

Sapwood area drives growth in mountain conifer forests

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Summary

1. It is expected that climate warming will enhance tree growth of mountain conifer forests in cold regions. However, trees have shown unstable, age-related and site-dependent growth responses to climate throughout the past century, but information on the drivers controlling such responsiveness at the site and tree scales is lacking. We evaluated whether such changing growth responses are more influenced by site features, such as altitude, or by tree features, such as size and sapwood area.

2. We quantified the growth trends at the site and tree levels in Iberian *Pinus uncinata* forests using dendrochronology. Tree-ring width was converted to basal area increment (BAI) to assess the relationships between growth and site and tree variables over three time periods (1901–1994, 1901–1947, 1948–1994) using structural equation models.

3. Trees were older at higher altitudes, and the amount of sapwood decreased as trees aged. BAI trends were lower in the period 1948–1994 than in the period 1901–1947, that is, tree growth is decelerating, despite BAI values of both periods showing the reverse pattern. Sapwood area and, to a minor extent, tree age were the main positive and negative drivers, respectively, controlling BAI during the 20th century, whereas altitude played a minor role.

4. *Synthesis.* Our results highlight the relevance of tree individual characteristics as the main drivers modulating growth responses to climate warming. We conclude that climate warming will have a lower effect on radial growth in slow-growing high-elevation trees than in fast-growing low-elevation trees, which produce a greater sapwood area. Trees may become relatively insensitive to climate as they age and reach a size-related functional threshold linked to reduced sapwood production.

Key-words: altitude, basal area increment, dendrochronology, *Pinus uncinata*, plant population and community dynamics, Pyrenees, structural equation models, tree ageing

Introduction

Air temperatures during the late 20th century were higher than during any other period of the last 500 years and are likely to be the highest of the past 1000 years (Jones *et al.* 2009). In the European mountains, Diaz & Bradley (1997) reported a warming trend since the 1950s leading to some of the warmest decades of the instrumental records in the last half of the past century. The length of the growing season has also potentially increased in mountain forests of temperate and cold areas where tree growth is mainly constrained by low temperatures (Menzel & Fabian 1999; Tardif *et al.* 2003; Wieser *et al.* 2009). In these areas, regional climate models predict temperature increases by 1.4–5.8 °C during the 21st century (IPCC 2007).

However, in a warmer scenario, tree growth in mountain forests may also be affected by additional site and tree factors. In addition, potential trade-offs or relationships at the tree level between several features such as radial growth rate, leaf and sapwood production and life span can explain their different individual growth responses (Loehle 1988).

Global warming and related changes such as rising atmospheric CO₂ concentrations are affecting tree growth (Soulé & Knapp 2006). Rates of radial growth are reported to have recently increased over broad areas of mountain conifer forests in Europe and North America (Graumlich 1991; Boisvenue & Running 2006). Despite these observations, other studies have suggested that warming may not consistently lead to increased growth in cold-limited forests (Lloyd & Fastie 2002; Harsch *et al.* 2009). Others have noted a recent site-dependent loss in growth responsiveness to the temperature rise (Briffa *et al.*

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1998). Such contrasting growth patterns also appear among nearby forests and coexisting trees and thus challenge our understanding of tree growth responses to climate warming (Wilmking *et al.* 2004). These diverse findings demand a much better understanding of the interactions between site conditions and tree characteristics at regional and local scales to disentangle how these features may modulate the individual growth responses to climate warming.

At the site level, altitude and other local conditions have been shown to control recent growth trends in mountain conifer forests (Tardif *et al.* 2003; Carrer *et al.* 2007; Littell, Peterson & Tjoelker 2008). Hence, mountain forests are characterized by a high spatial variability among sites and trees in their responsiveness to climate (Bunn, Waggoner & Graumlich 2005). A critical evaluation of such variability may help to disentangle the roles of local conditions such as elevation and topography (e.g. aspect) in mediating recent growth trends.

At the tree level, studies performed across altitudinal gradients have shown that growth depends on changes in sapwood area (Vertessy *et al.* 1995). Sapwood area and basal area increment (BAI) are tightly related in conifers (Sellin 1994; Knapic & Pereira 2005), and the former is closely linked to the growth efficiency of trees in terms of wood produced by needle area (Waring 1987). In *Pinus ponderosa* forests, size-related growth constraints explained the decline in growth efficiency which translated into a reduction of sapwood area (McDowell *et al.* 2007). The role of sapwood as a growth driver may depend on age-dependent changes in the stem hydraulic conductivity (Spicer & Gartner 2001). Consequently, sapwood area might modulate the growth responses of mountain conifer forests to recent climate warming.

In the case of Iberian mountain conifer forests, a rise in temperatures accompanied by an increase in climatic variability has driven trees recent growth trends (Camarero 1999; Andreu *et al.* 2007). In fact, the contrasting climatic conditions between the first and the second halves of the 20th century were also reflected in the radial growth patterns of *Pinus uncinata*, the dominant species in Iberian high-elevation forests, which showed an increased temporal variability in growth towards the very warm last half of that century (Tardif *et al.* 2003). Pyrenean *P. uncinata* tree line forests also showed enhanced radial growth during the late 20th century (Camarero & Gutiérrez 2004). Therefore, the Iberian *P. uncinata* subalpine forests offer a valuable system to evaluate whether growth throughout the past century was modulated by local site conditions (e.g. altitude, topography) or by intrinsic tree features (e.g. size, sapwood production). In this study, we aim to evaluate these effects at the site and tree levels for three distinct periods of the 20th century (1901–1947, 1948–1994 and 1901–1994). Previously, Tardif *et al.* (2003) speculated on a possible warming-induced ‘relaxation’ of the altitude-mediated control of tree growth in these forests during the 20th century. Consequently, we hypothesize that tree features, such as size and sapwood production, were the main drivers of tree growth during the 20th century in these high-elevation forests and that altitude played a minor role in constraining tree growth.

Materials and methods

STUDY SPECIES

Pinus uncinata Ram. is a long-lived, slow-growing and shade-intolerant conifer which shows a large ecological amplitude regarding topography (slope, exposure, altitude) and soil type (Ceballos & Ruiz de la Torre 1979). Based on xylogenesis studies, spring cambial resumption in *P. uncinata* starts in May and most of the tree ring (ca. 80% of the annual width) is formed between June and July (Camarero, Guerrero-Campo & Gutiérrez 1998). Radial growth in Pyrenean *P. uncinata* forests is enhanced by warm autumn and spring temperatures in the seasons before and during tree-ring formation, respectively (Tardif *et al.* 2003).

STUDY SITES

We sampled 27 *P. uncinata* sites located across the whole geographical range of the species in the Iberian Peninsula to capture most of the ecological variability experienced by this pine. We sampled 25 sites located in the Pyrenees and two relict populations of the Iberian System located in the Soria and Teruel provinces (Fig. 1, Table 1). Pyrenean forests are usually low-density, high-elevation stands with isolated trees reaching the alpine tree line (Fig. 1). The two relict populations of *P. uncinata* located in the Iberian System constitute the southern and western geographic limits of the species distribution (Ceballos & Ruiz de la Torre 1979).

The macroclimate of the Pyrenees is strongly influenced by east–west and north–south gradients with increasing Mediterranean conditions (e.g. warm and dry summers) eastwards and southwards, whereas continental conditions prevail in the Central Pyrenees (Del Barrio, Creus & Puigdefàbregas 1990). Mean annual temperature and total precipitation in the studied sites ranged from 2.0 to 4.9 °C and from 1200 to 2000 mm, respectively, with the coldest and warmest months being January (mean –2.0 °C) and July (mean 12.5 °C) (Camarero 1999). In the study region, there was a rise in temperature but no significant change in precipitation during the period 1901–1994 (Fig. S1 in Supporting Information).

Most of the Pyrenean sites (eighteen sites) were located within or near protected areas; therefore, these areas are not likely to have been disturbed by logging for much of the 20th century. Six sites were sampled within or near the Ordesa y Monte Perdido National Park (42° 40' N, 00° 03' E; established in 1918), and twelve sites were sampled in the Aigüestortes i Estany de Sant Maurici National Park area (42° 35' N, 00° 57' E; established in 1955) (Fig. 1).

