

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

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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 (Bošela 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 (Plíva, 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 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 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 (Štěpánek et al., 2009, 2011). The database for the studied areas included data on the daily average, minimum, and maximum temperatures (T_{avg} , T_{min} , and T_{max} , 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 (0–0.4 m) and subsoil (0.41–1.3 m), 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).

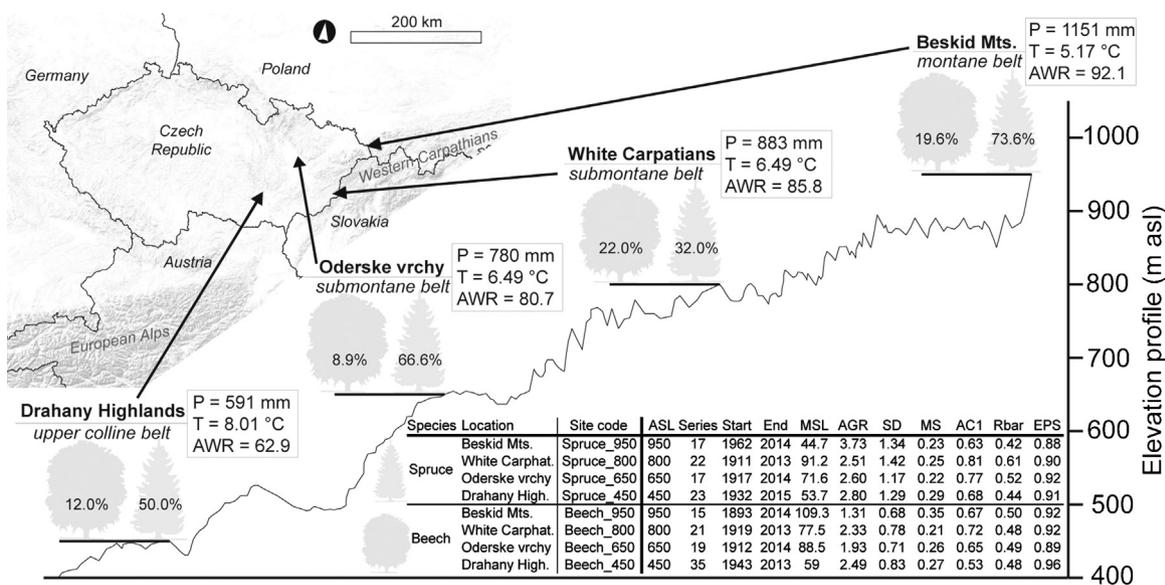


Fig. 1. The location of each study site in the map is accompanied by the average annual temperature (T), total precipitation (P), and relative available water in the soil at 0–130 cm (AWR) depths for the period 1961–2013. Black numbers in the tree habitus indicate the percentages of spruce and beech in the areas. The table presents basic statistics of the regional raw TRW chronologies: ASL, above sea level (m); MSL, mean segment length (year); AGR, average growth rate (mm/year); SD, standard deviation; MS, mean sensitivity; AC1, first order autocorrelation; Rbar, mean inter-series correlation (calculated in Arstan); EPS, minimum expressed population signal.

2.3. Sampling strategy, tree-ring data and statistical analysis

The selected sites cover a wide altitudinal range from 450 to 950 m asl to represent a transect of the common area of spruce and beech occurrence. All selected stands were mixed stands with group-wise distribution (beech group and spruce group in one stand). Because the between-tree variability within a site is much higher than the within-tree variability around the stem circumference (Bošela et al., 2014b), one core per tree was sampled at breast height (1.3 m) using a Pressler borer (Haglof Company Group, Sweden) with a 5 mm inner diameter. To avoid compression wood (in spruce) and tension wood (in beech), core sampling was performed along the contour line. All samples were measured (at an accuracy of 0.01 mm) using a TimeTable device with a measurement length of 78 cm (SCIEM, Vienna, Austria). The obtained TRW series were cross-dated and corrected for missing and false rings using both PAST4 (Knibbe, 2004) and COFECHA (Grissino-Mayer, 2001; Holmes, 1983).

