

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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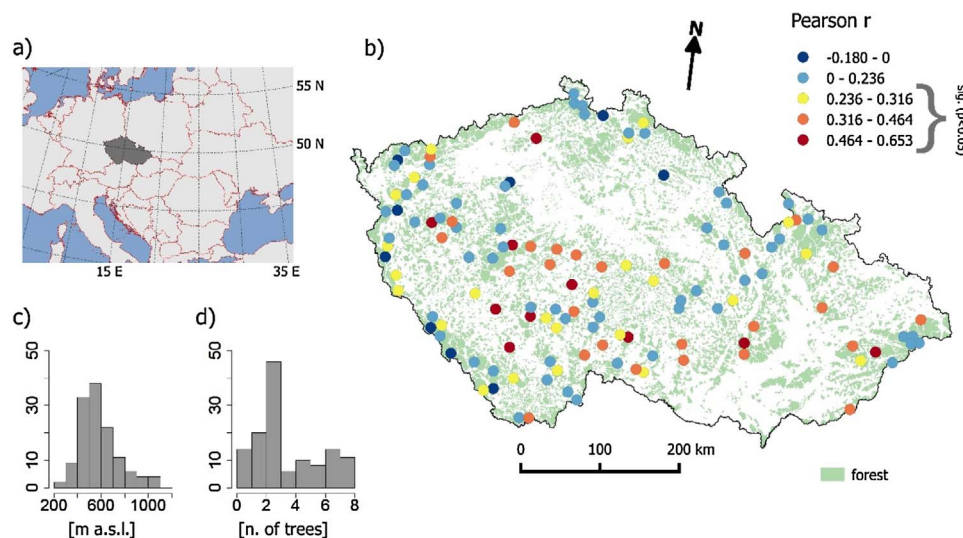


Fig. 1. (a) Position of the Czech Republic in Europe; (b) distribution of analysed plots across the Czech Republic with Pearson correlation coefficient between observed and modelled tree-ring width site series indicated by colours; (c) distribution of plots along elevation gradient; and (d) distribution 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 (Laverne 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 (Rydvall 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 km² 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 km²) 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

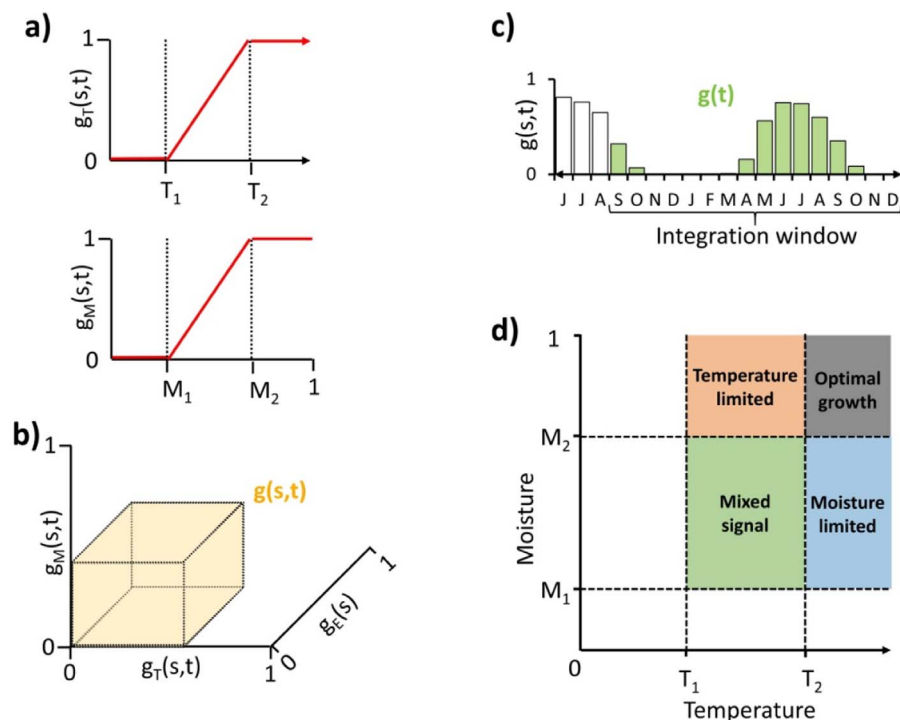


Fig. 2. Visualization of individual steps of the modified VS-Lite model (Tolwinski-Ward et al., 2011; Acevedo et al., 2016): (a) conversion of monthly resolved temperature and moisture to partial monthly growth responses; (b), calculation of overall monthly growth response; (c) integration of individual monthly growth responses to level of tree-rings; and (d) classification of individual months based on dominant limiting condition. See text for abbreviation definitions and more detailed description.

annual temperature of 0.28 °C per decade (most significant in summer), together with a shift in precipitation from summer to winter observed during the last 50 years (Brázdil et al., 2009) recently resulted in increasing frequency of drought (Brázdil et al., 2015). The spring drought effect in lowlands is amplified by the recent decrease in the amount of snow and by earlier snowmelt (Potopová et al., 2016). This increases the vulnerability of forests growing at dry limit of their ecological amplitude, with their productivity found to be significantly correlated with the drought index (SPI) during the growing season (Cienciala et al., 2016).