FIELD SAMPLING AND DENDROCHRONOLOGICAL METHODS

From 1994 until 2010, we sampled 642 living trees following standard dendrochronological methods. At each site, from 5 to 65 dominant trees (mean \pm SE = 24 \pm 3 sampled trees per site) were randomly selected for sampling. The number of trees sampled per site depended on the density of trees within each sampled plot. Except for a few cases, distance between trees was sufficient to avoid capturing local effects on tree growth due to spatial autocorrelation. The geographical position of sampled trees was registered with GPS (accuracy \pm 5 m). Topographic (altitude, slope, aspect) and biometric (dbh, diameter at breast height measured at 1.3 m; tree height) variables were registered for each tree. All individuals were cored at 1.3 m using a Pressler increment borer taking two or three cores per tree (n = 1296 cores). We measured the sapwood

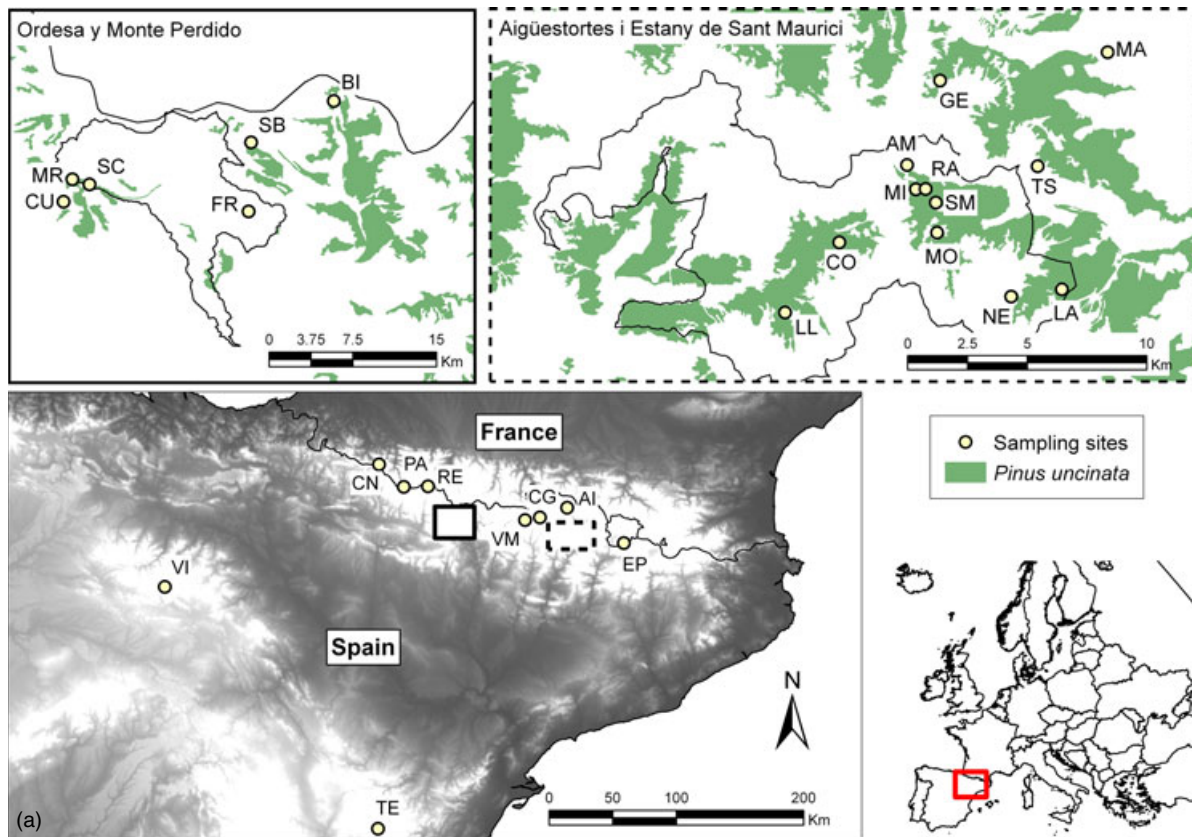


Fig. 1. Sampled *Pinus uncinata* sites in the Iberian Peninsula (a, white indicates high-elevation areas). The area delineated by the solid and dashed lines includes Ordesa y Monte Perdido (upper left map) and Aigüestortes i Estany de Sant Maurici National Parks (upper right map). Shaded areas in upper maps correspond to *P. uncinata* sites. The southernmost sites VI and TE are located in the Iberian System mountains. (b) Views of old *P. uncinata* trees in sites NE and SC (see sites codes in Table 1).

Table 1. Geographical, topographical and ecological characteristics of the sampled *Pinus uncinata* sites. Stands were arranged from east to west. Sites' codes are as in Fig. 1. Age was determined from cores taken at 1.3 m

Site (code)	Latitude (N)	Longitude (E/W)	Elevation (m a.s.l.)	Aspect	Slope (°)	Dbh (cm)	Height (m)	Sapwood (cm)	Age (years)
Estansys de la Pera (EP)	42° 27'	1° 35' E	2360	SW	30 ± 0	65.2 ± 11.0	7.8 ± 2.0	5.5 ± 2.6	339 ± 117
Mata de València (MA)	42° 38'	1° 04' E	2019	N-NW	19 ± 10	43.2 ± 3.6	12.0 ± 3.1	5.2 ± 1.7	237 ± 72
Estany de Lladres (LA)	42° 33'	1° 03' E	2120	NW	35 ± 12	52.1 ± 9.8	8.3 ± 1.6	5.0 ± 1.9	313 ± 123
Airoto (AI)	42° 42'	1° 02' E	2300	W	47 ± 29	58.5 ± 13.5	7.4 ± 1.6	6.7 ± 2.1	288 ± 100
Tessó de Son (TS)	42° 35'	1° 02' E	2239	N-NE	42 ± 14	74.5 ± 18.8	9.3 ± 3.8	7.4 ± 4.1	346 ± 202
Estany Negre (NE)	42° 33'	1° 02' E	2451	SE	35 ± 18	71.0 ± 26.0	6.6 ± 1.9	4.4 ± 1.9	411 ± 182
Estany Gerber (GE)	42° 37'	0° 59' E	2268	W	15 ± 15	53.5 ± 14.6	6.9 ± 1.4	4.8 ± 2.2	426 ± 147
Estany d'Amitges (AM)	42° 35'	0° 59' E	2390	S-E	40 ± 21	69.0 ± 26.0	9.3 ± 3.8	5.7 ± 2.2	355 ± 106
Mirador (MI)	42° 35'	0° 59' E	2180	SE	33 ± 18	55.1 ± 25.8	7.6 ± 2.3	4.6 ± 2.0	401 ± 132
Ratera (RA)	42° 35'	0° 59' E	2170	N	40 ± 5	28.3 ± 8.1	10.4 ± 2.0	–	380 ± 146
Sant Maurici (SM)	42° 35'	0° 59' E	1933	S-SE	16 ± 15	38.2 ± 5.7	13.7 ± 1.7	4.2 ± 1.2	204 ± 23
Monestero (MO)	42° 34'	0° 59' E	2280	SE	28 ± 13	64.4 ± 16.1	9.3 ± 2.1	5.0 ± 2.4	346 ± 110
Corticelles (CO)	42° 34'	0° 56' E	2269	W-NW	24 ± 17	83.1 ± 28.8	10.7 ± 3.8	4.9 ± 2.7	509 ± 177
Barranc de Llaçs (LL)	42° 32'	0° 55' E	2250	N-NW	44 ± 38	71.7 ± 20.0	10.5 ± 2.5	5.0 ± 2.5	616 ± 175
Conangles (CG)	42° 37'	0° 44' E	2106	S-SW	43 ± 15	56.0 ± 14.5	6.4 ± 2.7	4.7 ± 2.8	318 ± 117
Vall de Mulleres (VM)	42° 37'	0° 43' E	1800	N-NE	34 ± 13	69.0 ± 26.0	9.8 ± 1.8	5.2 ± 2.6	437 ± 184
Bielsa (BI)	42° 42'	0° 11' E	2000	E	88 ± 4	45.1 ± 9.4	7.7 ± 3.0	4.7 ± 1.5	270 ± 67
Sobrestivo (SB)	42° 40'	0° 06' E	2296	S	38 ± 2	61.7 ± 17.5	7.6 ± 1.7	4.1 ± 1.7	341 ± 97
Foratarruego (FR)	42° 37'	0° 06' E	2031	W	37 ± 11	49.5 ± 18.3	8.3 ± 2.9	5.5 ± 1.9	433 ± 50
Senda de Cazadores (SC)	42° 38'	0° 03' W	2247	N	49 ± 12	60.9 ± 16.5	9.4 ± 1.6	4.3 ± 2.0	337 ± 145
Mirador del Rey (MR)	42° 38'	0° 04' W	1980	SW	25 ± 10	53.3 ± 15.3	10.9 ± 4.6	–	117 ± 18
Las Cutas (CU)	42° 37'	0° 05' W	2150	S-SW	20 ± 5	33.3 ± 8.3	9.9 ± 2.5	4.4 ± 2.8	129 ± 16
Respomuso (RE)	42° 49'	0° 17' W	2350	S	70 ± 19	49.5 ± 15.1	7.6 ± 1.5	6.1 ± 4.1	280 ± 83
Pic d'Arnousse (PA)	42° 48'	0° 31' W	1940	NW	32 ± 4	65.4 ± 5.1	9.4 ± 0.7	9.0 ± 4.6	248 ± 83
Valdelinares-Teruel (TE)	40° 23'	0° 38' W	1800	SW-W	10 ± 5	63.8 ± 12.4	10.2 ± 1.8	5.8 ± 4.9	214 ± 107
Larra-La Contienda (CN)	42° 57'	0° 46' W	1750	SW	38 ± 24	46.4 ± 14.0	7.8 ± 2.2	3.8 ± 1.3	350 ± 108
Castillo de Vinuesa (VI)	42° 00'	2° 44' W	2050	W	21 ± 1	85.6 ± 23.0	9.4 ± 2.9	6.7 ± 2.4	368 ± 148

