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Original Article

European beech in its northeasternmost stands in Europe: Varying climate-growth relationships among generations and diameter classes

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ABSTRACT

Age, genetics and social status of trees affect their sensitivity to environmental factors, and information about such effects is needed for comprehensive assessment of growth potential. Climatic sensitivity of radial increment (i.e., tree-ring width) of introduced European beech (*Fagus sylvatica* L.) of different generations and social status, growing in its northeasternmost stands in Europe, was studied by dendroclimatological methods. At present, the studied stands occur outside of the natural distribution area of the species, providing opportunity to study adaptability and potential growth of beech in novel environments under changing climate. The sensitivity of radial growth to climatic factors was modulated by the generation and social status (size) of trees. The first generation trees, which were propagated from the material transferred from the northern Germany, were highly sensitive to climatic factors and showed wide spectrum of responses. The dominant trees were particularly sensitive to June precipitation, indicating sensitivity to water deficit in summer. The suppressed trees were mainly sensitive to temperature in the dormant period. Tree-ring width of the second generation trees, which were propagated from the first generation stands, was mainly affected by water deficit in summer, yet the local factors, modulated the mechanisms of response. In one stand, tree-ring width was affected by conditions during the formation of tree-ring, indicating direct influence of weather conditions on xylogenesis. In the other stand, tree-ring width was correlated to weather conditions in the preceding year, suggesting influence via carbohydrate reserves. The effect of social status on climatic sensitivity in the second generation stands was considerably weaker, likely due to the natural and anthropogenic selection of the material best adapted for local conditions. The effect of climatic factors on radial growth of beech has shifted during the 20th century. The effect of autumn temperature has weakened, likely due to warming; the effect of factors related to water deficit in summer has intensified that could be related to both, changes in climate and ageing. The observed climate-growth relationships suggested that conditions in winter have become suitable for beech, yet careful selection of sites/regions with appropriate hydrological conditions appear necessary to counteract the increasing effect of water deficit, hence to ensure productivity of future beech sites in Latvia.

1. Introduction

In Europe, northward expansion of European beech (*Fagus sylvatica* L.) is expected by the end of the 21st century in response to climatic changes (Hickler and Vohland, 2012; Kramer et al., 2010); however, considering slow dispersion of propagules (Saltre et al., 2013), assisted migration appears important issue for wider spread of the species (Björkman and Bradshaw, 1996; Vitt et al., 2010). Introduction of forest reproductive material suitable for warmer climates has been advised as one of the means for mitigation of the effects of warming climate on forestry (Winder et al., 2011), thus broadening perspectives for a wider (commercial) application of beech in the hemiboreal zone. Such introductions would require adjustments in forest management practices that creates necessity for comprehensive information about the benefits and environmental risks of the novel species (Burton, 2012).

Sensitivity of populations growing near the species distribution limits to environmental factors is largely determined by the genetics (provenance) (Peuke et al., 2002), which affects the adaptive capacity (Aitken et al., 2008; Kreyling et al., 2014). In this regard, experimental plantations, particularly near or outside the natural range of the species, serve as good indictors of adaptability and potential growth of species in novel environments under changing climate (Isaac-Renton et al., 2014; Kreyling et al., 2014; Vetaas, 2002). At present, the northeasternmost experimental stands of beech, which are located outside of its natural distribution range and have reached maturity, occur in the western part of Latvia (Augustaitis et al., 2015; Bolte et al.,

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Table 1
Description of the studied stands of European beech and descriptive statistics (mean value, range, and standard deviation) of stem diameter at breast height (DBH) and number of measured tree-rings for sampled trees. CI—confidence interval.

	Young 1	Young 2	Mature
Location	57.2505° N, 22.6993° E	57.2464° N, 22.6264° E	57.2504° N, 22.7209° E
Area, ha	1.7	2.2	2.0
Year established (stand age at sampling, years)	1956 (60)	1951 (65)	1889 (127)
Initial density, ind. ha^{-1}	4000	4000	3800
Admixture	Pure beech	Oak, 20%	Birch, 20%
Mean DBH ± CI, cm	25.86 ± 3.03	26.85 ± 3.12	28.95 ± 3.26
Range DBH, cm	10.4–46.3	12.4–48.5	14.1–49.6
St. dev. DBH, cm	9.9	9.8	10.5
Mean length of series ± St. dev., number of tree-rings	44.4 ± 9.7	56.2 ± 4.7	106.6 ± 14.0

2007), where the species has been planted on ca. 40 ha of forest land. Good survival, productivity and self-regeneration of these stands suggest that conditions in the western part of Latvia have been suitable for beech (Bolte et al., 2007; Dreimanis, 1995), yet little information is available about its growth variation (Augustaitis et al., 2015; Jansons et al., 2015).

