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UNIVERSITÀ DEGLI STUDI DI TORINO

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TITLE

Summer climate variability over 250 years differently affected tree species growth in a mesic *Fagus-Abies-Picea* old-growth forest

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ABSTRACT

Sustainable forest management has to consider the long-term effects of climate change on species growth to develop adaptation measures. In this perspective, dendrochronology provides valuable information on climate-growth relationships over long time periods. Tree-ring analyses in mixed stands can elucidate how different species respond to climate change within the same environmental conditions. However, few studies have investigated such stands, especially in South-Eastern Europe. In the forest reserve of Lom, in Bosnia and Herzegovina, we had the opportunity to study three co-occurring species (silver fir, Norway spruce, European beech) in an old-growth forest characterized by reduced human and natural disturbances, and a climate favourable to the tree species. We evaluated tree growth response to climate on inter-annual and decadal time scales over about 250 years. Response to inter-annual climate variability changed over the study period. Climate signal in beech was generally low, with a negative correlation to April temperature in the last decades. In fir and spruce, the positive effect of current spring temperature decreased, while the negative effect of previous summer temperature considerably increased over the last century. At the decadal scale, divergent responses have been detected among species: spruce was mostly negatively affected by summer temperature whereas summer precipitation benefited fir growth, probably reducing high temperature stress. Beech showed a peculiar delayed response, and protracted drought periods led to severe growth reductions. Despite a temperature increase over the last three decades, fir did not experience any growth reduction, while a strong decline was evident in spruce and beech productivity. Mesic sites are commonly underrepresented in tree-ring research. In our analysis, covering about 250 years, we observed that climate also affects species-specific growth patterns in these areas. Within a global change perspective, specific divergent responses are likely to occur even where current environmental conditions appear to be not limiting for tree species. Future management strategies should consider these outcomes.

Keywords: Climate change; decadal growth fluctuation; mixed forest; moving window; old-growth; tree ring.

1. INTRODUCTION

Current increase in temperature and CO₂ atmospheric concentration is expected to enhance plant growth in temperate ecosystems and, as a consequence, carbon sequestration (Ciais et al., 2005; Hember et al., 2012). However, during the last decades, both positive and negative trends in productivity have been reported in many temperate forests, depending on species and site (Boisvenue and Running, 2006; Linares and Camarero, 2012a). Besides CO₂ atmospheric enhancement and climate warming, variation in precipitation and climate extremes regime, lengthening of the growing season, nitrogen and sulphur deposition, changes in land management practices and disturbance regime have been identified as major drivers of observed growth trends (Magnani et al., 2007; Bellassen et al. 2011; Babst et al., 2012; Bradford et al., 2012).

Nevertheless, it is essential to place current variations within the context of long-term variability, to understand whether observed patterns are unprecedented or reversible temporal fluctuations. Tree-ring analysis represents a valuable tool for this, as it allows variations in tree growth patterns to be studied over long time periods, and to investigate relationships between trees and environmental factors, such as climate. Most dendrochronological research has been conducted on trees growing near their environmental limits, as they have a more evident response to climate. However, processes observed in such conditions can only be barely indicative of climate change influence on most forested areas (Carrer et al., 2012), which do not lie at the altitudinal or latitudinal limits of species distributions (Drew et al., 2013).

A central aspect of research on forest adaptation to climate change is evaluating the different responses of species. However, site conditions can confound species-specific responses (Eilmann and Rigling, 2012). To exclude site effect, a few studies have been conducted on response to inter-annual climate variability in co-occurring species (e.g., Battipaglia et al. 2009; Schuster and Oberhuber, 2013), but to date, very few studies have evaluated climate effects on decadal growth fluctuations in mixed stands (Wilson and Elling, 2004; Bouriaud and Popa, 2009). Such trends are often not considered, as they are affected by size-age relationships, stand dynamics and disturbances (Cook et al., 1990), and climate signal is considered hardly detectable. However, the effect of decadal climate variations on tree growth can be observed in old living trees even in a forest stand, when other factors influencing growth, such as disturbances, are limited and/or randomly distributed (Bouriaud and Popa, 2009; Aakala and Kuuluvainen, 2011).

Future carbon sink estimates and forest management strategies should be driven by detailed information on different tree species response to climate change. As recent variations in growth trends, and in tree response to climate, have not followed a uniform pattern in Europe (Spiecker, 1999; Mäkinen et al., 2002; Babst et al., 2013), there is a need to investigate tree species response to climate in different areas, especially those not previously much explored, such as mesic forests in Eastern Europe (Bošela et al., 2013; Poljanšek et al., 2013). In the current study, we aimed to evaluate growth patterns and response to climate over the last few centuries of three widely distributed tree species, i.e. European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.), in an old-growth forest in Bosnia and Herzegovina. As the three species co-occur in the same stand, it was possible to study their response to climate within the same environmental conditions. Moreover, in the study area the three species grow vigorously, allowing

species sensitivity to climate change to be studied in not-limiting conditions. Lastly, the forest has scarcely been affected by humans, and there were no signs of intermediate or large scale disturbances over the last centuries affecting tree growth patterns (Bottero et al., 2011; Motta et al., 2011). To better understand the climate influence on the species growth, we aimed to answer the following research questions: in the three species, (1) Is the inter-annual growth response to climate similar, and stable over time? (2) Is there an effect of decadal climate variations on growth trends?

On the basis of observed climate-growth relationships, we then discuss recent growth trends in comparison to those we observed in previous periods, and those reported for the same species in other regions of Europe.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in the Lom forest reserve (298 ha, 44°27' N, 16°28' E, 1250 - 1500 m a.s.l.) in the Dinaric Alps, Bosnia and Herzegovina. Annual precipitation averages 1600 mm, with maximum in December (173 mm) and minimum in July (108 mm), and mean annual temperature in the lower part of the reserve is 5.0 °C, with maximum in August (13.3 °C) and minimum in February (-3.9 °C) (Maunaga, 2001). The morphology has typical karst characteristics, such as limestone outcrops and deep cavities, with reduced soil water holding capacity. Shallow soils (dark soil and shallow brown) are predominant, and water deficit can occur during summer (Maunaga, 2001).

