Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate

Irantzu Primicia [a,*], Jesús Julio Camarero [b], Pavel Janda [a], Vojtch Čada [a], Robert C. Morrissey [a], Volodymyr Trotsiuk [a], Radek Bače [a], Marius Teodosiu [c,d], Miroslav Svoboda [a]

[a] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Praha 6 – Suchdol, 16521 Prague, Czech Republic
[b] Instituto Pirenaico de Ecología (IPE, CSIC), Avda. Montañana 1005, Apdo. 202, 50192 Zaragoza, Spain
[c] National Institue for Research-Development in Forestry "Marin Drăcea", Eroilor 128, 077190 Voluntari, Romania
[d] Faculty of Forestry, University Ştefan cel Mare Suceava, Universităţii 13, 720229 Suceava, Romania

ARTICLE INFO

ABSTRACT

Stands and trees may exhibit different climate–growth responses compared to neighbouring forests and individuals. The study of these differences is crucial to understanding the effects of climate change on the growth and vulnerability of forests and trees. In this research we analyse the growth responsiveness of primary Norway spruce forests to climate as a function of different stand (elevation, aspect, slope, crowding, historic disturbance regime) and tree (age, tree-to-tree competition) features in the Romanian Carpathians. Climate–growth relationships were analysed using Pearson correlation coefficients between ring-width indices (RWIs) and climate variables. The influence of stand and tree characteristics on the RWI responses to climate were investigated using linear mixed-effects models. Elevation greatly modulated the climate–growth associations and it frequently interacted with competition intensity or tree age to differentially influence growth responsiveness to climate. Old trees were more sensitive to climate than young trees, but while old tree's response to climate highly depended on elevation (e.g. positive influence of summer temperature on old trees' RWIs at high elevations, but negative effect at low elevations), differences of the young trees' response across the elevation gradient were less evident. The severity of the past disturbance also modified the climate–growth associations because of contrasting canopy structures. Our results suggest that although an increase in temperature might enhance growth at high elevations, it may also induce growth declines due to drought stress at lower elevations, particularly for old trees or trees growing under high levels of competition, which may increase their vulnerability to disturbances.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

In European forests tree growth is constrained by low temperatures in northern regions and at high elevations, and by low water availability in warmer southern regions or in drought-prone, low-elevation sites (Babst et al., 2013). Although climate is acknowledged as a major driver of growth, site and tree features can modify how individual trees respond to climatic variables at different spatial scales (Galván et al., 2014). Classical dendroclimatological studies have focused on trees with similar response to climate and on the summarizing of those responses in a mean growth series or site chronology for the whole stand (Fritts, 2001). Typically, site and tree selection are intended to enhance the climate signal (Cook and Kairiukstis, 1990; Schweingruber, 1996). However, trees show divergent climate–growth associations from their neighbours within a stand, because growth responsiveness to climate depends on site and tree characteristics like forest composition (Pretzsch and Dieler, 2011), tree-to-tree competition intensity (Linares et al., 2010) or tree age and size (Carrer and Urbinati, 2004; Martín-Benito et al., 2008; Szeicz and MacDonald, 1994).

The differential sensitivity of tree individuals to climate implies they are differentially adapted to varying levels of climatic stress being for example more or less drought-responsive individuals

(Galván et al., 2014). Studying the variability of the climate–growth response at the individual tree scale provides valuable ecological information on how trees respond to climate and how these responses determine forest dynamics (Carrer, 2011; Rozas, 2014). Identifying growth patterns and trends at the stand and tree scales is therefore crucial when forecasting how climate change will affect forest dynamics and tree adaptation to new climatic scenarios (Aitken et al., 2008), especially if drought and natural disturbances (e.g., beetle outbreaks) are thought to increase in the future (IPCC, 2007; Seidl et al., 2014).

Norway spruce (*Picea abies* (L.) Karst.) is one of the most widespread conifers in the European temperate forests (Spiecker, 2003), usually occupying mesic and managed sites and showing reduced growth in response to cold temperatures or low water availability during the growing season (Aakala and Kuuluvainen, 2011; Büntgen et al., 2007; Mäkinen et al., 2003, 2002). Primary forests of Norway spruce are very rare in Europe because of a long history of anthropogenic influence. Natural disturbances (e.g., windstorms, bark beetle outbreaks) are the major drivers of primary Norway spruce forest dynamics (Lännenpää et al., 2008; Shorohova et al., 2008; Svoboda et al., 2014; Trotsiuk et al., 2014), and could also influence the climate–growth response of trees (Rozas, 2001).

