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Hydraulic efficiency compromises compression strength perpendicular to the grain in Norway spruce trunkwood

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Abstract

The aim of this study was to investigate bending stiffness and compression strength perpendicular to the grain of Norway spruce (*Picea abies* (L.) Karst.) trunkwood with different anatomical and hydraulic properties. Hydraulically less safe mature sapwood had bigger hydraulic lumen diameters and higher specific hydraulic conductivities than hydraulically safer juvenile wood. Bending stiffness (MOE) was higher, whereas radial compression strength lower in mature than in juvenile wood. A density-based tradeoff between MOE and hydraulic efficiency was apparent in mature wood only. Across cambial age, bending stiffness did not compromise hydraulic efficiency due to variation in latewood percent and because of the structural demands of the tree top (e.g. high flexibility). Radial compression strength compromised, however, hydraulic efficiency because it was extremely dependent on the characteristics of the “weakest” wood part, the highly conductive earlywood. An increase in conduit wall reinforcement of earlywood tracheids would be too costly for the tree. Increasing radial compression strength by modification of microfibril angles or ray cell number could result in a decrease of MOE, which would negatively affect the trunk’s capability to support the crown. We propose that radial compression strength could be an easily assessable and highly predictive parameter for the resistance against implosion or vulnerability to cavitation across conifer species, which should be topic of further studies.

Keywords

Compression strength perpendicular to the grain; Conduit wall reinforcement; Hydraulic efficiency; Modulus of elasticity in bending; Norway spruce; Structure–function relationships; Vulnerability to cavitation; Wood shrinkage

Introduction

Conifer tracheids have to maintain both water transport and mechanical support, leading to a potential tradeoff between these wood functions (Gartner 1995; Hacke et al. 2001; Pitterman et al. 2006; Sperry et al. 2006; Domec et al. 2009). Mechanical and hydraulic demands change during a tree’s life. Stems of young trees have to be flexible to cope with snow loads and less vulnerable to drought stress because they have a shallow root system (Rosner et al. 2007). Enhanced allocation in foliage increases requirements for mechanical support, water

storage, and water- and nutrient transport (Mencuccini et al. 1997; Mattheck 1998; Spatz and Bruechert 2000). Therefore, the tree trunk of an older tree has to guarantee high hydraulic efficiency as well as mechanical stiffness in bending and compression strength in the axial wood direction. The tree top, however, has to be still flexible in bending to withstand wind and snow loads, but also more resistant to cavitation because higher negative pressures develop up in the crown (Gartner 1995; Rosner et al. 2006; Domec et al. 2009).

High wood density is a common strategy to guarantee both mechanical stiffness and low vulnerability against cavitation and implosion. An increase in density, achieved mainly by narrowing lumen diameter rather than increasing cell wall thickness (Hannrup et al. 2004; Pitterman et al. 2006; Sperry et al. 2006), goes along with a decrease in hydraulic efficiency. A density-based tradeoff between the hydraulic wood functions has been reported for the main conifer trunk (Domec and Gartner 2002a, 2003; Bouffier et al. 2003; Rosner et al. 2006; Domec et al. 2009), across species (Piñol and Sala 2000; Hacke et al. 2001; Maherali et al. 2004; Pitterman et al. 2006; Sperry et al. 2006) and for different clones of the same species (Rosner et al. 2008) but not necessarily for very young conifer stems (Rosner et al. 2007; Mayr et al. 2003) or branch systems (Mayr et al. 2005; Burgess et al. 2006). Since an increase in density comes at an increase in construction cost, trees might have developed strategies to guarantee both mechanical strength and high hydraulic efficiency. An increase in bending stiffness and compression strength parallel to the grain can be guaranteed as well by variation of cell wall chemistry, microfibril angle, tracheid length, arrangement of the cell wall layers and latewood percentage (Mencuccini et al. 1997; Ezquerro and Gil 2001; Gindl 2001; Jagels and Visscher 2006; Domec et al. 2009). Moreover, the further away tracheids are from the central axis of the trunk, the more they increase the strength of the trunk (Larjavaara and Muller-Landau 2010). Within a tree trunk, bending stiffness as well as compression strength along the grain (axial direction) and hydraulic efficiency are therefore not necessarily conflicting wood functions. Does a tree also manage to guarantee both mechanical strength perpendicular to the grain and high hydraulic efficiency? To our knowledge, no experimental studies exist where hydraulic properties of sapwood were related to compression strength perpendicular to the grain.

