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RADIAL COMPRESSION STRENGTH CAN PREDICT THE HYDRAULIC VULNERABILITY OF MATURE NORWAY SPRUCE SAPWOOD

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ABSTRACT

Hydraulic testing of isolated sapwood from mature tree trunks is time-consuming and prone to errors, whereas the measurement of compression strength is a standardized and rapid wood technological application. In this study, we aimed to analyze if compression stress perpendicular to the grain relates to hydraulic vulnerability of mature Norway spruce (*Picea abies*) trunk wood with an expected narrow vulnerability range. The sample-set comprised 52 specimens originating from 34 trees harvested in Sweden. Before mechanical testing, the P_{50}, i.e., the water potential resulting in 50 % of hydraulic conductivity loss, was estimated on small sapwood beams employing the air injection method. Compression strength perpendicular to the grain was defined as the first peak of a stress-strain curve (peak stress) when the wood is subjected to radial compression. Peak stress ranged between 1,65 MPa and 5,07 MPa, P_{50} between -2,98 MPa and -1,98 MPa. We found a good correlation between the peak stress and P_{50} ($r = 0,80$; $P < 0,0001$). This provides further evidence that peak stress in radial compression and P_{50} are both extremely dependent on the characteristics of the "weakest" wood part, i.e., the highly conductive earlywood. We conclude that the radial compression strength is a good proxy for P_{50} of mature Norway spruce trunk wood.

Keywords: Biomechanics, cavitation, hydraulic vulnerability, Norway spruce, radial compression strength, sapwood.

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INTRODUCTION

Knowledge about the hydraulic performance of long-living plants under drought stress is of high importance for future forestry strategies under the impact of global change (Brodribb *et al.* 2020). Conifers in particular face a high risk in terms of drought-induced forest dieback (McDowell and Allen 2015, Rosner *et al.* 2018, Klein *et al.* 2019).

Water transported in the sapwood from the roots to the crown is in a metastable state (i.e. under tension). According to the cohesion-tension theory, the driving force for the sap flow comes mainly from needle transpiration (Tyree and Zimmermann 2002, Venturas *et al.* 2017). Due to the metastable state, the water columns inside the conduits are likely to break when the water tension increases above a certain level.

The breakage of the water columns; i.e. cavitation, followed by an embolism (Tyree and Sperry 1989, Rockwell *et al.* 2014), induces a reduction in the hydraulic conductivity of the plant, which impairs the water supply of the transpiring needles. Cavitation would result in a total loss of hydraulic conductance in the absence of any regulative mechanisms of transpiration (Comstock 2002).

Plants, therefore, respond by closing their stomata, which should reduce transpiration and keep the water tension below a critical cavitation threshold value, preventing further embolisms (Tyree and Zimmermann 2002). After stomatal closure, water is still lost, but, at a much lower rate. However, if drought stress continues, a critical cavitation threshold is reached and gas emboli spread throughout the sapwood resulting in a massive loss of hydraulic conductance.

An important functional trait for estimating vulnerability to cavitation of sapwood is the P_{50}, i.e., the water tension resulting in 50 % loss of hydraulic conductivity (Figure 1). P_{50} is of high relevance for our understanding of tree survival since it corresponds to the mortality thresholds of conifers (Choat *et al.* 2018). The loss of 50% of hydraulic conductivity has been entitled “the point of no return” for conifers; however, some conifer species can survive much higher conductivity losses (Adams *et al.* 2017, Hammond *et al.* 2019, Mantova *et al.* 2021).

Most studies on hydraulic failure are conducted on branches or young stems of saplings and not on mature sapwood. Hydraulic testing of isolated sapwood from mature tree trunks is destructive (the whole tree has to be harvested), time-consuming, prone to errors, and can only be performed on fresh, never-dried specimens (Cochard *et al.* 2013). Therefore, anatomical traits (e.g. wall/lumen ratio) or wood density have been tested for their reliability to serve as proxies for vulnerability to cavitation (Hacke *et al.* 2001, Domec *et al.* 2009, Bouche *et al.* 2014, Rosner *et al.* 2016, Rosner *et al.* 2021).

