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Research paper

Increasing moisture limitation of Norway spruce in Central Europe revealed by forward modelling of tree growth in tree-ring network

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ABSTRACT

Planted even-aged forests dominated by Norway spruce (*Picea abies*) progressively replaced mixed natural forests in large parts of Central Europe during past centuries due to the productivity-motivated preferences of forest owners. These managed forests have become vulnerable to climate change, specifically to increasingly severe drought. To evaluate the response of trees to warming, we collected samples from a randomized landscape inventory grid of 7 × 7 km to account for spatial gradients in climate/growth interactions in the entire forested part of the Czech Republic. The purely climate-driven forward growth model − Vaganov-Shashkin "Lite" − was calibrated by real (observed) radial growth series to identify a course of climatic limiting factors on an intra-annual scale. Relative proportions of moisture and temperature limited parts of total tree-ring width were determined as well as trends in limiting conditions over the period 1940–2012 and along the elevation gradient. Significant match between modelled and observed growth was shown in 47% of the grid cells. The coherence between modelled and observed site series was significantly improved when individual grid cells were aggregated into elevation belts. In grid cells below 600 m, from 51 to 58% of tree-ring width was formed under moisture-limited conditions, with the proportion of growth under optimal conditions being minimal. The effect of drought stress was outweighed by earlier spring onset of growth, resulting in positive trends in total tree-ring width above 500 m. About 26% of tree-ring growth has occurred under optimal climatic conditions at elevations above 800 m, where, moreover, 45% of total annual growth was temperature limited. Except for one medium-elevation belt, the proportion of growth under moisture-limited conditions significantly increased during the period analysed. Recent warming and increasing frequency of drought events deepened the divergence in growth trends between low-elevation areas and stands at medium and high elevations.

1. Introduction

Norway spruce (*Picea abies*) is a cold-adapted, drought-sensitive species (Zweifel et al., 2009; Lévesque et al., 2013; Zang et al., 2014), and it is thus highly vulnerable to the increasing frequency and severity of drought events associated with recent climate change (Spinoni et al., 2015; Brázdil et al., 2015). Decrease in productivity, reversal of carbon balance and even large-scale dieback have already been observed near the moisture limit of Norway spruce distribution (Schutt and Cowling, 1985; Solberg, 2004; Ciais et al., 2005). Moreover, drought also acts as a predisposing factor for local insect and fungal outbreaks, further increasing mortality (Marçais and Bréda, 2006; Svoboda et al., 2010). On the other hand, spruce growth can also be promoted by increasing temperature as its growth range includes temperature limited montane zones (Wilson and Hopfmueller, 2001; Mäkinen et al., 2002, 2003; Leal et al., 2007; Hartl-Meier et al., 2014; Ponocná et al., 2016). Increasing growth in mid-elevations has been attributed to earlier onset of cambial activity due to higher spring temperatures (Gričar et al., 2014; Rathgeber et al., 2016). The contrasting responses of spruce stands to climate change in different regions bring uncertainty about future forest productivity and health in Europe (Lindner et al., 2014). Specifically, the sustainability of recent productivity increases (Pretzsch et al., 2014) is questionable, due to the lack of studies quantifying opposing influences of temperature and drought on growth dynamics.

Dendrochronology represents an effective approach for retrospective identification of environmental factors influencing tree-growth (Schweinguber, 1996). Indeed, many of the above-mentioned findings about growth-environment interactions of Norway spruce were derived

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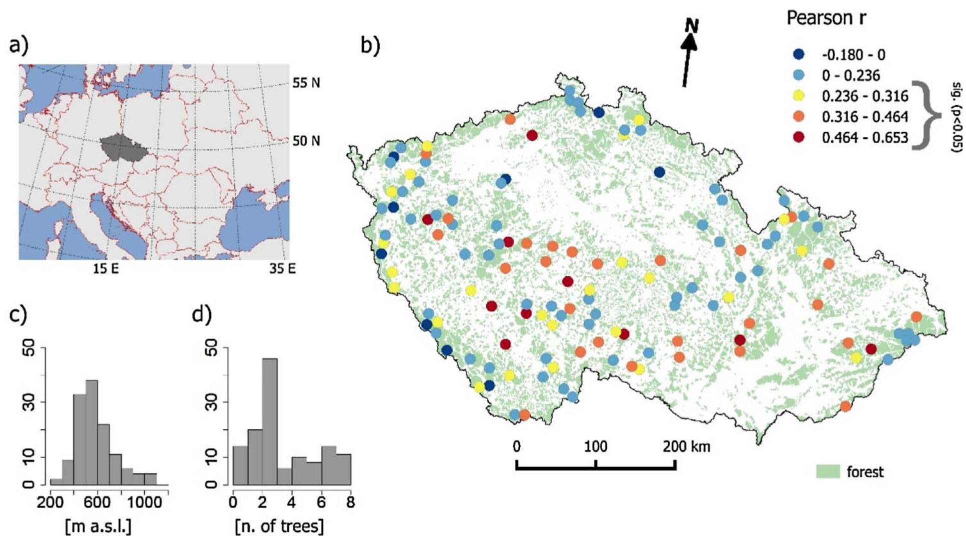

