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LETTER to *JPH*

Chronology of hydraulic vulnerability in trunk wood of conifer trees with and without symptoms of top dieback

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Abstract

There is evidence that recently occurring top dieback of Norway spruce (*Picea abies* (L.) Karst.) trees in southern Norway is associated with drought stress. We compared functional wood traits of 20 healthy looking trees and 20 trees with visual signs of top dieback. SilviScan technology was applied to measure cell dimensions (lumen and cell wall thickness) in a selected set of trunk wood specimens where vulnerability to cavitation (P_{50}) data were available. The conduit wall reinforcement ($(t/b)^2$) was a good proxy for P_{50}. Cell dimensions were measured on wood cores of all 40 trees; theoretical vulnerability of single annual rings could be thus estimated. Declining trees tended to have lower $(t/b)^2$ before and during a period of water deficit (difference between precipitation and potential evapotranspiration) that lasted from 2004 to 2006. The results are discussed with respect to genetic predisposition.

Introduction

In southern Norway, recently occurring top dieback in 40-50 years old forest stands of Norway spruce (*Picea abies* (L.) Karst.) is thought to be associated with climatic extremes (Hentschel et al. 2014). In this region, the period between 2004 and 2006 was characterized by high water deficits during the growing season, estimated as the difference between the cumulative precipitation and the potential evapotranspiration (see Fig 1 in Hentschel et al. 2014). During this period, trees with symptoms of top dieback (Fig. 1) showed lower intrinsic water-use efficiency that is associated with increased stomatal conductance (Hentschel et al. 2014) and produced wood with lower density, indicating higher vulnerability to cavitation (Rosner et al. 2014). Functional traits for estimating hydraulic vulnerability gain increasing importance as screening tools because hydraulic experiments are labour intensive or prone to errors (Cochard et al. 2013). In this study, we extend an existing dataset (Rosner et al. 2014) with tree samples and derive functional traits for hydraulic vulnerability from tracheid dimensions assessed by SilviScan technology (Evans 1994). Thereafter we document how these proxies changed over the years in 20 healthy looking and in 20 declining trees in order to learn more about the predisposing factors for top dieback in Norway spruce in southern Norway.

Figure 1: Norway spruce tree with symptoms of top dieback (middle) among healthy looking trees. Photo: Isabella Børja

Materials and Methods

Ten healthy looking trees and ten trees with visual signs of top dieback such as dry tops and needle yellowing in the top (Fig. 1) were selected in Sande (Lat. (N) 59°35', Long. (E) 10°12') and Hoxmark (Lat. (N) 59°40', Long. (E) 10°45'), respectively (n = 40 trees). For a previous study (Rosner et al. 2014), 24 trees (6 symptomatic and 6 non-symptomatic trees per site) were harvested in order to assess vulnerability to cavitation (P_{50}) of the trunk wood by means of the pressure collar technique (Domec and Gartner 2002). Wood cores taken at breast height and small wood beams, where P_{50} data were available (Rosner et al. 2014), were analyzed with SilviScan technology. Wood density, radial- and tangential tracheid diameters and wall thickness were thus available in 25 µm radial measurement steps. For each single annual ring, a conduit wall reinforcement, i.e. wall (*t)* to lumen (*b*) ratio, was calculated as $(t/b)^2$ (Hacke et al. 2001). The conduit wall reinforcement was not derived from the whole ring dataset but from wood with a density < 700 kg/m³ that comprises early wood and transition wood but not latewood (Dalla-Salda et al. 2014).

Results

P_{50} was strongly related to conduit wall reinforcement ($r^2 = 0.71$, $P < 0.001$, $n = 19$); $(t/b)^2$ could be thus used as good proxy for vulnerability to cavitation (Fig. 2).

After 2005, height and radial increments showed different trends in trees with symptoms of top dieback compared to healthy looking trees (Figs. 3a-b). Before 2004, symptomatic trees investigated in our study produced slightly higher radial increments than healthy looking trees. The differences were however not significant. After 1999, $(t/b)^2$ was lower in almost all annual rings of symptomatic trees (Fig. 3c); thus before, during and after a period with water deficit (2004 – 2006). In 2000, the difference was statistically significant. Steadily increasing $(t/b)^2$ after 2006, resulting in a higher $(t/b)^2$ of symptomatic trees in 2010, can be interpreted as a reaction to stress.