The reserve was established in 1956 in an old-growth mixed montane forest. The most widespread vegetation type is *Piceo-Abieti-Fagetum illyricum*, with Norway spruce, silver fir and European beech as the most frequent tree species. Spruce and fir trees can exceed 120 cm in diameter and 40 m in height, and the largest beech trees grow to over 70 cm and 35 m. Previous studies (Bottero et al., 2011; Motta et al., 2011; Garbarino et al., 2012) pointed out that forest dynamics are characterized by small-scale processes, while no intermediate, large, or stand replacing disturbances were recorded. Evidence of past human activities (selective logging) were observed only near the reserve borders.

2.2. Field sampling and tree-ring analysis

During 2008 and 2009, covering an area of approximately one squared kilometre in the lower part of the reserve, we sampled 34 Norway spruce, 35 silver fir and 47 European beech trees among dominant and co-dominant individuals. Diameter at breast height (dbh) was recorded, and two cores were taken from each tree at 1.30 m above ground level.

Ring width was measured to the nearest 0.01 mm in the laboratory and cross-dating accuracy was checked using COFECHA (Holmes, 1983). Cores not reliably cross-dated were excluded from the analyses. We obtained 64 series (34 trees) for spruce, 63 (35) for fir, and 85 (44) for beech.

To remove age-size related trends, raw ring width series were detrended using cubic smoothing splines with 50% frequency-response cutoff equal to 200 years using the ARSTAN program (Cook, 1985). This method

partially removed multi-century trends, possibly related to multi-century climatic fluctuations, but was able to keep most of the year to year and decadal variability. Mean chronologies for each species were calculated as the bi-weight robust mean of detrended individual series (Cook, 1985), and truncated when one of the following criteria was not met: (i) sample size < 5 series; (ii) mean correlation among series < 0.50 over 50 year windows; (iii) EPS (Expressed Population Signal) < 0.85 over 50 year windows (Wigley et al., 1984). For the mean chronologies, we calculated mean sensitivity (MS) to assess the high-frequency variations (Fritts, 1976), the first-order autocorrelation (AC) to measure the influence of previous year's growth on the current ring, and the mean correlation between trees (\bar{R}), measuring the common growth forcing among trees within the plot. To distinguish between inter-annual and decadal growth variations, the chronologies were filtered with 20 years cubic spline functions (with 50% frequency response cutoff). The splines were considered to represent the decadal growth variations (low-pass filtered chronologies, LP), while the ratio between the mean chronologies and the 20 years splines represented inter-annual growth variations (high-pass filtered chronologies, HP) (Mäkinen et al., 2002; Wilson and Elling, 2004; Bouriaud and Popa, 2009).

2.3. Climate data

Recent surface land temperature estimations at global or macro-regional level allow tree response to climate to be studied over a longer period than using local meteorological stations. For temperature we used the recently developed global land-surface temperature estimation by Rohde et al. (2011), spanning from 1753 to 2011 for Bosnia and Herzegovina. For precipitation, as a monthly resolved dataset covering the whole study period was not available, we used the seasonal precipitation reconstruction by Pauling et al. (2006) for European land areas (30°W to 40°E, 30° to 71°N), covering the period 1500–2000. Similarly to tree ring series, climate data were filtered with 20 years cubic spline functions (50% frequency response cutoff) to separate inter-annual and decadal variations (Bouriaud and Popa, 2009; Aakala and Kuuluvainen, 2011).

2.4. Response to climate

Climate effect on inter-annual growth variations (HP chronologies) for the period 1753-2008 (1753-2000 for precipitation, depending on data availability), and the stability of response for 50 year moving windows over the same period were assessed with bootstrap correlation, using Dendroclim 2002 (Biondi and Waikul, 2004). Parameters between June of the year prior to ring formation and current September were considered. As sample age increases throughout the span of a chronology derived from living trees, and tree age can affect response to climate (e.g. Carrer and Urbinati, 2004), we wondered whether ageing of trees in our sample could modify this response. We therefore compared change in climate signal over the study period in chronologies from young (first 33% of age distribution) and old (last 33%) trees for each species. For the same time period, influence of decadal climate variations on species growth fluctuations (LP chronologies) was quantified by Pearson's correlation. Significance level was corrected on the adjusted degrees of freedom, to account for the autocorrelation in the smoothed series (Mackas et al., 2001; Wilson

and Elling, 2004). To identify a possible delay in tree response to climate variations, we calculated correlation between the most important climate descriptors and growth in the successive years.

3. RESULTS

3.1. Growth patterns

The longest individual series of all the species exceeded 400 years (Tab. 1), but we considered a chronology since 1650 for Norway spruce, 1700 for silver fir, and 1720 for European beech as well replicated.

Differently to spruce and fir, beech series presented a few (less than 0.5%) missing rings, and some micro-rings, which enhanced the mean sensitivity of the species chronology.

Inter-annual growth variations were significantly correlated in fir and spruce ($r = 0.67$, $p < 0.001$), whereas beech was unrelated to the conifers (fir-beech, $r = 0.12$, n.s.; spruce-beech, $r = 0.07$, n.s.).

Decadal growth variations within the same species showed a common pattern for most of the period (as evidenced in Fig. 1). Higher standard error during the first decades was related to reduced sample size.

Correlation between species LP chronologies were not significant (fir-spruce, $r = 0.31$; spruce-beech, $r = 0.44$; fir-beech, $r = 0.06$). A growth decline occurred over the last 20-30 years in spruce and beech, but not in fir.

