(k_{100,}\)) was measured again af-
after recutting the specimens. Initially, the pressure chamber was
pressurized to 0.5 MPa, and the pressure was subsequently in-
creased after each conductivity measurement in steps of 0.5 or
1.0 MPa until more than 95% loss of conductivity (PLC)
occurred. The PLC at a given P was calculated as:

\[
\text{PLC} = \left( \frac{k_{100} - k_{100,}}{k_{100}} \right) \times 100 \tag{1}
\]

where \(k_{100}\) is the flow rate at full saturation.

In some specimens, specific conductivity was up to 10%
higher after exposure to low pressures between 0.5 and 1 MPa
than at full saturation (Domec et al. 2007). As a reference
value for constructing vulnerability curves, the initial conduc-
tivity at full saturation was chosen and values higher after the
first pressure increases were excluded from the analysis
(Rosner et al. 2006). Hydraulic vulnerability curves were fit-
ted by the least square method based on a sigmoidal function
to calculate \( \Psi_{50} \), the potential at which 50 PLC occurred
(Pammenter and Vander Willigen 1998).

Relative water loss (RWL; %) caused by the air over-
pressure was calculated as:

\[
\text{RWL} = \left( 1 - \frac{\text{actual fresh mass} - \text{dry mass}}{\text{saturated mass} - \text{dry mass}} \right) \times 100 \tag{2}
\]

Dry mass was obtained by drying wood specimens at 103 °C
to constant mass. The RWL was related to the pressure applied
with a cubic function, and the overpressure resulting in 50% RWL
was calculated (\(\Psi_{RWL,50}\)) (Rosner et al. 2006).

Mechanical properties
Mechanical traits comprised bending strength (\(\sigma_b; \text{Pa}\) ) and
bending stiffness (MOE, modulus of elasticity; Pa) as well as
compression strength (\(\sigma_a; \text{Pa}\) ) and compression stiffness in the
axial direction (E, Young’s modulus; Pa) of saturated green
wood.

Mechanical testing was performed with a Zwick/Roell
Z100 SW5A universal testing machine (Ulm, Germany) at
ambient temperature (~22 °C). A crosshead speed of 1 mm
min\(^{-1}\) was chosen for the compression tests and 3 mm
min\(^{-1}\) for the bending tests, respectively. The span width for the
3-point bending tests was 80 mm. An 80-mm span width
means that deflection of the beam was mainly influenced by
the axial stiffness of the material, and less so by shear de-
formation. Because of the design of the test set-up, measured
MOE was mainly determined by the axial stiffness of the spec-
imens. Specimens were loaded up to fracture and unloaded af-
after a force drop of 10% of the maximum force (\(F_{\text{max}}; \text{N}\) ). We
calculated \(\sigma_b\) as the maximum bending moment divided by the
section modulus of the specimens. We calculated \(\sigma_a\) as \(F_{\text{max}}\)
divided by the cross-sectional area of the specimens (m\(^2\)). Val-
ues of MOE and E were derived from the stress–strain curves
between 10 and 40% and between 35 and 50% of \(F_{\text{max}}\), respec-
tively.

Basic density
Basic density was determined as dry mass after drying at
103 °C to constant mass divided by the volume in the fully sat-
urated green state.

Sample numbers and statistics
Hydraulic tests were performed on 5–6 sapwood specimens
per tree and bending and compression testing was made on
7–10 sapwood specimens per tree taken from randomly cho-
sen positions around the circumference. Compression wood
(if present) was excluded from the measurements. Sixty trees
were investigated.

Values are given as means ± standard error (SE). All traits
followed a normal distribution. Significant differences for
clones, sites and their interaction were tested by factorial analysis of variance (ANOVA). Clones and sites were assumed to be fixed effects. Associations between two variables were examined by linear or nonlinear regression analyses. Nonlinear regression models were quadratic and S-models, where 

\[ y = e^{b_0 + b_1/x} \]

The Pearson correlation coefficient was used to associate traits on a single tree basis as well as on a clonal mean basis. We investigated relationships between two variables on a single tree (each site \( n = 30 \)) as well as on a clonal mean basis at each site (each site \( n = 6 \)) and on a clonal mean basis across sites (\( n = 6 \) and \( n = 12 \) for regression lines in the figures). Regression slopes were analyzed by the Student’s \( t \)-test for site-specific differences. Differences between mean values and regression slopes were accepted as significant if \( P \leq 0.05 \).

