



Climatic drivers of forest productivity in Central Europe



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ABSTRACT

Climate is an important driver of forest health, productivity, and carbon cycle, but our understanding of these effects is limited for many regions and ecosystems. We present here a large-scale evaluation of climate effects on the productivity of three temperate tree species. We determine whether the National Forest Inventory data (NFI) collected in the Czech Republic (14,000 plots) and Slovakia (1,180 plots) contains sufficient information to be used for designing the regional climate-productivity models. Neural network-based models were used to determine which among 13 tested climate variables best predict the tree species-specific site index (SI). We also explored the differences in climate-productivity interactions between the drier and the moister part of the distribution of the investigated species. We found a strong climatic signal in spruce SI (R 0.45–0.62) but weaker signals in fir and beech (R 0.22–0.46 and 0.00–0.49, respectively). We identified the most influential climate predictors for spruce and fir, and found a distinct unimodal response of SI to some of these predictors. The dominance of water availability-related drivers in the dry-warm part of a species' range, and vice versa, was not confirmed. Based on our findings, we suggest that (i) the NFI-based SI is responsive to climate, particularly for conifers; (ii) climate-productivity models should consider the differences in productivity drivers along ecological gradients, and models should not be based on a mixture of dry and moist sites; and (iii) future studies might consider the subset of influential climate variables identified here as productivity predictors in climate-productivity models.

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1. Introduction

The reliable assessment of forest productivity, including the effects of climatic drivers and other perturbations, has been increasingly recognized as crucial to forest management planning and climate change mitigation efforts (Hanewinkel et al., 2012; Nabuurs et al., 2013; Wamelink et al., 2009). While the effect of site climate on forest productivity has traditionally been central to the interest of foresters (Bontemps and Bouriaud, 2013; Skovsgaard and Vanclay, 2008, 2013; Socha et al., 2016), a forest's capacity to sequester carbon and exert control on climate has recently highlighted the bi-directional nature of forest-climate interactions (Becknell et al., 2015; Brovkin et al., 2009).

To investigate the environmental control of forest productivity and carbon cycle, researchers have focused on both the rule of fun-

damental ecophysiological processes (Coops et al., 2005; Zhou et al., 2005) and on the statistical associations between the environment and productivity indicators (Aertsens et al., 2010; Antón-Fernández et al., 2016). Although the latter approach provides only a limited understanding of the underlying processes (Adams et al., 2013; Pretzsch et al., 2015), it can guide management decisions, provide information about the main drivers of and changes in forest productivity (Bošel'a et al., 2014; Charru et al., 2010; Kint et al., 2012; Pretzsch et al., 2014), and support the development of empirical forest models (Pretzsch et al., 2008; Trasobares et al., 2016).

Here, we used an empirical approach to investigate the effects of climate on forest productivity in two countries in central Europe—the Czech Republic and Slovakia. To facilitate such investigation, we used extensive datasets of the National Forest Inventory (NFI) from the two countries. The NFI is a main source of forestry data in many countries and supports assessment of forest resources (Vidal et al., 2016) and research (e.g., Gasparini et al., 2013; Kovač et al., 2014). The data were also used for the development of growth-climate models and assessment of the effects of climate

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change on forests (Charru et al., 2010). The high spatial resolution of these data and the large number of inventory cycles that span many decades in some countries (e.g., from 1923 to the present in Sweden, Fridman et al., 2014) have facilitated cross-scale and interdisciplinary research through the integration with other forestry and environmental data (e.g., Kovač et al., 2014; Tomppo et al., 2008).

In Central Europe, forest productivity research has been conducted only on smaller scales (Bošel'a et al., 2013a; Socha, 2008; Socha et al., 2016), and thus the current study represents the first regional assessment of climatic effects on forest productivity. Forest productivity in this region is mainly driven by climate-oro-graphic patterns and soil nutrient availability (Bošel'a et al., 2013a). Recent research has recognized the inter- and intraspecific differences in temperate tree growth and productivity (George et al., 2015; Suvanto et al., 2016) as well as differences in the productivity of different mixtures of species (Bošel'a et al., 2015; Pretzsch et al., 2012, 2015). Such findings have been used in forest management planning and parameterization of forest models for the region (Bošel'a et al., 2013b; Hlásny et al., 2014a; Lexer et al., 2002; Pretzsch et al., 2014). We investigate here three widespread tree species that have high commercial and ecological importance and that constitute some of the original forest communities in Central Europe: Norway spruce (*Picea abies* L. Karst), European beech (*Fagus sylvatica* L.), and silver fir (*Abies alba* Mill.).