2.2. Dendrochronological and climatic datasets

All CzechTerra grid cells with centres located in forests dominated by Norway spruce were visited during 2014 or 2015. Three to eight randomly selected trees were cored next to the plot borders. This resulted in a dataset of 1246 spruce tree-ring width time series available for 266 plots. All cores were dried and a thin layer of wood was sliced off from each core using a core microtome (Gärtner and Nievergelt, 2010) to highlight the tree-ring boundaries. Tree-ring widths were measured with 0.01 mm precision of using TimeTable and the software PAST4 (Knibbe, 2004). To identify anomalies in tree-ring sequence (e.g., missing rings), all series were cross-dated visually using the pattern of wide and narrow rings (Yamaguchi, 1991) and verified by the Gleichläufigkeit index (Cook and Kairiukstis, 1990).

Only the time series whose span covered the period 1940–2012 were used in further analysis. This restriction resulted in a reduction of the dataset to 500 tree-ring width series from 129 plots. The age trend was removed from all series in a double detrending process – this included a negative exponential and a smoothing spline with 50% frequency-response cutoff at 67 years (Cook and Peters, 1981). This combination of detrending functions is appropriate for managed, even-aged forest stands with limited levels of competition (negative exponential) as well as for stands with heterogeneous vertical structure of trees (spline). It is important to note that the applied individual detrending approach retains high-frequency variability in tree-ring width indexed series, but removes virtually all low-frequency variability (Peters et al., 2015). Finally, the series from the same plots were

averaged into observed site series (TRW_{obs}). All processing of tree-ring width series was performed in R (R Core Team, 2016), using packages detrendR (Campelo et al., 2012) and dplR (Bunn, 2008).

Environmental datasets required by the Vaganov-Shashkin “Lite” forward model (VS-Lite; described in further detail below) include mean monthly temperatures and monthly precipitation sum, together with the latitude of each sampling plot (Tolwinski-Ward et al., 2011). VS-Lite further calculates soil moisture availability from temperature and precipitation using the National Oceanic and Atmospheric Administration’s Climate Prediction Centre (CPC) “Leaky Bucket” model (Huang et al., 1996). Precipitation and air temperature time series for given sites were prepared based on quality-controlled and homogenized station measurements distributed across the Czech Republic (Štěpánek et al., 2013). The calculations for individual grid cells were based on geostatistical interpolation, improved by standardization of neighbouring station values to the altitude of a given location by use of regional regression analysis (Štěpánek et al., 2011).

2.3. Modelling of growth response to climate

The response of tree growth to climatic conditions was described using the VS-Lite forward model, which approximates the non-linear response of growth based on monthly temperature and moisture availability (Tolwinski-Ward et al., 2011). Dimensionless partial growth responses of month s and year t to temperature ($g_T(s,t)$) and moisture ($g_M(s,t)$) are represented by ramp functions, whose shape is set by a pair of parameters indicating minimal monthly temperature/moisture required to initiate growth (T_1 , M_1) as well as by another pair of parameters representing temperature/moisture above which an increase of the climate parameter will not result in increasing growth (T_2 , M_2) (Fig. 2a). In this approach, the next step is a calculation of overall growth response for each month $g(s,t)$, which in the original version of the VS-Lite model equals the lower of $g_T(s,t)$ and $g_M(s,t)$, weighted by the ratio of monthly mean day length to day length of the summer solstice ($g_E(s)$). However, we followed a recommendation of Acevedo et al. (2016), and modified the original version of the VS-Lite model using product t -norm, which means using multiplied partial growth responses ($g_T(s,t) \cdot g_M(s,t)$) instead of their minimum (Fig. 2b). This

Table 1
Equations used to calculate cumulative indexes of growth under different limiting conditions.

Index	Equation
Index of temperature limited growth	$g_T(t) = \frac{\sum_{s=Io}^{If} g_T(s, t) * g_E(s)}{g(t)}; \text{ if } g_T(s, t) \in (0; 1) \wedge g_M(s, t) = 1$
Index of moisture limited growth	$g_M(t) = \frac{\sum_{s=Io}^{If} g_M(s, t) * g_E(s)}{g(t)}; \text{ if } g_M(s, t) \in (0; 1) \wedge g_T(s, t) = 1$
Index of mixed signal growth	$g_{MIX}(t) = \frac{\sum_{s=Io}^{If} g_T(s, t) * g_M(s, t) * g_E(s)}{g(t)}; \text{ if } g_T(s, t) \in (0; 1) \wedge g_M(s, t) \in (0; 1)$
Index of climate unlimited growth	$g_{UN}(t) = \frac{\sum_{s=Io}^{If} g_E(s)}{g(t)}; \text{ if } g_M(s, t) = g_T(s, t) = 1$

