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Inter- and intra-specific variation in drought sensitivity in *Abies spec.* and its relation to wood density and growth traits

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ABSTRACT

Understanding drought sensitivity of tree species and its intra-specific variation is required to estimate the effects of climate change on forest productivity, carbon sequestration and tree mortality as well as to develop adaptive forest management measures. Here, we studied the variation of drought reaction of six European *Abies* species and ten provenances of *Abies alba* planted in the drought prone eastern Austria. Tree-ring and X-ray densitometry data were used to generate early- and latewood measures for ring width and wood density. Moreover, the drought reaction of species and provenances within six distinct drought events between 1970 and 2011, as identified by the standardized precipitation index, was determined by four drought response measures. The mean reaction of species and provenances to drought events was strongly affected by the seasonal occurrence of the drought: a short, strong drought at the beginning of the growing season resulted in growth reductions up to 50%, while droughts at the end of the growing season did not affect annual increment. Wood properties and drought response measures showed significant variation among *Abies* species as well as among *A. alba* provenances. Whereas *A. alba* provenances explained significant parts in the variation of ring width measures, the *Abies* species explained significant parts in the variation of wood density parameters. A consistent pattern in drought response across the six drought events was observed only at the inter-specific level, where *A. nordmanniana* showed the highest resistance and *A. cephalonica* showed the best recovery after drought. In contrast, differences in drought reaction among provenances were only found for the milder drought events in 1986, 1990, 1993 and 2000 and the ranking of provenances varied at each drought event. This indicates that genetic variation in drought response within *A. alba* is more limited than among *Abies* species. Low correlations between wood density parameters and drought response measures suggest that wood density is a poor predictor of drought sensitivity in *Abies spec.*

1. Introduction

Terrestrial plants have developed various strategies to avoid or reduce drought induced stress. Such strategies encompass, amongst others, anatomical or physiological adjustments like reduction of leaf area (Le Dantec et al., 2000), reallocation of biomass from the crown to stem and roots (DeLucia et al., 2000), stomatal closure (Sperry, 2000) or altering gene expression patterns of proteins (Wang et al., 2003). One important milestone in the evolution of terrestrial plants had been the development of woody tissue, especially of xylem conduits, which allows them to transport water along a soil-plant-atmosphere continuum to greater heights efficiently (Breda et al., 2006; Sperry et al., 2008). This mechanism also bears risks, especially when soil-water is limited under strong evaporative demand: if the water flow within the xylem conduits is disrupted cavitation may occur causing irreversible damages to the water transport system (Choat et al., 2012). A tree's vulnerability to cavitation depends on many factors such as the pore diameter in conduit walls (i.e. the greater the diameter, the higher the vulnerability) (Zimmermann, 1978) and conduit wall reinforcement (i.e. the greater the reinforcement, the lower the vulnerability) (Hacke et al., 2001). However, to measure these anatomical characteristics and to estimate a tree's vulnerability to cavitation requires sophisticated preparation

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and measuring techniques and the ultimate destruction of the given sample. Thus, less time-consuming measures of wood traits were tested as indicators of cavitation- and drought-sensitivity. In Norway spruce (*Picea abies* L.), Rosner et al. (2014) found a negative relationship between wood density and the pressure potential necessary to induce 50% (P_{50}) and 88% (P_{88}) loss of hydraulic conductivity, respectively. Similar strong relationships were also found for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Dalla-Salda et al., 2011). Other studies focused on growth performance instead of hydraulic performance and used ring width changes as response variable in order to avoid destructive measurements (e.g. Battipaglia et al., 2009; Eilmann and Rigling, 2012; Orwig and Abrams, 1997; Pasho et al., 2011).

The understanding of drought sensitivity of individual trees, provenances, tree species and entire forest ecosystems is an issue of utmost importance, as some ecosystems worldwide have experienced and more are expected to undergo significant increases in the frequency, duration and severity of drought periods due to climate change (Allen et al., 2010; Beniston et al., 2007). In forest ecosystems, drought periods were found to result in reductions of the gross primary productivity and led to carbon emissions (Ciais et al., 2005) as well as to increased tree mortality either due to direct die-offs or indirectly via boosted insect outbreaks (Allen et al., 2010). Consequently, among different silvicultural adaptation methods, the planting of different provenances of the present species or even the planting of alternative tree species has been suggested as effective management option (e.g. Berry et al., 2002; Bradley St Claire and Howe, 2007; Hamann and Wang, 2006; Jandl et al., 2015; Matyas, 1996; Rehfeldt et al., 1999).

