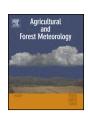
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# Temporal changes in the climate sensitivity of Norway spruce and European beech along an elevation gradient in Central Europe



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#### ARTICLE INFO

# Article history: Received 26 October 2016 Received in revised form 17 February 2017 Accepted 26 February 2017

Keywords: Czech Republic Drought Fagus sylvatica Picea abies Temperature Tree-ring width chronology

#### ABSTRACT

Norway spruce has experienced unprecedented forest declines in recent decades, leading to extensive salvage logging. Currently, because of the conversion of conifer forests into more natural mixed forests in Central Europe, spruce has begun to be replaced, mainly by European beech. The frequently discussed changing climate has a crucial effect on the vitality of both species. To improve our understanding of spruce and beech responses to climate change, including more frequent temperature and drought extremes, we investigated the impact of temporal climate variability on the growth of these species along an elevation gradient. In total, 79 spruce and 90 beech trees were used to build species-specific tree-ring width chronologies representing the altitudinal range in which both species grow (450, 650, 800, and 950 m asl) under the conditions of the Czech Republic. The climate–growth relationship indicates strong dependence of spruce and beech tree-ring growth on spring temperature (Mar–May) at all sites and summer (Jun–Aug) water availability at lower altitudes. Significant temporal shifts in the climate–growth relationships of both species indicate an increasing negative effect of summer temperature and positive effect of water availability in summer. The increasing drought and temperature sensitivity of both species suggest a significant impact of the predicted climate change on such forest ecosystems. Discussion emphasizes the current importance of adaptive forest management strategies.

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#### 1. Introduction

Projected scenarios of the climate change show that air temperature across the Czech Republic will on average increase between 2.0 °C (representative concentration pathway (RCP) 4.5 scenario) and 4.1 °C (RCP 8.5 scenario) by the end of the 21st century compared with the reference period (1981–2010; e.g. Štěpánek et al., 2016). Predictions of annual precipitation indicate slight increases of approximately 7–13% for RCP 4.5 and 6–16% for RCP 8.5. The largest increase is predicted for winter precipitation, which may increase by 35% by the end of the 21st century (but also remain unchanged according to some of the climate models). An opposite type of change is expected for summer precipitation and according to some global circulation models, precipitation may significantly decrease compared with the present.

Although mean change of precipitation according to the ensemble of global climate models shows in its annual total slightly increasing tendency, it is not nearly enough to offset drying of the landscape driven by increased temperatures, lower air humidity, and in some months increased global radiation. An overall increase in drier conditions with an increasing frequency, intensity, and duration of temperature extremes is expected (e.g., Tebaldi et al., 2006), in line with the decreasing soil moisture content reported in the past 55 years over the region (Trnka et al., 2015).

Climatic fluctuations will very likely have a substantial impact on forest ecosystems (Spiecker, 2003). Nevertheless, recurrent drought events may have an even more severe effect on tree vitality manifested in significant growth reductions (Lévesque et al., 2016) or even tree mortality (Allen et al., 2010). The primary mechanisms of drought-induced tree mortality are hydraulic failure (McDowell et al., 2008) and carbon starvation (Adams et al., 2009). Biotic agents, such as insects and pathogens, can amplify or be amplified by both carbon starvation and hydraulic failure (McDowell

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et al., 2008). The final consequences can lead to fluctuation of the ecological and geographical ranges of different tree species and a changing species composition in forests (Bolte et al., 2010; Rigling et al., 2013).

Norway spruce (Picea abies L. Karst) and European beech (Fagus sylvatica L.) belong to the most widespread and socio-economically valuable species representative of European forest ecosystems (Euforgen, 2009). Norway spruce, as a fast-growing softwood species, was planted far beyond the limits of its natural range in recent centuries, particularly in Central Europe (Spiecker, 2003). In forestry, these limits can be expressed as ecological and growth optima. The ecological optimum is a combination of site and climatic conditions which are optimal for growth, existence, and reproduction of the tree species in natural biocenosis (Walter, 2011). The growth optimum is defined as conditions under which tree species can achieve the maximum wood production and the maximum wood quality (Plíva, 2000). Such spruce monocultures show demonstrable reductions in resistance to natural hazards such as storms, droughts, or insects (Griess et al., 2012). Therefore, even-aged spruce monocultures have been converted into more stable mixed uneven-aged forests, leading to an increased proportion of deciduous trees where European beech predominates (Knoke et al., 2008; Pretzsch et al., 2014). The high reproduction potential and production potential of beech and its relatively wide ecological valence are the reasons for planting beech in Central European areas affected by spruce declines over recent years (Ammer et al., 2008).