Conduits carrying water under negative pressure (Zimmermann 1983) bear the risk of implosion (Hacke et al. 2001), which has so far only been measured in conifer leaves (Cochard et al. 2004; Brodribb and Holbrook 2005). The mechanical stress response to negative water pressure can be observed in sapwood tissues that are fully saturated with liquid water. Negative water pressure can slightly change the cell shape of conduits and induces dimensional variations without removal of bound water (Alméras and Gril 2007; Perré 2007). A tree trunk is therefore submitted to diurnal stem diameter changes which are strongly related to sap flow rate and xylem water potential (Neher 1993; Herzog et al. 1996; Cochard 2001; Offenthaler et al. 2001; Peramaki et al. 2001; Ueda and Shibata 2001; Zweifel et al. 2001; Alméras et al. 2006; Conejero et al. 2007). The relationship between diurnal stem diameter variations and changes in stem water potential is supposed to be influenced by the elastic properties of the sapwood (Neher 1993; Irvine and Grace 1997; Alméras and Gril 2007; Alméras 2008). Radial dimensional changes induced by negative pressure are thus strongly related to wood structure (Rosner et al. 2009). Greater resistance to cavitation requires a safer design for resisting implosion, because the cell walls have to withstand higher tensile strain before cavitation occurs (Hacke et al. 2001; Pitterman et al. 2006; Domec et al. 2009). Accordingly, hydraulically more vulnerable conifer sapwood under the same negative pressure is more prone to deformation than hydraulically safer conifer wood (Rosner et al. 2009). Conifer tracheids have generally high hydraulic safety margins so that the water columns collapse before the conduit would implode (Hacke et al. 2001; Pitterman et al. 2006; Domec et al. 2009). Tensile stresses in a water-filled conduit are supposed to increase with decreasing double wall to span ratio, which is based on the fact

that both mechanical strength and stiffness increase with increasing wood density (Hacke et al. 2001; Hacke and Sperry 2001; Pitterman et al. 2006; Sperry et al. 2006; Domec et al. 2009). Stress induced by negative pressure should be therefore directly related to the elastic properties of the sapwood (Neher 1993; Irvine and Grace 1997; Peramaki et al. 2001; Hölttä et al. 2002), which can be assessed by mechanical testing (Alméras et al. 2006). Whereas high bending strength, bending stiffness and compression strength along the grain can be guaranteed by high mean wood density or latewood percentage (Raiskila et al. 2006; Rosner et al. 2007, 2008; Domec et al. 2009), radial compression strength perpendicular to the grain is extremely dependent on the “weakest” wood parts. Norway spruce wood “fails” first in those wood parts where density reaches minimum values within an annual ring (Müller et al. 2003).

The aim of this study was to investigate bending stiffness and radial compression strength of Norway spruce (*Picea abies* (L.) Karst.) trunkwood with differences in hydraulic efficiency, defined as the flow rate at full saturation. Norway spruce wood from the tree top has smaller earlywood lumen diameters but higher tracheid double wall to span ratios than older trunkwood (Rosner et al. 2009). Hydraulic lumen diameters (Kolb and Sperry 1999) and most likely hydraulic efficiency and vulnerability to cavitation should be thus lower in juvenile than in mature Norway spruce sapwood. We hypothesize that a tradeoff between hydraulic efficiency (estimated as hydraulic lumen diameters) and bending stiffness does not necessarily exist at the tissue (whole ring) level because high flow rates can be achieved together with high bending stiffness by a combination of highly conductive earlywood compartments and high latewood percentage. It is also hypothesized that hydraulic efficiency compromises radial compression strength perpendicular to the grain on the tracheid as well as on the tissue level, because hydraulic efficiency and radial compression strength depend both strongly on the properties of the mechanically “weakest” wood parts within an annual ring. Both hypotheses were tested across cambial age (on juvenile and mature wood together) and for both cambial age classes separately. Anatomical investigations in this study were conducted at the tracheid level. The authors are aware of the fact that tracheid dimensions and parameters calculated from tracheid dimensions give only a rough estimate for hydraulic efficiency and vulnerability to cavitation as the major resistance is situated at the bordered pits (Hacke et al. 2004; Mayr et al. 2005; Sperry et al. 2006; Rosner et al. 2007).

