Preliminary indications for diverging heat and drought sensitivities in Norway spruce and Scots pine in Central Europe

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Massive and increasing tree mortality is currently observed in the two conifer species Norway spruce and Scots pine in Central Europe. Consecutive dry years are made responsible for this phenomenon. Leaf trait measurements, in specific leaf osmotic potential ($\pi_{osm}$) and leaf water potential at turgor loss ($\pi_{tlp}$), indicate that the underlying mechanisms for tree mortality are most likely different between the two species. $\pi_{tlp}$ of spruce was highly negative, revealing a potentially high drought tolerance of the species. $\pi_{tlp}$ of Scots pine was less negative, suggesting a higher susceptibility to drought stress. I conclude that the mortality of Norway spruce might be caused by rising temperatures and that the summer temperatures in the past years were beyond the species thermal tolerance threshold. Overall, I want to highlight and enhance the discussion that the search for suitable species for a climate change adapted forest should go in both directions, i.e., species should be chosen to make the forest fit for both increasing drought and heat stress.

Keywords: Tree Mortality, Water Stress, Heat Stress, Physiological Limitations, Conifers

Introduction

Climate-change induced forest mortality is currently a rapidly emerging trend (Allen et al. 2010). This means that many forests have lost their ability to sustain the global biogeochemical cycle or their function in providing vital habitat, and valuable ecosystem services for human communities (Cobb et al. 2017). A good understanding of the drivers, general patterns, and severity of changes can help to apply mitigation strategies to reduce economic and cultural consequence (Allen et al. 2010). In Europe, Norway spruce and Scots pine have been the two most important timber species for the forestry sector over centuries (for historic background see Hartig 1791, Stromer Von Reichenbach 1968). Especially, those two economically very important conifer species have been massively affected by accelerated tree mortality in recent years across Europe (Allen et al. 2010). In the past, the main cause of mortality in Norway spruce was wind disturbance with consecutive disastrous bark beetle outbreaks (Eriksson et al. 2007). The increasing frequency of summer drought and heatwaves has replaced wind disturbance as the main cause of Norway spruce mortality (Hentschel et al. 2014). In Central Europe, the massive mortality of Scots pine is a relatively new phenomenon in many areas and came for many forest managers and decision-makers almost unexpected (Kunert 2019), especially as Scots pine has been thought to be relatively drought tolerant. Hence, drivers and mechanisms causing tree mortality are not always clear.

This study presents the leaf osmotic potential ($\pi_{osm}$) as a physiological measure that is directly related to a species drought tolerance. $\pi_{osm}$ can be translated into the leaf water potential at turgor loss ($\pi_{tlp}$) and represents the permanent wilting point (Bartlett et al. 2012). The aim of this study was to verify if water limitation explains the accelerated mortality in Norway spruce and Scots pine from a leaf hydraulic perspective and to present a comparison to the regional species pool.

Methods

Study area

The collection of the plant material took place in the surroundings of Ammerndorf in the rural district of Fürth in Middle Franconia, Germany (49° 24′ 36.0″ N, 10° 49′ 39.3″ E). The forest management history of the district is influenced strongly by Peter Stromer, who initiated a reforestation approach in the year 1368, turning the formerly depleted mixed-species forests (probably Scots pine, birch, and oak) into pure stands of Scots pine (Pinus sylvestris L. – Stromer Von Reichenbach 1968). The area is characterized by a very patchy forest distribution. Approximately 30% of the area is currently stocked with forest and the rest is used for agriculture. The main tree species cultivated in the area are Scots pine, followed by Norway spruce (Picea abies Karst.). The two conifer species make up 80% of the forest area and the other 20% by broadleaved species, with European oak (Quercus robur L.) being the most important species and the invasive black cherry (Prunus serotina Ehrh.) rapidly taking over the understory. The area has experienced various dramatic and cascading die-off events in the last two years following three very dry summers and heatwaves in 2015, 2016 and 2019 (Klemmt et al. 2018). Bark beetle outbreaks have killed about 30% of the spruce trees and a complex combination of fungi are accelerating the mortality of pine (Kunert 2019). In some stands, all

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Results

The main results of this study are summarized in Fig. 1. The 75th and 25th percentiles of the species pool were -2.01 and -2.60 MPa for $\pi_{\text{osm}}$. Mean $\pi_{\text{osm}}$ lies at -2.33 ± 0.33 MPa and mean $\pi_{\text{osm}}$ at -2.04 ± 0.40 MPa. The two target species had a $\pi_{\text{osm}}$ of -2.64 ± 0.10 MPa and -1.93 ± 0.065 MPa. Common broad-leaved species like Quercus robur and Fagus sylvatica had a $\pi_{\text{osm}}$ of -2.68 ± 0.17 MPa and -2.62 ± 0.02 MPa, respectively. $\pi_{\text{osm}}$ was at -2.46 ± 0.20 MPa and -2.39 ± 0.02 MPa.