3.2. Response to inter-annual climate variability

Response to inter-annual climate variations over the whole study period (Tab. 2) evidenced some differences between species, even if for both fir and spruce the most important climate driver was temperature and, to a lesser extent, precipitation of previous growing season.

The effect of climate on the three species varied considerably over the study period (Fig. 2 and 3), but was quite consistent in different age classes (Fig. S1). Temporal changes in the response were rather similar in fir and spruce. In both species, the previous year's summer temperature had a moderate negative effect on growth in the first decades of the period, no effect at the end of the 19th century, while in the 20th century July and August had a strong negative effect (Fig. 2 and 3). Mild temperatures during winter and early spring (previous December to current April) for fir, and to a lesser extent for spruce, benefited growth for most of the period, but had a scarce effect in the second half of the 20th century. Current summer temperature (June to August) positively affected the two conifer species in some periods between the 18th and 19th centuries, while the correlation was not significant in the 20th century or, in some periods, turned negative, especially for spruce. As regards precipitations, previous summer benefited growth patterns of both species for most of the period, but not in the second part of the 20th century (Fig. 3). Current spring precipitation positively affected fir during the 19th century, while summer precipitation influenced both species in the first decades. The effect of other precipitation parameters was less evident and not consistent during the study period. As expected from the low correspondence between conifer species and beech chronology, response to climate in beech was rather different to that in spruce and fir, and was in general rather weak. Temperature in

previous autumn had a positive effect on beech for some periods, but not in the last decades (Fig. 2 and 3). Effect of temperature during other seasons was not stable, and negative correlations with April temperature emerged during recent years. For the whole period, a precipitation signal was almost absent in beech chronology (Fig. 3).

3.3. Decadal response to climate

A negative effect of summer temperature on decadal growth variations (LP chronologies) was observed for all the species, even if with different modes (Tab. 3). Fir growth was slightly negatively affected by temperature, but only May reached $p < 0.10$. Spruce was by far the most affected species. Decadal growth variations in spruce were clearly negatively related to summer temperature for most of the period (Fig. 4). Even beech growth was related to summer temperature. For this species, we observed a better match shifting summer temperature parameters backwards a few years (Tab. 3, Tab. S1 in Supplementary Material). This possibly indicates a long-term effect of climatic conditions on this species. Relationships between growth fluctuations and temperature in other seasons were not significant, but were almost always negative, confirming the negative effect of high temperatures on species performances.

Decadal variations in precipitation had a moderate effect on spruce, while there was a fairly good correspondence between fir growth and summer precipitation (Tab. 3). Correlation between precipitation and beech chronology was negative, and increased shifting climate parameters backwards a few years (Tab. 3, Tab. S1), but did not reach $p < 0.10$.

4. DISCUSSION

4.1. Non-stationary response to inter-annual climate variability

The analyzed European beech, Norway spruce and silver fir trees approximated the maximum age recorded for the species (for all three, 500-600 years, Badeau et al., 1996; Di Filippo et al., 2012; Castagneri et al., 2013). The availability of long tree ring series and climate reconstructions allowed us to study, to our knowledge for the first time, variation in inter-annual response to climate for the three co-occurring species over about 250 years.

Silver fir and Norway spruce response to climate changed considerably over the study period, with quite similar patterns for both species. The patterns observed in the first period were similar to those observed on mesic sites, where mild temperatures in winter, spring and/or summer generally promote fir and spruce growth rates, while abundant precipitation in the previous year can reduce the negative effect of too warm conditions (Büntgen et al., 2007; Kern and Popa, 2007; Cailleret and Davi, 2011; Castagneri et al., 2012; van der Maaten-Theunissen et al., 2013). Over the centuries, the positive effect of winter and spring temperature decreased, the negative effect of previous year's temperature increased, and the effect of current summer temperature passed from slightly positive to slightly negative. The positive effect of the previous year's precipitation ceased. A negative effect of previous and current summer temperature has generally been

observed in sites with dry summers (Mäkinen et al., 2002; Lebourgeois, 2007; Aakala and Kuuluvainen, 2011; Caillaret and Davi, 2011; Carrer et al., 2012), where increased evapotranspiration causes physiological stress, depressing growth in both the current and successive year. We speculate that, with the increasing temperature trend over the last period, the inter-annual response of the two species shifted from that typical of temperate sites to that of warmer sites. Tree age variation over the study period does not seem to account for non-stationary growth-climate relationships, as the youngest and oldest trees in our dataset showed similar responses.

For most of the period, beech sensitivity to inter-annual climate variability was low, as observed in other regions (Dittmar et al., 2003; Lebourgeois et al., 2012). However, this does not necessarily indicate a lack of sensitivity, but rather a complex response to climate, affected by discrete events. As a masting species, typical climate growth relationships could be obscured by deviation in the allocation flow during mast years (Di Filippo et al., 2007). Moreover, it is well known that beech is very sensitive to late frost at the beginning of the vegetative period (Caillaret and Davi, 2011). We observed that some of the narrowest rings corresponded to strong temperature decreases from April to May, and the two smallest rings of the 20th century (1928 and 1952) matched late frost events registered in Bavaria (Dittmar et al., 2006). The presence of such events certainly altered the correlation between ring width and monthly climatic variables. The negative effect of April temperature that emerged in recent decades could indicate increased frost risk.

4.2. Climate and growth decadal variations

Our study highlights the importance of assessing the effect of climate on decadal growth variations in mesic forests. Despite fairly abundant precipitations, and temperature range within the species requirements, decadal climate variations clearly affected tree growth patterns.