Non-climatic, size- and age-related growth trends, and other factors (e.g., competition) were removed from the individual TRW series by applying cubic smoothing splines with a 50% frequency cutoff at 32 years to preserve high frequency (inter-annual) variations for climate-growth analysis (Cook and Peters, 1981) in ARSTAN software (Cook and Krusic, 2005). TRW indices were calculated as residuals after an adaptive power transformation (Cook and Peters, 1997). The site-specific chronologies were calculated using bi-weight robust means. Internal signal strength was assessed with the inter-series correlation (Rbar), the expressed population signal (EPS; Wigley et al., 1984), and mean sensitivity indicating the relative year-to-year variability. Principal component analysis (PCA) was carried out in STATISTICA (Statsoft, Inc.; Prague, Czech Republic) software for the common period (1962–2013) to investigate the main growth variance among site-specific indexed chronologies.

We employed redundancy discriminate analysis (RDA; Legendre and Legendre, 1998) to display the most important growth-driving climate factors for both species at all sites. This analysis was proven to be an effective method in assessment of the relationship (Friedrichs et al., 2009). The relationships between the residual chronologies and temperature means, AWR means,

and precipitation sums (starting from June of the previous year to August of the year of tree-ring formation – referred to as “the current year”) were analyzed for the common period 1962–2013. RDA ordination axes were constrained to be linear combinations of climate variables (Legendre and Legendre, 1998). RDA analysis with forward selection was conducted in the R software Vegan package (Oksanen et al., 2016). Comparisons of variables were based on the Akaike information criterion (AIC) and p -values (<0.05) from Monte-Carlo permutation tests.

To assess the temporal variability in the growth-climate relationship along the elevation gradient, moving correlation coefficients were calculated for 20-year windows using Statistica software (Statsoft, Inc.; Prague, Czech Republic) over the common period (1962–2013). Mean temperature and AWR values for the spring (Mar–May) and summer (Jun–Aug) seasons of the current year were correlated with the site residual chronologies. Precipitation sums were not used for the moving correlations because of very strong dependency between both factors (see Section 2.1). The negative pointer years were analyzed for each species-specific site, truncated at a minimum sample replication of five TRW series. A reduction in TRW that was 40% greater than the average TRW in the previous 4 years and was observed in at least 30% of the trees indicated a pointer year (Schweingruber et al., 1990).

3. Results

3.1. TRW chronologies

Species-specific TRW chronologies covering the common period of 1962–2013 revealed robust signal strength, confirmed by very reliable values of Rbar and EPS (Fig. 1). Common variance within the TRW series, expressed by high values of the Rbar statistic, implies climatic control of regional spruce and beech growth (Büntgen et al., 2010). EPS did not drop below 0.89, which indicates that the species-specific TRW chronologies represented a theoretical population at these sites reliably (Wigley et al., 1984). The high first-order autocorrelation of the raw TRW chronology indicates great temporal memory. The influence of juvenile wood on TRW was confirmed by the relationship between the mean segment lengths and the average growth rate, where decreasing TRW

