

Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy

GIANLUCA PIOVESAN*, FRANCO BIONDI†‡, ALFREDO DI FILIPPO*,
ALFREDO ALESSANDRINI* and MAURIZIO MAUGERIS§

*Dendrology Laboratory, DAF, University of Tuscia, Viterbo, Italy, †DendroLab, Department of Geography, University of Nevada, Reno, NV, USA, ‡School of Earth Sciences, Stanford University, Stanford, CA, USA, §Istituto di Fisica Generale Applicata, Milan, Italy

Abstract

Productivity of old-growth beech forests in the Mediterranean Basin was measured by average stem basal area increment (BAI) of dominant trees at two mountain sites in the Italian Apennines. Both forests could be ascribed to the old-growth stage, but they differed markedly with regard to elevation (1000 vs. 1725 m a.s.l.), soil parent material (volcanic vs. calcareous), mean tree age (less than 200 years vs. 300 years), and stand structure (secondary old-growth vs. primary old-growth forest). Drought at the two sites was quantified by the self-calibrated Palmer Moisture Anomaly Index (Z-index), and by the self-calibrating Palmer Drought Severity Index (PDSI) for summer (June through August) and the growing season (May through September). Dendroclimatological analyses revealed a moisture limitation of beech BAI at interannual (water availability measured by Z-index) and decadal scales (water availability measured by PDSI). Both BAI and water availability increased from 1950 to 1970, and decreased afterwards. Trees were grouped according to their BAI trends in auxological groups (growth-type chronologies), which confirmed that growth of most trees at both sites declined in recent decades, in agreement with increased drought. Because BAI is not expected to decrease without an external forcing, the patterns we uncovered suggest that long-term drought stress has reduced the productivity of beech forests in the central Apennines, in agreement with similar trends identified in other Mediterranean mountains, but opposite to growth trends reported for many forests in central Europe.

Keywords: basal area increment, climate variability, dendrochronology, European beech, growth variation, old-growth forest, Palmer Drought Severity Index, spline trend, tree-ring analysis

Received 12 October 2006; revised version received 10 September 2007 and accepted 8 January 2008

Introduction

Drought, due to increased temperature and/or decreased precipitation, has affected different biomes during recent decades (Dai *et al.*, 2004; Angert *et al.*, 2005). In Europe, severe regional heat waves (e.g. summer, 2003) can considerably reduce primary productivity (Ciais *et al.*, 2005). Evaluating the potential for drought impacts on terrestrial ecosystems under global warming scenarios requires local estimates of growth trends in relation to climatic ones. Among European regions, the Mediterranean Basin could be most affected by climate change linked to global warming in the 21st

century (Schröter *et al.*, 2005). Since the 1970s, drought spells have become more frequent in the Mediterranean Basin (e.g. McCabe & Palecki, 2006), and natural forest productivity in the northern portion of the basin appears to have declined (Boisvenue & Running, 2006). In coming decades, changes in climate and land use are likely to cause water shortages, increased risk of forest fires, northward shifts in the distribution of species, and loss of agricultural products. According to Jump *et al.* (2006), increasing temperature caused growth decline of beech (*Fagus sylvatica* L.) stands located in the Montseny Mountains of Catalonia (northeast Spain) at the lower elevational limit for the species. Because a comparable fall in basal area increment (BAI) was reported for the central Apennines (Italy) by Piovesan *et al.* (2005a), this climate-related decline is not an isolated phenomenon,

Correspondence: Gianluca Piovesan, fax +39 0761 357250, e-mail: piovesan@unitus.it

but may be occurring at the southern edge of this species range elsewhere in Europe. On the other hand, satellite-based observations over the past two decades have identified a 'greening' trend in the northern mid-to-high latitudes (40–70°N), suggesting enhanced plant growth in the Mediterranean region (e.g. Nemani *et al.*, 2003; Xiao & Moody, 2005). To clarify these issues, especially at local scales, it is necessary to obtain additional ground-truth information on forest productivity trends and their forcing factors, both climatic and non-climatic ones, such as changes in land use and management practices.

Besides repeated timber inventories, dendrochronological data are another ground-truth, nondestructive source of information on interannual to interdecadal changes in forest growth (Biondi, 1999). Tree-ring records can effectively be used to understand how forest growth is influenced by environmental changes, including climate, at multiple spatial and temporal scales (Fritts, 1976; Cook & Kairiukstis, 1990). Because the climatic 'sensitivity' of wood growth is usually higher near the edge of a species range, these methods are also particularly well suited to evaluate long-term forest productivity at the low-latitude limit (rear edge) of tree species (Hampe & Petit, 2005). In the Mediterranean Basin, in addition to the above-mentioned studies on beech, dendroecological research on silver fir (*Abies alba*) in the Pyrenees has suggested that the period of moisture stress now extends from the summer into early autumn (Macias *et al.*, 2006).

Old-growth beech forests in the Italian Apennines provide a unique opportunity to explore climate–tree growth relationships in an area of the Mediterranean Basin that is at the southern limit of beech geographical range. Previous research, which was focused on inter-annual growth variations, indicated that beech radial growth in Central Italy is limited by water deficit during the summer (Piovesan *et al.*, 2005b). For this study, we identified two mountain beech forests where human impacts, wildfire, or stand-wide disturbances have not occurred for several decades, and at least since 1950. Our objective was to test if beech growth in the Apennines has decreased because of drought, with emphasis on the relationship between beech BAI and both temperature and precipitation in Central Italy. Measured BAI of dominant trees was used as an indicator of forest productivity, and then compared with climatic indices at both interannual and interdecadal time scales. BAI is much less dependent on changes in tree age/size than ring-width records (Biondi, 1996, 1999; Hogg *et al.*, 2005; Nakawatase & Peterson, 2006). BAI of individual trees is usually the result of complex interactions between climate, topography, stand composition and density, soil quality, tree age, and local

competition (e.g. Sterba *et al.*, 2002; Hein & Dhôte, 2006). Empirical, single-tree models of BAI proposed in the literature have not given much consideration to climatic variability (e.g. Wykoff *et al.*, 1982; Thürig *et al.*, 2005). Recently, BAI predictions in an oak–beech mixed stand were found to be biased, most likely because climate had not been factored in (Hein & Dhôte, 2006).

Long-term basal area growth of individual dominant trees can be represented by sigmoid growth models (Colbert *et al.*, 2004). Dendroecological research has shown that the age/size trend in BAI of dominant, healthy trees should be positive or at least approaching an asymptotic level for many decades (e.g. Rubino & McCharty, 2000; Choi *et al.*, 2001; Poage & Tappeiner, 2002). A decrease in BAI is considered evidence that the tree has entered a declining-senescent phase (Phipps, 1984; Olano & Palmer, 2003; also see Fig. 1 in Duchesne *et al.*, 2003). Moreover, sharp reductions of BAI are characteristic of diseased individuals, as in the case of *Castanea dentata* trees attacked by chestnut blight (McEwan *et al.*, 2006), and steep BAI declines are commonly related to tree mortality (Bigler & Bugmann, 2004). However, little is known on what truly controls tree longevity, particularly with regard to the start of a senescent phase (Martínez-Vilalta *et al.*, 2007), which may also be influenced by biomolecular differences between species (Flanary & Kletetschka, 2005). In conifers, attaining old age is often marked by the transition to 'strip-bark' growth forms, characterized by a band of trunk that remains alive and continues to grow after the rest of the stem has died (e.g. LaMarche, 1969; Matthes *et al.*, 2002).

Drought is a climatic factor that can decrease BAI, potentially triggering growth declines in entire forest populations (Desprez-Loustau *et al.*, 2006). Drought effects on BAI have been reported at the interannual (e.g. Bouriaud *et al.*, 2005) to the multidecadal time scale (e.g. Jump *et al.*, 2006). While the interannual relationship between BAI and climate can be quantified using records that have been prewhitened to remove autocorrelation, lower frequency connections are more difficult to demonstrate. In closed-canopy forests, where dominant species are usually shade tolerant (as is the case for *F. sylvatica*), growth is influenced by competitive processes, to the extent that growth of dominant trees can be affected by changes in density even in old age (Bebber *et al.*, 2004). A similar effect has also been found in old-growth forests of fire-adapted, shade-intolerant species, where dominant trees have been adversely impacted by greatly increased density of smaller individuals after the start of fire suppression programs (e.g. Biondi *et al.*, 1994; Biondi, 1996). Additional factors that need to be taken into account when describing long-term changes in BAI are large wind-

throw disturbances, which can influence radial growth for several years (Haywood, 2002). Finally, in beech forests, it has been found that thinning effects on BAI tend to be stronger during periods of favorable climate (Goff & Ottorini, 1993).