The negative effect of summer temperature on all the species growth was probably related to water deficit during warm periods. Temperate tree species, like those we studied, are not adapted to a warm climate, and can markedly react to moisture stress (Spiecker, 1995; Granier et al., 2008; Battipaglia et al., 2009). Although annual precipitation at the site averages 1600 mm, the karst environment reduces soil water holding capacity, thus water availability would probably be more limited than expected. Elevated evapotranspiration during warm summers, rather than low precipitation, probably caused water stress in the stand. High evaporating demand induces a decrease in water potential, causing stomatal closure at the cost of reduced CO₂ assimilation (Bréda et al., 2006). Furthermore, recent studies (King et al., 2013) demonstrated that temperature has a greater influence than precipitations on stem water dynamics.

Summer water shortage seems to play a key role for tree growth in the study site, but the three species showed a partially different response to decadal climate variations. Silver fir growth was rather stable over three centuries, and strong depressions never occurred. Growth rate was reduced during periods with high summer temperature, but high evapotranspiration was compensated for by precipitation (Lebourgeois, 2007; Battipaglia et al., 2009; van der Maaten-Theunissen et al., 2013). On the contrary, almost all growth fluctuations in spruce corresponded to summer temperature variations. The shallow root system is not able to

uptake deep water, and the species has a rather limited water reserve capacity (King et al., 2013; Schuster and Oberhuber, 2013). In addition, given that fir and beech are more adapted to higher temperature than spruce (Kern and Popa, 2007; Bouriaud and Popa, 2009; Bolte et al., 2010), its greater sensitivity to warm summers is not surprising.

Differently from conifer species, decadal climate fluctuations seem to have a lag effect on beech. One-year delayed effects of drought on beech growth have already been reported: reduced reserves in tree organs, fine root mortality, and xylem dysfunction could negatively affect growth in the years following drought (Granier et al., 2008; Meier and Leuschner, 2008). However, the long-term effects of repetitive drought years have not yet been investigated. In the study site, the species encountered a strong growth depression over the period 1860-1880. A growth decline over the same period has been documented in other forest stands in Central Italy (Piovesan et al., 2008), Albania and Macedonia (Tegel et al., unpublished), and the Czech Republic (Becker and Grissino-Mayer, ITRBD database). We believe this depression was caused by a severe drought that occurred during 1850-1870 in both Eastern Europe (Van der Schrier et al. 2006; Büntgen et al. 2010) and the Mediterranean Basin (Nicault et al., 2008).

4.3. Recent trends and future perspectives

Within the context of multi-century global warming, decadal climate variations can affect forest ecosystems and, as a consequence, forest growth and carbon accumulation rates, with profound implications for forest management at a broad scale. Similarly to other macro-regions, a remarkable temperature increase has occurred in Southern Europe over the last 30 years. To date, few studies have compared current growth rates with those in the past centuries in mesic forests. Our analysis covered about 250 years, and we assessed if recent growth trends in the three analyzed species are unprecedented, or periodic fluctuations.

The three species reacted differently to recent climate variations. In the past centuries, silver fir was the less sensitive species to decadal temperature variations. The recent growth trend confirmed this pattern, as fir growth was rather stable during the last decades. Our results are remarkable considering the dramatic growth variations recently observed in other European countries. In Central and Eastern Europe, a strong decline was widely observed during the 1970s and 1980s, mainly caused by SO₂ emissions, with a successive growth recovery (Bigler et al., 2004; Elling et al., 2009; Büntgen et al., in press). Our study area was less affected by pollutant emissions than other Central and Eastern European regions (Diaci et al., 2011), thus fir did not experience an evident growth decline. However, unlike beech and spruce, fir did not benefit from reduced summer temperatures during the 1970s and 1980s, possibly due to a moderate pollution stress. In Spain, fir has recently undergone drought-induced decline (Linares and Camarero, 2012b). Lack of reduced growth in our study site was not surprising, as fir sensitivity to climate depends on regional environment (Carrer et al., 2010), and the Pyrenees are generally dryer than the Balkans. We conclude that, with reduced pollution, and in environmental conditions similar to those studied, fir can be more competitive than co-occurring less thermophiles species, such as spruce.

The latter species was strongly negatively affected by enhanced summer temperature, as extensively observed in other mesic sites (Spiecker, 1995; Lebourgeois, 2007; Aakala and Kuuluvainen, 2011). The current growth depression was the most severe over the last three centuries in the study site, and we observed comparable growth fluctuations only in the late 16th century, a period characterized by high climate variability (Poljanšek et al., 2013). It is well known that prolonged growth reduction can lead to tree mortality (Bigler et al., 2004; Dobbertin, 2005). At present, however, we cannot estimate whether current decline is reversible or not. Similarly to what has been observed in other regions (e.g. Bolte et al., 2010) our analysis indicates that climate warming poses a threat to the future performance of Norway spruce, especially where it is competing with more warm-adapted species.

Although the climate effect was less evident than in spruce, beech was affected by climatic decadal variations, and the current growth depression, evidenced in many other sites in South-Western and Central Europe (Jump et al. 2006; Piovesan et al., 2008; Charru et al., 2010), can be explained by water deficit related to enhanced temperatures. The species already experienced, and overcame, a strong decline over the period 1860-1880, probably due to prolonged drought. However, climate projections do not forecast a water availability increase in the next decades (Beniston et al., 2007), thus a growth recovery seems to be unlikely.

5. CONCLUSIONS

Forest managers and landscape planners should consider different species response to climate change for both productivity assessment, silvicultural strategies, and CO₂ mitigation policies. As a matter of fact, a decreased capacity to assimilate carbon is occurring in beech and spruce in the study area, and the better adapted fir does not seem to benefit from the reduced performance of co-occurring species, nor to compensate for their lost carbon assimilation. Over the study period, beech and spruce demonstrated to be able to recover from unfavourable periods. However, current climate changes are unprecedented. Further enhanced temperatures could severely affect tree performance, and consequently forest dynamics and species composition. With the likely temperature increase in the future (IPCC, 2007; Poljanšek et al., 2012, 2013), fir and more warm-adapted species could out-compete spruce in forest stands with environmental conditions similar to those studied. More frequent and protracted droughts (Beniston et al., 2007) could even threaten beech. Models on future precipitation scenarios are not concordant but, if mean precipitation decreases (Maracchi et al., 2005), even fir could experience water stress and consequently growth reduction in the near future.