In this study we investigate how tree (age, tree-to-tree competition) and stand (elevation, aspect, slope, plot crowding, historic disturbance regime) features modulate climate growth relationships of primary Norway spruce forests in the Romanian Carpathians. The study forests are considered temperature-sensitive because they represent the upper part of the spruce distribution in the Carpathians but do not reach the alpine tree line (Čejková and Kolář, 2009; Treml et al., 2012; Wilson and Hopfmueller, 2001). Our main objectives were to determine the main climatic variables influencing Norway spruce growth and to elucidate how stand and individual tree conditions influence the trees' growth responses to climate. Our working hypotheses were that: (i) Norway spruce growth is mainly limited by temperature as elevation increases; and (ii) those trees under more stressful conditions (e.g. old trees or trees growing in dense, high-elevation stands or under high-severity disturbance regime) will exhibit higher sensitivity to climate variables.

2. Material and methods

2.1. Study area

The study was conducted in five sites within two localities, the Călimani and Giumălau Mountains of the Eastern Romanian Carpathians. We sampled fifty pure Norway spruce plots, 21 in Călimani and 29 in Giumălau, between 1249 and 1653 m a.s.l. (Table 1). Mean annual temperature is 3.3 and 6.2 °C with a mean annual precipitation of 822.7 and 715.8 mm for Călimani and Giumălau, respectively (Supplementary Material, Fig. A.1). The bedrock is composed of andesites (Seghedi et al., 2005) and phyllite in Călimani, and of gneiss in Giumălau (Balintoni, 1996), and podzols are the most common soils in both ranges (Valtera et al., 2013). For a more detailed description of the study area see Svoboda et al. (2014).

2.2. Data collection and processing

A stratified random design based on a 2-ha grid cell size was used to sample each site. Circular plots 1000 m^2 in size were established at each grid intersect; however, in plots with a high tree density (>500 trees ha^{-1}) and homogenous structure, plot size was reduced to 500 m^2 ($n = 20$). Stands with evidence of past logging, grazing, and stands close to formerly grazed areas were not sampled. In each plot, spatial location, species, and diameter at breast height (DBH) of all living trees $\geqslant$ 10 cm were recorded; crown area of five randomly selected canopy trees was estimated using the crown width of two orthogonal axes. Physiographic attributes such as slope, aspect, and elevation were recorded for each plot.

2.2.1. Dendrochronological methods

In 2011, we cored 25 (for 1000-m^2 sample plots) or 15 (for 500-m^2 sample plots) randomly selected dominant or co-dominant trees per plot. One radial core per tree was extracted at 1.0 m above ground level for growth analysis and age determination. The cores were air-dried, mounted on wood boards, and shaved with a razor blade until annual growth rings were clearly visible. For cores that missed the pith, the number of missing rings was estimated using the method of Duncan (1989). Samples were visually cross-dated using pointer years (Yamaguchi, 1991), and verified using the COFECHA program (Holmes, 1983). Annual tree ring widths were measured to the nearest 0.01 mm using a stereomicroscope and a LintabTM sliding-stage measuring device in conjunction with TSAP-WinTM software (Rinntech, Heidelberg, Germany). Tree-ring width series were standardized and detrended by fitting a 50-year cubic spline with a 50% cut-off frequency to remove age- and size-related trends (Cook and Peters, 1981). Autoregressive modelling removed most of the temporal autocorrelation (usually of first order) to obtain residual series of dimensionless ring-width indices (RWI). Individual tree RWI were averaged at the locality (Călimani, Giumălau) and plot scales to develop master chronologies for each scale. Series detrending and chronologies building were done using the Dendrochronology Program Library (*dplR*) package (Bunn, 2010) in the R software (R Core Team, 2013).

For each locality chronology, several descriptive dendrochronological statistics (Fritts, 2001) were calculated either from the raw tree-ring series (mean and standard deviation of ring width; AC,

Table 1
Physiographic parameters and stand structural characteristics of the study plots. Competition index was calculated only for those trees which zone of influence did not extend outside the plot boundary.

Locality	Călimani				Giumălau
Sites	C2	C3	C4	C5	G1
Mean (range) elevation (m a.s.l.)	1626 (1599–1653)	1484 (1415–1549)	1557 (1505–1601)	1558 (1512–1598)	1430 (1249–1571)
Mean (range) slope (°)	38 (33–43)	22 (16–28)	28 (25–32)	20 (15–23)	29 (17–38)
No. plots	4	6	6	5	29
Mean (±SD) tree density (stems ha^{-1})	365 ± 88	803 ± 107	408 ± 168	432 ± 130	516 ± 257
Mean (±SD) diameter at breast height (cm)	37.1 ± 3.4	23.9 ± 4.3	38.3 ± 7.9	39.7 ± 5.6	31.8 ± 9.2
Mean (±SD) basal area (m^2 ha^{-1})	46.3 ± 7.1	41.5 ± 12	53.2 ± 7.4	61 ± 4.1	47.6 ± 14.6
No. sampled trees	63	122	99	103	421
No. trees with competition index	43	82	72	73	258
Mean (range) tree age at 1 m (yrs.)	188 (84–257)	68 (56–78)	171 (51–276)	146 (53–237)	133 (50–304)