$g_T(s, t)/g_M(s, t)$ = partial growth response to temperature/moisture in month s and year t ; $g_E(s)$ = ratio of mean day length in month s to day length of summer solstice; Io/If = first/last month of integration window; $g(t)$ = total annual growth.

results in partly distorting the concept of “single most limiting factor” (Fritts, 1976) originally used in VS-Lite and smooths the transition between temperature and precipitation limitation, because a mixed signal of temperature and moisture is modelled for conditions in which both partial growth responses enable growth (> 0) but are not optimal (< 1) (Acevedo et al., 2016). Finally, the sum of respective $g(s, t)$ over integration period is calculated for each year ($g(t)$) (Fig. 2c), which after z-standardization gives modelled annual ring width index (TRW_{mod}). All the above described steps are expressed as mathematic equations in Supplementary Appendix 1.

In addition to the above described modelling of tree-ring width we also introduced four cumulative indices of proportion of growth under different limiting environmental conditions (Fig. 2d; Table 1). For each year (i.e., integration window), we separately summed all monthly growth responses for which the partial growth response to temperature was suboptimal (i.e., lower than 1) and the partial growth response to moisture was optimal (i.e., equals 1). This sum was further divided by $g(t)$, which gave the *index of temperature limited growth* ($g_T(t)$). This index represents the part of annual growth in year t that took place in conditions of temperature limitation. The *index of moisture limited growth* ($g_M(t)$) was calculated analogously, as the proportion of overall growth responses in months with suboptimal moisture and optimal temperature conditions. The *index of climate unlimited (optimal) growth* ($g_{UN}(t)$) integrates growth responses for months for which both temperature and moisture conditions were optimal for tree growth. Finally, growth responses in months with suboptimal conditions of both temperature and precipitation are summed in the *index of mixed signal growth* ($g_{MIX}(t)$). All the above-described indexes can be understood as a simple separation of total yearly growth into parts with different climatic limitations (Acevedo et al., 2016).

It is important to note that due to the simplicity of VS-Lite, the algorithm cannot model negative response of growth to extremely high temperatures (Fig. 2a). However, the negative response to high temperatures is incorporated through calculation of moisture availability based on precipitation and temperature (Tolwinski-Ward et al., 2011). The above-described index of temperature limited growth thus integrates the proportion of growth limited only by low temperature in wet months. On the other hand, growth during extremely hot months is summed into the index of moisture limited growth, when drought is the main limiting factor.

VS-Lite model requires a total of 12 input parameters. Four temperature and moisture response parameters (T_1 , T_2 , M_1 and M_2) were specifically set for each plot using a Bayesian parameter estimator (Tolwinski-Ward et al., 2013), calibrated over the whole period 1940–2012. This approach estimates the best combination of climate response parameters to fit TRW_{mod} to TRW_{obs} . The span of the integration window of VS-Lite model was set from the previous year's September to the current year's December, as the best performance of the model was documented with this setting (Breitenmoser et al., 2014), and this results in comparable levels of autocorrelation in

observed and simulated site series (Tolwinski-Ward et al., 2011). Although integration of October through December of the current year is not supported by phenology and xylogenesis of Norway spruce in the temperate zone (Hájková et al., 2012; Rossi et al., 2008), the VS-Lite model skilfully modelled negligible values of growth for November and December. October growth partly contributing to total tree-ring width was modelled in some years only for the sites at the lowest elevations (i.e., below 600 m), which we believe is realistic for our study area. Moreover, the use of the default span for the integration window ensures comparability of our results with results of other network-based forward modelling studies (Breitenmoser et al., 2014).

Parameters related to CPC “Leaky Bucket” soil moisture model were set to their default values, with the exception of “Root (bucket) depth”. Because the mature Norway spruce is usually shallow-rooting in forest soils, with more than 90% of the fine roots in the uppermost 0.5 m of the soil profile (Puhe, 2003) and, moreover, rooting depth was significantly reduced in Central Europe due to acid deposition and soil nutritional depletion (Braun et al., 2005), we used the value of 500 mm for this parameter (instead of the default value 1000 mm). All calculations related to the VS-Lite model and the Bayesian parameter estimator were performed using the latest version of MATLAB scripts (available at <http://ftp.ncdc.noaa.gov/pub/data/paleo/softlib/vs-lite>; version v2.3; Tolwinski-Ward et al., 2011) with only minor modification reflecting the product t-norm (Acevedo et al., 2016).

2.4. Data analysis

The performance of the model in each grid cell was quantified using Pearson correlation coefficient and root-mean-square error (RMSE) between modelled and observed site series. Additionally, we averaged all modelled tree-ring width site series of plots within each elevation belt and assessed their correlation with the average of the belt's observed site series. Plots were grouped into six elevation belts (below 400, 400–500, 500–600, 600–700, 700–800 and above 800 m a. s. l.) to ensure proper replication of site series in the aggregated series of each elevation belt (at least 11 plots per level). This approach follows the finding of Breitenmoser et al. (2014) of stronger coherence between modelled and observed growth after spatial aggregation of tree-ring chronologies. We focused on differences along the elevation gradient because it explains a higher proportion of variability between chronologies than latitudinal or longitudinal gradients when analysed over spatial domains comparable with the Czech Republic (Mäkinen et al., 2002; Leal et al., 2007; Hartl-Meier et al., 2014).