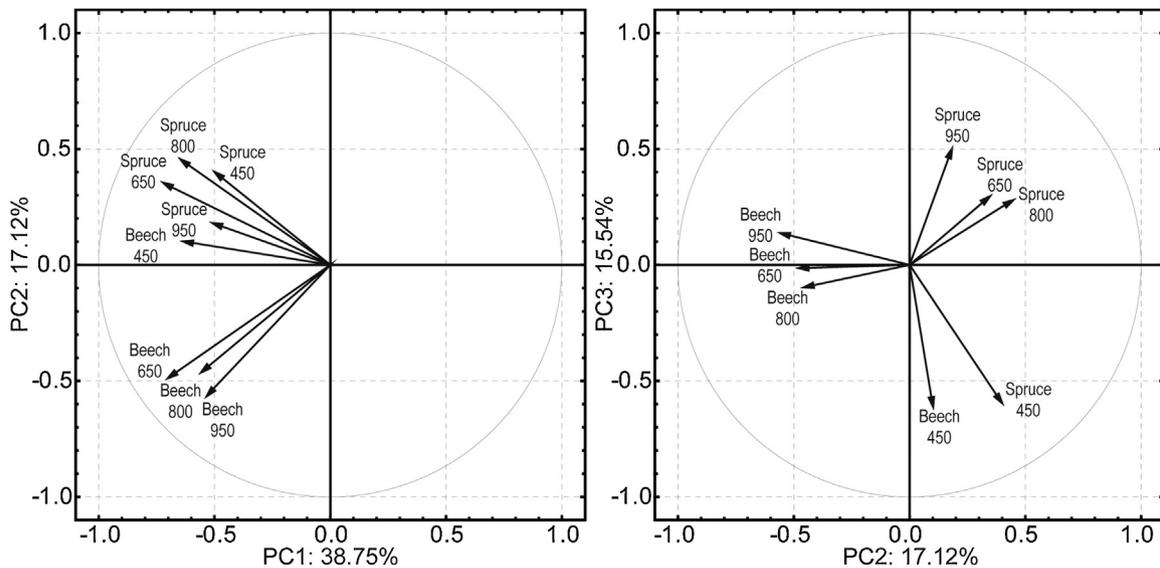


Fig. 2. PCA of indexed TRW chronologies for the common overlap period of 1962–2013.

was accompanied by increasing lengths of the series. The highest year-to-year variability, expressed as the mean sensitivity, was observed for Beech_950 and Spruce_450 (Fig. S2).

PCA revealed differences in the indexed TRW chronologies between the two species and four sites for the common period of 1962–2013 (Fig. 2). The first PCA axis explained >38% of the common variance of all chronologies. The second and third axes divided the chronologies into three groups: spruce and beech at the lowest site, beech above 650 m asl, and spruce above 650 m asl. The mean inter-chronology correlations between the regions revealed a higher common growth pattern among the spruce chronologies ($r = 0.495$) than among the beech chronologies ($r = 0.360$).

3.2. Climate–growth relationship

The influence of independent climatic variables on TRW growth showed the main differences between species and elevations (Fig. 3). The positive effect of mean temperature on TRW growth (mainly spruce) prevailed during the current Mar–May (spring season), except for the lowest site where the effect was negative. Conversely, the positive impacts of precipitation and AWR in the current Jun–Aug (summer season) were restricted to sites below 800 m asl. AWR better reflects water availability for a tree at the lower sites than precipitation (Fig. 3). High values of AWR in the previous Sep–Nov (autumn season) enhanced particularly spruce growth at 450 and 650 m asl. At the highest site (950 m asl), beech was mainly controlled by temperature (positively) and AWR (negatively) from previous December to current February (winter season).

The correlation coefficients within the 20-year moving window emphasized the significant effects of mean temperature and AWR values on spruce and beech TRW, as presented in Fig. 3. However, these patterns have changed over the past 30 years (Fig. 4). The positive effect of spring temperature on spruce TRW slightly increased at the highest elevation but decreased to a significantly negative effect at the lowest (driest) elevation. In contrast, the beech response to the temperature means in the same period was quite stable at all sites except for the lowest site, where it dropped into a significant negative impact. Spring AWR effect on TRW of both species positively increased at the lowest site, whereas Spruce_950 showed a negative influence of AWR over the past decade. The correlation coefficients for summer temperature generally decreased

for both spruce and beech. The negative impacts of summer drought on both species at all sites increased considerably.

3.3. Negative pointer year analysis

The negative pointer years were analyzed separately for each species and site. The most negative pointer years were calculated for Beech_950 (34) and Spruce_450 (27). It was found that 100% of the trees responded negatively at the Beech_650 site in 1927, the Beech_950 site in 1996, and the Spruce_450 site in 2012. The trees at all sites responded negatively only in 2003. Compared with the normal period, the frequency and intensity of negative pointer years have markedly increased from 1991 to the present (Fig. 5).

4. Discussion and conclusion

4.1. Climate–growth relationship

In this study, we explored the climate–growth relationship of Norway spruce and European beech in detail along the elevation gradient from 450 to 950 m asl (Fig. 1) where both the species explored form mixed forests. However, the ecological and growth optima of both species do not fall precisely within this gradient. The lowest study site lies outside the ecological and growth optima for spruce, at the border of the beech growth optimum, and within the beech ecological optimum. The highest study site lies outside the ecological and growth optima for beech and the spruce growth optimum, but within the spruce ecological optimum. Therefore, the PCA of the spruce and beech TRW chronologies showed differences between species and sites (Fig. 2). This finding suggests different sensitivities of the species- and site-specific chronologies to the macroclimate. The differences were also reflected in the highest year-to-year variability observed for Beech_950 and Spruce_450. Both sites lay outside of the species growth and ecological optima.