The estimation of transverse (radial or tangential) compression strength is a more standardized and rapid wood technological application than hydraulic testing and can also be applied to dried samples (Gindl *et al.* 2003, Müller *et al.* 2003, Huang *et al.* 2020). Wood is an anisotropic material and its mechanical strength is lowest in the transverse direction, i.e. perpendicular to the grain (Gindl *et al.* 2003, Thelandersson and Larsen 2003). Knowledge about the compression stress behavior of wood perpendicular to grain is important for designing timber structures (Zhong *et al.* 2022).

Rosner and Karlsson (2011) found for Norway spruce (*Picea abies*) that maximum peak stress calculated from stress-strain curves for radial compression is strongly related to the tracheid wall/lumen ratio. The latter is a functional trait that is a good proxy for vulnerability to cavitation among conifer species (Hacke *et al.* 2001) and within a conifer tree trunk (Rosner 2013). In the study of Rosner and Karlsson (2011) anatomical proxies of Norway spruce (*Picea abies*) specimens with a wide range of compression strength and vulnerability to cavitation; juvenile wood with low vulnerability and mature wood with high vulnerability (Rosner 2013), were related to compression strength perpendicular to the grain.

In this study, we aimed to analyze if compression stress perpendicular to the grain relates to hydraulic vulnerability of solely mature Norway spruce (*Picea abies*) trunk wood with an expected narrower vulnerability range. We related the peak stress of a stress/strain curve of compression perpendicular to the grain to P_{50}, to test the potential of biomechanical testing for the establishment of proxies for P_{50}.

MATERIAL AND METHODS

Plant material

The sample set comprised 52 specimens originating from 34 Norway spruce (*Picea abies* (L.) H. Karst.) trees harvested in southern Sweden; 20 in Tönnersjöheden (33 specimens) and 14 in Vissefjärda (19 specimens). Information about the trees can be found in Luss *et al.* (2019). Wood samples were taken from the outer sapwood at 1 m from the ground containing annual rings 17-19. Before mechanical testing, the P_{50}, i.e., the water potential resulting in 50 % loss of hydraulic conductivity, was estimated on small sapwood beams with a length of 120 mm (Figure 1) employing the air injection method (Cochard *et al.* 2013).

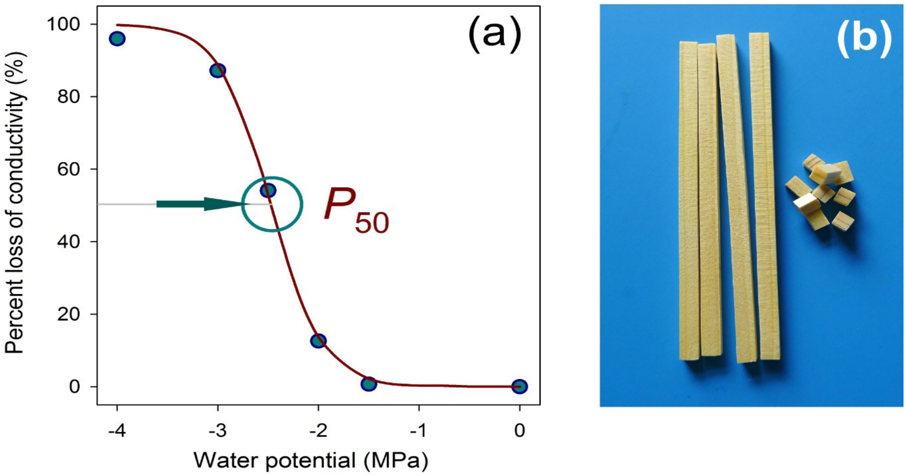

Figure 1: Hydraulic vulnerability curve for estimation of P_{50}, i.e. the pressure application (“water potential”; applied pressure with negative prefix) resulting in 50 % conductivity loss and (a) sapwood specimens for hydraulic and mechanical testing (b) The arrow points at P_{50}.