Materials and methods

Plant material and sample preparation

The sample set of 25-year-old Norway spruces (*Picea abies* (L.) Karst.) from a clonal trial in Southern Sweden is described in Rosner et al. (2009). We harvested four ramets of, in each case, three fast growing clones, which showed no significant differences in tree height and diameter at breast height. Harvesting was achieved during a wet period in June 2004. Wood bole segments, 0.2–0.3 m in length, were taken immediately after felling at the tree top (2nd whorl) and at 1.3 m height from the ground. Wood bole segments were debarked and split along the grain. Split samples of the outer sapwood zone were kept frozen at -18°C for some weeks until further preparation steps (Mayr et al. 2003; Rosner et al. 2006). Standard beams were produced from the outer sapwood taken at 1 m from the ground containing annual rings 17–19 (mature wood) and at the tree top, comprising annual rings 1–2 (juvenile wood). The preparation of fully saturated standard beams (6 mm tangential, 6 mm radial, and 100 mm longitudinal) is described elsewhere (Rosner et al. 2009).

Radial dimensional changes, vulnerability to cavitation and hydraulic conductivity

Acoustic emission (AE) was monitored with the μ DiSP™ Digital AE system from Physical Acoustics Corporation (Princeton Jct, PA, USA). Preamplifiers (40 dB) were used in connection with resonant 150 kHz R15C transducers over a standard frequency range 50-200 kHz. Data in a frequency range between 100 kHz and 300 kHz were recorded with a detection threshold of 30 dB (0 dB = 1 μ V input). Extraction of the relative AE energy (also referred to as “PAC-Energy”) was carried out with AE Win® software (Physical Acoustics Corporation).

The AE transducer was positioned on the tangential face of the fully saturated standard beam using an acrylic resin clamp which is described in Rosner et al. (2009). The clamp assembly allows determination of dimensional changes by means of a load cell (DMS, Type 8416-5500, range 0-500 N; amplification with an inline amplifier for DMS, Type 9235; Burster, Gernsbach, Germany) which is positioned between the AE transducer and the mounting screw of the clamp. The contact pressure between transducer and wood specimen was set to 30 N (Jackson and Grace 1996; Beall 2002) at the beginning of dehydration at ambient conditions (25°C, 30% r.h.). The whole clamp assemblage was placed on a balance (resolution 10⁻³ g, Sartorius, Göttingen, Germany) and water loss of the standard beams was quantified automatically every 10 min. AE and shrinkage testing was done until the contact pressure reached a constant value, which took <24 h. Absolute shrinkage (micrometer) was calculated by relating the total radial shrinkage (digital gauge, accuracy 1 μ m, Mitutoyo Corporation, Japan) to the total coupling pressure decrease (Rosner et al. 2009). Courses of radial dimensional changes of juvenile and mature wood are shown in Fig. 1a. The parameter “maximum cumulative radial deformation due to negative pressure” (SHR_m), is defined as the maximum radial dimensional change before the partial recovery of the cumulative dimensional change starts. The recovery is only partial because it is overlaid by cell wall shrinkage, which is initiated when the first tracheids reach fiber saturation. Circles mark the positions of SHR_m in Fig. 1a.