Materials and methods

Study sites

Two old-growth beech forests characterized by minimal human disturbance during the last 50 years were chosen in Central Italy (Fig. 1 and Table 1). The first site (CIM) is located on Monte Cimino (Viterbo Province, Latium), between 950 and 1050 m a.s.l., and is an old-growth secondary forest (58 ha) in the demographic transition stage (according to Frelich, 2002), passing

from an impressive single-layer canopy, where trees can reach >40 m in height, to an old, yet multiaged, structure. It is dominated by a widespread even-aged cohort (120–150 years old) that has suffered mortality in consequence of windthrows and glaze storms (Piovesan, 1998; Di Filippo *et al.*, 2005); the last timber logging occurred in 1947–1949. Soils have developed from a volcanic bedrock, are generally deep (>1 m), and were classified as Vitrandic Hapludalf (Lorenzoni *et al.*, 1995) following the Soil Taxonomy of the US Soil Survey Staff (1992). Site topography is gently sloping. The second stand (VCH) grows between 1600 and 1800 m a.s.l. in Valle Cervara (L'Aquila Province, Abruzzi), and is an old-growth, primary, multicohort forest (Frelich, 2002) distributed over 24 ha, with an uneven age structure that includes the oldest known *Fagus* tree (more than 500 years old) in the Northern Hemisphere (Piovesan

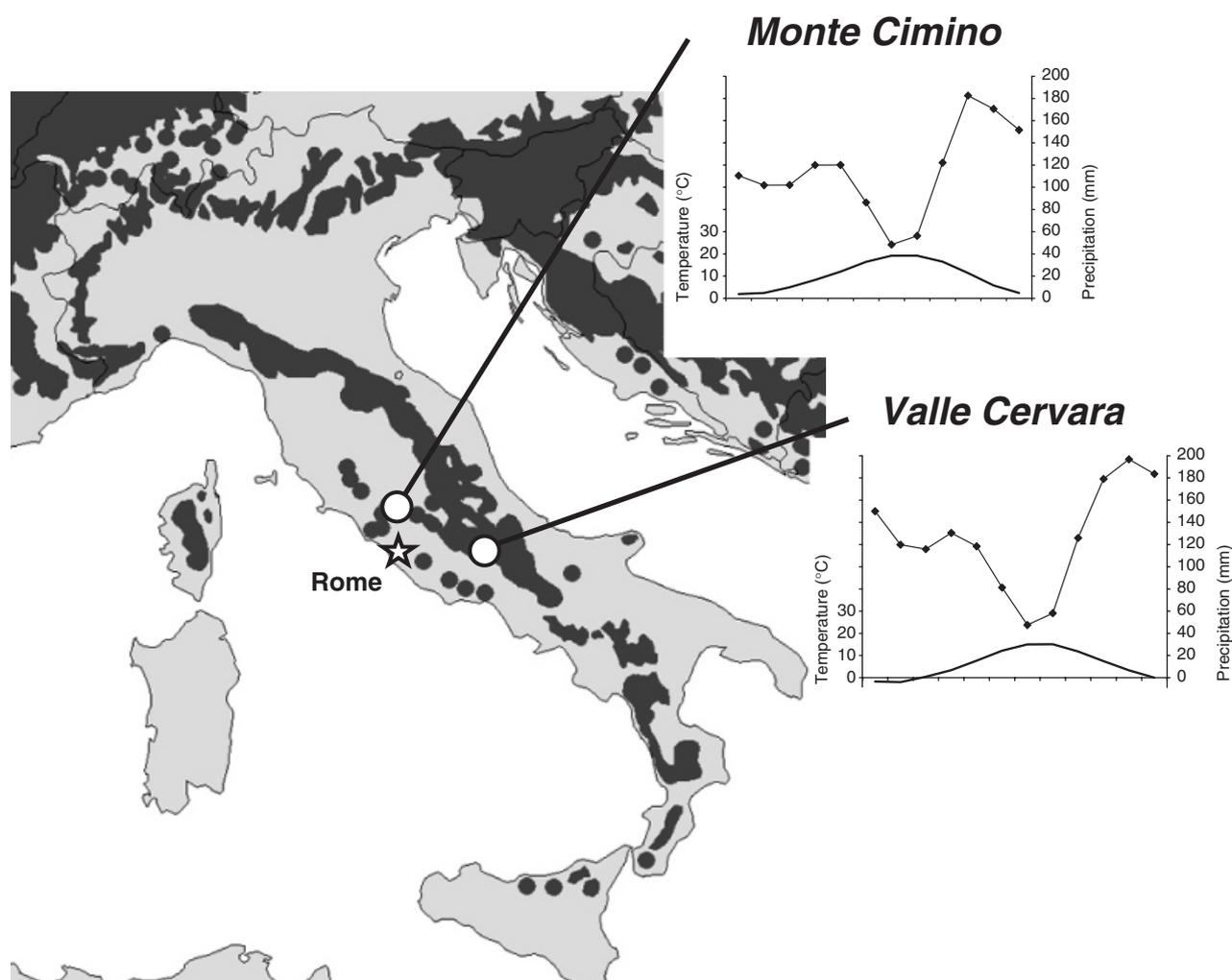


Fig. 1 Geographic distribution of *Fagus sylvatica* in Italy (dark area; Von Wuehlich, 2006), together with the location of study sites, and their climatic features, expressed by Bagnouls–Gaussen diagrams (line: temperature; line with diamonds: precipitations) calculated for the period 1890–2002.

Table 1 Geographic and structural features of the two sampled sites

| Site | Site code | Latitude (°) | Longitude (°) | Elevation (m a.s.l.) | Main aspect | Slope (%) | <i>t</i> (cm) | <i>N</i> (n ha ⁻¹) | <i>G</i> (m ² ha ⁻¹) | <i>H</i> (m) | <i>V</i> (m ³ ha ⁻¹) | Sampled trees | DBH (cm) | <i>N</i> _{rings} (years) |
|---------------|-----------|--------------|---------------|----------------------|-------------|-----------|---------------|--------------------------------|---|--------------|---|---------------|-------------|-----------------------------------|
| Monte Cimino | CIM | 42.4181 | 12.2350 | 1000 (950–1050) | – | 0–35 | 12.5 | 132 | 42 | 41 | 555 | 34 | 63 (35–100) | 131 (109–189) |
| Valle Cervara | VCH | 41.8690 | 13.6230 | 1725 (1600–1850) | W | 5–55 | 7.5 | 532 | 39 | 32 | 497 | 30 | 69 (55–100) | 306 (121–503) |

t, diameter-at-breast-height threshold used in field measurements; *N*, number of trees per hectare; *G*, basal area per hectare; *H*, mean height of the three to four tallest trees in the stand (stature); *V*, volume of living trees per hectare; DBH, mean and range of sampled trees diameters; *N*_{rings}, mean and range of rings counted on cores from sampled trees.

et al., 2005a). The terrain is sloping, soils are developed on calcareous bedrock, have variable depth (40–100 cm), and were classified as Eutrochreptic Rendolls.

Climatic data

Site-representative temperature series were constructed starting from the gridded version of the Italian long-term climate dataset (Brunetti *et al.*, 2006), which is available from ISAC/CNR, the Institute for Atmospheric Sciences and Climate of the Italian National Research Council. The grid has 1° resolution, both in latitude and in longitude. It is based on 67 observing stations, interpolated with a Gaussian weighting function constructed to have weight of 0.5 for station distance equal to the mean distance (*d*) of one grid point to the next. Each grid point record was calculated under one of the following conditions: (i) a minimum of two stations at a distance lower than *d* or (ii) a minimum of one station at a distance lower than *d*/2. The grid value computation was then performed considering all stations within a distance of 2*d*. Grid values were calculated from station anomalies with respect to the 1961–1990 period (Brunetti *et al.*, 2006).

The site-representative temperature series used in this paper were constructed by (i) calculating a weighted average of the four nearest grid point series, with weights defined according to the distances of the grid points from the sites, and (ii) by adding to the resulting anomalies the 1961–1990 monthly normal values of the sites. Such normal values (Table 2) were estimated using data from the Italian Hydrological Service, taking into account all available information on the altitude-dependence of monthly temperature for different areas of Italy (see Mennella, 1972, 1973). Stations used to estimate normal values at Monte Cimino are Montefiascone (555 m), Rocca di Papa (760 m), Vallepiedra (825 m), Vallombrosa (955 m), Monte Cavo (956 m), and Camaldoli (1111 m). Stations used to estimate the normal values of Valle Cervara are Capracotta (1421 m), Monte Terminillo Air Force station (1875 m), and Campo Imperatore (2125 m).

Site-representative precipitation series were constructed with a similar approach and are based on the 111 series of the ISAC/CNR dataset (Brunetti *et al.*, 2006). For precipitation, however, we used gridded series expressed as absolute values rather than as anomalies, because (i) the use of additive anomalies could give rise to negative absolute values, (ii) the use of anomalies could give rise to strong outliers because in the Mediterranean area there are stations with very low summer normal values. In order to avoid biases due to missing data, such absolute-value gridded series were constructed according to a method described in

Table 2 Estimated (1961–1990) monthly normal temperature values (°C) for the two sites

| | January | February | March | April | May | June | July | August | September | October | November | December |
|---------------|---------|----------|-------|-------|------|------|------|--------|-----------|---------|----------|----------|
| Monte Cimino | 2.4 | 3.0 | 5.2 | 8.5 | 12.1 | 16.3 | 19.3 | 19.1 | 16.6 | 11.6 | 5.9 | 2.6 |
| Valle Cervara | -1.4 | -1.4 | 0.7 | 3.6 | 7.8 | 12.1 | 15.1 | 15.1 | 11.9 | 7.6 | 3.3 | 0.1 |

Brunetti *et al.* (2002). Information from the Italian Hydrological Service was also used, but instead of individual stations we employed available climatologies (e.g. Mennella, 1967) to apply a correcting factor for each site. Such correcting factors were selected in order to have a long-term mean total annual precipitation of 1350 mm at Monte Cimino and 1500 mm at Valle Cervara (Boni *et al.*, 1986), and were 1.68 for Monte Cimino and 2.12 for Valle Cervara. The relatively large size of these corrections were caused by the fact that stations used to construct the records of the grid points including Monte Cimino and Valle Cervara were at lower elevations and had lower mean total annual precipitation, due to a strong elevation–precipitation relationship in the Apennines (Mennella, 1972, 1973).