Long-term trends in total annual growth ($g(t)$) and proportions of growth under different limiting conditions averaged for all plots as well as for individual elevation belts were quantified using linear regression over the period 1940–2012. To identify possible drivers of the recent changes in growth, we also averaged partial monthly growth responses to temperature/moisture for each month in approximately 15-year-long periods (1940–1955, 1956–1970, 1971–1985, 1986–2000 and

2001–2012) and, subsequently compared values for the same month between periods.

We are aware that influence of climatic conditions on tree growth could have changed during the calibration period used in the Bayesian parameter estimator; therefore, we checked the stability of climate/growth relationships using three independent approaches. First, two additional runs of the Bayesian estimator for calibration windows 1940–1965 and 1940–1990 (i.e., approximately first 1/3 and 2/3 of timespan) were performed and the values obtained for T_1 , T_2 , M_1 and M_2 were compared with the respective values for the whole analysis period using one-way ANOVA. Second, the 21-year moving average of the Pearson correlation coefficient between TRW_{obs} and TRW_{mod} was calculated for each plot to identify the years with significant, abrupt increase/decrease in agreement between modelled and observed site series. Finally, we analysed the temporal stability of average residuals between TRW_{obs} and TRW_{mod} (the clustering of positive or negative residuals within a certain specific period).

3. Results

3.1. VS-Lite model performance

Correlation coefficients between observed and modelled tree-ring width site series ranged between -0.18 and 0.65 , with an average 0.24 (Fig. 1b). Positive correlations were significant ($p\text{-value} < 0.05$) for 61 of 129 plots (i.e., 47%); there was no plot with significant negative correlation. Correlation coefficient between modelled and observed series aggregated irrespective of elevation belt was 0.42 and was highly significant ($p\text{-value} < 0.01$) (Fig. 3). There was no clustering of high or low values of correlation coefficients within specific regions of the Czech Republic (Moran's $I = 0.03$); however, there was a decrease in

correlation and increase in RMSE between observed and modelled site series with increasing elevation. There is no effect of slope, stand density and number of cored trees per plot on correlations and RMSE (Fig. S1). The parameters of ramp functions of partial growth responses found by the Bayesian estimator averaged $4.5\text{ }^{\circ}\text{C}$, $13.4\text{ }^{\circ}\text{C}$, 0.05 and 0.43 for T_1 , T_2 , M_1 , M_2 , respectively (Table S1). There was no significant difference in any of the parameters between sites in different elevation belts (Table S1), and no difference between different calibration windows (Table S2).

The visual inspection of the modelled and observed aggregated series (Fig. 3a,b) supports their general agreement, although some specific parts of the calibration period lacked the synchrony (most obviously in the modelled 1973 negative pointer year and growth increase after 2007, the both at low elevations). However, moving correlation coefficients were stable over the whole analysed period, with only minor decrease in average correlation coefficients in the 1970s and 1980s (Fig. S2). Average residuals varied symmetrically around zero, however, since the turn of the millennium they became slightly biased to values below zero (Fig. S3). Residuals had a normal distribution over the whole period analysed (Shapiro-Wilk test; $p\text{-value} = 0.66$).

3.2. Partial monthly growth responses

Partial monthly growth responses averaged for individual months reveal that the growing season (i.e., period with $g(s,t) > 0$) lasted from April to October (with minor negligible growth modelled also for March and November for sites below 600 m) (Fig. 4). On average, the spruce growth was moisture-limited from May to August with the rest of the growing season being temperature limited. The partial growth response to moisture was stable over the year with only a minor decrease during the second half of the growing season. Partial growth responses to