Acoustic emission data filtering was achieved with Vallen VisualAE™ software (Vallen Systeme GmbH, Munich, Germany). A mean AE energy value was calculated for 10-min time steps. Relative cumulative AE energy data were obtained by relating the stepwise cumulative mean AE energy values/10 min to the sum of all mean AE energy values/10 min. Mean AE energy/10 min was referenced to the nearest 5% relative water loss (R) step. The relationship between *R* and positive pressure was assessed on a parallel sample set of six juvenile and 12 mature wood beams (Rosner et al. 2006). After soaking and weighing, air pressure was applied to the lateral sides of the samples, while the transverse ends protruded from a double-ended pressure chamber (PMS Instruments Co., Corvallis, OR, USA). Following pressure treatment, the samples were weighed again. Initially, the chamber was pressurized to 0.5 MPa, and the pressure was subsequently increased in steps of 0.5 MPa until >95% loss of hydraulic conductivity was reached. Juvenile wood samples were pressurized up to 7 MPa (n = 6), mature samples only up to 5 MPa (n = 12). Prior to pressure treatment, hydraulic conductivity at full saturation was determined on the parallel sample set as described in Rosner et al. (2008). Conductivity measurements were carried out under a hydraulic pressure head of 5.4 kPa with distilled, filtered (0.22 μ m), and degassed water containing 0.005 vol.% Micropur. Conductivity data were corrected to 20°C to account for the temperature dependence of fluid viscosity.

Dry weight of the AE testing specimens and the parallel sample set was obtained by drying wood samples at 103 °C to constant weight in order to calculate the relative water loss (*R*) and basic density (volume in the green state/dry weight). Cubic functions for juvenile and mature wood given in Rosner et al. (2009) were used to relate *R* of AE and shrinkage testing specimens to the positive pressure applied. Acoustic vulnerability curves were fitted by the

least square method based on a sigmoidal function (Pammenter and Vander Willigen 1998) in order to calculate P_{50} , the potential at which 50% of cumulative AE energy occurred, which corresponds well to 50% loss of conductivity in Norway spruce trunk wood (Rosner et al. 2006).

Mechanical properties

Mechanical properties comprised bending stiffness [modulus of elasticity (MOE) in bending] and compression strength perpendicular to the grain (stress peak σ_r). Shrinkage testing specimens were stored at 20°C and 65% r.h. for a few days resulting in an equilibrium moisture content of 10.5% (Müller et al. 2003). 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 was chosen for the compression tests and 3 mm/min for the bending tests, respectively. The span width for the three-point bending tests was 80 mm (Rosner et al. 2008). Specimens were loaded up to fracture in the case of bending specimens. MOE was derived from the stress-strain curves between 10 and 40% of maximum stress.

Six cubes with a dimension of 6 mm × 6 mm × 6 mm were cut from the outer ends of the bending test specimens by means of a circular saw. Specimens were loaded in the radial direction perpendicular to the grain. Specimens were loaded up to the first stress peak (σ_{peak}) and unloaded after the subsequent increase in stress of >10% of σ_{peak} (Fig. 1b). σ_r was calculated as the peak force σ_{peak} divided by the area of the cross-section of the specimens. The compressive behavior of wood perpendicular to the grain is characterized by no clear failure of the material (Müller et al. 2003; Juodeikiene and Norvydas 2005). During testing, a clearly defined maximum load could thus not be obtained. We therefore avoided to calculate the Young's MOE and used σ_r instead to characterize mechanical properties in the radial wood direction of our small specimens.

Hydraulic lumen diameter and conduit wall reinforcement

Wood cubes (6 mm × 6 mm × 6 mm) from the reminders of the bending test samples were re-soaked in a mixture of distilled water, ethanol and glycerin (1:1:1). Transverse sections with a thickness of 20 µm were prepared on a sliding microtome. Sections were stained with Methylene blue and mounted in Euparal (Merck, Darmstadt, Germany). Radial lumen diameters were measured along five radial files of tracheids by means of a Leica DM4000M microscope interfaced with a digital camera and Leica image analysis software (Leica Microsystems Wetzlar GmbH, Germany). The mean hydraulic lumen diameter was calculated as $D_h = \Sigma d^5 / \Sigma d^4$, where d was the individual tracheid diameter (Kolb and Sperry 1999).

Conduit wall reinforcement, $(t/b)_h^2$, was determined as described in Hacke et al. (2001). The radial lumen diameter, b , was measured on two adjacent tracheids with diameters within ±10% of D_h , and wall thickness, t , as the distance across the double cell wall between both tracheids. Mean conduit wall reinforcement for each specimen was calculated from 60 single measurements.