From the above climatic data, we quantified drought stress at Monte Cimino and at Valle Cervara using monthly self-calibrated Palmer Moisture Anomaly Index (Z-index) and Palmer Drought Severity Index (PDSI; Palmer, 1965; Wells *et al.*, 2004; Van Der Schrier *et al.*, 2006). Z-index and PDSI series were computed using the software developed by the US National Agricultural Decision Support System at the University of Nebraska, Lincoln (<http://nadss.unl.edu/>). Z-index and PDSI values are based on a water budget soil model, and they show short-term (Z-index), as well as cumulative long-term (PDSI) dry and wet conditions (Heim, 2002). At Monte Cimino, the available water holding capacity (AWC = 220 mm), required for PDSI computations, was calculated by Salter's formula (Salter & Williams, 1967) using texture and depth data, for each horizon of the soil, reported in the literature for that site (Lorenzoni *et al.*, 1995). At Valle Cervara, AWC (190 mm) was obtained by averaging data calculated with the same method for beech forests environmentally and geographically close to that site (De Nicola *et al.*, 2006).

Growth time-series development and statistical analyses

At each site, increment cores were extracted at breast height (1.3 m from the ground) with an increment borer. A total of 30 dominant or codominant trees were sampled at Valle Cervara, and 34 at Monte Cimino, taking one or two cores per tree. Stem BAI was computed using crossdated ring-width series (for dendro-

chronological procedures, see Piovesan *et al.*, 2005b). Past annual BAI was estimated by subtracting twice the annual ring width (w_t) from the annual outside bark diameter (DBH_{*t*}; see LeBlanc, 1992), as follows:

$$\text{BAI}_t = \frac{\pi}{4} \left[\text{DBH}_t^2 - (\text{DBH}_t - 2w_t)^2 \right].$$

A raw BAI chronology was built for each site as the average by year of individual-tree BAI series. Prewhitened (i.e. without time-series autocorrelation) BAI chronologies were produced for each site using the following formula:

$$\bar{I}_t = \phi_p(B) \left[\frac{\sum_{i=1}^{i=n_t} (\text{BAI}^{0.5} - y)_{it}}{n_t} + c_{it} \right],$$

where \bar{I}_t is the prewhitened chronology value at year t ; n_t is the number of samples for year t , with $n_t \geq 10$ (e.g. McEwan *et al.*, 2006); BAI is the crossdated BAI of sample i for year t ; y the BAI value of sample i for year t computed by fitting a cubic smoothing spline with a 50% frequency response at a 50-year period (Cook & Peters, 1981); c_{it} the constant added to sample i in year t so that the standardized chronology has a mean equal to 1; and $\phi_p(B)$ the autoregressive operator of order p , chosen according to multiple criteria described by Biondi & Swetnam (1987). The program ARSTAN was used for computations (Cook & Holmes, 1986). We calculated the expressed population signal (EPS, a primary tool in evaluating tree-ring chronology quality; Wigley *et al.*, 1984) over the entire period of the raw and the prewhitened chronologies using 50-year moving windows with a 49-year overlap (Di Filippo *et al.*, 2007).

Growth–climate relationships were quantified over a period that was common to all wood samples, starting in 1890 (Monte Cimino: 1890–1996; Valle Cervara: 1890–2002), in order to avoid changes in variance due to sample depth (Wigley *et al.*, 1984; Frank *et al.*, 2006). According to previous results (Piovesan *et al.*, 2003, 2005b), indicating summer drought and May precipitation/temperature as the major factors controlling radial growth at the study sites, we chose mean temperature, total precipitation, mean Z-index (for high-frequency climatic analysis), and PDSI (for low-frequency climatic analysis) of May, summer (June–August), and growing period (May–September) as predictors. The Z-index

does not include a persistence factor, hence it is more indicative of monthly variability than the PDSI (Heim, 2002). Correlations were estimated over the period 1890–1996, matching current year BAI with climatic data of the current year (t), as well as 1 ($t-1$) and 2 ($t-2$) years before ring formation. Moving correlation functions (MCF; Biondi, 1997) were obtained by matching prewhitened BAI chronologies with climatic data over a 50-year moving window using the program DENDROCLIM2002 (Biondi & Waikul, 2004); in this latter analysis, the period covered for VCH is 1890–2002. The bootstrap method (Efron & Tibshirani, 1986; Guiot, 1991) was used for computing and significance testing (Biondi & Waikul, 2004).

Individual BAI 50-year splines (Cook & Peters, 1981), computed by the program ARSTAN, were converted to original units ($\text{cm}^2 \text{yr}^{-1}$) by squaring them to measure long-term growth variation for each tree. In order to represent low-frequency variability in climate, 50-year splines were also fit to PDSI monthly values. The mean spline BAI chronology, calculated as the arithmetic mean of all individual BAI splines, and the growth-type chronologies (GTC) were compared with the climate splines over the past 50 years (Holman & Peterson, 2006).

Within each site, individual splines were grouped by means of hierarchical cluster analysis (HCA), using $(1-r)$, with r being the Pearson product-moment correlation coefficient, as the linkage algorithm and the 'average' metric for within-cluster distance (Stenson & Wilkinson, 2004). We used a two-step agglomerative procedure, performing HCA over the whole period under analysis (i.e. 1890–1996 in CIM, 1890–2002 in VCH) in the first step, and on the more recent period (1950–1996 and 1950–2002, respectively) in the second one. By this approach, splines were divided into homogeneous 'growth types', which combined both long-term and current productivity variation groups. GTCs were then produced by averaging individual splines joined by the two-step HCA. This procedure was chosen to adopt an individual-tree approach (see for instance LeBlanc, 1992), as an alternative to computing an average site chronology. Finally, within each site we calculated each tree's average BAI for different decades, and compared it with the mean DBH¹ of the corresponding period. This allowed us to evaluate the presence of shifts in the growth-diameter relationship, which was quantified using simple linear regression. Differences between intercepts were then tested using a t statistic (<http://department.obg.cuhk.edu.hk/index.asp?scr=1280>).

¹Arithmetic average of reconstructed annual DBH at the beginning and at the end of the decade.

Tree-ring data from a European beech network in Central Italy (see Piovesan *et al.*, 2005b) were also used to compute BAI trends, for comparison with Monte Cimino and Valle Cervara. Even though those other areas could not properly be considered old-growth forests, because in most cases harvesting took place at least up to the 1980s, this comparison provided a broader context for the analysis. Using the same statistical methods described earlier, the 13 BAI (11 sites + VCH + CIM) chronologies were tested for growth trends related to elevation.

Results

The two sites were characterized by different lengths of raw BAI chronologies (Fig. 2). Up to the first half of the 19th century, the BAI series from Valle Cervara showed low level of growth. The old-growth status of this beech forest implies that trees may remain in the understory for centuries, undergoing severe competition from dominant trees before they are able to access the canopy (Piovesan *et al.*, 2005a). This initial suppression is likely to account for the low growth rates; another potential explanation could be climatic limitation during the Little Ice Age (Luterbacher *et al.*, 2006). Both BAI series first culminated at the beginning of the 20th century (this pattern was more pronounced at CIM), then peaked a second time (slightly higher) in the late 1960s to early 1970s, and since then growth had declined at both sites. Statistics of both raw and prewhitened BAI chronologies are given in Table 3. Mean BAI at Monte Cimino was significantly greater than at Valle Cervara in 1890–1996 ($P < 0.0001$ using a two-tailed t -test) and in 1950–1996 ($P < 0.01$) (Table 3; Fig. 2), although sampled trees in 1890 were significantly smaller ($P < 0.0001$) at CIM than at VCH (mean diameter in this year was 21 and 43 cm, respectively). While this difference was still significant in 1950 (49 vs. 58 cm, $P < 0.001$), present-day mean dimensions (Table 1) are similar, because of higher growth rates over time at CIM. Greater productivity at the CIM site is also suggested by its greater mean tree height (Table 1). This difference between the two sites is likely to be related to different soil fertility, linked to parent material (volcanic at CIM vs. calcareous at VCH). Furthermore, trees at the CIM site, which is at lower elevation than VCH, can benefit from a longer growing season (see Di Filippo *et al.*, 2007). The lower mean age of trees samples at CIM, compared with those sampled at VCH (see Table 1), may also have contributed to this difference in mean growth rates.

Data variability, as indicated by standard deviations (SDs), was similar between the two sites (Table 3). Mean sensitivity (MS) values were higher for VCH (but the

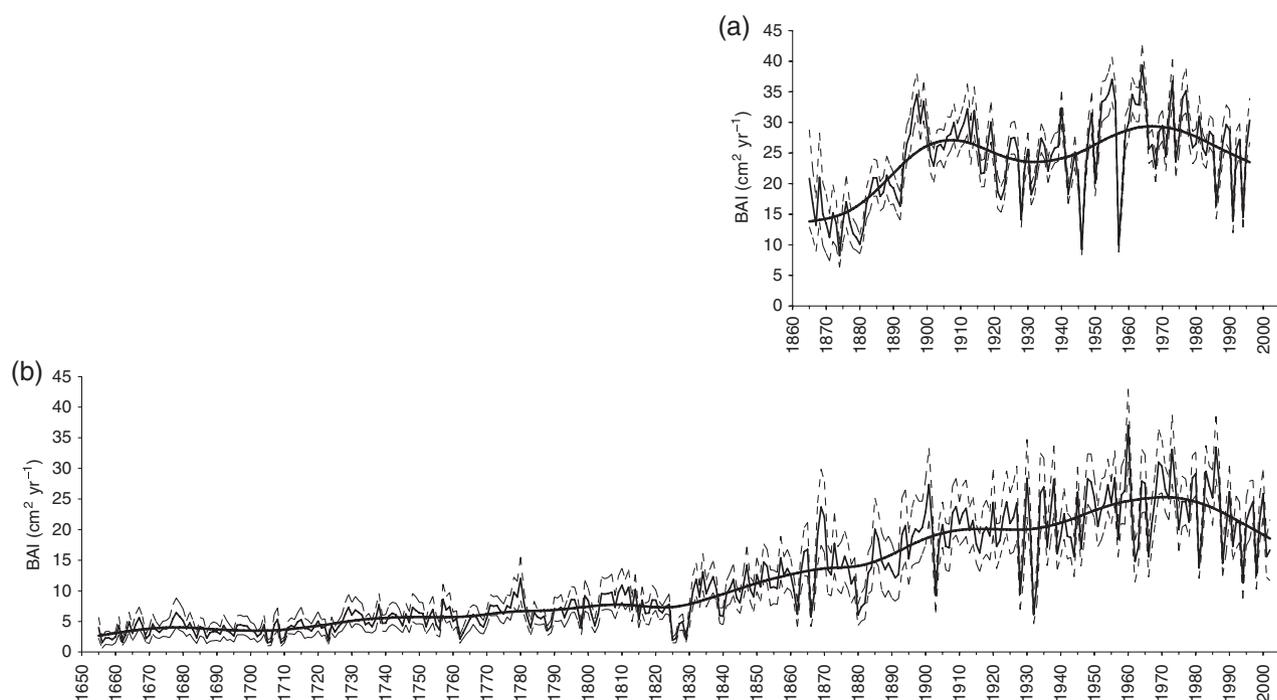


Fig. 2 Mean raw basal area increment (BAI) chronologies with more than 10 trees per year for Monte Cimino (a) and Valle Cervara (b). Bold line: 50-year cubic smoothing spline; dashed lines: ± 1 SE.