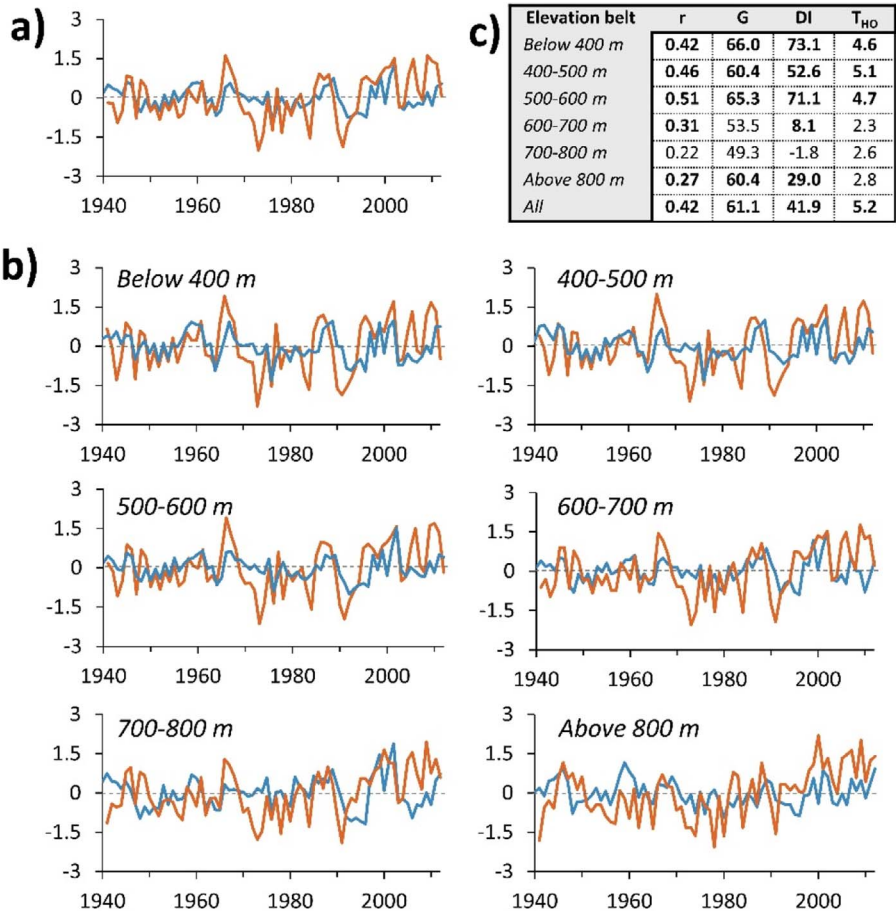


Fig. 3. Observed (blue) and modelled (orange) tree-ring width aggregated series averaged (a) for all plots; (b) for individual elevation levels; and (c) statistics of modelled-observed aggregated series coherence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
 r = Pearson correlation coefficient, G = Gleichläufigkeit index, DI = Date index, T_{HO} = t-test (Cook and Kairiukstis, 1990); bold indicates significance level with $p\text{-value} < 0.05$ (r , G) or values exceeding commonly used thresholds of 5 (DI) or 3 (T_{HO})

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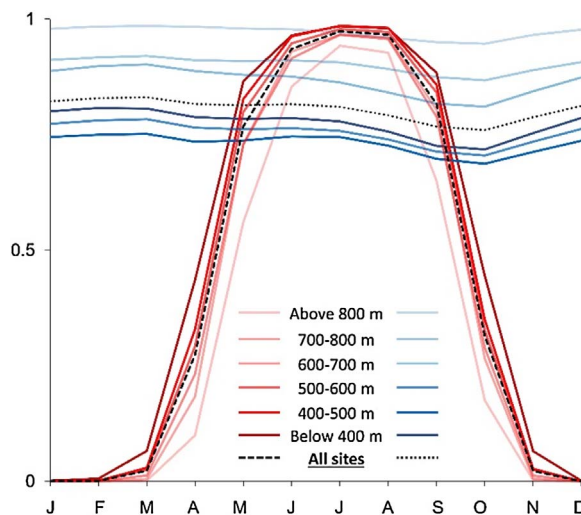


Fig. 4. Partial growth responses to temperature (shades of red) and moisture (shades of blue) for individual elevation belts and whole study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature/moisture tended to decrease/increase respectively with increasing elevation (Fig. 4). The average growing season was shorter at higher elevations than lower elevations (due to low partial growth responses to temperature in spring and autumn).

The partial monthly growth responses to temperature increased during the analysed period mainly for April and May (Fig. 5a) due to a significant increase in mean temperature of both months (Fig. 5b). However, the partial growth responses to temperature were more stable during autumn. The partial growth response to moisture varied mainly in August; however, with no apparent trend (maximum was achieved during 1956–1970 period and minimum in 1971–1985).

3.3. Proportions of growth under different limiting conditions

The proportions of growth under moisture, temperature, mixed signal and no climatic limitation significantly differed along the elevation gradient. On average, more than 45% of total annual growth was in moisture-limited conditions, almost 14% was limited by temperature, more than 28% of growth was governed both by moisture and temperature (mixed signal), and more than 12% of growth proceeded under optimal monthly climatic conditions (Fig. 6a,c). Although these proportions remained almost identical for the three lowest elevation belts, the respective proportions of annual growth during temperature limitation or optimal climatic conditions increased with elevation above 600 m from less than 7% to 45% and from 6% to 26%, respectively (Fig. 6b,c). In contrast, the proportion of total annual growth that occurred during moisture-limited conditions declined with increasing

elevation from almost 58% to 7%. The highest proportion of growth under mixed conditions (35%) is modelled to have been in medium elevations (500–700 m) and the lowest proportion in upper elevations (less than 22%). Elevation belts located below 500 m showed frequent years without any growth occurring under optimal climatic conditions (i.e., $g_{UN}(t) = 0$).