Our results regarding the long-term climate–growth relationship suggest distinct differences between the tree species and elevation gradients. It is well known that temperature is the most important climate factor for spruce growth at high elevations (Harti-Meier et al., 2014) and high latitudes (Suvanto et al., 2016). A warmer spring temperature of the current year enhanced spruce growth at elevations above 650 m asl (Fig. 4). Rising spring temperatures leading to an earlier start of the growing season and

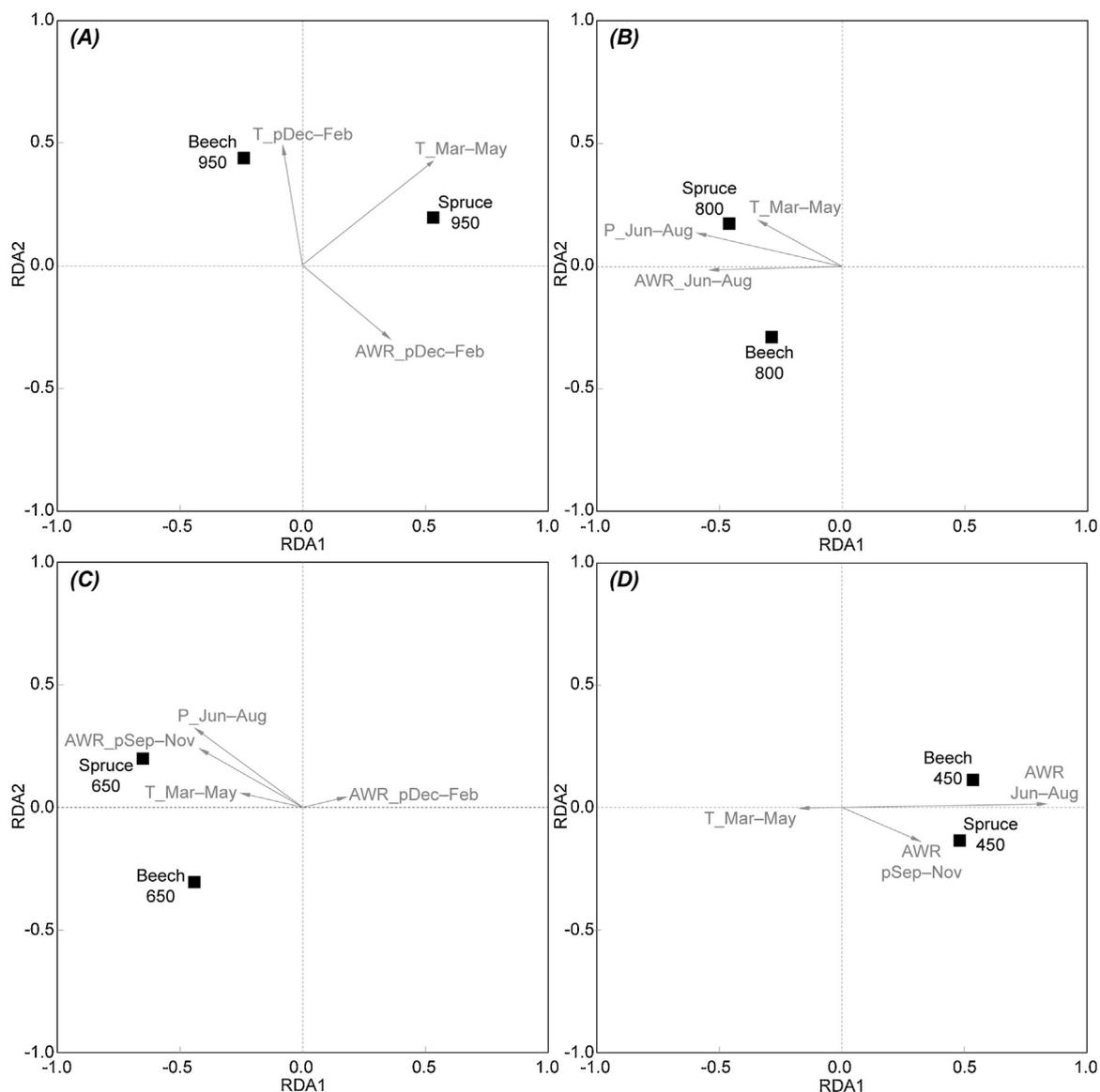


Fig. 3. Plot of the redundancy discriminant analysis portraying the climate–growth relationships (for the common period of 1962–2013) of Norway spruce and European beech at different elevations, of 950 m (A), 800 m (B), 650 m (C), and 450 m (D) asl. The site chronologies are depicted as symbols and significant climatic variables as vectors. Vector length indicates the strength of the significant climate variables ($p < 0.05$). The resultant vectors indicating roughly the same direction as the site symbols demonstrate a high positive correlation and vice versa: opposite direction shows a negative correlation. Vectors crossing at right angles correspond to a near zero correlation (ter Braak and Prentice, 1988). Mean temperature (T) and AWR values and precipitation (P) sums for different seasons of the previous (p) and current growing season were considered. Months are abbreviated using the first three letters.