### Results

**Growth, wood density and hydraulic and mechanical parameters: site and clonal effects**

Mean tree height and DBH were significantly smaller at the dry than at the wet site. Crown percent was higher at the dry site than at the wet site, whereas there were no significant differences in \( H/D \) ratio and basic density between sites (Table 2). Hydraulic conductivity at full saturation and mechanical properties had significantly higher values at the wet site than at the dry site. Only two of the six clones studied—the two fast-growing clones—showed significantly lower hydraulic vulnerabilities at the dry site than at the wet site (\( P < 0.05 \), Figure 1a), whereas hydraulic vulnerability in the slowest-growing clone was slightly (but not significantly) higher at the dry site than at the wet site. Therefore, mean hydraulic vulnerability (\( \Psi_{50} \)) of single trees did not differ between sites (Table 2). All traits investigated showed clone-specific differences, with the exception of crown percent (Table 1). Clone × site interactions were found for wood density, hydraulic vulnerability, and all mechanical properties assessed, except Young’s modulus.

### Relationships between growth, wood density and hydraulic and mechanical parameters

Vulnerability to cavitation and hydraulic conductivity increased with DBH (Figures 1a–c) and crown percent (Figures 2a–c), but decreased with the \( H/D \) ratio (Figures 2f–h). Values of \( k_{100} \) increased with increasing height growth (Figure 1h). Relationships between hydraulic wood functions and growth traits were generally stronger at the wet site than at the dry site (Table 3). Mechanical properties tended to increase with \( H/D \) ratio (Figures 2i–j), but decrease with growth (Figures 1d, 1e, 1i and 1j) and crown percent (Figures 2d and 2e).
Basic density was significantly lower in trees with rapid growth and high crown percentage, but higher in trees with high $H/D$ ratios (Table 3). Vulnerability to cavitation and hydraulic conductivity were negatively related to basic density (Figures 2k–m), whereas mechanical strength and stiffness increased significantly with increasing basic density (Figures 2n and 2o). The site-specific relationships assessed were mainly significant on a single tree basis (Table 3), but less often on a clonal mean basis (Figures 1 and 2).

Relationships between wood biological functions, growth traits and basic density became stronger when the analysis was performed for clonal means across sites ($n = 6$ clones). Clonal means of $k_{s100}$ were significantly positively correlated with DBH ($r = 0.97, P < 0.01$) and negatively correlated with basic density ($r = -0.94, P < 0.05$), but not with tree height. Clonal means of $\Psi_{50}$ were positively correlated with $DBH$ ($r = 0.82, P < 0.01$) and to crown percent ($r = 0.87, P < 0.05$), but negatively correlated with $H/D$ ratio ($r = -0.93, P < 0.01$) and basic density ($r = -0.85, P < 0.01$). Clonal means of the mechanical properties $\sigma_a$, $\sigma_b$, and $E$ decreased with increasing DBH ($r = -0.89, -0.95$ and $-0.83$, respectively, $P < 0.05$). Clones with denser wood had significantly higher $\sigma_a$, $\sigma_b$ ($r = 0.96$ and $-0.88$, respectively, $P < 0.05$) than clones with less dense wood. Regression slopes for the relationships between tree height and $E$ (Figure 1i), DBH and MOE (Figure 1e) and between MOE and basic density (Figure 2o) differed significantly between sites ($P < 0.01$). Basic density at breast height was strongly negatively related to DBH ($r = -0.91, P < 0.01$) and to crown percent ($r = -0.98, P < 0.001$). The mechanical properties $\sigma_a$, MOE and $E$ were therefore also negatively correlated with crown percent ($r = -0.95, -0.93$ and $-0.92$, respectively, $P < 0.01$). The $H/D$ ratio was significantly positively correlated to $\sigma_a$ ($r = 0.95, P < 0.01$).