Values are means ± SD.

length in the field, because the sapwood-heartwood was usually evident. In some selected cores from trees of contrasting dbh and age ($n = 140$), we checked these visual field estimates by applying bromocresol green stain on recently collected cores in the laboratory (Kutscha & Sachs 1962). Field and laboratory estimates of sapwood length were significantly related ($R^2 = 0.81$, $P < 0.001$). The diameter, excluding bark, and the sapwood length were converted to basal area and sapwood area, respectively, assuming a circular shape of the stem.

Each core was mounted and sanded with sandpapers of progressively finer grain until tree rings were clearly visible (Stokes & Smiley 1968). Then, the samples were visually cross-dated and measured to a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating was evaluated using the program COFECHA, which calculates cross correlations between individual series of each core and a master chronology, obtained averaging all measured series in each site (Holmes 1983).

Tree-width series were converted to BAI considering two radii per tree (inside bark) and assuming concentric circularity. BAI removes variation in growth attributable to increasing stem circumference and captures changes in growth better than linear measures such as tree-ring width (Biondi & Qeadan 2008). BAI series for dominant healthy trees usually show an early suppression phase before a rapid increase and a stable senescent phase (Duchesne, Ouimet & Morneau 2003). In the case of declining radial growth trees, BAI may show a long-term decrease before tree death (Jump, Hunt & Peñuelas 2006). Sharp

BAI reductions are also characteristic of stressed or dying trees (Piovesan *et al.* 2008). The annual BAI was calculated as follows:

$$\text{BAI} = \pi(r_t^2 - r_{t-1}^2) \quad \text{eqn 1}$$

where r_t and r_{t-1} are the stem radii in the current (year t) and previous (year $t-1$) years. In the cases of cores without pith, the distance to the pith was estimated by fitting a template of concentric circles with known radii to the curve of the innermost rings (Norton, Palmer & Ogden 1987). This allowed the estimation of the missing radius length to transform it into the number of missing rings. Conversion of the radius length into rings was carried out using a subset of cores with pith ($n = 17$ cores), and considering the innermost 40 rings, by using a regression calculating the mean number of rings (y) for the estimated distance to the pith (x): $y = 0.0109x$ ($R^2 = 0.99$, $P < 0.001$). In those trees in which the central core section could not be estimated because the innermost rings did not curve ($n = 250$ trees), we used the dbh of each tree to estimate the tree radius (r) inside bark using this formula:

$$r = [(dbh - (b_1 + b_2)]/2 \quad \text{eqn 2}$$

where b_1 and b_2 are the widths of the bark measured in two opposite sides of the stem in the field in a subset of trees ($n = 131$). We also estimated tree age at 1.3 m for each tree based on the calculated number of missing rings and considering the core reaching the maximum number of rings for each tree. Finally, we calculated

the BAI of each core, and then, we obtained BAI averages for each tree and site. Throughout the study, we considered and compared the BAI data for three different periods to assess temporal changes. We considered mean BAI annual values (in cm^2) for the period encompassing most of the 20th century (1901–1994) or for two sub-periods of equal span including most of the first (1901–1947) and second (1948–1994) halves of the past century. We also calculated BAI trends ($\text{cm}^2 \text{year}^{-1}$) based on the slopes of linear regressions between time and BAI.

Then, we examined the correlations between potential predictor variables, BAI and BAI trends, by calculating Pearson correlation coefficients between them at the site ($n = 27$) and tree ($n = 642$) levels. To summarize the relationships among topographic (altitude, aspect, slope), tree (basal area, height, tree age, sapwood area) and growth variables (BAI averages and trends for the three periods described before), we performed a Principal Component Analysis (PCA). The PCA was performed on standardized variables, and it was based on the correlation matrix among variables to avoid problems arising from different units and variances. The common within-site variability in BAI was quantified as the percentage of variance explained by the first principal component. Statistical analyses were carried out using the R package (R Development Core Team 2011).

THEORETICAL MODEL OF TREE GROWTH FOR MOUNTAIN COLD-CONSTRAINED FORESTS

We built a theoretical and conceptual model of tree growth based on the effects of decreasing air temperature with increasing altitude negatively affecting radial growth (Fig. 2). Such negative effects are exerted through a shortening of the growing season and a reduced rate of cambial division in cold high-elevation sites (Fritts 1976; Rossi *et al.* 2007). Less growth, and thus reduced BAI, and decreased sapwood production are also expected as altitude increases, because stem growth is closely linked to sapwood area (Vertessy *et al.* 1995). Tree growth and size (basal area, height) will also be comparatively lower in high-elevation stands (Yokozawa & Hara 1995; Petit *et al.* 2010). Several studies have also revealed that sapwood and basal area covary following allometric functions in conifers and that sapwood area is closely linked to the total cross-sectional area of living branches and to total needle area (Sellin 1994; Longuetaud *et al.* 2006), despite some studies showing that growth does not only depend on the sapwood amount (Yang & Murchison 1992). In addition, BAI and sapwood area decrease as trees age (Spicer & Gartner 2001). Furthermore, the negative relationship between tree life span and growth efficiency reported for several species may also explain

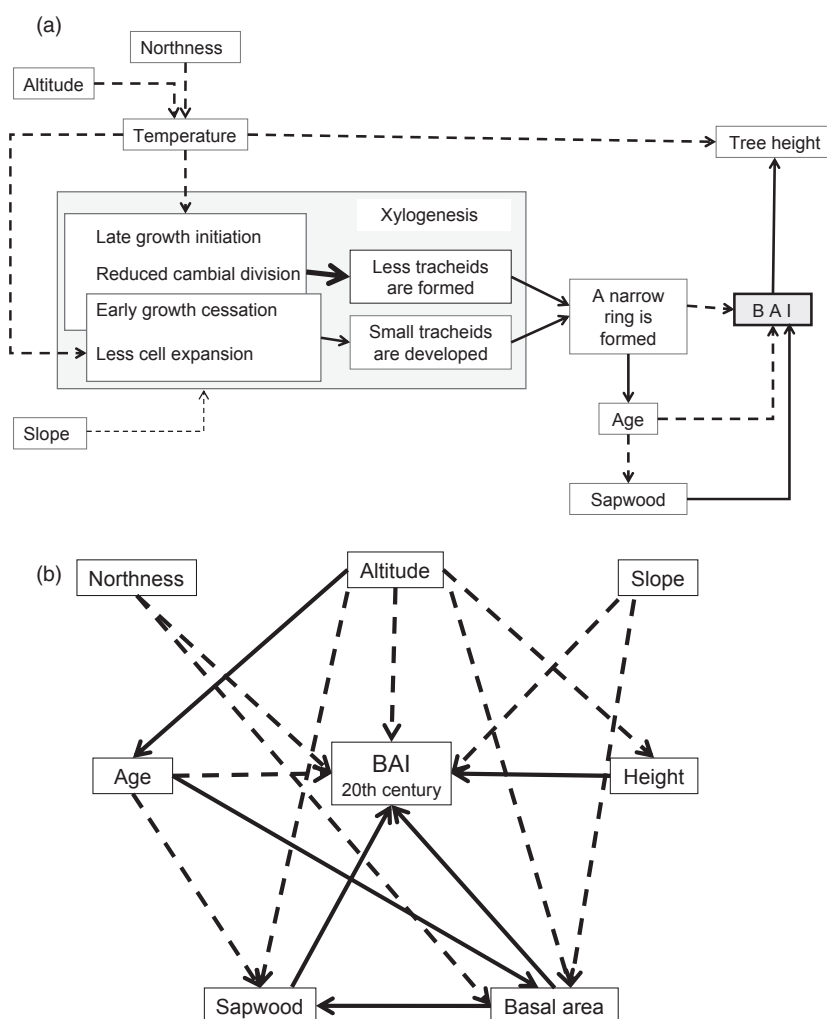


Fig. 2. Proposed (a) theoretical model of basal area increment based on hypotheses and relationships among altitude, temperature and growth and (b) conceptual model derived from it and adjusted according to previous knowledge of environment–growth relationships in *Pinus uncinata*. Positive and negative effects are indicated by solid and dashed lines, respectively.

this age-related growth decline (Martínez-Vilalta, Vanderklein & Mencuccini 2007; Black, Colbert & Pederson 2008). Finally, we also expect a positive association between radial and height growth and hypothesize that BAI will increase as tree height augments for trees with similar age (Ryan, Binkley & Fownes 1997).