therefore higher effective global radiation support photosynthetic activity and, thus, faster carbon fixation (Kolář et al., 2015). Moreover, warm, but not dry, spring conditions benefit the onset of cambial activity (Jyske et al., 2014; Prislan et al., 2013) and phenological phases (Fu et al., 2013; Kolář et al., 2016), leading to an extended growing season. However, the increasing spring temperature at the lowest (driest) site has an opposite effect on both species, which contributes to soil drying.

The positive impact of temperature decreases with decreasing elevation and water availability begins to become the essential factor limiting tree growth (Sidor et al., 2015). In this study, trees growing at lower (below 800 m asl) sites benefited from humid climate conditions, particularly during the previous autumn and current summer. Many studies have indicated that annual ring formation is strongly influenced by previous-year climate conditions (e.g., Scharnweber et al., 2011; Tegel et al., 2014). Dry conditions in the previous autumn can cause depletion of structural carbohydrate reserves that are crucial for the initial stage of

tree-ring formation in the following year (Rybníček et al., 2010; van der Maaten, 2012). However, we found that radial growth (spruce rather than beech) at lower sites depended mainly on AWR and precipitation of the current summer. Similar conclusions have been presented from many other studies of temperate forests (e.g., Friedrichs et al., 2009; Hartl-Meier et al., 2014). The summer period is extremely important for tree growth because cambial activity reaches a peak, and most of the TRW is generated at this time of year alone (e.g., Giagli et al., 2016). The influence of the available water supply proved to be more important in the top soil layer compared with deeper layers (results are not presented). Soil drying can lead to high mortality of fine root biomass (Leuschner et al., 2004), which is essential for water supply of trees and nutrient exploitation (Bolte and Villanueva, 2006; Brunner et al., 2015). Given that spruce maintains shallow vertical rooting, beech has been inferred to exhibit a higher competitive ability belowground (Bolte and Villanueva, 2006). These findings indicate that spruce trees, with their shallow roots, react more sensitively to drought variability than beech (e.g.,