**Tradeoffs between wood functions**

Hydraulic vulnerability was significantly positively related to hydraulic conductivity on a single tree basis (Table 3), as well as on a clonal mean basis at the wet site (Figure 3b). Across sites, clonal means of $\Psi_{50}$ and $k_{s100}$ were strongly related to each other ($r = 0.89, P < 0.05, n = 6$). Hydraulic vulnerability was negatively related to bending strength and stiffness (Table 3), but regression lines of the clonal means differed significantly between sites ($P < 0.05$, Figures 3c and 3d). The overpressure resulting in 50% RWL was a good predictive trait for hydraulic vulnerability (Figure 3a), with the relationship reaching maximum values when calculated for clonal means across sites ($r = 0.98, P < 0.001, n = 6$). Hydraulic conductivity was negatively related to mechanical strength and stiffness at both sites (Table 3). Across sites, clonal means of $k_{s100}$ increased with decreasing $\sigma_a$, MOE and $E$ ($r = -0.93, -0.97$ and $-0.92$, respectively, $P < 0.01, n = 6$).

**Discussion**

**Genetic and environmental determination of wood biological functions**

In accordance with the study of Hannrump et al. (2004), we found high variability in basic density among clones (Table 2) and strong positive relationships between basic density and mechanical strength and stiffness (Niklas 1992, Rozenberg and Cahalan 1997). Vulnerability to cavitation and hydraulic conductivity of mature wood also varied considerably among clones, as has been shown for juvenile wood of Norway spruce (Rosner et al. 2007) and other species (Cochard et al. 2007).
Trees with high growth efficiency had higher hydraulic conductivity (Mencuccini and Grace 1996, Rosner et al. 2007) but also higher hydraulic vulnerability to cavitation (Domec and Gartner 2003, Cochard et al. 2007). Clonal variability in hydraulic properties of mature Norway spruce wood was more strongly influenced by DBH than by tree height (Figures 1a–c and 1f–h). The linear relationship between vulnerability to cavitation and tree height at the wet site was distorted by one clone, the trees of which had high $H/D$ ratios and thus the growth characteristics of a suppressed tree (Figures 2f and 2g). The strong negative relationship between vulnerability and $H/D$ ratio suggests that sociability affects hydraulic vulnerability. Because of this clone, $\Psi_{50}$ showed a clone $\times$ site interaction, whereas clonal ranking for $k_{s100}$ was similar at both sites (Table 2). Site conditions had a significant effect on hydraulic conductivity, but only the two fastest-growing clones showed less vulnerability to cavitation at the dry site than at the wet site. This result is in accordance with the studies of Kavanagh et al. (1999) and Bouffier et al. (2003), who found lower hydraulic conductivities in Douglas-fir and ponderosa pine populations growing on drier sites, but no site-specific differences in the vulnerability parameter $\Psi_{50}$. However, Bouffier et al. (2003) observed that another vulnerability parameter, the PLC induced by 3 MPa overpressure, showed site-specific differences.

We calculated PLC for several pressures, but found no differences between sites (data not shown). Bouffier et al. (2003) also reported that ponderosa pines had enhanced height growth at wetter sites. We also found more significant differences in tree height than in diameter between the dry and wet site. The most striking difference between sites was in crown percent, a parameter hardly influenced by genetics (Table 2), but altered by physiological age and by stand density (Deleuze et al. 1996, Kantola and Mäkelä 2004). We suppose that the Norway spruce trees were in a physiologically younger stage at the dry site than at the wet site because of their higher crown percentages and slightly lower $H/D$ ratios (Table 2). Tree shape has a profound effect on the mechanical stress distribution in the tree stem. In young, moderately tapered trees (lower $H/D$ ratios), stress is maximum in the lowest third of the stem.
Table 3. Relationships between growth traits, wood density and wood biological functions of single trees; upper right: wet site (Tönnersjöheden, n = 30). Abbreviations: DBH = diameter at breast height; H = tree height; H/DBH = height/diameter at breast height; CP = crown percentage; BD = basic density; \( \Psi_{50} \) = applied air pressure causing 50% loss of conductivity; \( \Psi_{R WL50} \) = applied air pressure causing 50% loss of relative water content; \( k_{s100} \) = specific hydraulic conductivity at full saturation; \( E \) = Young’s modulus; \( \sigma_a \) = compression strength; MOE = modulus of elasticity; \( \sigma_b \) = bending strength. The significance of the correlation coefficients of the linear or quadratic model equations are indicated as: *, \( P < 0.01 \); and ***, \( P < 0.001 \).