Climate is one of the main factors that affects tree increment (Fritts, 2001), hence information about its climatic sensitivity is essential for assessment of future growth potential and necessary adjustments in management (Burton, 2012). Detailed information about the effect of climatic factors on tree growth can be obtained by retrospective analysis of tree-ring proxies (e.g., width), which act as a natural archive of the environment-growth interactions (Cook, 1985; Fritts, 2001). Trees growing close or even outside their natural distribution area have been considered as highly informative for such analysis due to pronounced effect of limiting factor(s) (Speer, 2010; Vetaas, 2002). The effect of climatic factors on tree growth is usually complex, modulated by regional, site and internal factors, which have to be considered when extrapolating the obtained relationships (Cook, 1985; Friedrichs et al., 2009; Fritts, 2001). Hence, the selection of empirical material (sample trees) influences the detectable climate-growth relationships (Carrer and Urbinati, 2004; Piutti and Cescatti, 1997).

Size and social status of trees within a stand, which depends on age, genetics, and micro-site factors, affects assimilation, maintenance costs, water transport (Peuke et al., 2002; Ryan et al., 1997) and carbon allocation (Genet et al., 2010). The synergy of these processes alters growth responses, hence sensitivity to particular environmental factors, resulting in a spectrum of growth patterns (Carrer and Urbinati, 2004; Piutti and Cescatti, 1997). Trees of different canopy status also have diverse water use efficiency (Granier et al., 2000; et al., 1997; Orwig and Abrams, 1997), implying varying sensitivity to the factors related to water deficit.

Besides the age- and size-related alterations in climatic sensitivity (Carrer and Urbinati, 2004), the sets of limiting factors can shift over time due to the changes in climate (Jansons et al., 2015; Lloyd and Fastie, 2002; Wilmking et al., 2004), as certain thresholds of environmental factors are exceeded (Speer, 2010). For example, improved growth of thermophilic species has been observed under warming climate (Kullman, 2008; Walther et al., 2002), while increasing temperature during the vegetation period might cause the opposite reaction, intensifying evapotranspiration and water deficit (Lindner et al., 2010; Wilmking et al., 2004). In addition, changing climate can cause diversification of growth patterns at a fine geographic scale, increasing the effect of micro-site conditions and competition (Briffa et al., 1998; Piutti and Cescatti, 1997; Wilmking et al., 2004).

Considering these factors, pooling of data from trees of different age/size might cause biased results, as environmental signals captured by xylogenesis might interfere (Fritts, 2001); nevertheless, only several studies have analysed the size- and age-related differences in sensitivity of tree growth (Carrer and Urbinati, 2004). Current studies from the eastern Baltic region, which have analysed pooled data from randomly selected trees, showed that radial increment of beech has been sensitive to both temperature in winter and water deficit in summer (Augustaitis et al., 2015; Jansons et al., 2015). However, there is still poor information about the diversity of growth responses within a stand and locality, as well as about the temporal changes in climatic sensitivity of growth. Hence, the aim of this study was to assess the sensitivity of tree-ring width (TRW) of beech of different generations (age) and stem diameter at breast height (DBH) classes to climatic (meteorological) factors at its northeasternmost experimental plantations (stands) in Europe. Regarding age (generation), we hypothesised that the older trees have been more sensitive to climatic factors than the younger ones. Additionally, we assumed that sensitivity has been affected by the social status within a stand (DBH class); accordingly, the dominant (larger) trees were more sensitive to drought related factors due to higher demand for water, while trees of smaller DBH (suppressed) were more sensitive to winter temperature due to lesser carbohydrate reserves and vigour (Gerard and Breda, 2014; Guy, 1990). We also assumed that, beside the age-related changes, the sets of the significant climatic factors have shifted during the 20th century due to warming of climate.

2. Material and methods

2.1. Study area

Study site was located in the northwestern part of Latvia (Table 1), representing lowland conditions; the elevation was ca. 100 m a.s.l. and the topography was flat. Soil was silty and well drained. The climate could be classified as moist continental, yet it was largely determined by the westerlies, which brought air masses from the Baltic Sea and the Atlantic. The mean annual temperature (± standard deviation) in the period 1940–2015 was +6.2 ± 1.0 °C; the mean monthly temperature ranged from −3.7 ± 3.6 in February to +16.5 ± 1.5 °C in July. Vegetation period, when the mean diurnal temperature exceeds +5 °C, mostly extended from mid-April to October. The mean annual precipitation sum was 667 ± 106 mm; the highest monthly precipitation occurred in summer months (June–August; 75 ± 30 mm). Climatic changes were mainly expressed as increase of the mean temperature, particularly during the dormant period and spring, and as extension of the vegetation period (Lizuma et al., 2007), while summer temperature and precipitation regimes were becoming more heterogeneous (Avotniece et al., 2010).

Three plantations (stands) of beech located within 5 km distance from each other, growing on rich sites (*Myrtilloso-polytrichosa-Oxalidosa*) were selected (Table 1). The age of the plantations differed; two stands (Young 1 and Young 2) were ca. 60 years old, and the third stand (Mature) was twice older; however, the DBH ranges were similar. The initial density of the plantations was ca. 4000 trees ha^{-1}. The older (Mature) beech stand was established by the reproductive material originating from wild stands in the northern Germany, yet the exact area of provenance was unknown. Two younger stands were established