Vulnerability to cavitation

Hydraulic vulnerability curves of mature trunk wood samples were made as described in Spicer and Gartner (1998) and Domec and Gartner (2001). Wood boles were debarked in the field and transported to the laboratory in plastic bags containing some tap water with 0,005 % Micropur (Katadyn Products, Wallisellen, Switzerland) in order to avoid bacterial growth. The fresh, never-dried sapwood samples were split along the grain (10 mm (radial) x 10 mm (tangential) x 200 mm (longitudinal)) and smooth tangential and radial surfaces were produced on a sliding microtome (6 mm (radial) x 6 mm (tangential), after microtoming).

Wood beams were thereafter shortened on a band saw to a length of 130 mm and re-cut several times with a razor blade. Samples were kept moist (at relative water contents much higher than at the fiber saturation point) during all preparation steps. Sapwood specimens were then fully saturated under low vacuum for 24 h at 4 °C in filtered, distilled water with 0,005 % Micropur. The final specimen length was 120 mm (Figure 1b). Sapwood area-specific hydraulic conductivity (Ks, $cm^2\ s^{-1}\ MPa^{-1}$) was measured under a hydraulic pressure head of 5,4 kPa with distilled and filtered water containing 0,005 % Micropur.

After the determination of the flow at full saturation, air overpressure was applied with a pressure collar (PMS Instruments, Corvallis, OR, USA) for one minute (Rosner *et al.* 2019) and the hydraulic conductivity measurement was repeated. The pressure in the collar was gradually increased in steps of 0,5 MPa or 1,0 MPa and after every pressure application, the hydraulic conductivity was measured.

The procedure was repeated until more than 80 % of the hydraulic conductivity at full saturation was lost. The pressure application resulting in 50 % conductivity loss (P_{50}) and 88 % conductivity loss (P_{88}) was calculated from exponential sigmoidal fittings (Pammenter and Vander Willigen 1998) of the relationship between percent loss of hydraulic conductivity and pressure application (Figure 1a).

Determination of the peak stress in radial compression

The stress/strain curves for Norway spruce wood in radial compression perpendicular to the grain show a typical pattern (Müller *et al.* 2003, Rosner and Karlsson 2011). The biomechanical functional trait "peak stress" was defined as the first peak of a stress-strain curve when the wood is subjected to radial compression, which eventually results in the densification of wood (Figure 2).

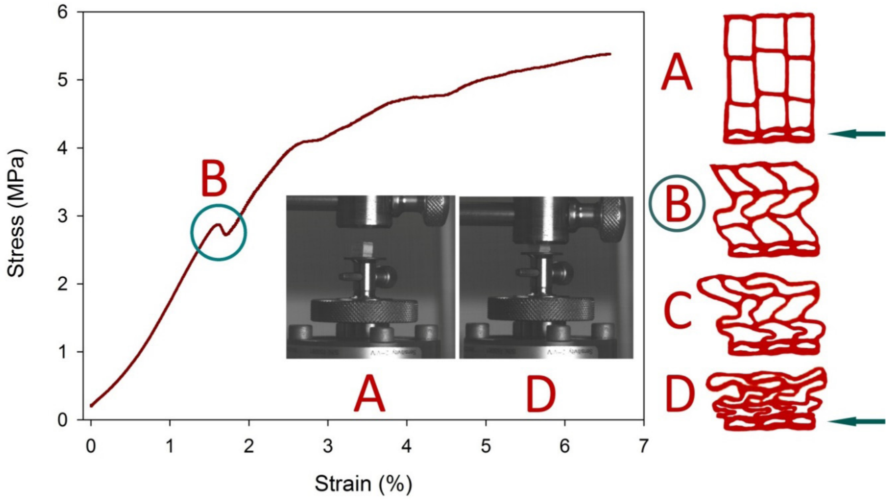

Figure 2: Stress-strain curve for radial compression of mature Norway spruce wood (left) and stages of the densification process of conifer wood (right, e.g. Aimene and Nairn 2015, Wu *et al.* 2022, Yan *et al.* 2022). Stage "A" in the inserts and drawings indicate the initial state, stage "D" full densification. Stage "B" marks the first peak stress in radial compression of Norway spruce sapwood; the position for acquisition of the parameter "peak stress" in radial compression. Arrows point at the latewood.