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Table 1

	<i>A. alba</i>	<i>P. abies</i>	<i>F. sylvatica</i>
Raw data			
Cores (trees)	63 (34)	64 (35)	85 (44)
Year	1593-2008	1580-2008	1581-2009
Mean ring width (mm)	1.204	1.139	0.924
Mean chronology			
Year	1700-2008	1650-2008	1720-2009
Mean sensitivity	0.169	0.185	0.310
Autocorrelation	0.290	0.334	0.249
Rbar	0.401	0.398	0.410

Descriptive statistics of the three species raw series and mean chronologies.

Table 2

Temperature	Jun-1	Jul-1	Au -1	Sep-1	Oct-1	Nov-1	Dec-1	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	JJA-1	SON-
<i>A. alba</i>		-0.31	-0.33	-0.19	0.14		0.16	0.16	0.17	0.26		-0.13						-0.32
<i>P. abies</i>	-0.27	-0.31	-0.31	-0.19	0.15					0.14								-0.40
<i>F. sylvatica</i>				0.15	0.23		0.13					0.16						0.1
Precipitation																		
<i>A. alba</i>																		0.26
<i>P. abies</i>																		0.30
<i>F. sylvatica</i>																		

Correlations between high-pass filtered (HP) chronologies and climate (temperature: 1753-2008; precipitation: 1753-2000) in the three species. Only Pearson's r values corresponding to $p < 0.05$ are reported.

Table 3

Current year	Temp May	Temp Jun	Temp Jul	Temp Aug	Temp JJA	Prec JJA
<i>A. alba</i>	-0.36 ⁺	-0.14 n.s.	-0.27 n.s.	-0.31 n.s.	-0.29 n.s.	0.48 [*]
<i>P. abies</i>	-0.26 n.s.	-0.50 ⁺	-0.64 [*]	-0.64 [*]	-0.71 ^{**}	0.32 n.s.
<i>F. sylvatica</i>	-0.08 n.s.	-0.35 n.s.	-0.51 n.s.	-0.36 n.s.	-0.48 n.s.	0.29 n.s.
Prev. 5 years						
<i>A. alba</i>	-0.37 ⁺	0.16 n.s.	-0.02 n.s.	-0.19 n.s.	-0.04 n.s.	0.31 n.s.
<i>P. abies</i>	-0.15 n.s.	-0.38 n.s.	-0.40 n.s.	-0.41 n.s.	-0.48 n.s.	0.34 n.s.
<i>F. sylvatica</i>	-0.28 n.s.	-0.47 n.s.	-0.55 ⁺	-0.42 n.s.	-0.57 ⁺	0.38 n.s.

Correlations between low-pass filtered (LP) chronologies and decadal climate variations in the current and previous five years (temperature: 1753-2008; precipitation: 1753-2000). Only climate parameters correlating with at least one species at $p > 0.10$ are reported. The symbols indicate level of significance: n.s., $p > 0.10$; +, $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$.

Fig. 1.

Three species low-pass filtered (LP) chronologies (thick line), with standard error envelopes (thin lines). Sample size is shown in grey at the bottom of the graphs.

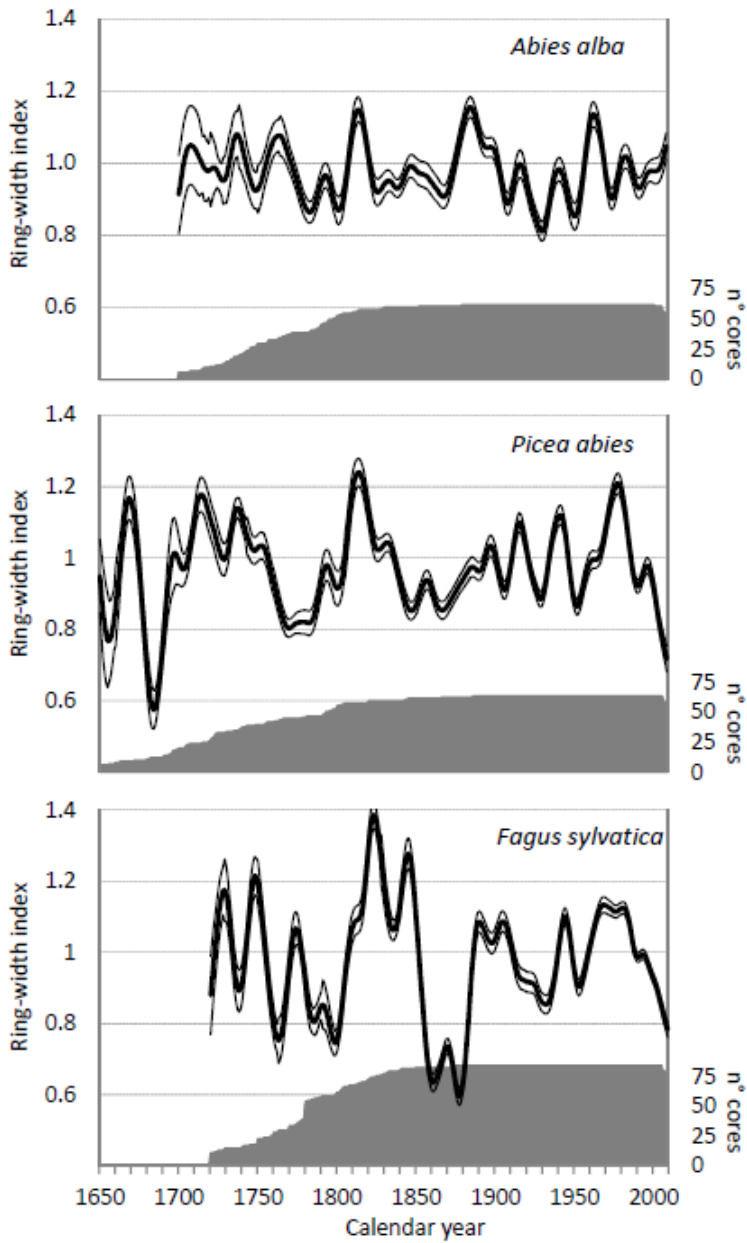


Fig. 2.