We also assumed that topographical variables (aspect, slope) may also affect BAI and postulate that trees will grow less in northern-oriented sites with steep slopes than in southern-oriented sites with gentle slopes. Furthermore, in previous studies, we found that mean tree age in *P. uncinata* stands usually increases with altitude (Camarero & Gutiérrez 1999). This positive altitude-age association may be due to a low growth rate and extended life span in these environmentally harsh sites (Bigler & Veblen 2009). Hence, we also speculate that growth will also be negatively affected by the increased longevity of trees at high altitudes as compared with those at low altitudes (Rossi et al. 2008).

STRUCTURAL EQUATION MODELS

Structural Equation Models (SEM) were calculated using the program EQS (Bentler & Wu 2002) and used as multivariate tools to statistically evaluate the postulated theoretical model of tree growth, that is, to determine the main factors potentially driving changes in BAI during the twentieth century for the three periods analysed (1901–1994, 1901–1947 and 1948–1994). First, we specified a theoretical model based on *a priori* assumed relationships among variables (Fig. 2) and on the previous knowledge and published works on

growth of mountain conifer species (see the previous section). Secondly, we tested whether the variance–covariance matrix obtained from observational data significantly differed from the matrix imposed by the hypothetical model (Grace 2006). SEMs are able to deal with the interdependence of variables and to decompose total effects in direct and indirect types, and they allow comparison of alternative models using indices of goodness of fit (Mitchell 1992). To estimate the standardized path coefficients, which quantify the strength of the associations among variables, we used a robust Maximum Likelihood method because all variables excepting BAI deviated from normality even after log-transformation (Bentler & Wu 2002).

The use of several indices to evaluate the model fitness provides a robust assessment of the fitted SEM (Jöreskog 1993). Hence, the models were evaluated using the chi-square (χ^2) test and its related probability level (*P*), as well as several complementary goodness-of-fit indices (AGFI, Adjusted Goodness-of-Fit Index; RMSEA, Root Mean Square Error of Approximation; AIC, the Akaike Information Criterion). Values close to zero for the χ^2 and RMSEA statistics and values close to one of the AGFI index would indicate that the evaluated models are consistent with the theoretical ones. Lower AIC values correspond to more parsimonious models. In relative terms, models with low AIC and high *P* values associated with χ^2 correspond to better fits than models with the reverse characteristics. In contrast to traditional significance testing, it is usually preferable to obtain non-significant χ^2 values which indicate that the predicted model is congruent with

Table 2. Basal area increment values and trends at the tree level for three selected periods of the 20th century

Site	No. trees/radii	Basal area increment (cm ²)			Trends in basal area increment (cm ² year ⁻¹)		
		1901–1994	1901–1947	1948–1994	1901–1994	1901–1947	1948–1994
EP	20/39	13.4 ± 7.8	12.2 ± 7.6	14.5 ± 8.4	0.04 ± 0.07	−0.03 ± 0.10	0.02 ± 0.11
MA	10/20	7.6 ± 2.1	7.4 ± 1.9	7.8 ± 3.3	−0.01 ± 0.06	−0.01 ± 0.10	−0.13 ± 0.13
LA	36/74	10.3 ± 5.5	10.2 ± 6.2	10.4 ± 5.4	−0.02 ± 0.08	−0.01 ± 0.13	−0.12 ± 0.19
AI	16/31	21.5 ± 10.3	19.7 ± 9.7	23.3 ± 11.6	0.06 ± 0.11	0.16 ± 0.17	−0.11 ± 0.19
TS	10/17	13.7 ± 11.2	13.8 ± 10.7	13.6 ± 12.5	−0.02 ± 0.11	−0.03 ± 0.19	−0.12 ± 0.15
NE	46/86	10.3 ± 7.5	9.8 ± 7.8	10.7 ± 7.5	0.01 ± 0.09	0.05 ± 0.14	−0.07 ± 0.24
GE	41/79	7.0 ± 4.1	6.5 ± 4.5	7.4 ± 3.9	0.01 ± 0.05	0.03 ± 0.08	−0.02 ± 0.09
AM	25/56	10.7 ± 7.0	10.4 ± 7.3	11.1 ± 6.8	0.01 ± 0.06	0.02 ± 0.11	−0.06 ± 0.15
MI	33/85	8.2 ± 7.0	8.4 ± 7.1	8.0 ± 7.1	−0.01 ± 0.05	0.02 ± 0.07	−0.06 ± 0.10
RA	5/13	6.3 ± 3.1	7.2 ± 4.5	5.4 ± 2.7	−0.05 ± 0.07	−0.06 ± 0.14	−0.07 ± 0.06
SM	20/40	5.9 ± 2.7	6.8 ± 3.2	5.0 ± 2.4	−0.04 ± 0.03	−0.06 ± 0.05	−0.05 ± 0.08
MO	30/76	16.1 ± 9.9	16.2 ± 9.8	16.0 ± 10.6	−0.01 ± 0.10	0.04 ± 0.19	−0.08 ± 0.25
CO	25/43	11.1 ± 7.6	10.8 ± 6.9	11.4 ± 8.8	0.01 ± 0.07	−0.01 ± 0.08	−0.04 ± 0.12
LL	17/17	11.1 ± 7.8	10.9 ± 8.0	11.5 ± 8.1	0.01 ± 0.08	0.03 ± 0.15	−0.11 ± 0.20
CG	25/54	12.1 ± 7.5	10.5 ± 6.7	13.7 ± 8.9	0.06 ± 0.10	0.02 ± 0.18	0.05 ± 0.21
VM	12/23	11.6 ± 9.9	11.6 ± 10.1	11.7 ± 10.0	−0.01 ± 0.05	−0.02 ± 0.07	−0.06 ± 0.13
BI	11/20	7.3 ± 4.2	6.9 ± 4.2	7.5 ± 4.4	0.01 ± 0.04	−0.05 ± 0.12	−0.02 ± 0.07
SB	53/95	11.1 ± 7.4	12.2 ± 9.5	10.0 ± 6.0	−0.05 ± 0.11	−0.02 ± 0.16	−0.10 ± 0.12
FR*	12/25	—	5.5 ± 2.4	—	—	−0.06 ± 0.08	—
SC	65/119	10.0 ± 5.7	10.4 ± 5.9	9.6 ± 5.8	−0.03 ± 0.06	−0.03 ± 0.16	−0.09 ± 0.12
MR	17/34	3.8 ± 2.3	2.2 ± 1.2	5.3 ± 3.8	0.06 ± 0.06	0.03 ± 0.04	0.05 ± 0.11
CU	10/20	10.2 ± 3.5	6.4 ± 2.9	13.2 ± 4.8	0.15 ± 0.09	0.19 ± 0.08	0.04 ± 0.13
RE	20/47	8.9 ± 5.1	8.4 ± 4.9	9.4 ± 5.4	0.01 ± 0.03	−0.02 ± 0.06	0.01 ± 0.08
PA	8/16	14.4 ± 6.4	13.2 ± 6.3	15.1 ± 7.0	0.06 ± 0.14	0.04 ± 0.40	0.19 ± 0.14
TE	35/68	14.3 ± 6.5	11.5 ± 5.6	15.8 ± 8.1	0.05 ± 0.11	0.19 ± 0.46	−0.11 ± 0.21
CN	25/57	5.7 ± 2.4	5.5 ± 2.6	5.6 ± 2.7	0.01 ± 0.04	−0.02 ± 0.05	0.08 ± 0.08
VI	24/42	11.7 ± 5.2	11.4 ± 5.3	12.0 ± 5.5	0.01 ± 0.07	−0.06 ± 0.14	0.02 ± 0.18

Values are means ± SD.

*Site FR had only three living trees covering the period 1901–1994 and it was excluded in further analyses.

the observed data. We also displayed the proportion of observed variance of dependent variables (R^2) and the measurement errors of tree variables.