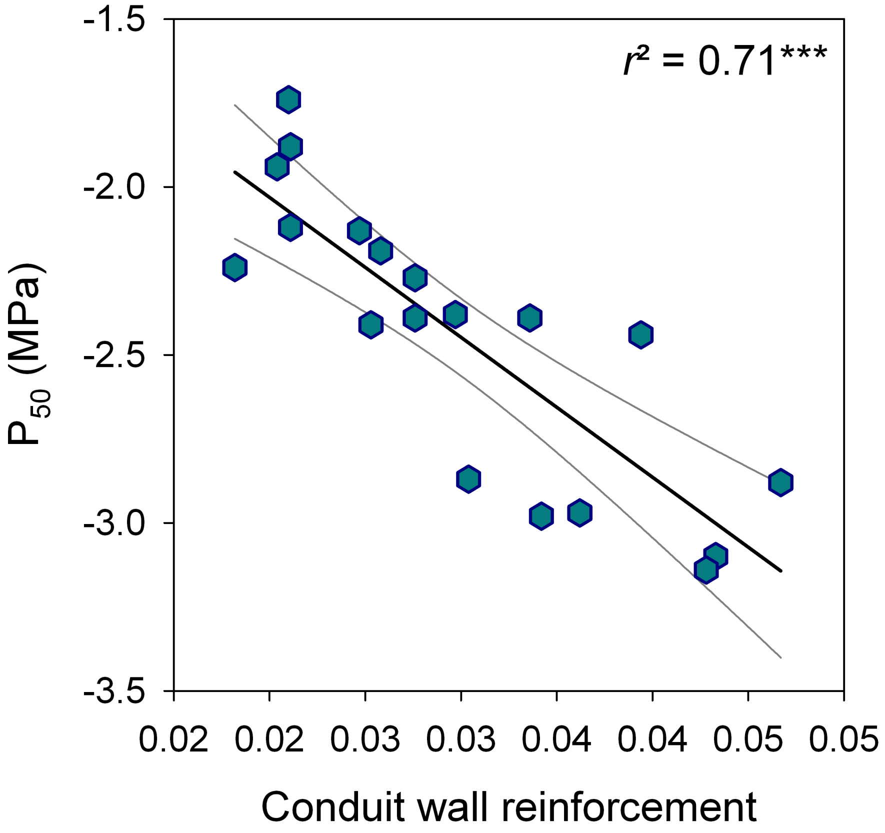

Figure 2: Linear relationship (regression line and 95% confidence interval) between conduit wall reinforcement $(t/b)^2$ and vulnerability to cavitation (P50).

Discussion

Producing wood with lower $(t/b)^2$ during periods of sufficient water supply can be a risky investment regarding hydraulic safety for Norway spruce trees. This "strategy" can lead to lower survival prospects under the impact of an extreme sudden drought because this species uses at least ten annual rings for axial water transport (Bertaud and Holmbom 2004). Due to irreversible embolism induced by drought stress (Choat et al. 2015), the hydraulic conductivity might get lost in more vulnerable annual rings. This can lead to an impairment of the water supply of the crown and thus to reduced growth. In addition, trees with top dieback tended to spend water; they had a predisposition to less strict stomatal control. Trees with both characteristics can most likely not cope with several drought periods during subsequent years (Hentschel et al. 2014).

Proxies for P_{50} can be useful tools to screen for provenances or individuals with higher hydraulic safety (Dalla Salda et al. 2009). Published relationships between t/b ratio and P_{50} are much stronger within a given species (e.g. Domec et al. 2009) than across conifer species (e.g. Bouche et al. 2014). Strong relationship between t/b ratio (thus $(t/b)^2$) and P_{50} within a tree of a given species exist due to the extreme changes of P_{50} and thus t/b or tracheid lumen diameters (Anfodillo et al. 2013) along a conifer trunk and the variability in P_{50} between different plant organs (Domec et al. 2009). This implies smart sampling strategies: in order to perform reliable comparisons between individuals of the same species, sapwood for hydraulic testing or for determination of functional proxies shall be collected from a given plant organ and from annual rings of comparable age (i.e. juvenile *versus* mature) at the same (relative) tree height.

Wood quality traits such as density (and most likely $(t/b)^2$) are highly heritable in Norway spruce. Recently, Chen et al. (2014) found that early selection for wood density is highly effective from rings 6–7. Starting at that age, selecting individuals for higher hydraulic safety in trunk wood could be possible. However, trunkwood safety covers only one aspect of drought sensitivity related to hydraulic architecture (see Hacke et al. 2015) and selected trees must be tested for their hydraulic performance in field experiments. In species such as Norway spruce, wood density is genetically negatively correlated with growth (Rosner et al. 2014). Thus, when selecting Norway spruce trees for higher hydraulic safety and/or more strict stomatal control, reduction in growth rate might have to be taken into account.