50 years moving window correlations between HP chronologies and monthly temperature parameters. In sky-blue, significant negative correlation; in blue, correlation with $r < -0.4$; in yellow, significant positive correlation; in red, $r > 0.4$.

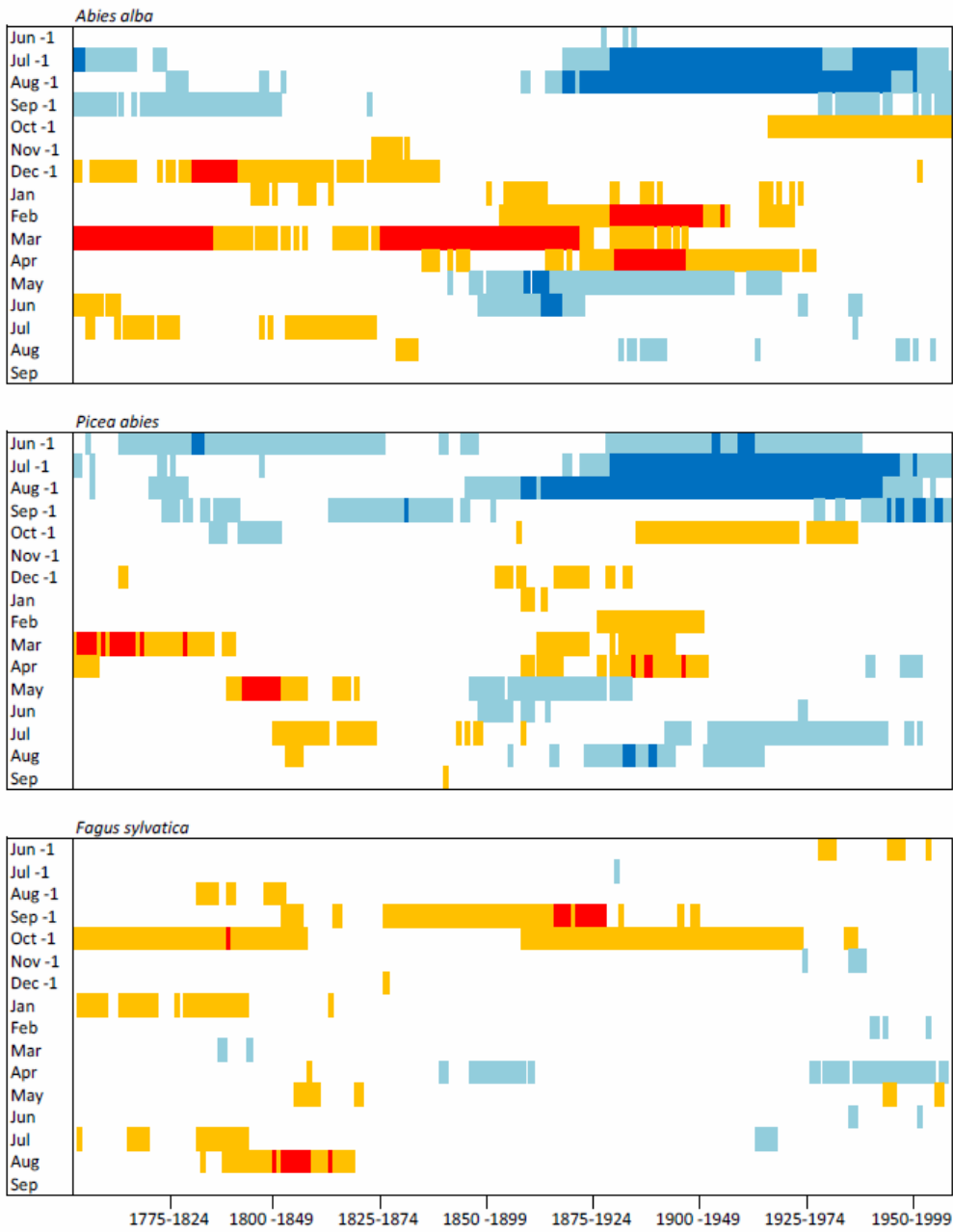


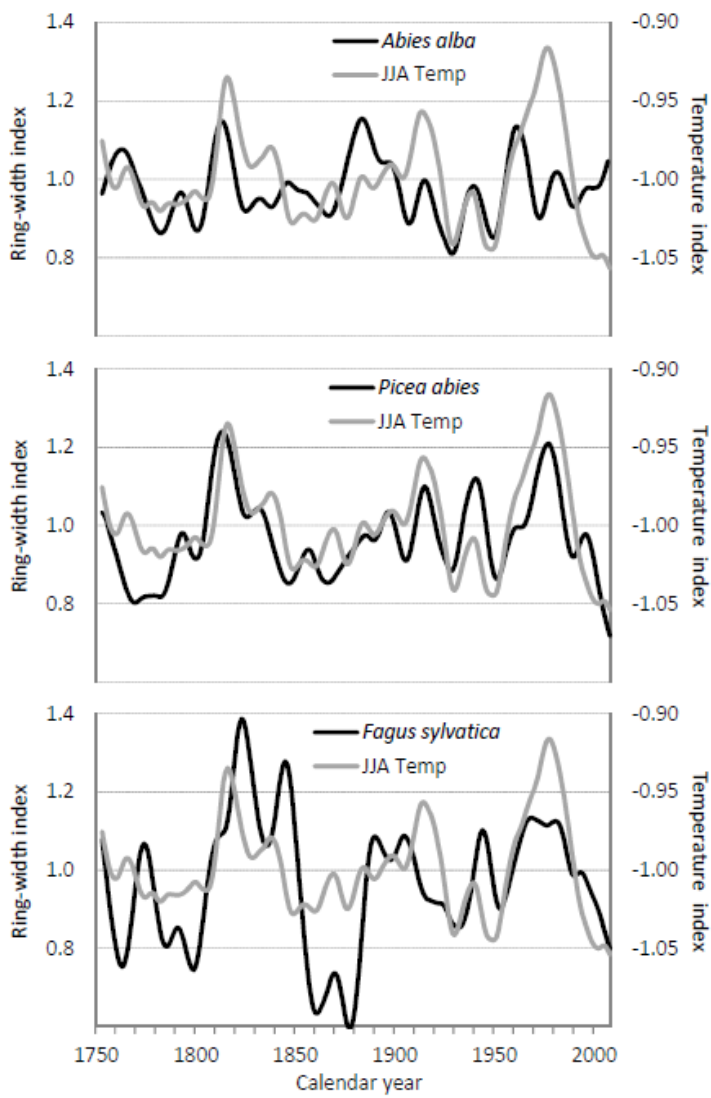
Fig. 3.

50 years moving window correlations between HP chronologies and seasonal temperature and precipitation parameters. In sky-blue, significant negative correlation; in blue, correlation with $r < -0.4$; in yellow, significant positive correlation; in red, $r > 0.4$.

JJA -1 is mean temperature (precipitation) of previous year June, July and August; SON -1 is previous year September, October and November; D-1, JF is previous year December and current January and February; MAM is current March, April and May; JJA is current June, July and August.