Norway spruce has been extensively planted in Central Europe, and the so-called secondary spruce forests are for the most part currently distributed at unsuitable sites (Ellenberg, 1986; Spiecker et al., 2004; Löf et al., 2010). This is thought to greatly amplify the vulnerability of such forests to biotic and abiotic stresses (Hanewinkel et al., 2010; Hlásny and Turčáni, 2013). Although the growth response of spruce to climate was found to be variable (Andreassen et al., 2006), and although spruce growth was strongly affected by air pollution and other non-climatic effects (Bošel'a et al., 2014), spruce growth was found to significantly accelerate in recent decades in Central Europe (Pretzsch et al., 2014). On the other hand, spruce growth was found to be much more sensitive to drought than the growth of beech and fir (Zang et al., 2014). Spruce also exhibited a substantially elevated mortality under an increasingly unfavourable climate (Neuner et al., 2014).

European beech is highly sensitive to climate (Fang and Lechowicz, 2006; Fotelli et al., 2009; Mellert et al., 2016), and this has generated concerns about the sustainability of the species across a large part of its distribution under climate change (Czúcz et al., 2011; Mette et al., 2013). Beech has exhibited decreased growth since ca. 1975 near the lower range of its distribution (Jump et al., 2006; Peñuelas et al., 2007). At the same time, beech has shown accelerated growth under standard growing conditions in Central Europe (Pretzsch et al., 2014), particularly in less productive sites (Bošel'a et al., 2016). Several authors found the ratio of mean temperature of the warmest month and annual precipitation (the Ellenberg quotient) to be a powerful predictor of beech vigour, growth, and mortality (Czúcz et al., 2011; Fang and Lechowicz, 2006; Jahn, 1991).

After a serious growth decline and even a dieback of silver fir in the period of 1970–1990, fir has experienced an unprecedented growth increase in central Europe (Bošel'a et al., 2014; Elling et al., 2009). Fir growth, however, has declined in the southern range of the species' distribution since 2000, which has suggested that drought may have recently become a factor limiting fir growth in some regions (Büntgen et al., 2014; Gazol et al., 2015; Linares and Camarero, 2012). The growth decline in 1970–1990 was attributed to high levels of air pollution, whereas the recent growth increase was likely associated with climate warming when that warming has not been coupled with a significant decrease in water availability (Büntgen et al., 2014).

To increase our understanding of forest productivity and climate interactions in Central Europe, we focused here on the following objectives: (i) to identify the extent to which the species-specific site productivity in Central Europe is controlled by climatic drivers; (ii) to determine which climate variables are the most important predictors of the region's forest productivity; (iii) to evaluate differences between climate control of forest productivity in the cool-moist and the warm-dry part of the ranges of spruce, beech, and fir; and (iv) to produce maps that show the sensitivity of species productivity to climate across the Czech Republic and Slovakia.

This research will extend the current knowledge of forest-climate interactions in Central Europe because it uses a novel experimental design and novel methods of data analysis. Moreover, the used data cover a substantial part of the ranges of the three species. While most previous studies used limited sets of climate predictors to explain observed growth and productivity patterns (e.g., Albert and Schmidt, 2010; Bošel'a et al., 2013a), and while these predictors were selected based on the prior hypotheses formulated by the researchers, we evaluate here an extensive predictor set using a data mining-like approach (Zaki and Meira, 2014). Data mining has the potential to reveal patterns that might be missed by other techniques but has been used in forestry research only rarely (e.g., Hlásny et al., 2011, 2014b; Pourtaghi et al., 2016; Sanquetta et al., 2013). We use neural network-based regression modelling, which has been found to have good data-fitting and predictive performance in many scientific fields including forestry (Aertsen et al., 2010; Moisen and Frescino, 2002). Given the increasing quantity of forestry data and improvements in computer performance, neural network-based modelling is likely to be increasingly used. We demonstrate here one field of application, including critical assessment of its advantages and disadvantages.

In support of the objectives, we test the hypothesis that effect of temperature and water availability-related variables is relatively balanced over the entire range of a species, while effect of water availability-related variables prevails in the warmer and drier part of the range and effect of temperature-related variables prevail in the cooler and moister part of the range (Briner et al., 2013; Walther et al., 2002). We also test the hypothesis that even though a broad set of climate variables are used as productivity predictors, there will be a substantial portion of the unexplained variance accounting for the non-climatic drivers of forest development, by the noise in the used response variable (Goelz and Burk, 1996), as well as by the conceptual limits to the use of the site index (SI) as an indicator of site productivity (Bontemps and Bouriaud, 2013).

2. Data and methods

2.1. Study area

The study area covered the territory of the Czech Republic (CZ) and Slovakia (SK) (Fig. 1). Both countries are in the temperate forest zone, with an oceanic climate prevailing in the CZ and a continental climate prevailing in SK (Rivas-Martínez et al., 2004; Table 1). A substantial climate-oro-graphic gradient in the region has resulted in a range of zonal vegetation communities, from open woodland and semi-arid oak forests to a mountain tree line formed by conifers. Both countries apply timber-oriented forest management with a focus on softwood timber.

2.2. National forest inventory (NFI) data and used response variable

We used the data from a single cycle of the NFI conducted in the CZ (2001–2004; 14,000 plots) and SK (2005–2006; 1,180 plots). The CZ NFI has plots distributed in a grid of 2 × 2 km. Two circular

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