Statistics

Statistical analysis was carried out with SPSS® 12.0. Values are given as mean ± standard error (SE). Mean values were tested for significance with the t test for independent samples, after analysis of variance and checking for normal distribution. Associations between two variables were examined using linear or non-linear regression analysis. The terminology “across cambial age” is used for pooled analyzes of juvenile and mature wood. Differences between mean values and relationships were accepted as significant if P was <0.05.

Results

Mature wood, which had higher dimensional changes at moderate moisture loss and lower resistance to cavitation, had bigger hydraulic lumen diameters (Fig. 2) and much higher specific hydraulic conductivities at full saturation (Table 1). Hydraulic lumen diameters were thus negatively related to the resistance to cavitation (Fig. 3e). Bending stiffness (MOE) was significantly higher in mature than in juvenile wood, whereas radial compression strength significantly lower in mature than in juvenile wood (Table 1).

Increased latewood percentage resulted in an increase of MOE (Fig. 4) with cambial age. Density showed no differences between juvenile and mature wood (Table 1). In mature wood, density was related to the latewood percentage ($r^2 = 0.67$, $P < 0.001$). We found, however, no such relationship across cambial age. The quadratic relationship between density and MOE ($r^2 = 0.25$, $P = 0.05$) was therefore rather weak. For mature wood, we found a strong relationship between density and MOE ($r^2 = 0.70$, $P < 0.01$). Across cambial age, the hydraulic lumen diameters showed no significant variation with density and had only a weak relationship with latewood percentage ($r = 0.30$, $P < 0.05$). In mature wood, however, hydraulic lumen diameters decreased significantly with increasing density ($r^2 = 0.39$, $P < 0.05$) and latewood percentage ($r^2 = 0.45$, $P < 0.05$). Vulnerability to cavitation did not significantly increase in specimens with lower density, but in specimens with higher latewood percentage ($r^2 = 0.45$, $P < 0.0001$) due to an increase in latewood percentage with cambial age.

The age dependent decrease in conduit wall reinforcement ($(t/b)_h^2$) was associated with lower resistance to cavitation (Fig. 3a) and radial compression strength (Fig. 3c). Resistance to cavitation was therefore strongly related to radial compression strength ($r^2 = 0.72$, $P < 0.0001$). Across cambial age, the relationship between MOE and $(t/b)_h^2$ was rather weak (Fig. 3b). In mature wood, MOE (Fig. 3b) increased, however, with increasing $(t/b)_h^2$. Maximum cumulative deformation due to negative pressure (SHR_m) increased with decreasing $(t/b)_h^2$ (Fig. 3d); SHR_m was therefore negatively related to radial compression strength (Fig. 5a). The increase in MOE with cambial age resulted, however, in a positive relationship between MOE and SHR_m (Fig. 5b).

Radial compression strength increased with decreasing hydraulic lumen diameters (Fig. 3g). High MOE (Fig. 3f) and high SHR_m (Fig. 3h) were found in wood with big hydraulic lumen diameters. In mature wood, MOE increased, however, significantly with decreasing hydraulic lumen diameters (Fig. 3f).

Discussion

Bending stiffness does not necessarily compromise hydraulic efficiency

Enhanced allocation in foliage increases requirements for mechanical support, water storage, and water- and nutrient transport (Mencuccini et al. 1997; Spatz and Bruechert 2000). Norway spruce wood is, however, designed to guarantee both high hydraulic efficiency and bending stiffness within the tree trunk.

Mechanical properties of Norway spruce wood with similar cambial age depend strongly on wood density (Raiskila et al. 2006; Rosner et al. 2007, 2008). Together with the microfibril angle, density is the most predictive trait for wood strength (Meylan and Probine 1969; Evans and Illic 2001; Lundgren 2004; Eder et al. 2009). Microfibril angles of juvenile spruce wood are very high and associated with a higher flexibility of young stems (Lichtenegger et al. 1999; Lindström et al. 1998). Increased mechanical support in the

longitudinal direction (bending and compression) can be achieved not only by increasing overall density or lower microfibril angles but also by varying latewood percentage (Rosner et al. 2007; Domec et al. 2009; Eder et al. 2009; Keunecke et al. 2009), tracheid length (Mencuccini et al. 1997; Ezquerro and Gil 2001), arrangement of the cell wall layers (Jagels and Visscher 2006), bordered pit frequency (Sirviö and Karenlampi 1998; Hacke et al. 2004) or by cell wall chemistry (Gindl 2001; Jungnikl et al. 2008). Some traits that increase bending stiffness and hydraulic conductivity, e.g. longer tracheids, are in turn associated with higher hydraulic vulnerability (Mencuccini et al. 1997; Rosner et al. 2007).