Fig. 4. June to August temperature and growth decadal variations in the three species. Temperature is reversed to better visualize common trends.



SUPPLEMENTARY MATERIAL

Fig. S1.

50 years moving windows for correlation between HP chronologies and monthly temperature parameters in young (33% youngest trees) and old (33% oldest) classes. In sky-blue, significant negative correlation; in blue, <-0.4 ; in yellow, significant positive correlation; in red, >0.4 . Time period is restricted to 1850-2008 as previous period was scarcely covered by young class chronologies.

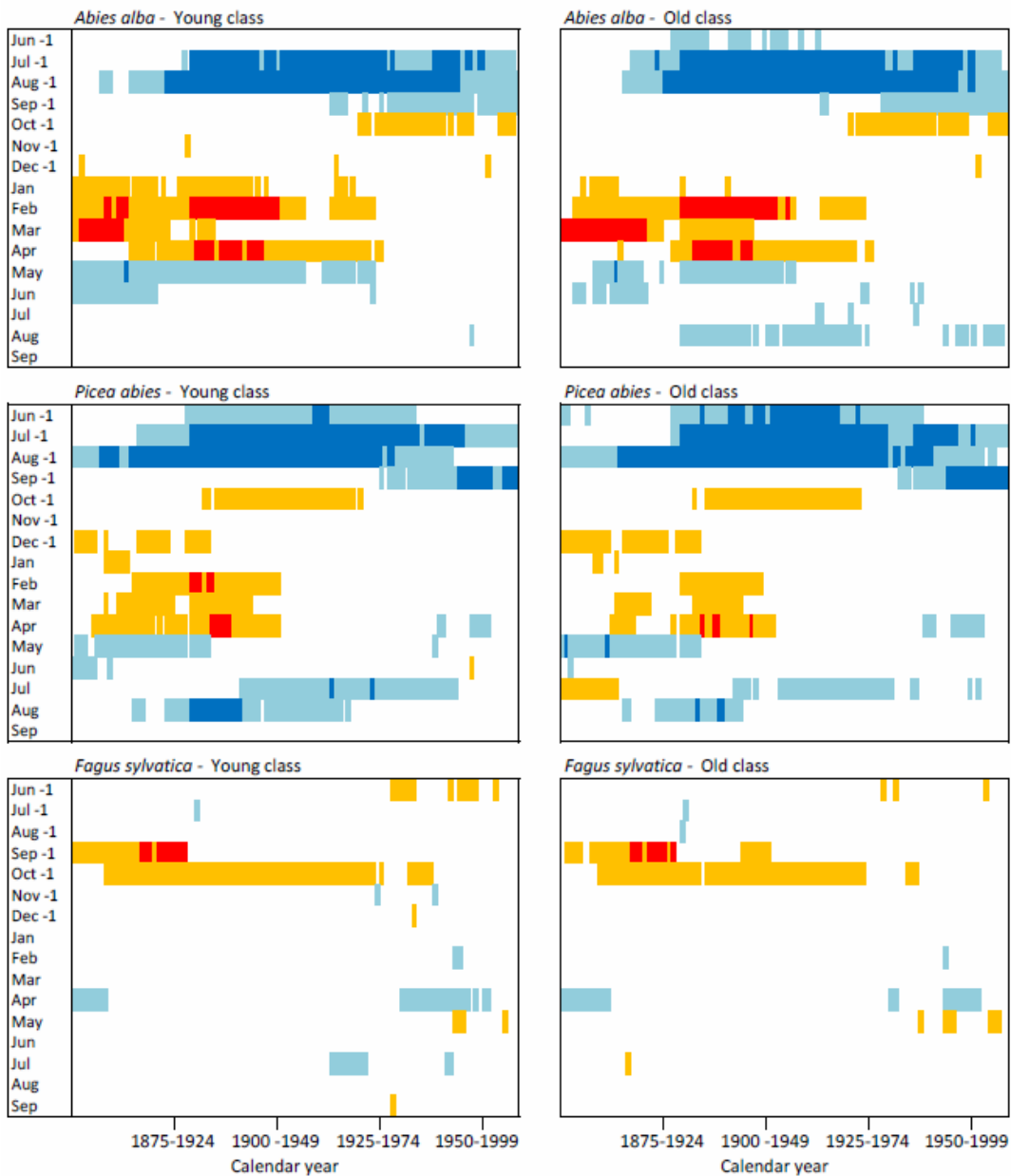


Table S1

Correlations between LP chronologies and May to August climate decadal variations shifted backwards by 10 years. The symbols indicate level of significance: n.s., $p > 0.10$; +, $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$.