There is a significant ($p < 0.05$) increasing temporal trend in the index of moisture-limited growth for all elevation belts except 700–800 m (Fig. 6b, Table S3). A significant positive trend is modelled also for total annual growth (i.e., tree-ring width) at sites above 500 m. In contrast, there were significant negative trends for proportions of mixed signal growth for three elevation belts (400–500, 500–600 and 700–800 m), and temperature-limited growth for belt above 800 m. The positive trend in proportion of growth under optimal climate was significant only for sites above 800 m. When averaged over all plots, model outputs display significant negative trends in proportions of mixed signal growth and temperature limited growth, and positive trends in total annual growth and growth under moisture-limited conditions (Fig. 6a).

4. Discussion

4.1. Temporal and altitudinal trends

Our study provided spatially detailed climate/growth responses of Norway spruce over an extensive area and allowed description of trends in basic climatic limiting factors of tree growth. We identified three general temporal trends in Norway spruce growth in the Czech Republic over the period 1940–2012. These consist of: (i) increasing total annual increments in sites above 500 m; (ii) increasing proportion of growth under moisture limitation; and (iii) slightly decreasing proportion of growth under temperature limitation or mixed conditions. We suggest that the recent increase in modelled tree-ring widths can be attributed to increasing temperature, as the growth is closely related with summer temperature in high elevations (Hartl-Meier et al., 2014; Ponocná et al., 2016). In these locations, the partial growth response to temperature is lower than the partial growth response to moisture during most of the growing season. Medium-elevation sites benefit especially from increasing spring (April–May) temperature allowing early cambial activity onset (Gričar et al., 2014; Giagili et al., 2016) and the extension of growing season (Pretzsch et al., 2014). In contrast to sites above 500 m, there was no significant trend in the modelled tree-ring widths for sites located below 500 m, probably due to interplay between the negative effect of drought stress in summer and positive effect of increasing temperature in spring (Čejková and Kolář, 2009; Hartl-Meier et al., 2014).

The gradual increase in proportion of growth under moisture limitation and the stability or decrease in proportion of growth under temperature limitation are probably linked to each other through increase of May temperature. In the temperate zone, May is among the

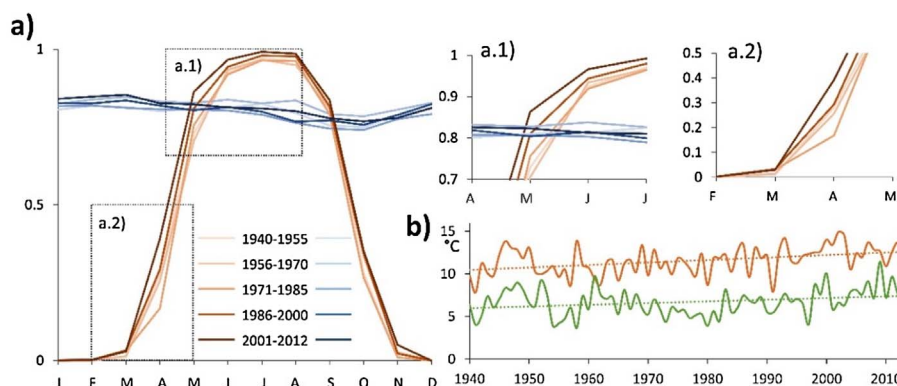


Fig. 5. (a) Temporal trends in partial growth responses to temperature (shades of red) and moisture (shades of blue) averaged over different periods; parts of growing season with the most important temporal changes in growth responses are zoomed in on in (a.1) and (a.2); (b) mean April (green) and May (orange) temperatures, with dotted linear trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