Dense latewood in combination with less dense earlywood should guarantee both mechanical stiffness and high flow rates (Domec et al. 2009). High density zones in juvenile wood, i.e. compression wood, can be compensated for flow reduction by structural characteristics of the first formed earlywood tracheids (Mayr et al. 2005). Overall density is therefore not necessarily strongly related to mechanical and hydraulic properties (Rosner et al. 2007). Accordingly, we found only a weak relationship between density and MOE and no relationship between density and hydraulic lumen diameters or vulnerability to cavitation across cambial age. High bending stiffness was mainly achieved by an increase in latewood percentage with cambial age (Fig. 4) rather than an increase in whole wood density. Across cambial age, no density-based tradeoff between hydraulic wood functions and MOE on the tissue (whole ring) level was therefore apparent in our specimens. MOE and hydraulic lumen diameters were, however, strongly negatively related in mature wood (Fig. 3f), indicating a clear density-based tradeoff between hydraulic efficiency and bending stiffness (Hacke et al. 2001) in wood with the same cambial age, which is probably under genetic control (Rosner et al. 2008). In juvenile wood, a more uniform distribution of density with small lumen diameters (Fig. 2b) and probably more air-seeding-safe bordered pits (Hacke et al. 2004; Domec et al. 2006) guarantee high hydraulic safety. A density-based tradeoff between hydraulic and mechanical wood functions (Gartner 1995; Hacke et al. 2001; Hacke and Sperry 2001; Domec and Gartner 2002a; Bouffier et al. 2003) is masked by structural compromises associated with the mechanical demands of the young trunk (Rosner et al. 2007). Keeping the young stem or the tree top in the upright position by formation of compression wood is an important biomechanical task (Lindström et al. 1998; Zobel and Sprague 1998; Mayr and Cochard 2003; Mayr et al. 2005). High flexibility against wind and snow loads is achieved by high spiral grain (Skatter and Kucera 1997) and microfibril angles of the S₂ cell wall layer (Meylan and Probine 1969; Lichtenegger et al. 1999; Lindström et al. 1998), which have similar (high) values in juvenile normal wood and compression wood (Gorišek and Torelli 1999). High microfibril angles together with low latewood percentage but overall small lumen diameters in juvenile wood might explain why juvenile wood showed lower bending stiffness but at the same time higher hydraulic safety than mature wood, although both had similar whole wood densities.

Hydraulic efficiency compromises radial compression strength perpendicular to the grain

Whereas high bending stiffness and hydraulic efficiency can be both guaranteed due to variation in latewood percentage (Domec et al. 2009) and microfibril angle (Meylan and Probine 1969; Bendtsen and Senft 1986; Lichtenegger et al. 1999; Evans and Illic 2001), radial compression strength perpendicular to the grain is extremely dependent on the “weakest” wood parts (Müller et al. 2003).

Hydraulic conductivity, vulnerability to implosion (Domec and Gartner 2002b; Domec et al. 2009) and deformation due to negative pressure (Rosner et al. 2009) depend strongly on the properties of conifer earlywood. Low vulnerability to cavitation implies high resistance against implosion in order to withstand deformation due to negative pressure (Rosner et al. 2009). Water-filled conduits experience large bending stresses that could lead to implosion under negative pressure if mechanical support of the surrounding cell walls was not