Results

BAI PATTERNS AND TRENDS AT THE SITE AND TREE LEVELS

All sampled living trees with BAI data were established before the 20th century, with maximum ages reaching 741 years in site GE. Considering the two sub-periods of the 20th century, the mean BAI per tree for the period 1948–1994 (mean \pm SE: 10.7 ± 0.4 cm²) was significantly higher ($F = 4.56$, $P = 0.03$) than the mean value for the period 1901–1947 (10.0 ± 0.3 cm²) (Table 2). However, the BAI trends of both sub-periods showed the reverse pattern and differed among periods being significantly ($F = 39.2$, $P < 0.001$) lower in 1948–1994

(mean \pm SE: -0.05 ± 0.01 cm² year⁻¹) than in 1901–1947 (0.02 ± 0.01 cm² year⁻¹) (Table 2).

At the site level, three sites showed positive and significant ($P < 0.05$) BAI trends in the 1901–1947 sub-period and one site in the 1948–1994 sub-period, and most sites (38%) showed negative BAI trends in both analysed sub-periods. Approximately 32% of sites showed positive BAI trends followed by negative ones for the 1901–1947 and 1948–1994 sub-periods, respectively, whereas 15% of sites showed the reverse pattern and the remaining 15% of sites showed positive trends for these sub-periods. At the tree level, 28% of the individuals presented negative BAI trends in the 1901–1947 and 1948–1994 sub-periods, whereas 36% showed positive and negative BAI trends in these sub-periods, in that order. At the individual level, 11% of all trends were negative and significant in the 1901–1947 sub-period and 22% in the 1948–1994 sub-period, while 12% and 8% were positive and significant for the

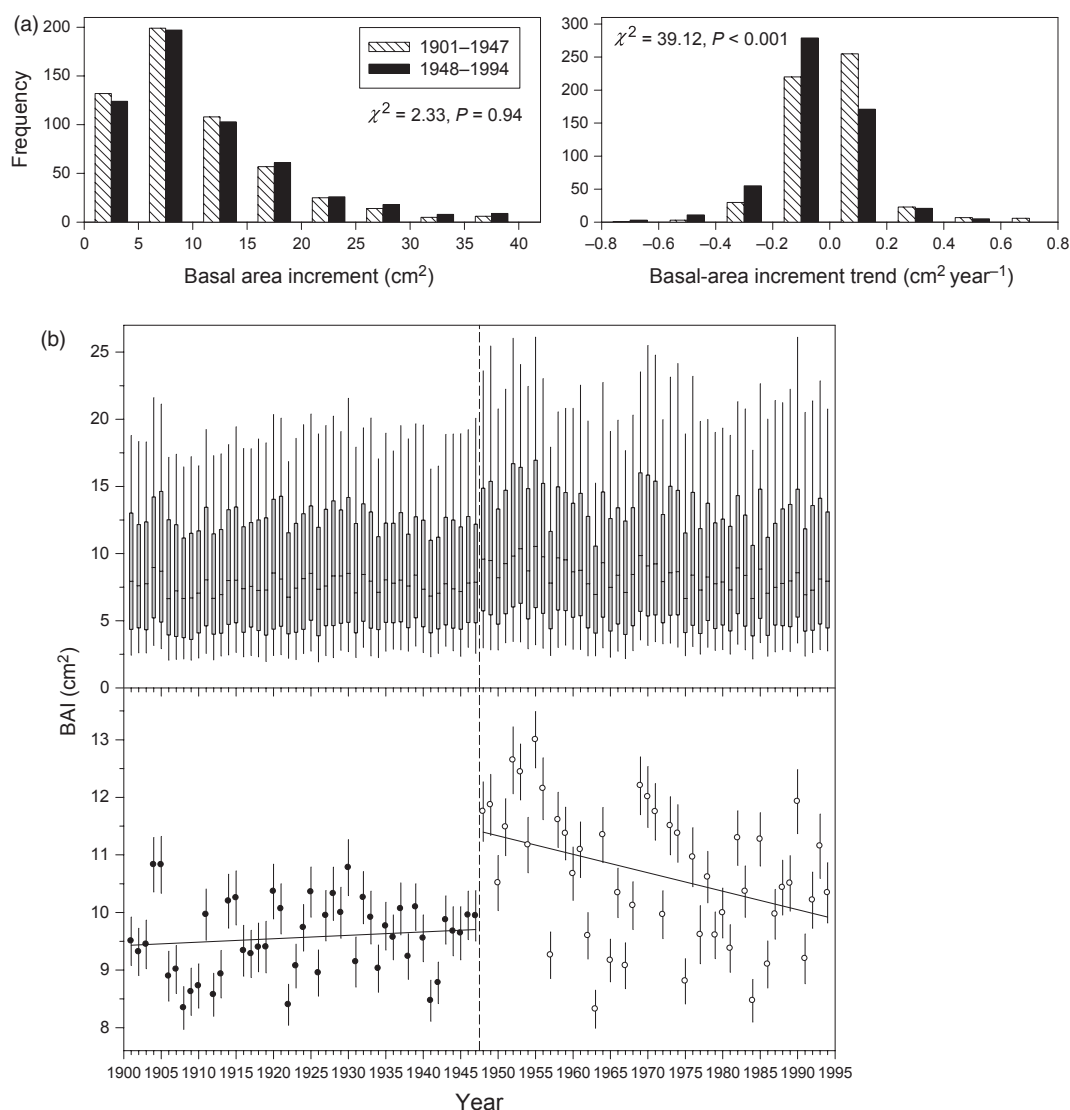


Fig. 3. Comparisons and related statistics (χ^2 , P) between the frequency of basal area increment (BAI) and its linear trends for the sub-periods 1901–1947 and 1948–1994 ($n = 642$ trees) (a) and temporal changes in BAI during the study period (1901–1994, box plots of annual BAI values) and the two sub-periods (lower graphs, mean annual BAI values and corresponding linear trends) (b).

aforementioned intervals. Lastly, 18% of trees presented negative trends followed by positive ones and 18% of trees showed positive trends throughout the 20th century.

The distribution of BAI values at the tree level did not differ among sub-periods but their trends were mostly higher in 1901–1947, when 53% of trees had positive BAI trends, than in 1948–1994 when only 36% of trees presented positive BAI trends (Fig. 3a). Only in one tree line site with relatively young trees (site CU), did we find a trend towards showing more positive BAI values in the later half compared with the early half 20th century, whereas in seven sites, the distributions of BAI trends differed between both sub-periods (Fig. S2 in Supporting Information). The BAI values of the two studied sub-periods were significant and positively related at the tree level ($r = 0.85$, $P < 0.001$), whereas the BAI trends were inversely related ($r = -0.28$, $P < 0.001$) (Fig. S3 in Supporting Information).

We found that the variability of BAI at the site level, assessed as the mean percentage of variance accounted for by the first principal component (PC1) of BAI of trees living

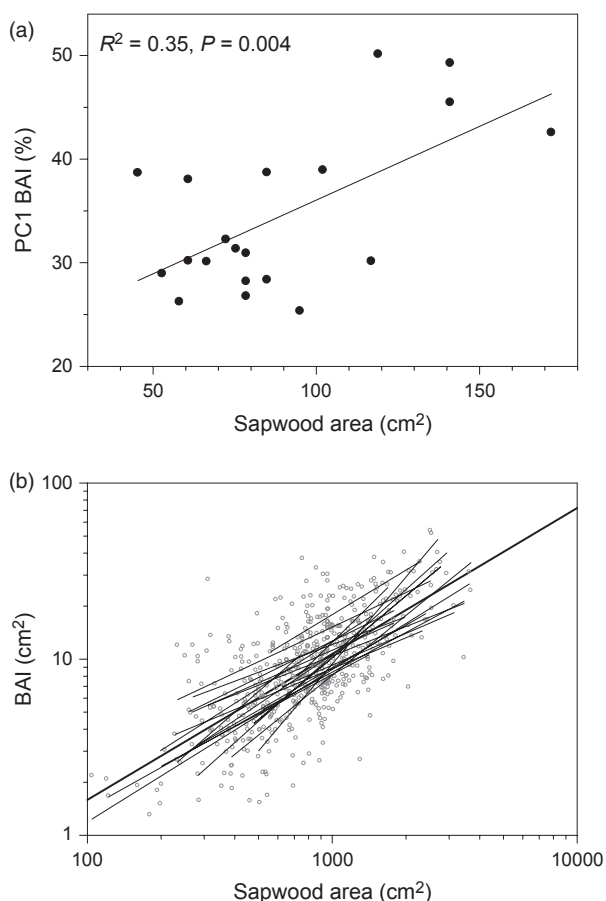


Fig. 4. Sapwood is the main driver of variability in basal area increment (BAI) among (a) and within sites (b), that is, among trees. The common within-site BAI variability was quantified as the percentage of variance accounted for by the first principal component (PC1, upper graph). The lowermost graph shows all individual tree values (symbols), the linear regression for all trees (thick line) and the site regressions (thin lines). Note the log–log scale in the lowermost graph.

within each site, has significantly (Mann–Whitney $U = 120.0$, $P = 0.012$) increased in 1948–1994 (mean 42%) compared with 1901–1947 (mean 36%), and such an increase was observed in 81% of all sites (Table S1 in Supporting Information). Exceptions to such rising trend were observed in sites dominated by relatively young trees (e.g. site MR), the two southernmost sites located in the Iberian System mountains (sites TE and VI) and two Pyrenean sites (sites BI and RE) (Table S1 in Supporting Information). Furthermore, this common BAI variability was positively related with sapwood area at the site level (Fig. 4a). Such positive association between sapwood area and BAI was also observed at the tree level for all sites (Fig. 4b).