Table 3 Summary information for the two raw (a) and prewhitened (b) chronologies over their entire length (period with at least 10 trees), and on selected sub-periods (only for raw chronologies)

| Site | <i>N</i> | Period | MV ($\text{cm}^2 \text{yr}^{-1}$) | SD ($\text{cm}^2 \text{yr}^{-1}$) | MS | A_1 | <i>p</i> | Period with EPS > 0.85 |
|----------------------------|----------|-----------|-------------------------------------|-------------------------------------|------|-------|----------|------------------------|
| (a) Raw chronology | | | | | | | | |
| Monte Cimino | 34 | 1865–1996 | 24.21 | 6.83 | 0.19 | 0.66 | – | 1850–1996 |
| | | 1890–1996 | 26.19 | 5.77 | 0.19 | 0.46 | – | |
| | | 1950–1996 | 27.75 | 6.29 | 0.22 | 0.33 | – | |
| Valle Cervara | 30 | 1655–2002 | 11.76 | 8.19 | 0.26 | 0.87 | – | 1640–2002 |
| | | 1890–1996 | 21.68 | 5.49 | 0.25 | 0.31 | – | |
| | | 1950–1996 | 24.01 | 5.43 | 0.25 | 0.19 | – | |
| (b) Prewhitened chronology | | | | | | | | |
| Monte Cimino | 34 | 1867–1996 | 1.00 | 0.10 | 0.10 | 0.02 | 2 | 1850–1996 |
| Valle Cervara | 30 | 1658–2002 | 1.00 | 0.13 | 0.15 | 0.00 | 3 | 1640–2002 |

N, replication; MV, mean value; SD, standard deviation; MS, mean sensitivity; A_1 , first-order autocorrelation; *p*, order applied in AR modeling.

difference was not significant), possibly in relation to the increasing importance of climatic control on tree-ring width with elevation (Piovesan *et al.*, 2005b). First-order autocorrelation was higher in CIM, possibly in relation to the younger age of trees in the subperiods analyzed. Both raw and prewhitened chronologies from the two sites showed EPS values > 0.85 during the entire study period, 1890–2002 (Table 3b). The moving EPS function for the CIM raw chronology had a sudden

drop in the first half of the 20th century (data not shown), possibly linked to timber logging that took place during the late 1940s (Piovesan, 1998).

High-frequency climatic signals in BAI

Bootstrapped correlation functions with climatic series during the study period revealed that summer climate up to 2 years before wood formation was related to BAI

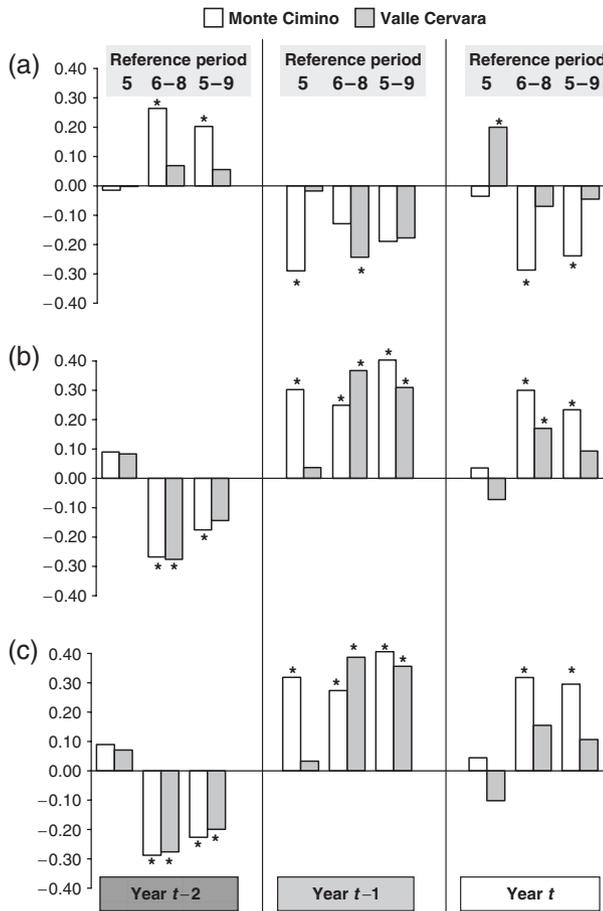


Fig. 3 Sample linear correlations of CIM and VCH prewhitened chronologies with mean temperature (a), total precipitation (b), and mean Z-index (c) for May (5), summer (6–8: June–August), and the growing period (5–9: May–September). The correlations were calculated for three different time lags during the period 1890–1996. Asterisks: bootstrapped 95% significant values.

(Fig. 3). Beech at CIM was limited by summer drought as shown by a negative correlation with temperature, a positive correlation with precipitation, and a positive correlation with the Z-index. Tree growth at VCH, which is positively correlated with summer precipitation, has a positive correlation with current May temperature, and a negative correlation with prior year summer temperature. At both sites, previous summer drought is the main factor limiting growth. However, a different response to climate 1 year before ring formation is evident for the month of May, which is highly correlated to the CIM chronology, but not to the VCH one (Fig. 3). Relationships between BAI and climate 2 years before wood growth are opposite to those identified for the 1 year lag: summer drought at year $t-2$ is positively correlated with wood growth at year t (Fig. 3).

Based on MCF with the Z-index, current year relationships between tree growth and summer climate at

CIM have been relatively stable through time (Fig. 4a). At VCH, correlations with May temperature have progressively increased as years passed, but in recent years dropped again to nonsignificant values (Fig. 4b). While at VCH correlations with prior year climate were relatively stable, at CIM correlations with prior year climate have progressively increased, becoming greater than those with current climate in the most recent periods (Fig. 4). The negative correlation identified between BAI chronologies and climate of year $t-2$ showed different behavior over time among CIM and VCH, with some periods not significant. Moving bootstrapped correlations between either raw or prewhitened BAI chronologies at the two sites (Fig. 5) show a decrease in common variability over time, as shown by the loss of significance during the most recent decades. This may be due to the reduced correlation between BAI and prior summer Z-index at VCH (Fig. 4b), considering how that climatic signal represented a major response that could synchronize growth variability at the two sites (Fig. 3).

Low-frequency climatic signals in BAI

Interdecadal patterns accounted for 11% of the annual variance in raw BAI chronologies at Monte Cimino (period 1950–1996), and 10% at Valle Cervara (period 1950–1996; 15% in the period 1950–2002). Similar interdecadal patterns (Fig. 6) were found at the two sites for summer PDSI (43% of the annual variability in 1950–1996, 49% in 1950–2002) and mean temperature (27% of the annual variability in 1950–1996, 44% in 1950–2002). BAI increased at both sites starting in 1950 and until the late 1960s (CIM) or the beginning of the 1970s (VCH), then it decreased until recent years, in synchrony with summer (or growing season) PDSI (Fig. 6a) and summer temperature (Fig. 6b). At CIM, BAI peaked at the same time as PDSI, while at VCH the decline in BAI had a 2–3 years delay compared with PDSI. Given that other potential mechanisms for tree growth decline could be ruled out at the two sites, we consider drought stress (especially when considered in combination with the high-frequency signals mentioned earlier) to be responsible for the drop (20% at CIM, 26% at VCH) in recent BAI values compared with those in the 1970s.