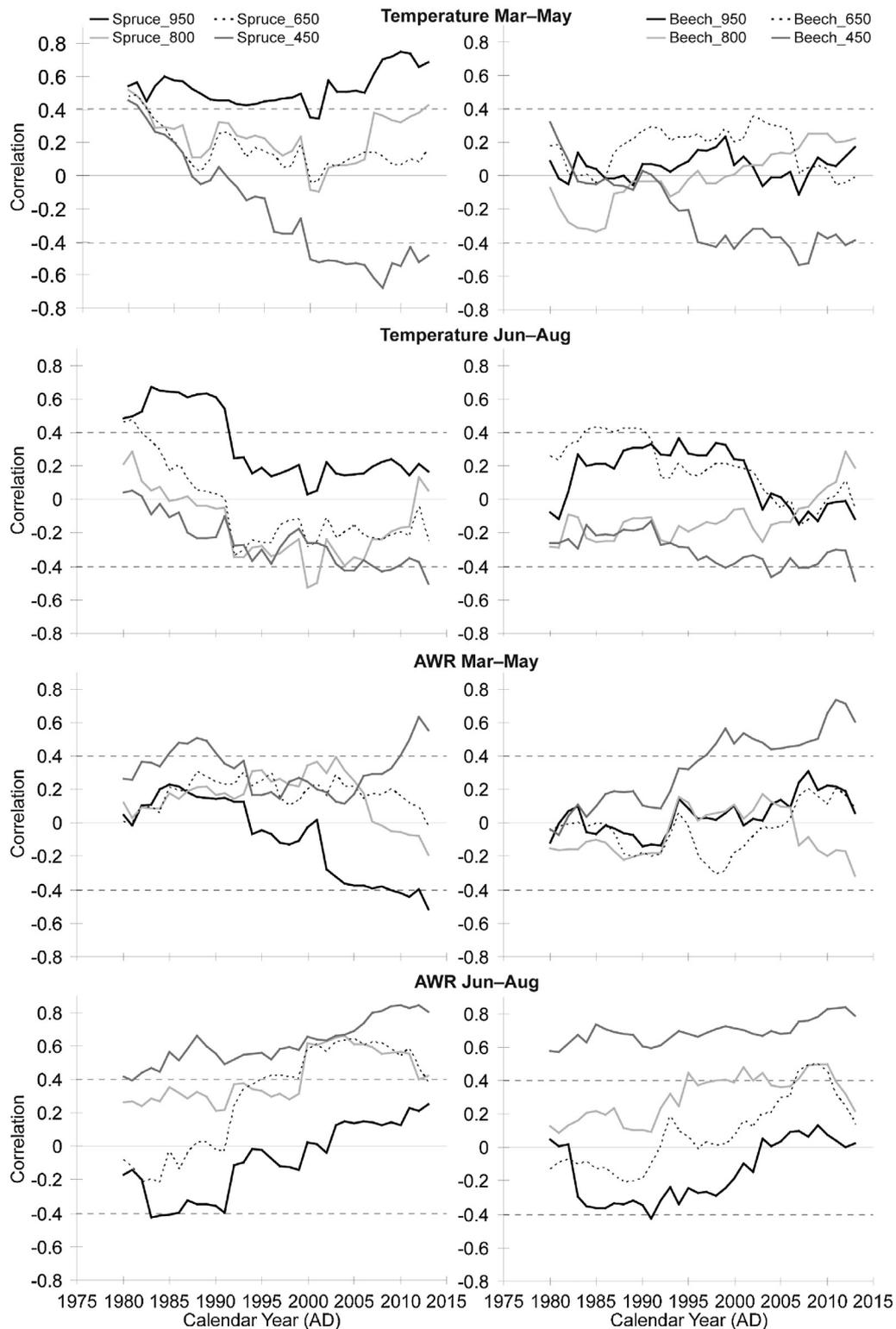


Fig. 4. Twenty-year moving Pearson's correlation coefficients between residual TRW index chronologies and mean temperature and AWR values for the Mar–May and Jun–Aug periods of the current growing season. The residual site chronologies of Norway spruce (left) and European beech (right) represent an elevation gradient of 450–950 m asl.

Bolte et al., 2010; Pretzsch et al., 2014). European beech growth is positively supported by mild winters (Fig. 4) as it has been identified as a particularly temperature-sensitive species (Drobyshev et al., 2014), showing high sensitivity to late frosts (Fischelli et al., 2014).

The long-term climate–growth relationship was characterized by sudden temporal shifts (Fig. 4). Given the fact that AWR better

reflects water availability for a tree, as was provided in the results, and strong correlation with precipitation was demonstrated; only AWR and temperature were used for moving correlations. Our results indicate an increased sensitivity of TRW to drought conditions. Temporal instability in the climate sensitivity of radial growth has been proven for various tree species in Europe (e.g., Bošel'a et al., 2014a; Büntgen et al., 2011; Dobrovolný et al., 2016).