DRIVERS OF BAI AT THE SITE AND TREE LEVELS

At the site level, BAI was positively related to sapwood and basal areas, while altitude affected negatively and significantly BAI trends in the period 1948–1994 (Table S2 in Supporting Information). No variable satisfactorily explained the different BAI trends among sites (results not shown). At the tree level, BAI for any period was strongly and positively related to sapwood and basal area and tree height, whereas age had a significant negative effect on BAI only in 1948–1994 (Table S2 in Supporting Information). Contrastingly, age negatively influenced BAI trends in the period 1901–1947, while sapwood area exerted a positive influence on BAI trends in the same period. The linear regressions fitted to BAI–sapwood area relationships for both sub-periods presented confidence intervals which did not overlap (1901–1947, mean \pm SD: 0.0088 ± 0.0005 ; 1948–1994, 0.010 ± 0.0005). This indicates that, despite the declining BAI trends of the late 20th century, the BAI increase as a function of sapwood area increment was proportionally higher in 1948–1994 than in 1901–1947 at tree level (Fig. S4 in Supporting Information). The first and second principal components of the PCA explained 30.3% and 14.9% of the total variability among trees, and they were mainly related to changes in BAI, basal and sapwood areas (PC1) and to BAI trends (PC2), respectively. Hence, the PCA confirmed the positive links between BAI and the basal and sapwood areas.

STRUCTURAL EQUATION MODELS OF BAI

The accepted SEMs show that BAI was predominantly positively related to the sapwood area and, to a minor extent, negatively influenced by age, whereas the associations of BAI with altitude and height were weak (Fig. 5). Sapwood area was mainly controlled by changes in basal area and, secondarily, in a negative way, by tree age. Basal area was mainly driven by tree age. The accepted SEMs for the two sub-periods also showed satisfactory goodness-of-fit indices, as did the model for the 1901–1994 period (1901–1947, $\chi^2 = 4.05$, $P = 0.26$, AGFI = 0.98, AIC = 40.05, RMSEA = 0.02; 1948–1994, $\chi^2 = 3.46$, $P = 0.33$, AGFI = 0.99, AIC = 39.46, RMSEA = 0.02). The percentage of BAI variability explained increased from 40% in 1901–1947 to 47% in 1948–1994

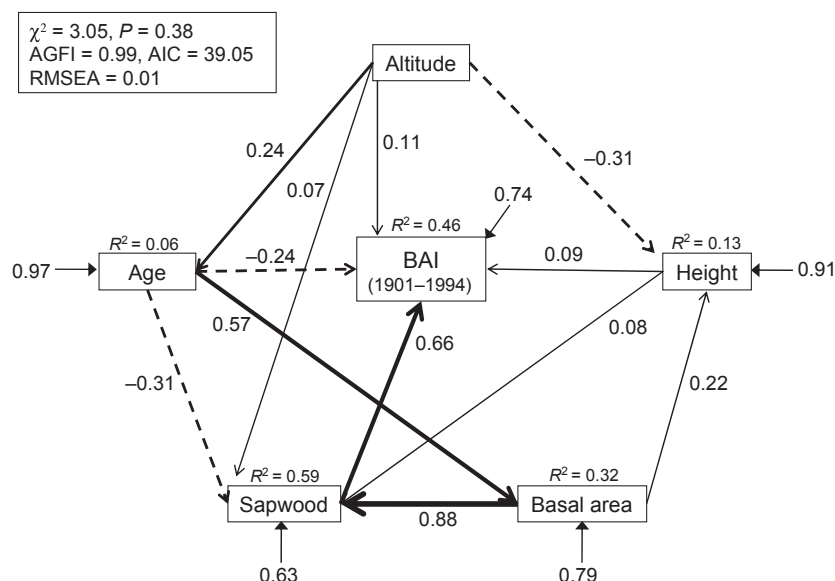


Fig. 5. Selected structural equation model of basal area increment as a function of several variables at the tree level and for the period 1901–1994. Goodness-of-fit statistics appear in the upper part. A non-significant ($P > 0.05$) χ^2 value indicates that the predicted model is congruent with the observed data. Positive and negative effects are indicated by solid and dashed lines, respectively. Arrow widths are proportional to the absolute value of standardized path coefficients (numbers located near arrows) which measure how strongly a variable affects another one. Only significant ($P < 0.05$) coefficients are displayed. The observed variances of dependent variables (R^2) explained by the model are also presented. The numbers located near the tree variables (age, height, sapwood area, basal area) are the measurement errors.

Table 3. Standardized path coefficients affecting basal area increment (BAI) for the structural equation models fitted to the sub-periods 1901–1947 and 1948–1994 (see also Fig. 5). The amount of explained variance (R^2) of BAI is presented in the lowermost line

Variables	Period	
	1901–1947	1948–1994
Sapwood area	0.59	0.68
Height	0.15	0.04
Altitude	0.14	0.09
Age	-0.18	-0.27
R^2 (%)	0.40	0.47

All coefficients were significant ($P < 0.05$).

because the positive influence of sapwood area on BAI was higher in the second than in the first analysed sub-periods, whereas the negative effect of age on BAI also became more important (Table 3).

Discussion

Sapwood area was the main driver of recent decelerating growth trends in Iberian mountain *P. uncinata* forests. Trees which produced more sapwood area also showed a higher BAI. Furthermore, this association between sapwood and wood production has increased in the last decades of the past century. In Iberian *P. uncinata* forests, BAI increased at higher rates in the first than in the second half of the 20th century, despite mean BAI being higher in the later sub-period. Such deceleration in BAI is not consistent with a widespread warm-

ing-related enhancement of growth during the late 20th century in mountain conifer forests (Graumlich 1991; Boisvenue & Running 2006). The reduction in the growth rates may be caused by the fact that trees reach the senescent phase when BAI stabilizes (Duchesne, Ouimet & Morneau 2003). The inverse relationship between age and growth rate has been widely documented in several tree species (Johnson & Abrams 2009). However, despite declining radial growth rates with age, trunk volume or whole-crown mass augment as trees get older (Sillett *et al.* 2010). The negative effects of tree age on BAI were similar between both analysed sub-periods of the 20th century. This agrees with numerous studies demonstrating how sapwood area decreases as trees age (Hazenberg & Yang 1991; Sellin 1994; Spicer & Gartner 2001). Nevertheless, the negative influence of age on BAI is becoming stronger based on our SEMs. The increasing influence of age on BAI can be mediated by changes in sapwood area, that is, older trees produced proportionately less sapwood area than younger ones in the late 20th century. Because trees whose ages were estimated using cores without pith were at least 30% of all sampled individuals, further research is on course to get better estimations of tree age, which would provide a more robust test of our ideas.

Why is radial growth becoming increasingly linked to sapwood area and tree age than before? The increasing length of the hydraulic pathway as trees age and accumulate biomass may be one of the answers, despite the fact that any potential loss in conductivity may be partially offset by decreased leaf-to-sapwood area ratios (Magnani, Mencuccini & Grace 2000; Zaehle 2005). Indeed, trees with different sapwood areas may also modulate their sapwood hydraulic conductivity and growth rates by keeping relatively stable values of water trans-

port efficiency (Medhurst & Beadle 2002). However, the ageing of conductive structures and the alteration of hydraulic networks of old trees and big stems (Martínez-Vilalta, Vanderkelen & Mencuccini 2007; McCulloh *et al.* 2010), and the harsh climatic conditions imposed by high altitudes may also contribute to explain a sharp decrease in hydraulic conductivity and sapwood production as trees grow and age, thus leading to sapwood-mediated declining growth trends. The harsh environmental conditions in high-elevation forests (low air and soil temperatures, frequent freeze-thaw events, elevated radiation and high wind speed; see Barry 2008) are consistent with the finding that trees tend to be older at higher elevations plausibly because of a reduction in radial growth rates and increased longevity (Bigler & Veblen 2009).