An analysis of BAI vs. diameter (the average of annual DBH at the beginning and at the end of the increment) confirmed their well-known direct relationship (e.g. Boncina *et al.*, 2007). This relationship, however, appears different for the period of maximum growth (1960–1969) compared with recent years (1987–1996; supplementary Fig. S1). At both sites, growth decreased from the earlier to the later decade in all size classes, and so did the overall mean BAI

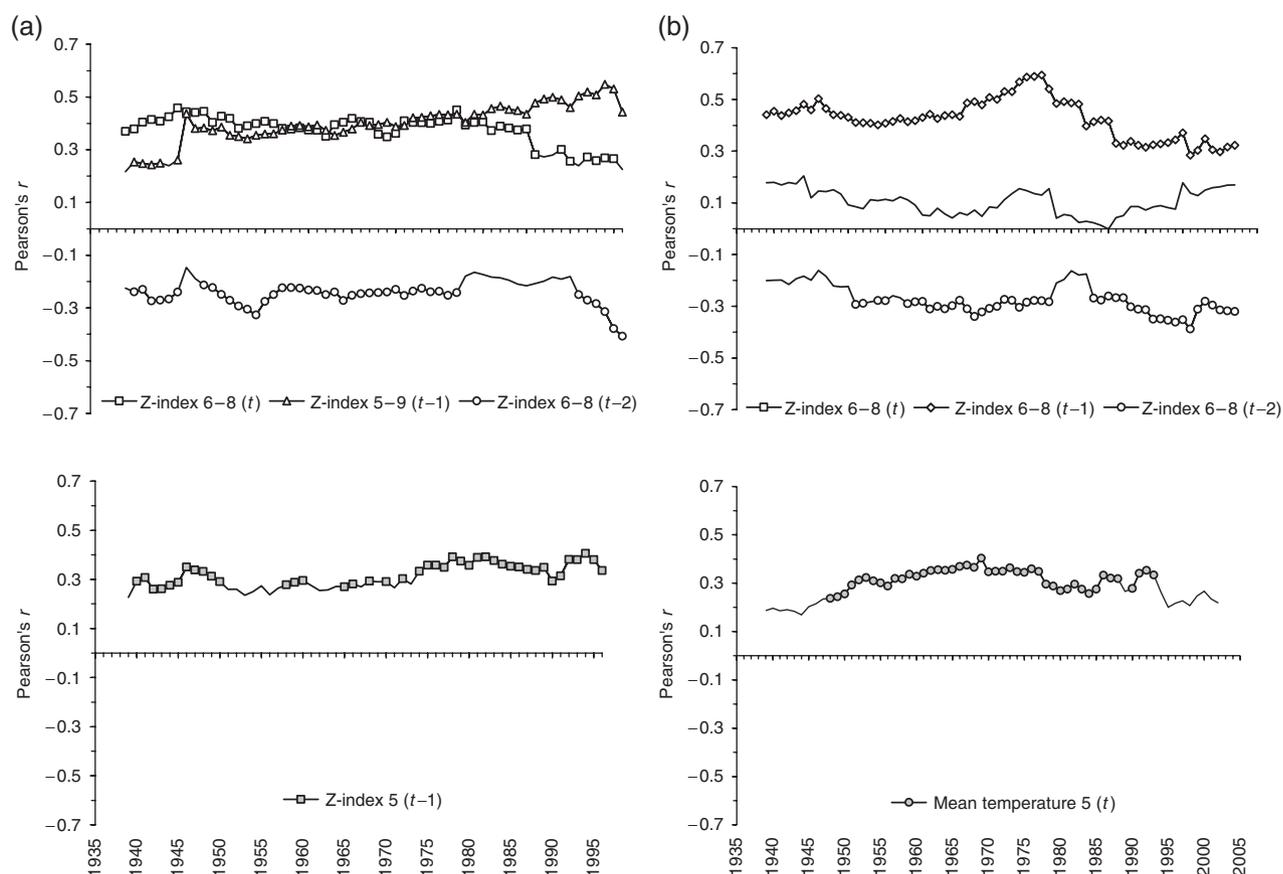


Fig. 4 Moving correlation functions (MCF) of CIM (a) and VCH (b) prewhitened basal area increment (BAI) chronologies with selected climate variables (see Fig. 3 for variables explanation). Each point corresponds to the end of a 50-year interval. Symbols represent intervals with significant correlation using bootstrapped 95% confidence intervals.

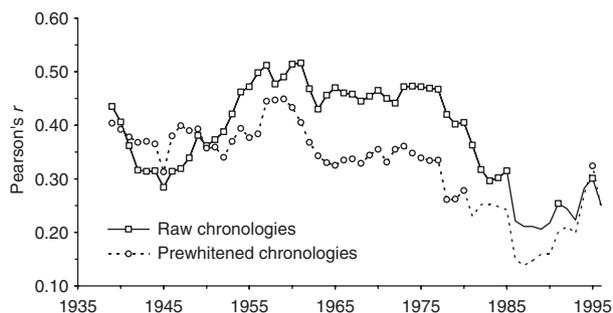


Fig. 5 Moving correlations between VCH and CIM raw and prewhitened basal area increment (BAI) chronologies. Each point corresponds to the end of a 50-year interval. Symbols represent intervals with significant correlation using bootstrapped 95% confidence intervals.

(CIM: from 30.71 to $24.19 \text{ cm}^2 \text{ yr}^{-1}$, $P < 0.01$ using a two-tailed paired t -test; VCH: from 24.09 to $20.42 \text{ cm}^2 \text{ yr}^{-1}$, $P < 0.01$). For the two periods, the regression between BAI and DBH (supplementary Fig. S1) shows different intercepts at both sites ($P < 0.001$ at CIM, with $n = 34$; $P < 0.01$ at VCH, with $n = 30$; t -test results from <http://>

department.obg.cuhk.edu.hk/researchsupport/Compare_2_regressions.asp). For equal DBH, trees at the CIM site grew faster than at the VCH site in 1960–1969, but less so in 1987–1996 (1960–1969: $P < 0.001$; 1987–1996: $P < 0.05$ based on a t -test of regression intercepts). In an attempt to separate size from age effects, we considered a total of 19 trees whose cores included the pith at the Valle Cervara site, where large age differences had already been found between trees of similar DBH (Piovesan *et al.*, 2005a). In 1987–1996, DBH and age were not significantly correlated, so they were used as predictors of BAI in a multiple regression ($r^2 = 0.67$, $n = 19$), which indicated a greater importance of DBH (standard coefficient = 0.82 , $P < 0.001$) than age (standard coefficient = -0.34 , $P < 0.05$). Similar results were obtained for the period 1960–1969.

Comparison with other beechwoods in Central Italy

BAI data obtained from a beech network in Central Italy (see Piovesan *et al.*, 2005b) for the same years used for CIM and VCH revealed a decrease in overall mean BAI,

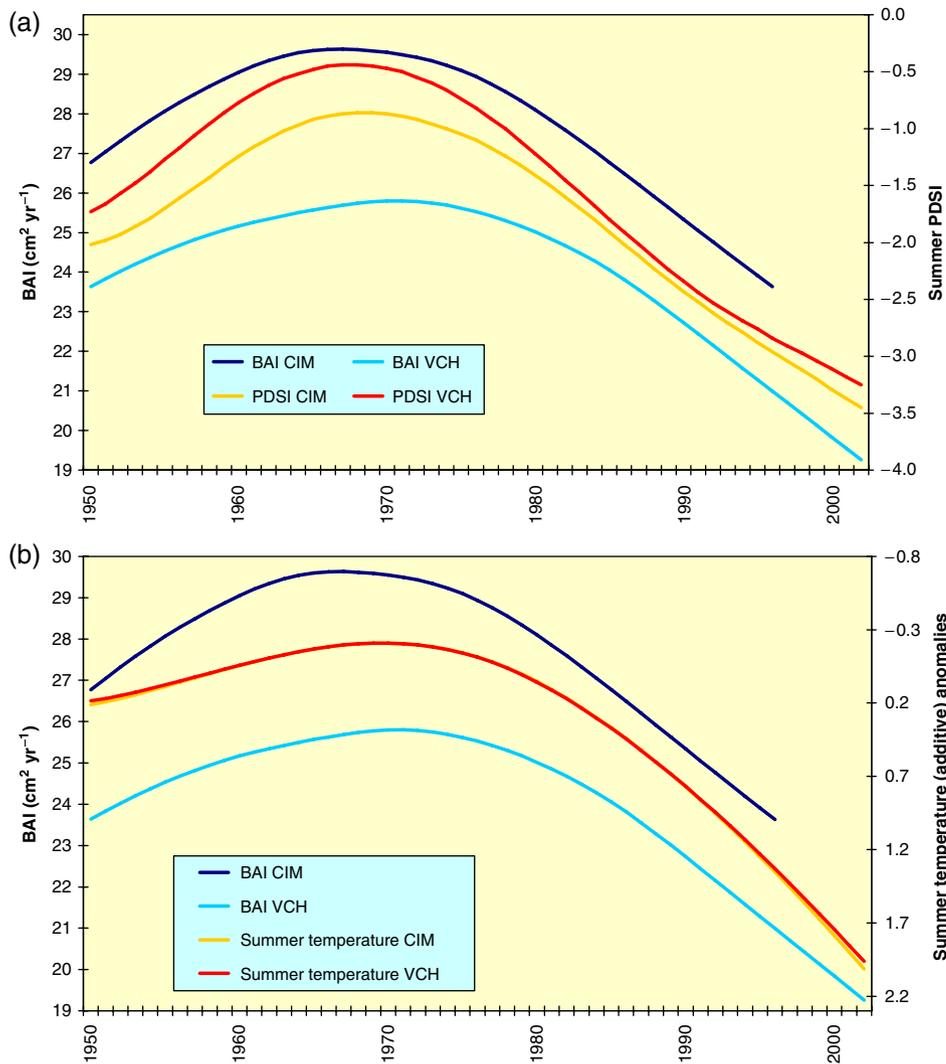


Fig. 6 CIM and VCH mean 50-year splines fit to annual basal area increment (BAI) during the last five decades, matched against 50-year splines fit to June–August mean Palmer Drought Severity Index (PDSI) (a) and temperature (b) for the same years.

from $34.75 \text{ cm}^2 \text{ yr}^{-1}$ in 1960–1969 to $28.33 \text{ cm}^2 \text{ yr}^{-1}$ in 1987–1996 ($P < 0.001$ using a two-tailed paired *t*-test). Elevation was an important factor, as BAI was inversely related to elevation (Fig. 7a and b; Piovesan *et al.*, 2005b), but even this relationship changed over time, becoming less pronounced in recent years. Beechwoods located at 450–1400 m a.s.l. (low hills to mountains), showed a decrease in BAI from 1960–1969 to 1987–1996 (range: -12% to -35%) (Fig. 7c). This pattern reversed at most sites between 1400 and 1700 m (high mountain beech forest); inside this belt only the old-growth forest of Valle Cervara was characterized by a decreasing growth trend. While a detailed analysis of these patterns should be subject of further research (taking in consideration also daily water balance and ecophysiological models; see Lebourgeois *et al.*, 2005), it is likely

that different management practices at some sites interfered with BAI changes linked to elevation by altering local competition processes.