Discussion

$\pi_{\text{osm}}$ measurements revealed that Norway spruce loses its turgor at a more negative leaf water potential. In contrary, Scots pine loses its turgor earlier with less negative leaf water potential. This means that Scots pine reaches its permanent wilting point earlier under water limitation than Norway spruce (Bartlett et al. 2012). This approach disregards possible differences in rooting depth of the two species and water accessibility during drought; however, various studies have shown that both species have

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**Fig. 1** - Mean values and standard deviation of the (A) water potential at turgor loss ($\pi_{\text{tlp}}$) and (B) osmotic leaf water potential ($\pi_{\text{osm}}$) of the target species and the most economically important broad-leaved species in Central Europe. The box plot presents $\pi_{\text{tlp}}$ and $\pi_{\text{osm}}$ of 32 woody species collected in the study area. Three individual (n = 3) for each species were sampled to measure $\pi_{\text{tlp}}$ and $\pi_{\text{osm}}$. Values for the box plot are based on the mean values of the 32 species. The upper and lower limits of the box plots represent estimates of the 75th and 25th percentiles.
most of their fine roots in the same soil layer and do not access layers deeper than 50 cm with a significantly different amount of fine roots (Jackson et al. 1996, Finer et al. 2007, Helmsaari et al. 2007). Hence, it can be assumed that both species are accessing water resources at the same soil layer and that from leaf hydraulic point of view Norway spruce is much more drought tolerant than Scots pine. Despite possible differences in rooting and soil water uptake pattern, Norway spruce has even lower $\pi_{w,\min}$ and $\pi_d$ than the 25th percentile of the species in the area. This means that Norway spruce might be potentially more drought tolerant than most other species, even more, tolerant to drought than oak and bee trees (Fig. 1). I conclude that the main underlying mechanism of accelerating Norway spruce mortality does not lie in water stress but rather in heat stress caused by heatwaves. In the last years a significantly increasing number of heatwaves, defined as at least three consecutive days with a maximum daily air temperature of $>30^\circ C$, has been observed in Central Europe (Tomczyk & Bednorz 2019). Norway spruce has been planted in many lowland areas near or at the edge of its thermal tolerance. Those temperature regimes during the heat waves are most likely reaching the thermal tolerance threshold (Curts et al. 2014, Cochar 2019) of the species leading to lethal heating of leaves (O’Sullivan et al. 2017). As higher altitudes are affected by heatwaves too, the thermal tolerance threshold could explain mortality in higher and cooler environments. To my knowledge there is no study on the thermal tolerance threshold of Norwegian spruce to support my speculation; most studies focus rather on the freezing tolerance of these species (e.g., combination of freezing and drought tolerance – Blödner et al. 2005). Similar mechanisms of tree mortality concerning heat might apply to the currently observed wilting of bee trees all over central Europe. From the leaf hydraulic perspective, European beech and oak have similar $\pi_{w,\min}$, however, species distributional range of European oak reaches trees all over central Europe. From the leaf hydraulic perspective, European beech and oak have similar $\pi_{w,\min}$ and $\pi_d$ than the 25th percentile of the species in the area. This means that Norway spruce might be potentially more drought tolerant than most other species, even more, tolerant to drought than oak

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**Conclusion**

Mortality in the two most economically important conifer species in Central Europe might be explained by two different mechanisms. Norway spruce might be more affected by being pushed to its thermal tolerance threshold, whereas Scots pine suffers from water limitation. However, both drought and heat are threatening forest ecosystems with progressing climate change and will be the most pressing task to be tackled by forest managers in the coming years. Therefore, the search for suitable species must account for the thermal tolerance threshold and a species’ drought tolerance.

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