sufficient. Resistance against implosion of adjacent tracheids increases with increasing double wall/span ratio (Hacke et al. 2001; Hacke and Sperry 2001). Dense wood is therefore more resistant to cell wall collapse (Alméras and Gril 2007). In conifer stems, conduit wall reinforcement is decreasing with cambial age because the increase in earlywood lumen diameter does not go along with a 1:1 increase in wall thickness (Hannrup et al. 2004; Pitterman et al. 2006; Sperry et al. 2006; Domec et al. 2009; Rosner et al. 2009). Pit membranes in juvenile wood appear to be less flexible (more resistant to air seeding) and less conductive than pit membranes in mature wood (Domec et al. 2006). All these specific characteristics make juvenile wood more resistant to air seeding and implosion than mature wood but result also in a lower hydraulic conductivity at full saturation. Biomass allocation demands highly conductive wood structures (Mencuccini et al. 1997). The increase in earlywood lumen diameter with cambial age goes along with a decrease in conduit wall reinforcement, because a proportional increase in cell wall thickness would be too costly for the tree (Pitterman et al. 2006; Sperry et al. 2006; Domec et al. 2009).

Transmission of negative pressure from a fluid through solid cell walls causes dimensional changes of wood tissues in response to water status (Offenthaler et al. 2001; Almras and Gril 2007). When cavitation occurs in a xylem conduit, the negative pressure is released so that the embolized conduit recovers its unstressed state (Hltt et al. 2002). Recently we showed that hydraulically less safe wood is more prone to deformation under the same negative pressure. The sensitivity to deformation under negative pressure is strongly dependent on the characteristics of the first formed earlywood cell rows (Rosner et al. 2009), which have a strong impact on the value of the hydraulic diameter ($D_h = \Sigma d^3 / \Sigma d^4$) and thus on hydraulic efficiency (if we exclude the impact of bordered pits). In the present study we proofed experimentally that maximum deformation due to negative pressure is strongly related to the compression strength perpendicular to the grain (Fig. 5a). Hydraulic diameters were negatively related to radial compression strength (Fig. 3g), giving strong evidence that a tradeoff exists between hydraulic efficiency and radial compression strength.

Density together with cell wall geometry is responsible for both elasticity and failure behavior of single tracheids in the transverse direction (Almras and Gril 2007; Keunecke et al. 2007). On the tissue level, we found, however, no significant relationship between density and radial compression strength. As can be seen in Fig. 1b, compressive behavior of wood perpendicular to the grain is characterized by no clear failure of the material (Juodeikiene and Norvydas 2005). After an initial linear elastic deformation, the stress-strain curve for radial compression of Norway spruce wood reaches a peak, where first cell wall buckling can be observed. After a slight decrease in stress, stress increases again; this corresponds to the collapse of the weak earlywood cells near the ring border (Mller et al. 2003). Spruce wood “fails” in the first formed earlywood cell rows, where density reaches minimum values within an annual ring. The critical buckling load is lowest in those cell rows characterized by tracheids with big lumen diameters and thin walls (Mller et al. 2003). Together with high density, a more homogenous cross-sectional tissue composition and cell wall geometry, as can be found in juvenile wood (Fig. 2b), has a positive influence on radial compression strength and stiffness (Almras and Gril 2007; Keunecke et al. 2007). Mature wood consists of low density earlywood and high density latewood (Fig. 2c). High variability in wood density within an annual ring might explain why whole wood density was no predictive trait for the radial compression strength.

Other wood anatomical features that are supposed to influence strength perpendicular to the grain are the microstructure of the tracheid cell wall and the amount of ray cells. On contrary to the negative relationship between microfibril angles and MOE in bending, high microfibril angles in the S_1 and S_3 (Bergander and Salmn 2000) or S_2 (Almras and Gril 2007; Keunecke et al. 2009) layers of the tracheid cell wall guarantee high compression

stiffness perpendicular to the grain. Microfibril angles in the S_2 cell wall layer are known to be very high in juvenile Norway spruce wood (Gorišek and Torelli 1999; Hannrup et al. 2004); this could additionally enhance compression stiffness and probably conduit reinforcement against implosion. Characteristic for juvenile wood is also that it has a higher number of wood rays per tangential wood area than mature wood (Rosner and Führer 2002). Radial MOE (Bergander and Salmén 2000) and radial compression stiffness (Keunecke et al. 2007) of Norway spruce wood increases with an increasing number of wood rays per volume.