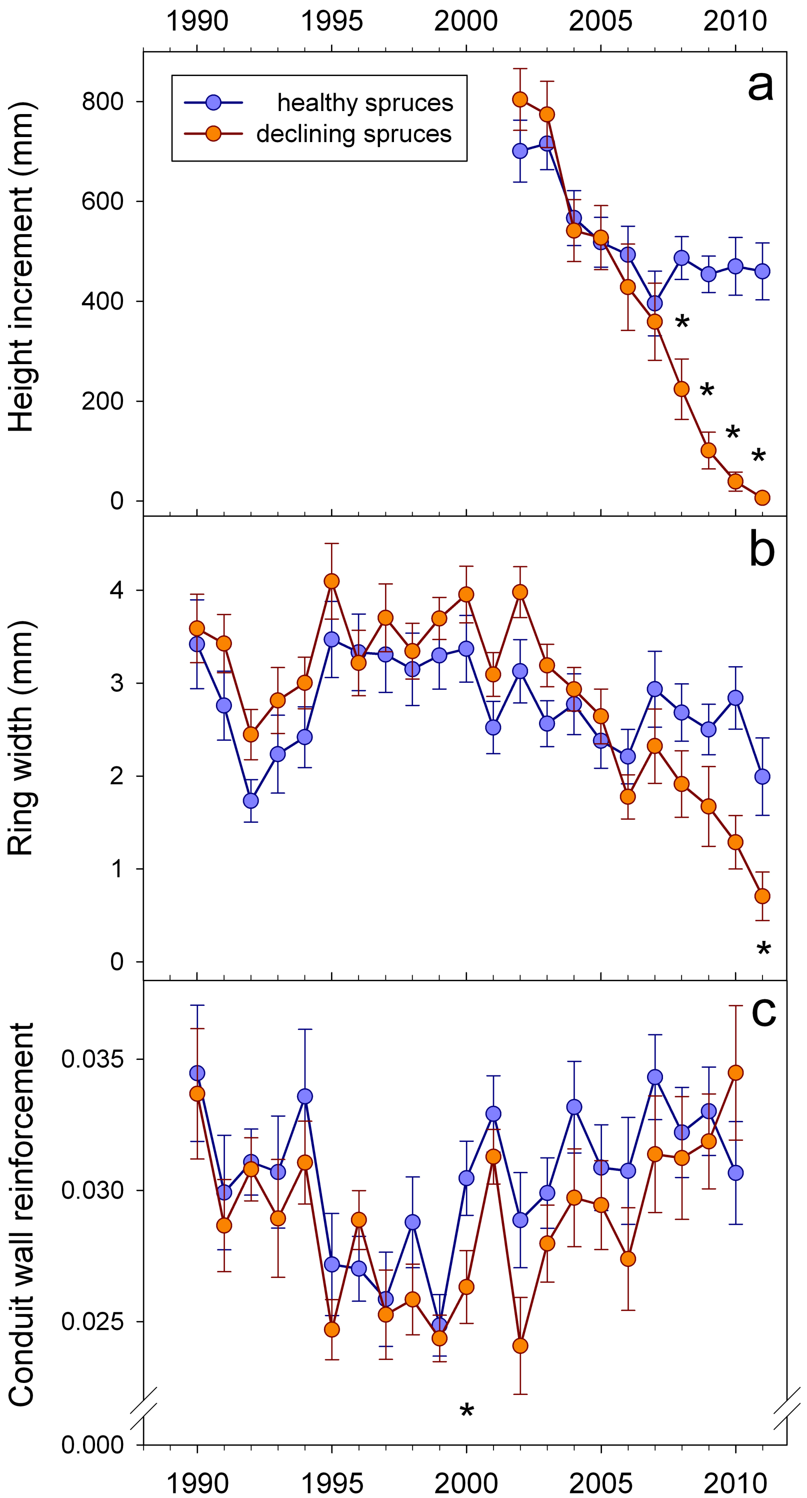

Figure 3: Time course of height increment (a), radial increment (b) and wall/lumen ratios of earlywood (c). Significant differences are indicated by "*".

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