Wood cubes with a longitudinal dimension of 6 mm were sawn from the small wood beams used for hydraulic testing (Figure 1). They were stored at 20 °C and 65 % r.h. for one week, which resulted in an equilibrium moisture content of 10,5 % (Müller *et al.* 2003). Mechanical testing was performed with a Zwick/Roell Z020 universal testing machine (Figure 2) at a crosshead speed of 0,3 mm/min - 0,4 mm/min. Deformation was measured by a laser extensometer (Xforce, Zwick/Roell). 184 small wood cubes (Figure 1) produced from 52 hydraulic testing wood beams (3-4 specimens/wood beam, Luss 2020) were loaded in the radial direction perpendicular to the grain.

Results were analyzed with the testXpert® II software. The trait "peak stress" (MPa, N/mm²) in radial compression was calculated as peak force (N) divided by the area of the cross-section (mm²) of the specimens (Figure 2). Each wood sample comprised 1-2 full annual rings. It is important to select solely samples with the complete parallel alignment of the annual rings to the tangential surface and to measure at least 6 repeats/hydraulic specimen, in order to be able, select 3-4 stress/strain curves that show a clear first peak to determine the trait "peak stress". This peak stress is equivalent to the turning point in a radial compression stress-strain curve when parts of the wood become permanently deformed after an initial linear elastic deformation (Gindl *et al.* 2003, Müller *et al.* 2003, Huang *et al.* 2020). The first cell wall buckling is observed at this deformation level in Norway spruce (*Picea abies* (L.) H. Karst.) wood (Müller *et al.* 2003).

RESULTS AND DISCUSSION

The peak stress for radial compression of mature Norway spruce (*Picea abies*) sapwood of the lower trunk ranged between 1,65 MPa and 5,07 MPa, P_{50} between -2,98 MPa and -1,98 MPa (Figure 3) and P_{88} between -4,19 MPa and -2,52 MPa. Strength in radial compression (Rosner and Karlsson 2011) and hydraulic safety (Domec *et al.* 2009, Rosner 2013) of outer conifer trunkwood decrease, whereas hydraulic tracheid diameters increase from the top to the base, i.e. "conduit widening", (Anfodillo *et al.* 2013, Olson *et al.* 2021).

The range of the peak stress for radial compression is therefore much wider within a Norway spruce (*Picea abies*) trunk than among mature wood of similar cambial age of different individuals (Rosner and Karlsson 2011). Even though the range of the peak stress was narrower than in our earlier work (Rosner and Karlsson 2011), we found a significant correlation between the mean peak stress and P_{50} ($r = 0{,}80$; $P < 0{,}0001$, n = 52) for mature Norway spruce (*Picea abies*) wood.

Radial compression strength depends on the characteristics of the "weakest" part of the growth ring, i.e., the highly conductive earlywood (Müller *et al.* 2003), and is related to P_{50}, which provides further evidence that the earlywood is the most important portion determining the mean vulnerability to cavitation (P_{50}) of trunk wood in mature Norway spruce (*Picea abies*). In mechanical testing, the first failure (cell collapse) occurs particularly in the first-formed tracheid rows (Müller *et al.* 2003, Aimene and Nairn 2015).

