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Norway spruce physiological and anatomical predisposition to dieback

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ABSTRACT

Top dieback on Norway spruce has frequently occurred in stands of southern Norway and it is a serious threat to the productivity and stability of economically important spruce stands. The underlying dieback mechanisms are unclear; often the whole stand is not affected, but only individual trees. Drought stress is hypothesized as a crucial trigger for the onset of symptoms; therefore, we studied the response-effect relationships of water limitation and tree specific traits. We analyzed year ring anatomy, i.e. wood density, as an estimate of drought vulnerability, and carbon and oxygen isotope composition of the year rings as an estimate of leaf physiology. At two sites in SE Norway, we grouped declining and symptomless trees in direct vicinity of each other into pairs for comparison of anatomical and physiological traits. For one site, we observed a distinct lower wood density and higher radial growth of declining trees in comparison with the healthy trees over several years. We identified high vulnerability to cavitation due to lower wood density as a trait of individuals prone to dieback. We observed lower intrinsic water-use efficiency (WUE_i) associated with increased stomatal conductance. The healthy trees had lower stomatal conductance, which most likely prevented water losses during dry periods. Within a population, we observed a trade-off between long-term growth performance under "average" conditions and a different response for "extreme" events. These resource strategies will be important for Norway spruce management, especially for regions facing an increase in the frequency of drought events.

1. Introduction

Temporal and spatial patterns of increased tree mortality have been documented around the globe (Allen et al., 2010; Choat et al., 2012). These mortality patterns are strongly related to climate change and, in particular, to the increase in frequency and intensity of heat stress and drought. In Southern Norway and Sweden, a top-dieback of Norway spruce (*Picea abies* L. Karst.) has been observed over the past decades and has primarily been attributed to drought and heat stress (Solberg et al., 1992, 1994; Barklund and Wahlstrøm, 1994; Wahlstrøm and Barklund, 1995). The dieback has triggered considerable concern, mainly because the afflicted trees are at the age of highest growth, i.e. usually 40–60 years old, and are dominant or co-dominant in highly productive stands. Typical symptoms appear first as a stunted top growth, needle discoloration and drying of the top (Solberg, 2004). While these dieback symptoms are widely recognized and described, the underlying changes in tree anatomy and the physiological causes that lead to the visible dieback symptoms and subsequent death are not well understood.

Tree responses to drought and heat stress over a growing season are manifold, but can be categorized as long- and short-term responses. Changes in wood anatomy fall under the long-term category, as trees optimize water transport pathways by adjusting tracheid cell size and shape as well as cell wall thickness to reduced soil water availability and higher evaporative demand. Two recent studies applying artificial drought conditions to Norway spruce reported a decrease in radial growth, since fewer tracheid rows are produced (Eldhuset et al., 2013; Jyske et al., 2010). Drought experiments with mature trees revealed only a slight increase in wood density due to an increase in tracheid cell

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wall thickness; lumen diameters were however not influenced (Jyske et al., 2010). The authors concluded that severe drought as predicted to occur more frequently in the future may reduce Norway spruce growth, but it is unlikely to result in large changes in wood properties. This is emphasized by the fact that an increase in wood density is achieved mainly by narrowing lumen diameter rather than increasing cell wall thickness (Hannrup et al., 2004; Pittermann et al., 2006; Sperry et al., 2006). The intrinsic wood anatomy of the water conducting tissue, however, determines the hydraulic conductivity as well as the hydraulic safety.

Wood density has been the most promising candidate to predict vulnerability to cavitation and thus drought sensitivity in mature Norway spruce trunk wood (Rosner et al., 2008). Rosner (2013), showed a clear and significant negative relationship between air seeding pressure or full embolism pressure on the one hand and wood density of Norway spruce on the other. Hence, a greater resistance to cavitation requires a safer design for resisting implosion, because the cell walls need to withstand higher tensile strain before cavitation occurs (Hacke et al., 2001). Tensile stresses in a water filled conduit should thus increase with decreasing double cell wall to span ratio, based on the assumption that both mechanical strength and stiffness increase with increasing wood density (Domec et al., 2009; Hacke and Sperry, 2001; Hacke et al., 2001; Pittermann et al., 2006; Sperry et al., 2006).

Short-term responses mainly occur at the leaf level whereby a reduction in stomatal conductance (g_s) reduces water losses to the atmosphere. This change in stomatal aperture subsequently reduces the amount of CO_2 diffusing through stomata reducing photosynthetic capacity (A). Consequently, the probability of tree mortality under drought is related to the balance between carbon uptake and water loss. Precise physiological mechanisms of drought related mortality is an active area of research (Anderegg et al., 2012), and it is unclear how important carbon starvation is compared to hydraulic failure (Sevanto et al., 2014), yet, the intensity and duration of drought stress (McDowell et al., 2008) most likely plays a large role in Spruce dieback. Stable isotopes have been widely used to address leaf level acclimation of A and g_s to environmental conditions (for a recent review see Werner et al., 2012). Photosynthetic carbon isotope fractionation and consequently the carbon isotope composition ($\delta^{13}C$) of plant organic matter is an indicator for the ratio of ambient (c_a) to leaf intercellular (c_i), more precisely, to chloroplastic (c_c) CO_2 concentration (Farquhar et al., 1982). Since c_i/c_a and c_i/c_c are strongly dependent on g_s and A, $\delta^{13}C$ is a direct indicator of intrinsic water use efficiency ($WUE_i = A/g_s$) (Farquhar et al., 1989), which is also recorded in the dateable tree ring archive (McCarroll and Loader, 2004).