Conclusion

A density-based tradeoff between MOE in bending and hydraulic efficiency was apparent in mature wood, but was masked across cambial age because of the mechanical demands of the young stem and due to variation in latewood percent. Across cambial age, high bending stiffness did therefore not compromise hydraulic efficiency. Compression strength perpendicular to the grain compromised, however, hydraulic efficiency because it was extremely dependent on the characteristics of the “weakest” wood parts. Structural compromises would be either too costly for the tree (i.e. increasing conduit wall reinforcement) or would result in a decrease of MOE in bending or axial compression stiffness (i.e. increasing microfibril angles). We propose that radial compression strength could be an easily assessable and highly predictive parameter for the resistance against implosion and thus also for the vulnerability to cavitation. These relationships should be tested in further studies either within one species or across species.

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Fig. 1.

Assessment of mechanic and shrinkage parameters. Courses of the radial dimensional changes during dehydration versus time (a) and the stress/strain curve for radial compression perpendicular to the grain (b) of juvenile and mature Norway spruce sapwood. *Circles* mark the positions for acquisition of the parameters “maximum cumulative radial deformation due to negative pressure” (SHR_m) and “peak force, radial compression” (σ_r)

Fig. 2. Wood anatomical characteristics change with cambial age. Transverse sections of juvenile (a, b) and mature (c, d) Norway spruce wood. *Reference bars* represent 50 μm (a, d) and 1,000 μm (b, c)

Fig. 3.

Hydraulics and mechanics related to conduit wall reinforcement and hydraulic diameter. Vulnerability to cavitation (**a, e**), modulus of elasticity in bending (**b, f**), radial compression strength (**c, g**) and maximum deformation due to negative pressure (**d, h**) plotted against the conduit wall reinforcement and hydraulic diameter of juvenile (*closed circles*) and mature (*open circles*) Norway spruce specimens. Only significant linear (**b, c, f-h**) quadratic (**a, d**) or cubic (**e**) relationships between parameters are indicated by *regression lines*. *Regression lines* are drawn across cambial age (all data points), except in **b, f**, where additional regression lines are given for mature wood (*dashed lines*)

Fig. 4. Modulus of elasticity in bending (MOE) plotted against the latewood percentage of juvenile (*closed circles*) and mature (*open circles*) sapwood specimens

Fig. 5. Maximum cumulative radial deformation due to negative pressure related to compression strength perpendicular to the grain (a) and modulus of elasticity in bending (b) of juvenile (closed circles) and mature (open circles) sapwood specimens. Significant linear relationships between parameters are indicated by linear regression lines

Anatomical, hydraulic, mechanical and shrinkage characteristics of juvenile and mature Norway spruce wood specimens (mean $\pm$ SE)

Table 1

Trait	Abbreviation	Juvenile wood	Mature wood	P
Hydraulic diameter (μm)	D_h	22.2 ± 0.2	36.1 ± 1.4	<0.0001
Wall reinforcement (dimensionless)	$(t/b)^2_h$	0.053 ± 0.001	0.033 ± 0.002	<0.0001
Latewood percent (μm)	LWP	6.5 ± 0.7	15.9 ± 1.4	<0.0001
Basic density (g/cm^3)	WD	0.40 ± 0.01	0.40 ± 0.01	>0.05
Specific hydraulic conductivity at full saturation ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1} \times 10^{-4}$)	k_{s100}	5.0 ± 0.9	37.8 ± 1.5	<0.0001
Air pressure corresponding to 50% cumulative AE Energy (MPa)	P_{50}	4.1 ± 0.1	2.4 ± 0.1	<0.0001
Modulus of elasticity (GPa)	MOE _b	6.4 ± 0.3	10.9 ± 0.7	<0.0001
Radial compression strength (MPa)	σ_r	7.6 ± 0.2	4.2 ± 0.3	<0.0001
Maximum cumulated radial deformation due to negative pressure (%)	SHR _m	-0.42 ± 0.07	-1.44 ± 0.39	<0.0001

Specific hydraulic conductivity was determined on a parallel sample set of six juvenile and 12 mature standard beams. All other traits were determined on the same juvenile ($n = 12$) and mature ($n = 12$) standard wood beams