A biophysical explanation of our results may also be found in the fact that as altitude increases, air and stem temperatures decrease, producing an increment in water viscosity and hence in the sap flux resistance (Grace 1983). This, together with the windy conditions in high altitude forests leading to drying effects, may cause an enhanced sapwood area to compensate this hindered sap flux in high altitude forests (Gates 1980; Gutiérrez *et al.* 1991). Therefore, rising temperatures in the sub-period 1948–1994 may have induced a decrease in water viscosity, leading to enhanced sap flux and a reduction in sapwood production leading to slowing down growth rates. Mechanistic approaches based on physiological measures such as long-term estimates of water use efficiency should further test this idea. For instance, the increasing atmospheric CO₂ concentration may stimulate tree growth through enhanced water use efficiency (Körner, Morgan & Norby 2007). However, rising CO₂ does not imply enhanced BAI as has been observed in many sites where regional climatic factors (e.g. rising temperatures) and tree features (e.g. vigour) were the major drivers of growth (Peñuelas, Canadell & Ogaya 2010; Linares & Camarero 2012).

Our findings suggest that any potential warming-induced enhancement of BAI will be mainly driven by sapwood production, which is mediated by tree age and altitude. Because slow-growing high-elevation trees are older than fast-growing low-elevation trees, we expect differential responses along the altitudinal gradient. Both xylogenesis studies and dendrochronological assessments of growth–climate relationships indicate that wood formation and growth responsiveness to climate are age dependent (Carrer & Urbinati 2004; Rossi *et al.* 2008) and modulated by site conditions (Tardif *et al.* 2003). Photosynthetic rates can also decrease as trees age (Yoder *et al.* 1994). Therefore, an increasing size-mediated constraint of xylogenesis, photosynthesis and hydraulic conductivity in old trees, usually located at high altitudes, would cause a more intense reduction of their growth and sapwood production than in low-elevation younger trees. Hence, high-elevation trees with intrinsically low growth rates will produce less sapwood and will live longer than the fast-growing trees that dominate downslope localities. Furthermore, forest density cannot explain this pattern as in the open, high-elevation stands most sampled trees were old and isolated individuals. Thus, we expect a minor effect of tree-to-tree competition on growth

trends of these subalpine forests. Concurrently, in similar *P. ponderosa* forests, size-related growth constraints explained the decline in growth efficiency assessed either as stemwood production per unit basal area or as sapwood area (McDowell *et al.* 2007).

The tight association between BAI and sapwood area suggests that climate, particularly temperature, is the main driver of changes in growth and in sapwood amount in the uppermost tree line (Paulsen, Weber & Körner 2000; Ettinger, Ford & HilleRisLambers 2011). Some studies indicate that climate warming is responsible for an observed growth enhancement of high-elevation trees in the last decades (Wiener *et al.* 2009). Others have projected more pronounced growth reductions for high- than for low-elevation conifer populations in mesic areas (Chen, Welsh & Hamann 2010). Tardif *et al.* (2003) suggested that the rising temperatures of the past century will ‘relax’ the altitude-mediated temperature constraints on growth, which will become more dependent on local factors. Overall, our data suggest that a more realistic projection of future growth and productivity responses of mountain forests to climate warming will be strongly affected by tree features (e.g. sapwood area) and secondarily by local factors (e.g. topography) modulating or buffering the regional effects of climate stress on growth (Case & Peterson 2005).

Our work complements other studies performed across altitudinal gradients in hardwood tree species showing that growth depends on changes in sapwood area (Vertessy *et al.* 1995). In contrast to previous research highlighting the intensity of competition for light as a main driver of tree growth along altitudinal gradients (Coomes & Allen 2007), our mainly low-density stands rule this out as a factor. Finally, our findings indicate that once trees reach a maximum age- or size-related functional threshold linked to a stagnant sapwood production, they will become relatively insensitive to climate variability.

Conclusions

We found that age-related changes in sapwood area were the main drivers of BAI in mountain *P. uncinata* forests. This finding and the temporal instability detected when comparing BAI values along the 20th century confirms that ecological research on climate–growth relationships should always involve detailed information at the individual level. Our results indicate that actively growing trees producing more sapwood area, and probably presenting a low leaf-to-sapwood area ratio, will show the highest growth stimulation in the forecasted warmer climatic conditions in cold mountain conifer forests.