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Lower Right: Dry Site (Rosner et al. 2006)</th>
<th>Upper Right: Wet Site (Tönnersjöheden, n = 30)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH</td>
<td>0.733***</td>
<td>0.733***</td>
</tr>
<tr>
<td>H</td>
<td>0.810***</td>
<td>0.810***</td>
</tr>
<tr>
<td>( k_{s100} )</td>
<td>0.531***</td>
<td>0.531***</td>
</tr>
<tr>
<td>( \Psi_{50} )</td>
<td>0.385*</td>
<td>0.385*</td>
</tr>
<tr>
<td>( \Psi_{R WL50} )</td>
<td>0.705***</td>
<td>0.705***</td>
</tr>
<tr>
<td>( \Psi_{k} )</td>
<td>0.385*</td>
<td>0.385*</td>
</tr>
<tr>
<td>( E )</td>
<td>0.715***</td>
<td>0.715***</td>
</tr>
<tr>
<td>( \sigma_a )</td>
<td>0.507**</td>
<td>0.507**</td>
</tr>
<tr>
<td>MOE</td>
<td>0.385*</td>
<td>0.385*</td>
</tr>
<tr>
<td>( \sigma_b )</td>
<td>0.507**</td>
<td>0.507**</td>
</tr>
</tbody>
</table>

Tradeoffs between wood biological functions

Basic density was a good predictor of hydraulic properties of mature Norway spruce wood: clonal variability in \( k_{s100} \) and \( \Psi_{50} \) were strongly dependent on basic density (\( r = -0.94 \) and \( -0.85 \), respectively). Maximum hydraulic conductivity and vulnerability to cavitation are supposed to be conflicting wood functions and if both functions are strongly related to wood density we expect a density-based tradeoff between them. In contrast to our results for juvenile trunkwood (Rosner et al. 2007), we found a density-based tradeoff between hydraulic vulnerability and hydraulic conductivity in mature Norway spruce trunk wood (Table 3, Figure 3b). Density-based tradeoffs in hydraulics are present within branch systems or within a trunk tree of the same species (Sellin 1991, Cochard 1992, Domec and Gartner 2001, 2002a, 2003, Bouffier et al. 2003, Rosner et al. 2006). The smallest and usually youngest branches tend to be less vulnerable than the largest branches. There is a tradeoff between efficiency and safety when comparing tracheids within a tree, where the most efficient conduits are also the most vulnerable (Boyer 1985, Lewis and Tyree 1985, Sellin 1991, Hargrave et al. 1994, Tyree et al. 1994, Tyree and Zimmermann 2002). Hydraulic tradeoffs in juvenile wood have been found across species (Piñol and Sala 2000, Hacke and Sperry 2001), but rarely in wood of the same cambial age originating from the same species (Kavanagh et al. 1999, Bouffier et al. 2003, Cochard et al. 2007). We suppose that there is a density-based tradeoff between \( k_{s100} \) and \( \Psi_{50} \) (\( r = 0.89 \) across sites) in mature wood because of its higher uniformity compared with juvenile wood. Other than in juvenile wood, a hydraulic tradeoff was not masked by structural compromises, such as light bands, or mechanical demands, such as spiral grain and production of compression wood (Mayr and Cochard 2003, Mayr et al. 2003, 2005, Rosner et al. 2007).