Growth-type chronologies (GTCs)

For the period under analysis (i.e. 1890–1996 in CIM, 1890–2002 in VCH), HCA divided 50-year splines fit to BAI data into two main groups at both sites. These groups had increasing (A) and decreasing (B) growth trends (supplementary Figs S2 and S3). At both sites, few trees showed variable growth trends (group C: 9% at CIM, 10% at VCH). While most trees at VCH were characterized by an increasing BAI trend (67% in group A, 23% in group B), CIM had a greater amount of trees with decreasing trend (44% in group A, 47% in group B).

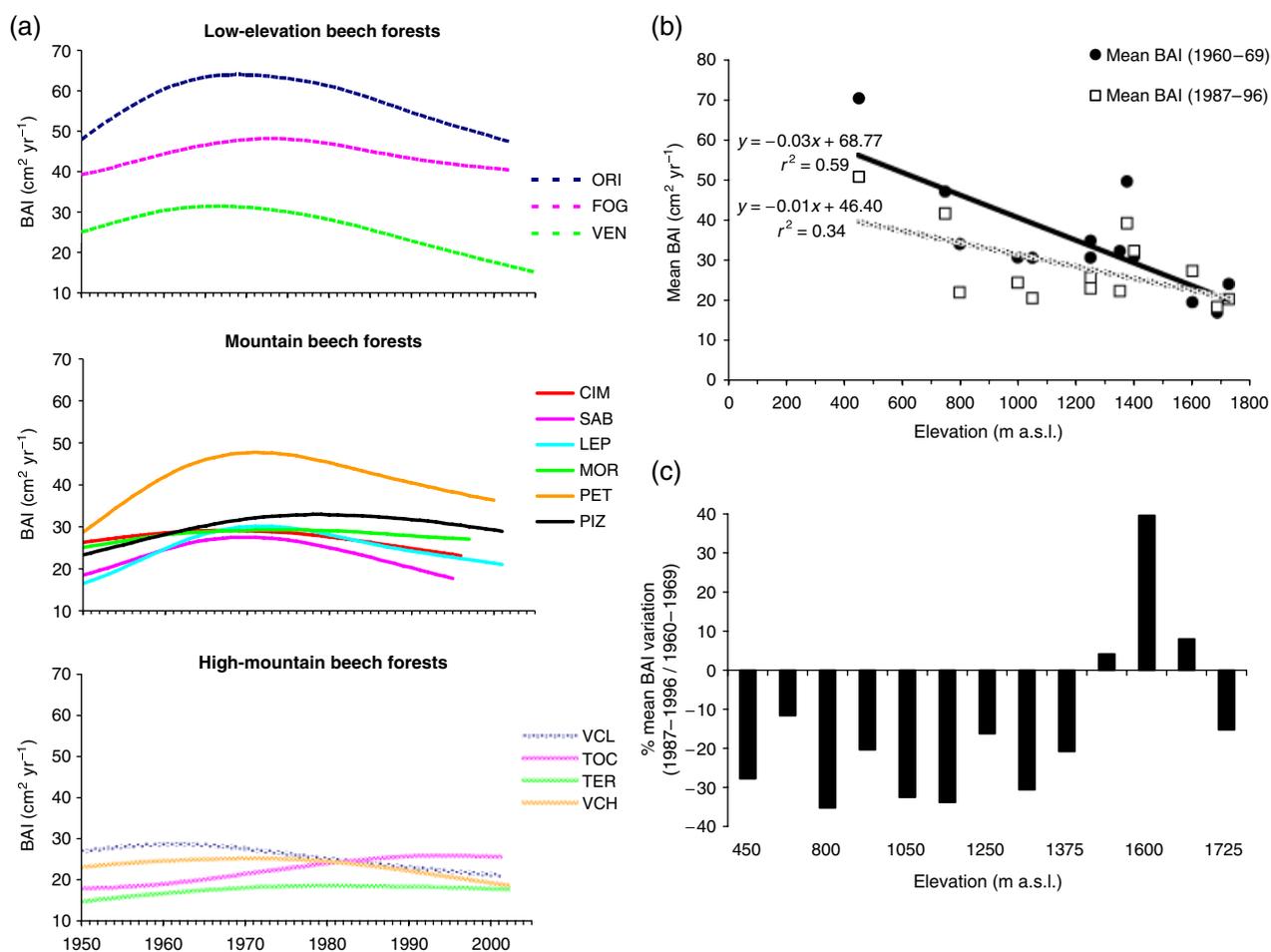


Fig. 7 Central Italy beech tree-ring network, composed of 13 sites (a) 50-year splines fit to mean raw basal area increment (BAI) chronologies (calculated on more than 10 trees per site), arranged according to low-elevation, mountain, and high-mountain sites (Piovesan *et al.*, 2005b). (b) Linear regression between mean BAI and elevation at these sites during the two reference periods 1960–1969 and 1987–1996. (c) Percent change in mean BAI for the two reference periods ($100 \times \text{BAI}_{1987-1996} / \text{BAI}_{1960-1969}$).

In the most recent decades (1950–1996 at CIM, 1950–2002 at VCH), most trees showed a decline of BAI (group d: 68% at CIM; 77% at VCH). Trees characterized by increasing BAI (group i: 32% at CIM; 17% at VCH) were also not the same trees included in group A. In fact, only 17% of the trees at VCH, and 18% at CIM, showed an increasing BAI trend in both the longer (since 1890) and the shorter (since 1950) period; these trees formed group Ai. At VCH, 50% of the trees culminated their increment in the years 1969–1974, then BAI splines decreased. A similar growth behavior was present at CIM (26% of trees), with just a few years difference (1960–1965) in culmination. Together these trees were categorized as group Ad. Another group of trees (Bd; 35% at CIM and 23% at VCH) showed an overall decrease (stronger at CIM than at VCH), but with two partial reversals at the beginning of the 1900s and in 1960–1974.

Tree diameter in 1890 was reconstructed from measured DBH and past ring widths. We found that trees assigned by HCA to group B (decreasing) had greater 1890 DBH than those assigned to group A (increasing). At VCH and CIM, group B trees had a mean 1890 DBH of 50.1 and 26.3 cm, respectively, whereas group A trees had mean 1890 DBH of 40.3 and 17 cm, at the two sites ($P < 0.05$ at VCH; $P = 0.10$ at CIM, using a two-tailed *t*-test). At CIM, trees grouped by HCA under d (*decreasing*) had significantly greater ($P < 0.05$ using a two-tailed *t*-test) 1890 DBH (mean of 25.7) than trees grouped under i (*increasing*; mean of 13.6 cm). This suggests that dominant, bigger trees are most at risk of suffering BAI decline.

Discussion

Dendroclimatic studies have uncovered a moisture limitation of beech radial growth in the Apennines

(Biondi, 1993; Piovesan *et al.*, 2005b). For the two sites we considered, average annual BAI variability was mostly related to drought stress during the current summer at Monte Cimino (CIM), while May temperature was a more important signal at the higher elevation site, Valle Cervara (VCH). From a network of beech dendrochronological records (Piovesan *et al.*, 2005b), it was found that growing season drought has a greater impact at the lower elevations, from low hills (400–800 m a.s.l.) to mountains (1000–1400 m a.s.l.). At the highest elevations (1600–1900 m a.s.l.), beech becomes sensitive to May temperature, a response most likely mediated by the effect of late frosts and by a general reduction of moisture stress (Piovesan *et al.*, 2003; Di Filippo *et al.*, 2007). In our study, the main climatic signal in common between CIM and VCH was linked to drought during the growing season (longer at CIM than at VCH) in the year before wood formation. Moving correlations revealed that the prior summer signal decreased over time at VCH, thereby reducing the year-to-year correlation between BAI at the two sites. Summer drought was also directly related to BAI occurring 2 years later, and such delayed response has become more significant in recent times. The negative (positive) correlation between summer drought and BAI at 1 (2) year lags could result from an interaction with floral and masting processes, and the resulting allocation of photosynthates to either vegetative or reproductive parts (Piovesan & Adams, 2001; Richardson *et al.*, 2005; Di Filippo *et al.*, 2007). It is worth noting that increased aridity, which in our study decreased dendrochronological synchronization between the two sites, may also have the opposite result, as shown by increased agreement of moisture-stressed conifer tree-ring records from Spain (Macias *et al.*, 2006; Andreu *et al.*, 2007). Other studies have recognized summer drought as the main driver of beech BAI, either during the current year (Bouriaud *et al.*, 2005), the previous year (Piovesan & Schirone, 2000; Piovesan *et al.*, 2003; Jump *et al.*, 2006), or 2 years earlier (Piovesan & Schirone, 2000).

At decadal time scales, delayed responses do not appear, and the main driver of BAI at those lower frequencies is current (summer or growing season) PDSI. Over the past three to four decades, BAI declined at both sites, and our analyses identified a greater importance of temperature than precipitation in causing this drought-related pattern. Similarly, Jump *et al.* (2006) demonstrated that warming can reduce BAI by enhancing moisture stress, although they emphasized annual values, rather than growing season ones, as was done in our study. Overall, considering that we focused on two sites that differed markedly with regard to elevation, soil parent material, tree age, and stand structure, our

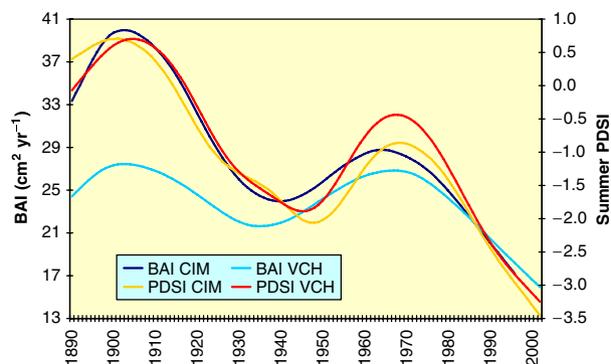


Fig. 8 Growth-type Bd at the CIM and VCH sites, matched against the 50-year spline fit to summer Palmer Drought Severity Index (PDSI) at the two sites.

findings support the notion that European beech in the Mediterranean biome will be adversely impacted by global warming, as increased summer drought stress overcomes any positive effects of an earlier growing season in the spring (see Angert *et al.*, 2005).