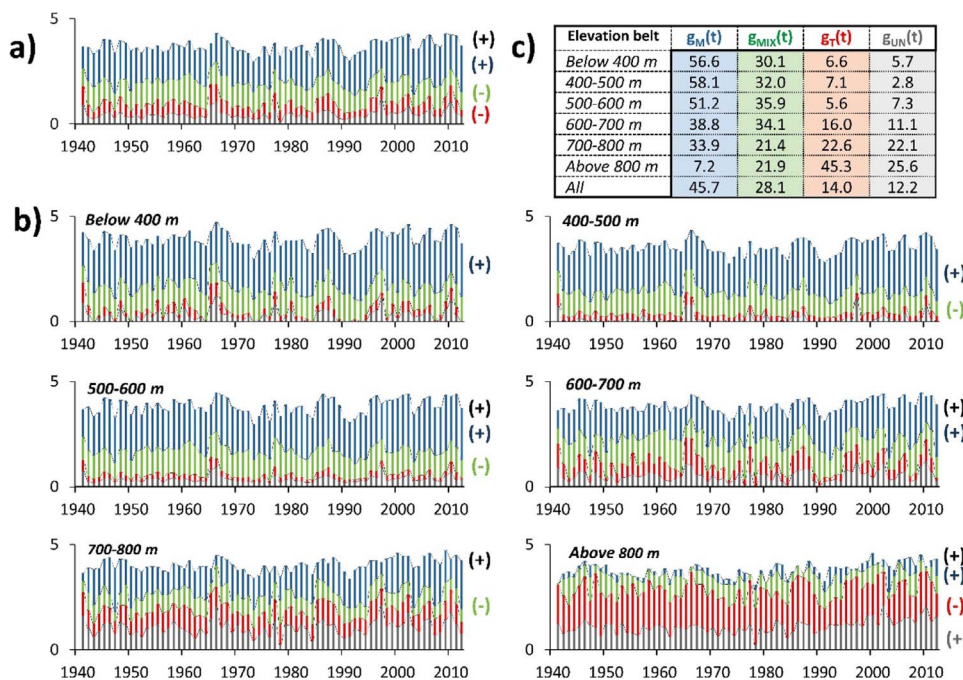


Fig. 6. Inter-annual variability of total annual growth separated into parts of temperature limitation (red), moisture limitation (blue), mixed limitation (green) or no climate limitation (grey) (a) averaged over all plots; and (b) different elevation belts, with (c) the proportions of individual limiting factors averaged over the period 1940–2012. Plus and minus signs on the right side of charts indicate significant (p -value < 0.05) linear trends in proportions of specific limiting factors (colour signs) or in total tree-ring width (black). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

months with the highest growth rates (Rossi et al., 2007; Cuny and Rathgeber 2016) as also indicated in VS-Lite by the average $g_E(\text{May})$ of studied plots being 0.92—the third-highest for a growing-season month (after June and July). At the beginning of the calibration period (1940–1955), the average partial monthly growth response to temperature for May equalled 0.73, substantially less than the average partial monthly growth response to moisture (0.81). Therefore, temperature and moisture limits on May growth were commonly classified as mixed, or, in wet years, as temperature-limited. Increasing May temperatures therefore led to decreasing intensity of temperature limitation in May, while moisture limiting conditions remained stable. Together, these two outcomes resulted in an increase of the proportion of moisture limited conditions on overall growth. This is mainly manifested in sites above 800 m, where the proportion of growth under temperature limitation is dominant, whereas the proportion of moisture limitation is only marginal, but with opposite and steep temporal trends.

The sampling network covered almost the complete altitudinal gradient of both planted and native Norway spruce stands in lowlands and mid-elevations of Central Europe. Along this gradient, relatively small changes in the proportions of climatic growth-limiting factors were observed for elevations under 600 m. There, the growth under moisture-limiting conditions exceeded 50% of total tree-ring width. Notably, for many years during the 1940–2012 period, the modelled growth conditions were never classified as optimal for any of the sites below 500 m. Prevailing moisture-limiting conditions at low elevations therefore have not allowed an increasing growth trend in response to rising temperature; this was also shown by non-significant changes in modelled ring widths. The importance of moisture availability on modelled tree growth is in-line with the significant correlation between recent basal area increment and drought index observed in the CzechTerra repeated inventory dataset (Cienciala et al., 2016). From 600 m towards the highest-located spruce stands, the proportion of growth not limited by climatic variables increased to reach about 26% in montane forests. The positive temporal trend in the amount of growth under climatically optimal conditions was significant only for the sites above 800 m, where, moreover, the growth limited by low temperatures was dominant. The recent temperature trends thus further increased the divergence in growth trends and climatic limiting factors between low (below 600 m) and high (above 600 m) elevations.

4.2. Temperature and moisture thresholds limiting tree growth

The threshold parameters of temperature response ramp functions found by the Bayesian parameter estimator (Tolwinski-Ward et al., 2013) are comparable with the ecological thresholds of Norway spruce growth reported by other dendroecological studies. The mean value of the minimal monthly temperature parameter (T_1) is similar to the minimal critical daily temperature (Rossi et al., 2008) and 6-day mean temperature (Tremblé et al., 2015) for onset of xylogenesis in coniferous species. Carrer et al. (1998) documented that spruce trees do not benefit from increasing monthly temperature above approximately 13 °C (T_2). Increase in mean monthly temperature above 13.5 °C in June results in shift from stimulating to limiting effect of temperature on tree growth (Sidor et al., 2015). The average values of all parameters are comparable with those estimated by Tolwinski-Ward et al. (2013) in North America and by Sánchez-Salguero et al. (2017) in the Iberian Peninsula. Moreover, T_1 and M_2 are similar to their most common values estimated by Breitenmoser et al. (2014) for sites at the global scale.

The individual threshold parameters do not significantly differ among different elevation belts, indicating that growth of spruce trees in the dataset of this study has been influenced mainly by physiological responses of cambium to climatic conditions rather than by local specific conditions of individual sites (e.g., soil properties, forest dynamics, disturbances). Moreover, the stability of thresholds over time indicates that physiological thresholds shaping the response of tree growth to climatic conditions are also temporally stable.