Mature conifer wood is supposed to adjust its resistance to embolism by increasing density at the cost of reducing hydraulic conductivity (Domec and Gartner 2003), and thus growth. In the clones we investigated, wood density was strongly nega-
tively related to DBH ($r = -0.91$), implying that the slower-growing Norway spruce clones are able to compensate for their lower growth rate by producing a safer xylem, thus high resistance to cavitation is genetically determined, but at the cost of growth (Hacke and Sperry 2001, Roderick and Berry 2001). Domec and Gartner (2002a) found hydraulic safety factor values less than half those for mechanical safety factors in Douglas-fir and concluded that wood structure in conifers has evolved primarily in response to requirements for hydraulic safety rather than for mechanical safety. Our Norway spruce clones with higher hydraulic safety had lower growth rates (Figures 1a and 1b), implying lower mechanical strength and stiffness to support the crown; however, basic density and stiffness were higher in the slower-growing clones (Figures 2d, 2e, 2i and 2j). Thus, we did not find a simultaneous increase in hydraulic conductivity and mechanical stiffness as reported for other conifer species (Mencuccini et al. 1997, Jagels et al. 2003, Jagels and Visscher 2006); mechanical strength and stiffness were negatively related to hydraulic vulnerability (Figures 3c and 3d) and to hydraulic conductivity (Table 3). Larger and more frequent pit membranes facilitate water transport, but require thicker secondary cell walls to compensate for a potential weakening of walls. Larger tracheids and thin cell walls increase flow rates, but raise the risk of implosion (Hacke and Sperry 2001).

Within a tree stem, a simultaneous increase in hydraulic efficiency and mechanical strength is advantageous, because an increase in height influences both the distance water must travel to transpiring leaves, and the magnitude of the bending moment of dynamic wind loading (Mencuccini et al. 1997). We found a simultaneous increase in mechanical stiffness and $k_{s100}$ within a Norway spruce trunk. Values of MOE measured in annual rings 1–3 were only half those measured in annual rings 17–19 (despite the higher density of the first annual rings), but $k_{s100}$ was much lower in annual rings 1–3 than in annual rings 17–19 (Rosner et al. 2007). The hydraulic and mechanical demands of a young trunk or the tree top (e.g., high hydraulic safety, flexibility, keeping the upright position by formation of compression wood) are, however, quite different from those of mature wood at breast height (Gartner 1995, Mattheck 1998). Although hydraulic conductivity was negatively related to mechanical strength and stiffness at both sites (Table 3) and across sites, we found indications of structural compromises that guarantee both hydraulic efficiency and mechanical strength. For example, trees at the wet site had significantly higher $k_{s100}$ and thus higher growth rates, but also higher mechanical strength and stiffness values than trees at the dry site. Although we found no significant differences in density between sites, high $k_{s100}$ and mechanical stiffness can be obtained simultaneously by modifying pit pore size, latewood density, microfibril angle or cell wall chemistry (Mencuccini et al. 1997, Gindl 2001, Ezquerra and Gil 2001, Jagels et al. 2003, Jagels and Visscher 2006). Mechanical properties were strongly negatively correlated to $\Psi_{50}$, but the relationship varied significantly between sites (Figures 3c and 3d). Structural compromises induced by differences in crown length and stem taper might also explain why regression lines between $\Psi_{50}$ and mechanical properties differed between the wet and dry sites.

\section*{Consequences for tree breeding}

Wood density was a good indicator of hydraulic vulnerability in mature Norway spruce wood, but not in juvenile wood (Rosner et al. 2007). Another easily measured vulnerability indicator, $\Psi_{RWL50}$, was strongly negatively related to $\Psi_{50}$ and to density. Wood density is genetically negatively related to growth in spruce species and both properties are highly heritable (Rozenberg and Cahalan 1997, Hannrup et al. 2004). Our results suggest that mechanical properties and vulnerability to cavitation are under strong genetic control. Selecting for growth may thus lead not only to a reduction in mechanical
strength and stiffness but also to a reduction in hydraulic safety if adequate precautions are not taken (Booker and Sell 1998, Domec and Gartner 2002a, Rozenberg et al. 2002, Cochard et al. 2007).

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