	Temp May	Temp Jun	Temp Jul	Temp Aug	Temp JJA	Prec JJA
<i>Abies alba</i>						
current year	-0.36 +	-0.14 n.s.	-0.27 n.s.	-0.31 n.s.	-0.29 n.s.	0.48 *
year -1	-0.40 +	-0.07 n.s.	-0.24 n.s.	-0.32 n.s.	-0.26 n.s.	0.48 *
year -2	-0.43 *	-0.01 n.s.	-0.20 n.s.	-0.31 n.s.	-0.22 n.s.	0.46 *
year -3	-0.43 *	0.06 n.s.	-0.15 n.s.	-0.29 n.s.	-0.16 n.s.	0.43 +
year -4	-0.41 +	0.11 n.s.	-0.09 n.s.	-0.25 n.s.	-0.10 n.s.	0.38 n.s.
year -5	-0.37 +	0.16 n.s.	-0.02 n.s.	-0.19 n.s.	-0.04 n.s.	0.31 n.s.
year -6	-0.31 n.s.	0.20 n.s.	0.04 n.s.	-0.13 n.s.	0.03 n.s.	0.23 n.s.
year -7	-0.23 n.s.	0.22 n.s.	0.10 n.s.	-0.07 n.s.	0.09 n.s.	0.15 n.s.
year -8	-0.15 n.s.	0.23 n.s.	0.16 n.s.	0.00 n.s.	0.15 n.s.	0.05 n.s.
year -9	-0.05 n.s.	0.23 n.s.	0.21 n.s.	0.07 n.s.	0.20 n.s.	-0.03 n.s.
year -10	0.04 n.s.	0.22 n.s.	0.25 n.s.	0.12 n.s.	0.24 n.s.	-0.11 n.s.
<i>Picea abies</i>						
current year	-0.26 n.s.	-0.50 +	-0.64 *	-0.64 *	-0.71 **	0.32 n.s.
year -1	-0.26 n.s.	-0.48 +	-0.61 *	-0.62 *	-0.69 *	0.36 n.s.
year -2	-0.25 n.s.	-0.45 n.s.	-0.57 *	-0.59 *	-0.65 *	0.38 +
year -3	-0.23 n.s.	-0.43 n.s.	-0.52 +	-0.54 *	-0.60 *	0.38 +
year -4	-0.20 n.s.	-0.40 n.s.	-0.46 +	-0.48 +	-0.54 +	0.36 n.s.
year -5	-0.15 n.s.	-0.38 n.s.	-0.40 n.s.	-0.41 n.s.	-0.48 n.s.	0.34 n.s.
year -6	-0.10 n.s.	-0.36 n.s.	-0.34 n.s.	-0.34 n.s.	-0.41 n.s.	0.30 n.s.
year -7	-0.04 n.s.	-0.35 n.s.	-0.28 n.s.	-0.26 n.s.	-0.35 n.s.	0.25 n.s.
year -8	0.01 n.s.	-0.34 n.s.	-0.23 n.s.	-0.18 n.s.	-0.29 n.s.	0.19 n.s.
year -9	0.06 n.s.	-0.33 n.s.	-0.18 n.s.	-0.11 n.s.	-0.24 n.s.	0.11 n.s.
year -10	0.10 n.s.	-0.33 n.s.	-0.14 n.s.	-0.04 n.s.	-0.19 n.s.	0.04 n.s.
<i>Fagus sylvatica</i>						
current year	-0.08 n.s.	-0.35 n.s.	-0.51 n.s.	-0.36 n.s.	-0.48 n.s.	0.29 n.s.
year -1	-0.12 n.s.	-0.39 n.s.	-0.53 +	-0.38 n.s.	-0.51 n.s.	0.32 n.s.
year -2	-0.16 n.s.	-0.42 n.s.	-0.54 +	-0.40 n.s.	-0.54 n.s.	0.34 n.s.
year -3	-0.20 n.s.	-0.44 n.s.	-0.55 +	-0.41 n.s.	-0.56 +	0.36 n.s.
year -4	-0.24 n.s.	-0.46 n.s.	-0.55 +	-0.42 n.s.	-0.57 +	0.38 n.s.
year -5	-0.28 n.s.	-0.47 n.s.	-0.55 +	-0.42 n.s.	-0.57 +	0.38 n.s.
year -6	-0.31 n.s.	-0.48 n.s.	-0.53 +	-0.41 n.s.	-0.56 +	0.38 n.s.
year -7	-0.32 n.s.	-0.47 n.s.	-0.50 n.s.	-0.40 n.s.	-0.55 +	0.37 n.s.
year -8	-0.33 n.s.	-0.47 n.s.	-0.46 n.s.	-0.38 n.s.	-0.52 n.s.	0.35 n.s.
year -9	-0.32 n.s.	-0.45 n.s.	-0.42 n.s.	-0.35 n.s.	-0.48 n.s.	0.32 n.s.
year -10	-0.29 n.s.	-0.43 n.s.	-0.36 n.s.	-0.32 n.s.	-0.44 n.s.	0.28 n.s.

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