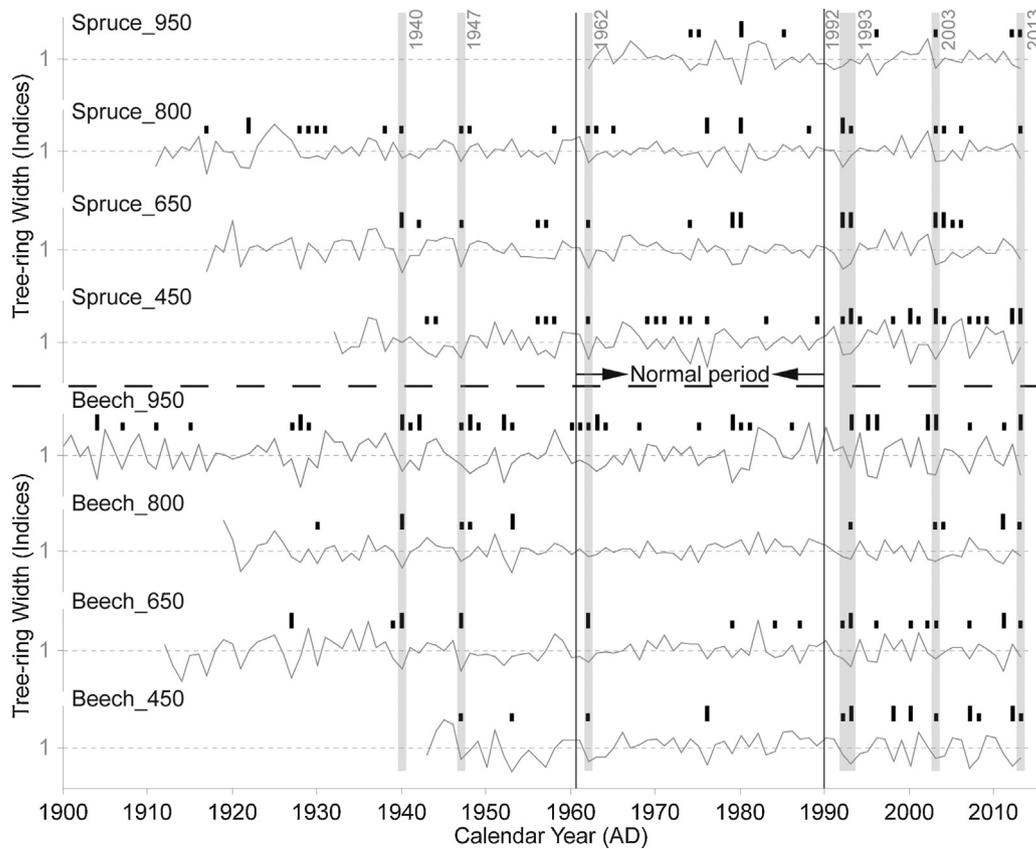


Fig. 5. Residual TRW chronologies of all Norway spruce and European beech sites with analysis of negative pointer years (short black line, at least 30% of the trees responded; long black line, more than 60% of the trees responded) for periods replicated in at least 10 trees at the site. Gray strips indicate years when negative pointer years were calculated for at least five sites.

There are different explanations for the deviations captured in these relationships. Mountain Norway spruce stands in Central Europe were mainly affected by enormous global emission loads during the second half of the 20th century, which was identified as one of the main factors responsible for substantial spruce declines and the reduction of the climate signal in radial growth. Although efficient pollution control has led to gradual recovery of TRW since the 1980s (Kolář et al., 2015), another forest decline followed in the early 1990s because of bark beetle outbreaks in areas such as the Western Carpathians (Vakula et al., 2015). Biotic factors such as pests (particularly bark beetles) tend to impact stands with reduced tree vitality, ultimately resulting in rapid tree mortality (Vacek et al., 2015). Warm and dry climate conditions can increase the frequency of bark beetles because drought affects the physiological conditions of trees and makes them susceptible to bark beetle attack (Vakula et al., 2015). Serious forest declines occurred after the extraordinary drought summer of 2003 in particular (Luterbacher et al., 2004). Moreover, the occurrence of heat waves, such as that observed in 2003, is expected to increase in the near future (Schär et al., 2004). Therefore, ongoing temperature increases and more concurrent frequent drought events may have essential impacts on tree vitality and, subsequently, on entire forest ecosystems. The given reasons leading to temporally unstable climate–growth relationships then cause that dendroclimatic reconstructions using TRW chronologies could not be performed (Büntgen et al., 2006; Prokop et al., 2016).

4.2. Negative pointer year analysis

Analysis of negative pointer years provided a deeper understanding of climate–growth relationships and confirmed the