Climate-growth relationships, analyzed based on comparisons of tree-ring width (TRW) chronologies and meteorological data, have been frequently studied in Central Europe for both spruce (e.g., Koprowski, 2013; Rybníček et al., 2012) and beech (e.g., Mölder and Leuschner, 2014). Most of these studies have presented the general conclusion that altitude is the leading factor controlling the main climate signal in temperate forests (Bošel'a et al., 2014a). Tree growth at high altitudes is particularly driven by growing season temperature and global radiation (e.g., Leonelli et al., 2016). A considerable increase in TRW has been observed mainly at high elevations during the past 20 years (e.g., Ponocná et al., 2016). Conversely, climate conditions at lower sites indicative of summer droughts cause narrow TRWs (e.g., Lebourgeois et al., 2010), particularly for drought-sensitive tree species, including Norway spruce (e.g., Lévesque et al., 2014) and European beech (Betsch et al., 2011; Rozas et al., 2015).

In light of the present climate change, comparative detailed multi-species studies are desirable as a contribution to the discussion of the climate-induced growth changes in different tree species (Castagneri et al., 2014; Hartl-Meier et al., 2015) and to formulate adequate adaptive forest management strategies, at least for the period corresponding to the species felling age. In particular, the past several decades have been indicated as very likely being the warmest period in Europe in the past 500 years (Luterbacher et al., 2004). Such climate forcing indisputably plays an important role in the temporal changes of climate–growth relationships, also reflected in tree vitality.

In this study, we exploited TRW measurements to better understand the temporal climate-induced changes in the growth of Norway spruce and European beech from four different sites and elevations. The study aims to investigate the long-term temporal variability of TRW in both species under conditions of climate change at the study sites, which were selected in order to represent regions lying in the ecological and growth optima as well as out of this range. We hypothesized that the lowest and the driest region is not suitable for ecological and economical growth of both species. The result of our investigation aims to contribute to the discussion on the essential forest adaptation strategies.

#### 2. Materials and Methods

#### 2.1. Study area

The climate sensitivity of radial growth in Norway spruce (P. abies L. Karst) and European beech (F. sylvatica L.) was analyzed in the eastern part of the Czech Republic (Moravia and Silesia). The ecological optimum of Norway spruce in Central Europe is located in the upper submontane, montane, and supramontane belts (Ellenberg, 2009), and the growth optimum varies between approximately 550 and 900 m asl (Pliva, 2000). On the other hand, the ecological optimum of European beech is in the upper colline and submontane belts, and the growth optimum ranges from approximately 450 to 700 m asl (Ellenberg, 2009; Plíva, 2000). The study area lies along the border between the Bohemian Massif and the Western Carpathians and covers the upper colline, submontane, and montane altitudinal vegetation belts (Chytrý, 2012). Given that Norway spruce and European beech both grow within an approximate altitudinal range of 400-1000 m asl in the territory of the Czech Republic, study sites were selected to represent this gradient. Site codes were defined to indicate species and elevations in meters above sea level (Fig. 1).

The lowest site (Drahany Highlands) is characterized by total annual precipitation lower than 600 mm and was chosen to represent one of the driest regions in the Czech Republic, southern Moravia. The Oderske vrchy is among the colder and windier areas because of its natural plateau character. The very rugged area of the White Carpathians is characterized by a short, mild, and wet summer. At the highest site (the Beskid Mountains), total annual precipitation can be higher than  $1100 \, \text{mm/year}$ . The seasonal values and trends of climate factors (temperature, precipitation, and relatively available water – AWR) at all study sites are presented in Figure S1. Generally, precipitation shows positive statistically significant (p < 0.05) Pearson's correlation with AWR (0.58 - 0.70). On the other hand, AWR correlates negatively (p < 0.05) with temperature (varies from  $-0.30 \, \text{to} -0.43$ ). No significant relationship was observed between temperature and precipitation.

#### 2.2. Climate data

Climate data covering period 1961–2013 were derived through interpolation from a set of nearby weather stations using locally weighted regressions including the effect of altitude. The interpolation was based on the total database of the Czech Hydrometeorological Institute, which includes data from 268 meteorological stations and 787 precipitation stations that represent the territory of the Czech Republic well. All observations of weather variables were tested for outliers and breaks through a detailed homogenization sequence, and gaps in missing data were filled (Stěpánek et al., 2009, 2011). The database for the studied areas included data on the daily average, minimum, and maximum temperatures (Tavg, Tmin, and Tmax, respectively), the daily sum of global radiation, mean daily wind speed, mean daily relative humidity, and the daily sum of precipitation. The sum of global radiation was corrected on the basis of the site aspect and slope. The SoilClim (Hlavinka et al., 2011) model was employed to estimate the daily values of the relative soil water content (AWR) for the top 1.3 m, which was used as one of the water availability proxies. Estimates of AWR for a particular grid took into account phenology of the canopy (i.e. deciduous forest) as well as the soil water holding capacity of the soil topsoil (0-0.4m) and subsoil (0.41-1.3m), the aspect and slope of the grid, influence of underground water as well as potential shading by the neighboring terrain. The first year was used to spin-up the soil moisture model. Most of the key climate factors can be considered simultaneously using this complex indicator (e.g., Trnka et al., 2011).

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