4.3. VS-Lite forward model performance

One of the principal presumptions of the VS-Lite model is dependence of tree growth on climatic conditions (temperature and precipitation) with no or only minor effect of other processes including e.g., competition, pollution or soil properties (Tolwinski-Ward et al., 2011). As most sampled plots were located in managed even-aged forests, the effects of competition in the observed series are reduced by thinning, as indicated by the nonsignificant effect of stand density on correlations between modelled and observed series. We also believe that the modelled proportions of growth-limiting conditions are realistic, since they match well the results derived from studies covering altitudinal gradients in Central Europe (e.g., Mäkinen et al., 2002;

Čejková and Kolář, 2009; Hartl-Meier et al., 2014; Sidor et al., 2016; Ponocná et al., 2016). Most of these studies identified three zones along the altitudinal gradient with more or less distinct borders: chronologies significantly correlating with precipitation (or drought indices) are found at the lowest elevations, the zone of complacent series with optimal climatic conditions is in the middle, while the temperature signal dominates at the highest elevations. A direct comparison of zone borders identified by different studies is not possible due to different climatic and other environmental conditions of study areas. However, the sites above 900 m display mainly a temperature signal in the northern part of our study domain (Ponocná et al., 2016). Moreover, the borders between zones were identified as being at approximately 700 m and 950 m in the mountain ranges of the southern Czech Republic (Wilson and Hopfmueller, 2001; Čejková and Kolář, 2009).

There was significant positive correlation between modelled and observed site series in 47% of the plots, which is slightly higher than in the global study of Breitenmoser et al. (2014), indicating an above-average climatic signal in our study area. The general decrease of correlation between modelled and observed site series with elevation can be attributed to two reasons. First, there is an increase in the modelled proportion of tree-ring formed under optimal climatic conditions, resulting in complacency and low sensitivity of modelled series to climatic variability at highest elevation belts. This is in line with the results of studies using response functions for climate-growth analysis, indicating a mixed climatic signal in those elevations (Hartl-Meier et al., 2014; Ponocná et al., 2016). Moreover, radial growth was suppressed at high elevations of Central Europe in the 1970s and 1980s due to air pollution (Kroupová, 2002).

The cluster of negative residuals between modelled and observed site series in the period since 2000 can possibly bias the results of trend analysis because of amplifying the modelled recent increase in growth. It is important to note that results identifying trends in total tree-ring width and proportions of growth under different climatic conditions were similar also for the period 1940–2000, i.e., before bias in residuals (Supplementary Appendix 2). The model had very small average residuals in the extremely dry years 1959, 1976, 2003 and 2007 (Brázdil et al., 2015), not supporting the recently observed poor performance of simple CPC “Leaky Bucket” model for identification of drought stress on tree growth (Mina et al., 2016). However, for the most recent and strongest dry years (i.e., 2003 and 2007), the model recorded negative residuals in up to two consecutive years, indicating slow recovery of growth after high intensity drought. This can be attributed to reductions in biomass and lifespan of fine roots during the years of extreme drought stress (Brunner et al., 2015), and this delayed response cannot be properly considered by the simple algorithm of VS-Lite.

When examined visually, the modelled aggregated series revealed an increasing trends, whereas there was almost no trend seen in observed site series. The lack of trends in the observed series is mainly due to the applied individual detrending approach resulting in removal of a trend component from the tree-ring series (Peters et al., 2015). This is why we also inspected the trends in raw series over the last 20 years. During that period, 133 individual series significantly increased ring width, while 87 series decreased. The distribution of trees with positive and negative trends is not influenced by tree age and study site elevation, with only a slight increase of the significantly responding trees (both negatively and positively) at the sites above 800 m (Fig. S4). This indicates that even though the growth of trees was stressed by prolonged drought in the last two decades, a high proportion of individual trees still retained positive trends in tree-ring widths, as also modelled by the VS-Lite algorithm.

We are aware that the number of trees per plot was limited, due to the network design of our study aiming at a regular spatial distribution of sampled trees over the whole Czech Republic. When inventory plots are distributed with proper density, even a single cored tree per plot has substantial potential for dendroclimatological purposes (Bošela et al., 2016). Although plot chronologies based on limited sample depth can

be biased due to specific (endogenous) signals of individual trees (Cook and Kairiukstis, 1990), our aggregation of plots into elevation belts emphasized common climatic signals (as indicated by randomization exercise in Supplementary Appendix 3).

5. Conclusions

The VS-Lite forward model performed well in modelling proportions of tree-rings formed under different climatic conditions after aggregation of individual site series into elevation belt chronologies. Low and high elevation sites differ in the dominant growth-limiting factor, however, they share a common trend of increasing proportion of tree-rings formed under moisture limitation. Although all elevation belts above 500 m exhibited growth increase in response to recent climate change, only at sites located above 800 m the growth increase was driven by a decrease in proportion of growth under temperature limitation and increase of growth in optimal climatic conditions. At mid-elevation sites, a positive trend of total growth was associated with significant increase in proportion of growth under moisture limitation. This makes sustainability of increasing growth of Norway spruce dependent on future trends in drought intensity. The lowest sites (below 500 m) with the most pronounced drought stress recorded only redistribution of annual growth from mixed conditions to moisture limitation with no trend in total growth during the last seven decades. This indicates that those sites are already near the moisture limit of Norway spruce distribution and thus especially sensitive to future drought events.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.07.015>.

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