The oxygen stable isotope composition ($\delta^{18}O$) of plant organic matter provides additional physiological information that allows for distinguishing between effects of stomatal conductance (as mainly affected by water availability/air humidity) and effects of changes in photosynthetic capacity (as additionally influenced by irradiance, temperature and nutrient availability) on $\delta^{13}C$. In addition to the $\delta^{18}O$ of the source water (Farquhar and Cernusak, 2005) and the biochemical fractionation between the carbonyl groups of organic matter and the surrounding reaction water (Sternberg, 2009), $\delta^{18}O$ of organic matter depends on the evaporative enrichment of the leaf water, which in turn is affected by the vapor pressure differences between leaf interior and ambient air (Dongmann et al., 1974) and transpiration (via the Péclet effect; c.f. (Farquhar and Lloyd, 1993)). Thus, $\delta^{18}O$ is strongly related to g_s but not to A. The dual-isotope approach combining $\delta^{13}C$ and $\delta^{18}O$ analyses can give deeper insights into the physiological control of water use and carbon gain affected by environmental conditions (Scheidegger et al., 2000; Grams et al., 2007; Gessler et al., 2009a,b; Barnard et al., 2012). However, there are assumptions mainly on the side of $\delta^{18}O$ that need to be fulfilled for a valid interpretation of the dual isotope approach: $\delta^{18}O$ of source water should be comparable between individuals or treatments compared. Moreover, g_s needs to be coupled to the evaporative demand of the atmosphere (Scheidegger et al., 2000) or a clear g_s *vs.* transpiration relationship has to be assumed (Gessler et al., 2009a) and the pathways for water movement within the leaf need to be constant (Ferrio et al., 2009).

The combined analysis of wood anatomy, xylem hydraulic properties and the isotopic composition of tree rings allows for the assessment of the short- and long-term drought responses (Panek, 1996; McDowell et al., 2003; Battipaglia et al., 2010). This approach is also suitable to retrospectively characterize changes in wood anatomy and canopy physiology of individual trees, and to relate these changes to climate trends or extreme events in the past. Moreover, intrinsic predispositions of individual trees can be discerned and related to the actual status of vitality. Therefore, we studied trees that displayed crown dieback symptoms (symptomatic trees; *sym*) and neighboring non-symptomatic (*non-sym*) trees at two sites in Southern Norway.

Extensive drought-induced mortality (the hypothesized reason for the dieback in our study) has been primarily attributed to either hydraulic failure (Peguero-Pina et al., 2011) or carbon starvation (Galiano et al., 2011). Carbon starvation, however, is most likely related to both the avoidance and occurrence of hydraulic failure, due to their impacts on assimilation, maintenance metabolism, phloem transport and defense (McDowell et al., 2011). Since our study trees were selected with respect to their comparability, tree dimensions and social status did not differ between *sym* and *non-sym* trees. Hence, we hypothesized that differences in the susceptibility to hydraulic failure and carbon starvation depend on the differences in anatomical properties and canopy physiological traits among individuals of a population. To test this hypothesis, we investigated long-term responses of trees by comparing wood density as measure for cavitation vulnerability. Short-term responses of canopy physiology were characterized retrospectively by analyzing late wood $\delta^{13}C$ and $\delta^{18}O$ isotope signatures from tree rings.

We expect that declining trees will be more highly sensitive to drought evidenced by (i) a higher vulnerability to cavitation related to a lower wood density of the xylem tissue (Hacke and Sperry, 2001; Rosner et al., 2008), and as a short-term response in dry years (ii) a stronger increase in water use efficiency due to stomatal closure as a safety mechanism to avoid to hydraulic failure, but leading to carbon starvation. Furthermore, (iii) we expect a stronger coupling between climate, tree growth and the intrinsic water use efficiency WUE_i of the *sym* trees as previously observed for declining Scot pine trees (*Pinus sylvestris* L.) by Voltas et al. (2013).

2. Material and methods

2.1. Study sites

This study was conducted at two different locations in SE Norway (Hoxmark: 80 m a.s.l., Lat. 59°40′19″N, Long. 10°45′11″E; Sande: 110 m a.s.l., Lat. 59°35′12″N, Long. 10°12′30″E). The study plot Hoxmark was located in Ås at the eastern site of the Oslo-fjord, whereas the study plot Sande was located in Vestfold County at the western site of the Oslo-fjord. Long term climatic conditions (2000–2010) were similar at both sites: mean annual air temperature was 6.5 °C and the average annual sum of precipitation was 926 mm. In addition, the Norwegian Meteorological Institute in Oslo Blindern (94 m a.s.l., Lat. 59°94′23″N, Long. 10°72′00″E) provided an estimate for the water availability within the growing seasons at the regional scale. Therefore the modeled, cumulative