The genus *Abies* encompasses, amongst others, ten species that are distributed around the Mediterranean, of which only one species (silver fir, *Abies alba* Mill.) is also part of temperate and alpine forests. In the low mountain ranges of western, southern, south-eastern and Central Europe, silver fir is a main component of the forest climax vegetation. Recent comparisons of tree species suggest that silver fir is more resilient to climate change (and associated phenomena like bark beetle outbreaks and storm damage) than other conifers of temperate forests (Zang et al., 2011). Currently economically less important Mediterranean firs have small, partially disconnected distribution ranges, but they could substitute *A. alba* or other conifers in temperate European forests if increasing temperatures and decreasing precipitation endanger present tree species compositions. However, a systematic analysis of drought sensitivity within the genus *Abies* and among populations of silver fir across several drought periods is not available so far.

In our study, data was taken from a long-term provenance trial comprising 10 provenances of *A. alba* and 5 Mediterranean *Abies* species. This trial site was established in 1970 with the explicit objective to investigate the drought reaction of *Abies spec* (Mayer et al., 1980) and located in eastern Austria, where severe summer droughts occur frequently (see for example Büntgen et al., 2010). In our analysis, we aim at the following questions: (i) Do the various species and provenances of the genus *Abies* respond differently to drought situations? (ii) Can wood properties (e.g. ring width, ring density) be used to predict the reaction of species or provenances to drought events? (iii) Does the climate at the origin of seed of a respective species or provenance explain its specific reaction?

2. Materials and methods

2.1. Trial site and plant material

The trial site is located in eastern Austria at the border of the sub-pannonian Vienna basin. It is placed on a moderate south-west slope at 290 m a.s.l. Mean annual air temperature is 8.6 °C and the annual precipitation sum is 650 mm with 270 mm during the vegetation period (ZAMG weather station "Hohe Warte" 1970–2010). Seed material of the Mediterranean fir species originated from Turkey and Greece and the provenances of silver fir from across its natural distribution area (Fig. 1). The trial was planted in 1970 as a randomized block-design with plant spacing of 0.5 × 1.0 m using two- and three-year-old seedlings (Mayer et al., 1980). In March 2012, all specimen, for which at least eight trees were available were sampled by taking two cores per tree at breast height (Table 1). This included ten provenances of *Abies alba*, four Mediterranean fir species (*A. bornmülleriana*, *A. cephalonica*, *A. cilicica* and *A. nordmanniana*), and the natural hybrid of *A. alba* and *A. cephalonica*: *A.* x *borisii- regis* (Mattfeld, 1926; Bella et al., 2014).

2.2. Core sample preparation, X-ray densitometry and removal of age-trend

Approximately 1.4 mm thick cross sections of each core, produced with a double-blade circular saw, were placed on microfilms and exposed to a 10 kV (24 mA) X-ray source for 25 min. Microfilms were analyzed using WinDENDRO 2009 (Regent Instrument, Quebec, CAN). This procedure provided measurements for mean ring density (RD), early-wood density (ED), late-wood density (LD), minimum density (MIND) and maximum density (MAXD) for each year as well as for ring width (RW), earlywood width (EW), latewood width (LW) and latewood proportion (LWP). Density parameters were measured in kg/m^3 while ring width parameters were measured to the nearest 0.001 mm. LWP expresses the relative proportion of latewood compared to total ring width and is therefore given in percentages. Values from the two cores of the same tree were averaged to reduce non-climatic effects (such as reaction wood and faults in the wood tissue) and to account for potentially missing data of the youngest and oldest tree rings. For further analysis of identification of drought years (see below), we removed the biologically caused age trend occurring in the short time series of ring width by using a flexible 15-year cubic smoothing spline that was fitted and visually evaluated using the dplr package of the software R (Bunn, 2010; R Development Core Team, 2008).

2.3. Identification of drought events and evaluation of performance under drought

To identify drought periods with subsequent effects on tree growth and wood density, we calculated the standardized precipitation index - SPI according to McKee et al. (1993). The SPI is based on monthly precipitation time series (in our case from 1970–2010) and relates the actual precipitation deficit to the mean and standard deviation of the time series. In contrast to drought indicators with fixed time scales such as the PDSI (Guttman, 1997; Vicente-Serrano et al., 2010), the SPI is able to identify and differentiate between frequently occurring short- and longer drought events, because the duration of the tested drought/precipitation period can be modified from few months up to years. We chose two different time scales (1- and 3-months, respectively) since these time spans represent biological meaningful periods of water-shortage for trees and are likely to occur in central Europe. For calculation of SPI we used the program *SPI SL 6* (NDMC, 2014). Years were considered as drought years, when they showed a severe or extreme shortage in water supply (severe drought: SPI ≤ -1.50; extreme drought: SPI ≤ -2.00) within the vegetation period (April to August). To assess a trees performance during these drought events, we calculated four indices of drought reaction following Lloret et al. (2011): resistance (Res), recovery (Rec), resilience (Rsl), as well as relative resilience (rRsl). Resistance can be characterized as a trees' ability to withstand a period of low water supply without showing a perceptible drop