Fig. 1. (a) Position of the Czech Republic in Europe: (b) distribution of analysed plots across the Czech Republic with Pearson correlation coefficient between observed and modelled tree-ring width site series indicated by colours; (c) distribution of plots along elevation gradient; and (d) distribution of number of trees analysed per plot.

from networks of tree-ring site chronologies subjected to correlation or response function analysis between tree-ring width and monthly resolved climatic data (Fritts, 1976; Cook and Kairiukstis, 1990). Such an approach, however, requires satisfying the assumption that linear coefficients of the climate/growth relationship during the analysed period (or span of moving window) are temporally stationary (Biondi, 1997; Carrer and Urbinati, 2001). Climatic processes influencing tree-growth are then considered as a "black box" that is described by only one statistic (e.g., correlation coefficient) over a period encompassing many growing seasons (Guiot et al., 2014)

However, inhomogeneity in climate/growth relationship has been observed in many parts of the world at various temporal and spatial scales (D'Arrigo et al., 2008). Moreover, it has been shown that growth does not react to climatic variables linearly, but that there are temperature and moisture thresholds beyond which wood formation does not proceed (Rossi et al., 2007, 2008). Recently, non-linear forward models estimating climate/growth responses of trees have appeared to serve as a useful tool to overcome the above-mentioned limitations of correlation or response function analysis (Vaganov et al., 2006; Evans et al., 2006; Guiot et al., 2014). Forward models benefit not only from using realistic algorithms describing climate/growth interactions, but also from more detailed description of processes behind tree-ring formation. For instance, forward models have been used as efficient tools for addressing changes in dominant growth-limiting environmental factors over different parts of single growing seasons (Anchukaitis et al., 2006; Touchan et al., 2012; Zhang et al., 2015; Mina et al., 2016) or among consecutive growing seasons (Lavergne et al., 2015). Moreover, inter-specific comparisons of calibrated climatic thresholds of modelled growth (Breitenmoser et al., 2014; Sánchez-Salguero et al., 2017) and comparisons among sites with local instrumental measurements of climatic data (Tolwinski-Ward et al., 2013) can identify species and regions with different response intensities to climate change. In addition, forward models consider solely climatic factors affecting tree growth and can be used to estimate the level of disturbance noise in observed site chronologies (Rydval et al., 2016).

To our knowledge, the advantages of forward modelling of tree growth based on climate variables have not been utilized to characterize climate/growth responses and growth trends of trees in a dense tree-ring network. We aimed to fill this gap using 129 data points covering approximately 14,000 km^2 of forest land dominated by Norway spruce in the Czech Republic. Norway spruce has been planted far outside its natural areal in Central and Eastern Europe since the early 19th century (Spiecker, 2003), and its current representation on all forested land exceeds 60% in Austria, 42% in the Czech Republic, and 26% in both Slovakia and Germany (Spiecker, 2004; Hlásny et al., 2011; Federal Ministry of Food and Agriculture, 2014). Even though dominance of Norway spruce in regional forest composition is of great economic importance (Hanewinkel et al., 2013), its future has become uncertain due to possible impacts of climate change. Increasing temperature limits Norway spruce growth and resilience through increasing drought frequency at low elevations (Zang et al., 2014), which makes this species sensitive to insect outbreaks on regional and sub-continental scales (Svoboda et al., 2010).

In the present study, we hypothesize that the proportion of spruce tree-rings formed under moisture limited conditions has increased in Czech Republic during recent decades due to climate warming. Moreover, we expect this proportion to be greatest at low elevations and the smallest at high elevations, where the influence of drought is of marginal importance. To test this hypothesis we parameterized a forward model of annually resolved tree-ring widths sampled in a network design across the Czech Republic covering a period of about seven decades (1940–2012). This allowed us to (i) disentangle climatic drivers limiting tree growth on an intra-annual scale; and (ii) analyse the elevational and temporal trend of each limiting climate variable effect on tree growth.

2. Material and methods

2.1. Study site

The study area is represented by the CzechTerra network of landscape inventory plots (Cienciala et al., 2016; Altman et al., 2017) covering the whole Czech Republic in a regular grid with cell size 7 × 7 km (Fig. 1). In total, there are 1599 plots distributed across the Czech Republic, of which 604 contain areas in the forest land-use category. The elevation range of the forested plots is from 139 to 1226 m a. s. l.

Approximately 35% (i.e., 28,000 km^2) of the Czech Republic is covered by forest, of which almost 75% are managed, productive forests. Natural species composition was significantly altered during centuries of active forestry management, and Norway spruce is now the dominant species (42% by area, 52% by volume; Cienciala et al., 2016), accompanied mostly by beech (9.1%) and oaks (7.8%). Norway spruce naturally covered only about 8% of the area at the highest elevations (Neuhäuslová and Moravec, 1997); however, it was introduced in middle and lower elevations as even-aged stands with generally short rotation periods.

The Czech Republic is characterized by a climate transitional between oceanic and continental conditions with significant intra-annual variability of most climatic parameters. An increasing trend of mean