The auxological groups used to compute GTCs of BAI confirmed that most trees at both sites showed a decline in recent years, in agreement with increased drought. The opposite pattern (i.e. BAI increase shown by a few trees) could be attributed to more localized processes, such as reduced competition from nearby plants, soil properties, and/or genetic differences. Trees in group Bd, showing BAI peaks at the turn of the 20th century and in 1960–1974 (indicating a 50–60 years cycle), were in tune with summer PDSI (Fig. 8), especially at the CIM site. It is interesting to note that PDSI reached a minimum in the 1940s, but the summer Z-index was extremely low in the late 1920s and early 1930s (data not shown), dry periods that correspond to tree-ring signatures (Piovesan *et al.*, 2003).

Relationships between stem DBH and BAI changed significantly over time, most likely because of climatic influences. Other authors have reported changes in DBH–BAI relations, although usually related to nonclimatic environmental processes (Brown, 1985; Hein & Dhôte, 2006). Because BAI was proportional to stem DBH, it is possible to infer that drought stress resulted in size-symmetric competitive processes (Weiner & Damgaard, 2006). Climatic impacts on tree growth will need to be included not only in radial increment models for individual trees (see Hein & Dhôte, 2006) but also in forest management plans. In fact, forest productivity has already been found to be sensitive to hydroclimatic variability at decadal time scales (Vose & Swank, 1994; Woollons *et al.*, 1997; Wensel & Turnblom, 1998). Dendroecological research is therefore well suited to supplement ecophysiological models with empirical information to improve the predictive ability of forest

growth process models (see Adams & Piovesan, 2005; Bunn & Goetz, 2006).

Beech tree-ring records for a number of Apennine forests demonstrated similarly decreasing BAI patterns. While Jump *et al.* (2006) identified negative trends only at the lower elevations in the Montseny Mountains, we found reduced BAI at most elevations in the central Apennines. However, this decrease was more pronounced at sites in the low hills and mountains (PET, LEP, SAB in Fig. 7; see also Piovesan *et al.*, 2005b) than in areas located at higher elevations and/or further from the sea. Because altitude generally exerts a strong control on beech growth (e.g. Di Filippo *et al.*, 2007), the weakening we uncovered in the BAI–altitude relationship (see Fig. 7) deserves to be further monitored in Mediterranean mountains. In a global warming scenario, dry periods will probably lead to productivity decreases (Morales *et al.*, 2007), especially on hilly beech stands, but also to dieback phenomena, potentially leading to local extinction. Multiple influences, such as different forest management practices (see Bascietto *et al.*, 2004), complicate the analysis of BAI trends along an elevation transect in this region. Nevertheless, the Valle Cervara site (VCH), which is an old-growth, primary beech forest at the upper limit of the species distribution (Piovesan *et al.*, 2005a), provides a unique opportunity for understanding past, present, and future impacts of climatic changes. Future research should be aimed at understanding how forest structure and management (e.g. McDowell *et al.*, 2006), together with topography (see Fekedulegn *et al.*, 2003), affect BAI, its changes at multiple time scales, and its relationship with climate, also considering more detailed water balance and ecophysiological models (see Lebourgeois *et al.*, 2005).

By comparing our results with growth models (e.g. Thürig *et al.*, 2005) and observations of BAI in beech forests (e.g. Jaworski & Paluch, 2002), it is clear that beech growth rates in the Apennines are much lower than those in central Europe. This happens in spite of a longer growing period (Lausi & Pignatti, 1972), most likely because of moisture limitation in the summer (more or less intense depending on elevation and climatic period). Trees whose BAI peaked at the beginning of the 1900s had reached dominant status by then, and the relationship of their BAI with drought assumes even greater relevance when viewed in relation to the long-held view that BAI reaches a maximum and then stabilizes (declining slowly). We have shown here that dominant trees can reach more than one BAI peak during favorable climatic periods, and experience a BAI decline because of adverse climates. Such climatically driven oscillations have to be taken into account for developing more realistic expectations of BAI trends.

Climatic influences on BAI trends are mediated by the ecoregion (or environmental zone; see Metzger *et al.*, 2005) where trees are located. In our study, for instance, Bd trees at the Monte Cimino site experienced a 40% BAI decline in the 1940s (Fig. 8), greater than the most recent one, and similar to the one reported by Jump *et al.* (2006) in the Montseny Mountains. Trembling aspen BAI can be reduced by as much as 50% following a dry spell (Hogg *et al.*, 2005). In other cases, drought seems to decrease BAI at interannual, but not longer, time scales (Fekedulegn *et al.*, 2003). In the Mediterranean biome, where moisture availability is critical for beech growth, increased drought since the turn of the 20th century (see also Dai *et al.*, 2004) is, therefore, linked to changes in forest productivity which are opposite to those in central Europe, where positive growth trends have been identified (e.g. Dhôte & Hervé, 2000; Boisvenue & Running, 2006).

Dry conditions in southern Europe started about 40 years ago (see Fig. 12 in Van Der Schrier *et al.*, 2006) in concomitance with increasing temperatures (Brunetti *et al.*, 2006) and with the positive phase of the North Atlantic Oscillation (NAO), which reduces winter precipitation in these Mediterranean areas (Stenseth *et al.*, 2002). A relationship between NAO variability and *F. sylvatica* tree rings was already reported by Piovesan & Schirone (2000). The quasiperiodic 50–60 years pattern identified in BAI was possibly linked to slowly changing oceanic conditions, such as those summarized by the Atlantic Multidecadal Oscillation and/or the Pacific Decadal Oscillation (McCabe & Palecki, 2006).

Overall, our results suggest that long-term drought stress has reduced the productivity of beech forests in Mediterranean mountains during recent decades. Considering that a BAI reduction can be followed by widespread deterioration of forest health (Duchesne *et al.*, 2003), our results call for increased monitoring of beech forest conditions, such as potential phytopathological outbreaks. In Central Italy, drought has already been linked to forest health decline in coastal and hilly areas dominated by deciduous oak species (e.g. Desprez-Loustau *et al.*, 2006; G. Piovesan, unpublished data). Even in boreal biomes, trees can be negatively affected by warming beyond physiological thresholds when there are no significant gains in effective precipitation (D'Arrigo *et al.*, 2004) or during dry periods (Barber *et al.*, 2000). Ecosystem modeling predictions for the Mediterranean area under some climate scenarios have highlighted a drop in net primary productivity because of drought, and the potential shift of several forests from carbon sinks to carbon sources (Morales *et al.*, 2007). At the beginning of the 2000s, large-scale vegetation 'browning' in the northern hemisphere, associated with a period of below normal precipitation, extended

to the Mediterranean Basin (Lotsch *et al.*, 2005). Further research is needed to reconcile the observed decline in beech BAI with remote sensing data, because Normalized Difference Vegetation Index (NDVI; see Lapenis *et al.*, 2005) increased even in Mediterranean areas until the late 1990s (Nemani *et al.*, 2003; Xiao & Moody, 2005).

To date, few studies have focused on ground-truthed, long-term, tree growth variation in Mediterranean mountains. Our investigation is the first one to suggest that drought, expressed in terms of PDSI, controls forest productivity at decadal scales in Apennine beech forests. Such control extends over a range of elevations, from the lower (CIM) to the higher (VCH) limit of beech distribution in Central Italy. These findings have implications for modeling tree growth at the landscape level in relation to forest management options and to carbon cycling estimates, especially with regard to the impact of climate variability.

Acknowledgements

This research was partially supported by Regione Lazio (PRAL project). F. Biondi thanks Stanford University for sabbatical support. We also thank Francesco Biondi, Anna Testi, and Cristina De Nicola for their contribution to soil analyses. Three anonymous referees provided suggestions that helped improve an earlier version of this manuscript.