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References

- Andreu, L., Gutiérrez, E., Macías, M., Ribas, M., Bosch, O. & Camarero, J.J. (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Global Change Biology*, **13**, 804–815.
- Barry, R.G. (2008) *Mountain Weather and Climate*. Cambridge University Press, Cambridge, UK.
- Bentler, P.M. & Wu, E.J.C. (2002) *EQS 6 for Windows User's Guide*. Multivariate Software Inc., Encino, CA, USA.
- Bigler, C. & Veblen, T.T. (2009) Increased early growth rates decrease longevity of conifers in subalpine forests. *Oikos*, **118**, 1130–1138.
- Biondi, F. & Qeadan, F. (2008) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, **64**, 81–96.
- Black, B.A., Colbert, J.J. & Pederson, N. (2008) Relationships between radial growth rates and lifespan within North American tree species. *Ecoscience*, **15**, 349–357.
- Boisvenue, C. & Running, S.W. (2006) Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology*, **12**, 862–882.
- Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G. & Vaganov, E.A. (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, **391**, 678–682.
- Bunn, A.G., Waggoner, L.A. & Graumlich, L.J. (2005) Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA. *Global Ecology and Biogeography*, **14**, 103–114.
- Camarero, J.J. (1999) Dinámica del límite altitudinal del bosque en los Pirineos y su relación con el cambio climático. PhD Thesis, Universitat de Barcelona, Barcelona.
- Camarero, J.J., Guerrero-Campo, J. & Gutiérrez, E. (1998) Tree-ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the Central Spanish Pyrenees. *Arctic and Alpine Research*, **30**, 1–10.
- Camarero, J.J. & Gutiérrez, E. (1999) Structure and recent recruitment at alpine forest-pasture ecotones in the Spanish Central Pyrenees. *Écoscience*, **6**, 451–464.
- Camarero, J.J. & Gutiérrez, E. (2004) Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change*, **63**, 181–200.
- Carrer, M. & Urbinati, C. (2004) Age-dependent tree ring growth responses to climate of *Larix decidua* and *Pinus cembra* in the Italian Alps. *Ecology*, **85**, 730–740.
- Carrer, M., Nola, P., Edouard, J.L., Motta, R. & Urbinati, C. (2007) Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. *Journal of Ecology*, **95**, 1072–1083.
- Case, M.J. & Peterson, D.L. (2005) Fine-scale variability in growth–climate relationships of Douglas-fir, North Cascade Range, Washington. *Canadian Journal of Forest Research*, **35**, 2743–2755.
- Ceballos, L. & Ruiz de la Torre, J. (1979) *Árboles y arbustos de la España Peninsular*. Escuela Técnica Superior de Ingenieros de Montes, Madrid, Spain.
- Chen, P., Welsh, C. & Hamann, A. (2010) Geographic variation in growth response of Douglas-fir to inter-annual climate variability and projected climate change. *Global Change Biology*, **16**, 3374–3385.
- Coomes, D.A. & Allen, R.B. (2005) Effects of size, competition and altitude on tree growth. *Journal of Ecology*, **95**, 1084–1097.
- Del Barrio, G., Creus, J. & Puigdefàbregas, J. (1990) Thermal seasonality of the high mountain belts of the Pyrenees. *Mountain Research and Development*, **10**, 227–233.
- Diaz, H.F. & Bradley, R.S. (1997) Temperature variations during the last century at high elevation. *Climatic Change*, **36**, 254–279.
- Duchesne, L., Ouimet, R. & Morneau, C. (2003) Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research*, **33**, 2074–2080.
- Ettinger, A.K., Ford, K.R. & HilleRisLambers, J. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, **92**, 1323–1331.
- Fritts, H.C. (1976) *Tree Rings and Climate*. Academic Press, London, UK.
- Gates, D.M. (1980) *Biophysical Ecology*. Springer-Verlag, New York, NY.
- Grace, J. (1983) *Plant-Atmosphere Relationships*. Chapman Hall, London, UK.
- Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.
- Graumlich, L.J. (1991) Sub-alpine tree growth, climate, and increasing CO₂ – an assessment of recent growth trends. *Ecology*, **72**, 1–11.
- Gutiérrez, E., Vallejo, V.R., Romañá, J. & Fons, J. (1991) The Subantarctic *Nothofagus* forests of Tierra del Fuego: distribution, structure and production. *Oecologia Aquatica*, **10**, 351–366.
- Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are tree-lines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.
- Hazenber, G. & Yang, K.C. (1991) The relationship of tree age with sapwood and heartwood width in black spruce, *Picea mariana* (Mill) B.S.P. *Holzforschung*, **45**, 317–320.
- Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 68–78.
- IPCC. (2007) *Climate Change 2007*. Cambridge University Press, Cambridge, UK.
- Johnson, S.E. & Abrams, M.D. (2009) Age class, longevity and growth rate relationships. Protracted growth increases in old trees in the eastern United States. *Tree Physiology*, **29**, 1317–1328.
- Jones, P.D., Briffa, K.R., Osborn, T.J., Lough, J.M., van Ommen, T.D., Vinther, B.M. et al. (2009) High-resolution palaeoclimatology of the last millennium: a review of current status and future prospects. *Holocene*, **19**, 3–49.
- Jöreskog, K.G. (1993) Testing Structural Equation Models. *Testing Structural Equation Models* (eds K. Bollen & J.S. Long), pp. 294–316. Sage, Newbury Park.
- Jump, S.A., Hunt, J.M. & Peñuelas, J. (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.
- Knapic, S. & Pereira, H. (2005) Within-tree variation of heartwood and ring width in maritime pinus (*Pinus pinaster* Ait.). *Forest Ecology and Management*, **210**, 81–89.
- Körner, C., Morgan, J. & Norby, R. (2007) CO₂ fertilization: when, where, how much? Terrestrial Ecosystems in a Changing World (eds J. Canadell, D.E. Pataki & L. Pitelka), pp. 9–21. Springer-Verlag, Berlin.
- Kutscha, N.P. & Sachs, I.B. (1962) Color Tests for Differentiating Heartwood and Sapwood in Certain Softwood Tree Species. USDA Forest Service, Forest Products Laboratory, Madison, WI. Wis. Rep. No. 2246.
- Linares, J.C. & Camarero, J.J. (2012) From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. *Global Change Biology*, **18**, 1000–1015.
- Littell, J.S., Peterson, D.L. & Tjoelker, M. (2008) Douglas-fir growth-climate relationships along biophysical gradients in mountain protected areas of the northwestern U.S. *Ecological Monographs*, **78**, 349–368.
- Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, **52**, 481–509.
- Loehle, C. (1988) Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research*, **18**, 209–222.
- Longuetaud, F., Mothe, F., Leban, J.M. & Mäkelä, A. (2006) *Picea abies* sapwood width: variations within and between trees. *Scandinavian Journal of Forest Research*, **21**, 41–53.
- Magnani, F., Mencuccini, M. & Grace, J. (2000) Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell and Environment*, **23**, 251–263.
- Martínez-Vilalta, J., Vanderklein, D. & Mencuccini, M. (2007) Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia*, **150**, 529–544.
- McCulloh, K., Sperry, J.S., Lachenbruch, B., Meinzer, F.C., Reich, P.B. & Voeelker, S. (2010) Moving water well: comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse-porous saplings from temperate and tropical forests. *New Phytologist*, **186**, 439–450.
- McDowell, N.G., Adams, H.D., Bailey, J.D. & Kolb, T.E. (2007) The role of stand density on growth efficiency, leaf area index, and resin flow in southwestern ponderosa pine forests. *Canadian Journal of Forest Research*, **37**, 343–355.
- Medhurst, J.L. & Beadle, C.L. (2002) Sapwood hydraulic conductivity and leaf area – sapwood area relationships following thinning of a *Eucalyptus nitens* plantation. *Plant, Cell and Environment*, **25**, 1011–1019.
- Menzel, A. & Fabian, P. (1999) Growing season extend in Europe. *Nature*, **397**, 659.
- Mitchell, R.J. (1992) Testing evolutionary and ecological hypotheses using path analysis and structural equation modelling. *Functional Ecology*, **6**, 123–129.
- Norton, D.A., Palmer, J.G. & Ogden, J. (1987) Dendroecological studies in New Zealand I. An evaluation of tree estimates based on increment cores. *New Zealand Journal of Botany*, **25**, 373–383.

- Paulsen, J., Weber, U.M. & Körner, C.H. (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic and Antarctic Alpine Research*, **32**, 14–20.
- Peñuelas, J., Canadell, J. & Ogaya, R. (2010) Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography*, **20**, 597–608.
- Petit, G., Anfodillo, T., Carraro, V., Grani, F. & Carrer, M. (2010) Hydraulic constraints limit height growth in trees at high altitude. *New Phytologist*, **189**, 241–252.
- Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A. & Maugeri, M. (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology*, **14**, 1–17.
- R Development Core Team. (2011) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org>.
- Rossi, S., Deslauriers, A., Anfodillo, T. & Carraro, V. (2007) Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, **152**, 1–12.
- Rossi, S., Deslauriers, A., Anfodillo, T. & Carrer, M. (2008) Age-dependent xylogenesis in timberline conifers. *New Phytologist*, **177**, 199–208.
- Ryan, M.G., Binkley, D. & Fownes, J.H. (1997) Age-related decline in forest productivity: patterns and process. *Advances in Ecological Research*, **27**, 213–262.
- Sellin, A. (1994) Sapwood-heartwood proportion related to tree diameter, age, and growth rate in *Picea abies*. *Canadian Journal of Forest Research*, **24**, 1022–1028.
- Sillett, S.C., Van Pelt, R., Koch, G.W., Ambrose, A.R., Carroll, A.L., Antoine, M.E. & Mifsud, B.M. (2010) Increasing wood production through old age in tall trees. *Forest Ecology and Management*, **259**, 976–994.
- Soulé, P.T. & Knapp, P.A. (2006) Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO₂ fertilization effect? *New Phytologist*, **171**, 379–390.
- Spicer, R. & Gartner, B.L. (2001) The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees, Structure and Function*, **15**, 222–229.
- Stokes, M.A. & Smiley, T.L. (1968) *An Introduction to Tree-ring Dating*. The University of Chicago Press, Chicago, IL.
- Tardif, J., Camarero, J.J., Ribas, M. & Gutiérrez, E. (2003) Spatiotemporal variability in tree growth in the Central Pyrenees: climatic and site influences. *Ecological Monographs*, **73**, 241–257.
- Vertessy, R.A., Benyon, R.G., O'Sullivan, S.K. & Gribben, P.R. (1995) Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, **15**, 559–567.
- Waring, R.H. (1987) Characteristics of trees predisposed to die. *BioScience*, **37**, 569–573.
- Wieser, G., Matyssek, R., Luzian, R., Zwerger, P., Pindur, P., Oberhuber, W. & Gruber, A. (2009) Effects of atmospheric and climate change at the timberline of the Central European Alps. *Annals of Forest Science*, **66**, 402.
- Wilmking, M., Juday, G.P., Barber, V.A. & Zald, H.S.J. (2004) Recent climate warming forces contrasting growth responses of white spruce at tree line in Alaska through temperature thresholds. *Global Change Biology*, **10**, 1724–1736.
- Yang, K.C. & Murchison, H.G. (1992) Sapwood thickness in *Pinus contorta* var. *latifolia*. *Canadian Journal of Forest Research*, **22**, 2004–2006.
- Yoder, B.G., Ryan, M.G., Waring, R.H., Schoettle, A.W. & Kaufmann, M.R. (1994) Evidence of reduced photosynthetic rates in old trees. *Forest Science*, **40**, 513–527.
- Yokozawa, M. & Hara, T. (1995) Foliage profile, size structure and stem diameter-plant height relationships in crowded plant populations. *Annals of Botany*, **76**, 271–285.
- Zaehle, S. (2005) Effect of height on tree hydraulic conductance incompletely compensated by xylem tapering. *Functional Ecology*, **19**, 359–364.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Common within-site variability of basal area increment at the tree level considering three time periods (1901–1994, 1901–1947 and 1948–1994).

Table S2. Pearson correlation coefficients of basal area increment and trends for the three studied periods as related to explanatory variables.

Figure S1. Trends in annual mean temperature and total precipitation in the study area for the period 1901–1994.

Figure S2. Comparisons for all sampled sites and related statistics (χ^2 , P) between the frequency of basal area increment (A) and its linear trends (B) for the sub-periods 1901–1947 and 1948–1994.

Figure S3. Relationships between mean basal area increment and its trend at the tree level for the sub-periods 1901–1947 and 1948–1994.

Figure S4. Associations between basal area increment and sapwood area for the sub-periods 1901–1947 and 1948–1994.

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