The Achilles' heel in transverse compression is at the transition between earlywood and latewood because of a sudden change in material mechanical properties (Huang *et al.* 2020). Even though conifers do have quite high hydraulic safety margins (Choat *et al.* 2012), cell wall collapse can occur in the thin-walled, first-formed, earlywood tracheids of living Norway spruce (*Picea abies* (L.) H. Karst.) trees (Rosner *et al.* 2018). Such irreversible mechanical damage is caused by the impact of extreme early summer drought when the water tension in the sapwood becomes too high (low water potential).

Particularly individuals selected for high growth that produce thin-walled earlywood with a low wall/lumen ratio and high radial shrinkage above fiber saturation are prone to such mechanical failure. The trait P_{88} (vulnerability for 88 % conductivity loss) was much weaker correlated to the peak stress ($r = 0{,}59$; $P < 0{,}0001$, n = 52). We suppose that at P_{88} water is already lost in transition wood and even in latewood parts (Rosner *et al.* 2012) and the trait "peak stress" does not reflect anatomical characteristics of these ring components. These components might be, however, crucial for survival of species which can cope with more than 50 % loss of hydraulic conductivity (Adams *et al.* 2017, Hammond *et al.* 2019, Mantova *et al.* 2021).

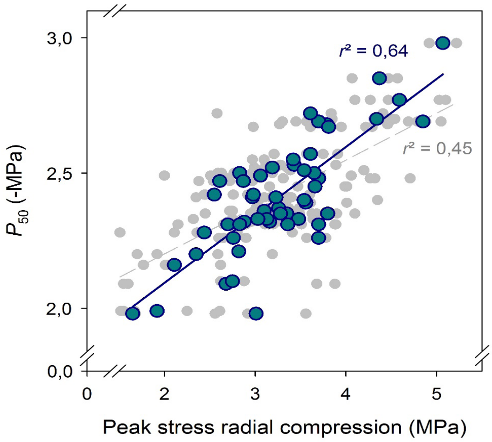

Figure 3: Linear relationships between peak stress in radial compression and vulnerability to cavitation (P_{50}) in mature Norway spruce wood (n = 52 mean value for wood beams (big dots)/184 single wood cubes (small dots)).

"Conduit widening" results in an optimization of hydraulic efficiency and safety due to an increase in (earlywood) tracheid diameter from tip to base (Anfodillo *et al.* 2013, Olson *et al.* 2021). In other words, tall trees need an efficient hydraulic conducting system, with much wider earlywood tracheids at the tree base than at the tree top. This comes at the cost of a decrease in mechanical strength perpendicular to the grain but not necessarily at the cost of mechanical strength and stiffness in the longitudinal direction (Rosner and Karlsson 2011).

Bending strength and stiffness and axial compression strength are strongly positively related to overall (basic) wood density (Dlouhá *et al.* 2018), whereby the latter is modified by the latewood percentage (Domec *et al.* 2009, Rosner 2013). Low density earlywood in combination with high density latewood guarantees both high sap flow and mechanical strength in the longitudinal direction; however, high flow is at the cost of hydraulic vulnerability and wood strength in radial direction, which explains why these two functional traits are related to each other.

CONCLUSIONS

We conclude that the "peak stress" in radial compression is a reliable proxy for vulnerability to cavitation of mature Norway spruce trunkwood and assume that radial compression strength and vulnerability to cavitation (P_{50}) are both dependent on the characteristics of the "weakest" wood part, i.e., the highly conductive earlywood. The advantage of this approach is that the functional trait "peak stress" in radial compression can be measured on dry samples and the measurements are quite fast and can be standardized for a broader application. Additional studies are needed to test if the relationship between radial compression strength and hydraulic vulnerability exists as well in other conifer species.

Authorship contributions

S.R.: Visualization, conceptualization, methodology, data analysis, investigation, data curation, writing – original draft, writing – review & editing. S.L.: Methodology, data analysis, investigation, data curation. J.K.: Supervision, investigation, writing – review & editing. N.K.: Investigation, writing – review & editing. All authors agree on the content of the manuscript.

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