significant drought sensitivity of trees from low elevations. Maximum negative pointer years were identified for sites where the woody plant species were outside of their ecological and growth optima. The increased frequency and intensity of negative pointer years after 1991 (Fig. 9) may be connected with the results of Brázdil et al. (2015), who concluded that increasing dryness for the past two hundred years throughout the territory of the Czech Republic peaked in 2004–2012. Marked drought spells in the Czech Republic (e.g., 1947, 1976, 1992, 1993, 2000, 2007, or 2012; Brázdil et al., 2009 and 2015; Potop et al., 2012) were reflected in negative pointer years, mainly in lower elevations. Only the unprecedented heat wave of 2003 was reflected in all TRW chronologies, regardless of tree species or elevation (Fig. 9). Summer 2003 is considered to have been the hottest summer of the past 500 years (Luterbacher et al., 2004). Nevertheless, tree growth at high elevations is mainly limited by temperature anomalies, while water availability is not a limiting factor. Negative extremes in 1979 and the following years were caused by the extremely cold and harsh winter of 1978/1979, at high elevations also accompanied by high values of SO₂ (Kolář et al., 2016). European beech sensitivity to late frosts (mentioned earlier) most likely led to the negative pointer years of 1962, 1986, 1993, 1995, 1996, 2002, and 2013. Additionally, mast years, which are strongly affected by temperature, can be considered another reason for growth reduction in European beech (Drobyshev et al., 2014). The last mast years of beech were recorded at the highest study site in 2007 and 2011 (Suchomel et al., 2016), corresponding to negative pointer years (Fig. 5). The above reasons may explain why the greatest number of negative pointer years was detected in the TRW chronology of Beech_950, lying outside of ecological and growth optima.

4.3. Implications for forest management strategies

Our results show that the replacement of Norway spruce by European beech in Central European forest stands is troublesome task. It is likely that the average climate conditions for beech will be more favorable in the montane belt but its growth and vitality will be probably still limited by climate extremes, as, for example, late frosts. European beech is highly sensitive to water availability in the colline belt, and its sensitivity will probably be further increased in submontane areas. High beech sensitivity to dry and warm episodes was also demonstrated by Betsch et al. (2011), Ciais et al. (2005), and Friedrichs et al. (2009). Modeling of the growth responses of European beech (Mátyás et al., 2009) predicts growth depressions and decreased vitality under stressful conditions, particularly at dry sites. In contrast, some authors have hypothesized that beech could be more resistant to abiotic and biotic stressors and that its competitive capacity (in comparison with Norway spruce) will increase under conditions of climate change (Bolte et al., 2010). On the basis of evaluation of tree rings, Dittmar et al. (2003) posited that European beech shows higher resilience than spruce and will be able to cope with periods characterized by decreased availability of water. It is probable that the responses of beech trees to climate changes will be different in various ecotypes and geographical regions as well as at various altitudes (i.e., vegetation belts) (Čermák and Holuša, 2011). Additionally, Bošela et al. (2016) suggested that vertically more diversified beech forests might be more stable under the future climate warming scenarios. Metz et al. (2016) found that beech is less drought stressed when growing in mixtures. In the current climate conditions, low-risk silviculture of Norway spruce is possible only at such low elevation sites (colline and lower submontane) where the change of macroclimate is compensated by hydric soil regime or mesoclimate, as, for example, in gleyic sites saturated with groundwater or at sites with north slope orientation. However, spruce silviculture is probably possible only as admixture at present. In these areas and in localities exhibiting forest decline of Norway spruce, it is difficult to avoid an increase in the proportion of beech in production forests. The change of species composition must not take a form of a simple replacement of Norway spruce with European beech.

The main aim of the change in the forest management should be the creation of structured mixed forests – application of the principles of continuous cover management forestry. Variations in tree age and dimension, forest density, as well as species composition will help to increase biological diversity and resistance. The use of natural regeneration may increase genetic diversity and improve the potential of forests to adapt to climate change. Besides controlling tree species composition, stand density management may also help to further adapt temperate forests to climate change (Ammer, 2017). Climate change shifts the realized niches of tree species; therefore, a structured mixed forest is the best option – it minimizes risks by spreading the risks over different species and ontogenetic stages and maximizes employment of natural forest processes. The process of transformation from even-aged forest stands to irregular forest stands and the application of principles of continuous cover management forestry are complicated in the colline belt because some of the suitable tree species are light-demanding species. Besides the underplanting of silver fir which is missing in many places, forest managers should also apply gaps (small clearcuts) with subsequent artificial regeneration of oaks (especially pendulate oak on waterlogged sites) or with the regeneration of other suitable shade low tolerant or intolerant trees (Bílek et al., 2013; Schütz, 1999). The predicted climate change in Central Europe will most likely lead to the altitudinal shift of the tree species ecological optimum. In relation to this, the current planting of tree species on the bottom border of the ecological optimum or out of the optimum is extremely risky (except the specific sites, mentioned earlier).

Planting of mixtures of species in their ecological optimal conditions is the basic measure to ensure forest health and productivity in the future.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.02.028>.

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