References

- Adams JM, Piovesan G (2005) Long series relationships between global interannual CO₂ increment and climate: evidence for stability and change in role of the tropical and boreal-temperate zones. *Chemosphere*, **59**, 1595–1612.
- Andreu L, Gutiérrez E, Macias M *et al.* (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Global Change Biology*, **13**, 804–815.
- Angert A, Biraud S, Bonfils C *et al.* (2005) Drier summers cancel out the CO₂ uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 10823–10827.
- Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Bascietto M, Cherubini P, Scarascia-Mugnozza G (2004) Tree rings from a European beech forest chronosequence are useful for detecting growth trends and carbon sequestration. *Canadian Journal of Forest Research*, **34**, 481–492.
- Bebber DP, Thomas SC, Cole WG *et al.* (2004) Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees*, **18**, 29–34.
- Bigler C, Bugmann H (2004) Predicting the time of tree death using dendrochronological data. *Ecological Applications*, **14**, 902–914.
- Biondi F (1993) Climatic signals in tree-rings of *Fagus sylvatica* L. from the central Apennines, Italy. *Acta Oecologica*, **14**, 57–71.
- Biondi F (1996) Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition? *Canadian Journal of Forest Research*, **26**, 1397–1406.
- Biondi F (1997) Evolutionary and moving response functions in dendroclimatology. *Dendrochronologia*, **15**, 139–150.
- Biondi F (1999) Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications*, **9**, 216–227.
- Biondi F, Myers DE, Avery CC (1994) Geostatistically modeling stem size and increment in an old-growth forest. *Canadian Journal of Forest Research*, **24**, 1354–1368.
- Biondi F, Swetnam TW (1987) Box-Jenkins models of forest interior tree-ring chronologies. *Tree-Ring Bulletin*, **47**, 71–95.
- Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers and Geosciences*, **30**, 303–311.
- Boisvenue C, Running SW (2006) Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology*, **12**, 862–882.
- Boncina A, Kadunc A, Robic D (2007) Effects of selective thinning on growth and development of beech (*Fagus sylvatica* L.) forest stands in south-eastern Slovenia. *Annals of Forest Science*, **64**, 47–57.
- Boni C, Bono P, Capelli G (1986) Schema idrogeologico dell'Italia centrale. *Memorie della Società Geologica Italiana*, **35**, 991–1012.
- Bouriaud O, Bréda N, Dupouey JL *et al.* (2005) Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Canadian Journal of Forest Research*, **35**, 2920–2933.
- Brown S (1985) Response of tree growth to changes in flooding regime in a mixed hardwood bottomland forest in southern Illinois. In: *Fifth Central Hardwood Forest Conference, Illinois, 15–17 April 1985* (eds Dawson JO, Majerus KA), pp. 203–208. Publication 85-05. Department of Forestry, University of Illinois Urbana-Champaign, Urbana-Champaign, IL.
- Brunetti M, Maugeri M, Monti F, Nanni T (2006) Temperature and precipitation variability in Italy in the last two centuries from homogenised instrumental time series. *International Journal of Climatology*, **26**, 345–381.
- Brunetti M, Maugeri M, Nanni T, Navarra A (2002) Droughts and extreme events in regional daily Italian precipitation series. *International Journal of Climatology*, **22**, 543–558.
- Bunn AG, Goetz SJ (2006) Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type, and vegetation density. *Earth Interactions*, **10**, 1–19.
- Choi J, Lorimer CG, Vanderwerker J *et al.* (2001) A crown model for simulating long-term stand and gap dynamics in northern hardwood forests. *Forest Ecology and Management*, **152**, 235–258.
- Ciais P, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.
- Colbert JJ, Schuckers M, Fekedulegn D (2004) Comparing models for growth and management of forest tracts. In: *Modelling Forest Systems* (eds Amaro A, Reed D, Soares P), pp. 335–346. CABI Publishing, Wallingford.
- Cook ER, Holmes RL (1986) *Users Manual for Program ARSTAN*. Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA.

- Cook ER, Kairiukstis LA (1990) *Methods of Dendrochronology: Applications in Environmental Science*. Kluwer Academic Publishers, Dordrecht, pp. 104–123.
- Cook ER, Peters K (1981) The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*, **41**, 45–53.
- Dai A, Trenberth KE, Qian T (2004) A global dataset of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *Journal of Hydrometeorology*, **5**, 1117–1130.
- D'Arrigo RD, Kaufmann RK, Davin N *et al.* (2004) Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles*, **18**, 1–7.
- De Nicola C, Fanelli G, Posillico M *et al.* (2006) Modello di distribuzione delle specie del sottobosco delle faggete dell'Appennino centrale in relazione ai parametri edifici. In: *SITE Atti XVI* (eds Cimmaruta R, Bondanelli P), p. 134. SITE, Parma.
- Desprez-Loustau ML, Marçais B, Nageleisen LM *et al.* (2006) Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*, **63**, 597–612.
- Dhôte JF, Hervé JC (2000) Changements de productivité dans quatre forêts de chênes sessiles depuis 1930: une approche au niveau du peuplement. *Annals of Forest Science*, **57**, 651–680.
- Di Filippo A, Biondi F, Cufar K *et al.* (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. *Journal of Biogeography*, **34**, 1873–1892.
- Di Filippo A, Piovesan G, Schirone B (2005) Le foreste vetuste: criteri per l'identificazione e la gestione. Atti del XIV Congresso Nazionale della Società Italiana di Ecologia, 4–6 Ottobre 2004, Siena. In: Carlo Gaggi, Valentina Nicolardi e Stefania Santoni (editori), *Ecologia. Atti del XIV Congresso Nazionale della Società Italiana di Ecologia*, 4–6 Ottobre 2004, Siena. <http://www.xivcongresso.societaitalianaecologia.org/articles/Di-Filippo-61.pdf>
- 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.
- Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science*, **1**, 54–75.
- Fekedulegn D, Hicks RR Jr, Colbert JJ (2003) Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *Forest Ecology and Management*, **177**, 409–425.
- Flanary BE, Kletetschka G (2005) Analysis of telomere length and telomerase activity in tree species of various life-spans, and with age in the bristlecone pine *Pinus longaeva*. *Biogerontology*, **6**, 101–111.
- Frank DC, Esper J, Cook ER (2006) On variance adjustments in tree-ring chronology development. In: *Tree Rings in Archaeology, Climatology and Ecology*, TRACE, Vol. 4 (eds Heinrich I *et al.*), pp. 56–66. ATR, Fribourg.
- Frelich LE (2002) *Forest Dynamics and Disturbance Regimes*. Cambridge University Press, Cambridge, UK.
- Fritts HC (1976) *Tree Rings and Climate*. Academic Press, London.
- Goff NL, Ottorini JM (1993) Thinning and climate effects on growth of beech (*Fagus sylvatica* L.) in experimental stands. *Forest Ecology and Management*, **62**, 1–14.
- Guiot J (1991) The bootstrapped response function. *Tree-Ring Bulletin*, **51**, 39–41.
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Haywood A (2002) Growth of advanced European beech trees in the transformation phase in the southern Black Forest. Inaugural-Dissertation zur Erlangung der Doktorwürde der Forstwissenschaftlichen Fakultät der Albert-Ludwigs-Universität Freiburg i. Brsg. <http://www.freidok.uni-freiburg.de/volltexte/1352/index.html>
- Heim RR Jr (2002) A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*, **83**, 1149–1165.
- Hein S, Dhôte JF (2006) Effect of species composition, stand density and site index on the basal area increment of oak trees (*Quercus* sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. *Annals of Forest Science*, **63**, 457–467.
- Hogg EH, Brandt JP, Kochtubajda B (2005) Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. *Canadian Journal of Forest Research*, **35**, 610–622.
- Holman ML, Peterson DL (2006) Spatial and temporal variability in forest growth in the Olympic Mountains, Washington: sensitivity to climatic variability. *Canadian Journal of Forest Research*, **36**, 92–104.
- Jaworski A, Paluch J (2002) Factors affecting the basal area increment of the primeval forests in the Babia Góra National Park, Southern Poland. *Forstwissenschaftliches Centralblatt*, **121**, 97–108.
- Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.
- LaMarche VC Jr (1969) Environment in relation to age of bristlecone pines. *Ecology*, **50**, 53–59.
- Lapenis A, Shvidenko A, Shepaschenko D *et al.* (2005) Acclimation of Russian forests to recent changes in climate. *Global Change Biology*, **11**, 2090–2102.
- Lausi D, Pignatti S (1972) Die phänologie der europäischen buchenwälder auf pflanzensoziologischer grundlage. *Phytocoenologia*, **1**, 1–63.
- LeBlanc DC (1992) Spatial and temporal variation in the prevalence of growth decline in red spruce populations of the northeastern United States. *Canadian Journal of Forest Research*, **22**, 1351–1363.
- Lebourgeois F, Brèda N, Ulrich E, Granier A (2005) Climate–tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees*, **19**, 385–401.
- Lorenzoni P, Mirabella A, Bidini D (1995) Soil genesis on trachytic and leucitic lavas of Cimini volcanic complex (Latium, Italy). *Geoderma*, **68**, 79–99.
- Lotsch A, Friedl MA, Anderson BT *et al.* (2005) Response of terrestrial ecosystems to recent Northern Hemispheric drought. *Geophysical Research Letters*, **32**, 1–5.

- Luterbacher J, Xoplaki E, Casty C *et al.* (2006) Mediterranean climate variability over the last centuries: a review. In: *Mediterranean Climate Variability* (eds Lionello P, Malanotte-Rizzoli P, Boscolo R), pp. 27–148. Elsevier, Amsterdam.
- Macias M, Andreu L, Bosch O *et al.* (2006) Increasing aridity is enhancing Silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. *Climatic Change*, **79**, 289–313.
- 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.
- Matthes U, Kelly PE, Ryan CE, Larson DW (2002) The formation and possible ecological function of stem strips in *Thuja occidentalis*. *International Journal of Plant Science*, **163**, 949–958.
- McCabe GJ, Palecki MA (2006) Multidecadal climate variability of global lands and oceans. *International Journal of Climatology*, **26**, 849–865.
- McDowell NG, Adams HD, Bailey JD *et al.* (2006) Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*, **16**, 1164–1182.
- McEwan RW, Keiffer CH, McCarthy BC (2006) Dendroecology of American chestnut in a disjunct stand of oak–chestnut forest. *Canadian Journal of Forest Research*, **36**, 1–11.
- Mennella C (1967) *Il Clima d'Italia*, Vol. primo. Fratelli Conte Editori, Napoli.
- Mennella C (1972) *Il Clima d'Italia*, Vol. secondo. Fratelli Conte Editori, Napoli.
- Mennella C (1973) *Il Clima d'Italia*, Vol. terzo. Fratelli Conte Editori, Napoli.
- Metzger MJ, Bunce RGH, Jongman RHG, Múcher CA, Watkins JW (2005) A climatic stratification of the environment of Europe. *Global Ecology and Biogeography*, **14**, 549–563.
- Morales P, Hickler T, Rowell DP *et al.* (2007) Changes in European ecosystem productivity and carbon balance driven by regional climate model output. *Global Change Biology*, **13**, 108–122.
- Nakawatase JM, Peterson DL (2006) Spatial variability in forest growth–climate relationships in the Olympic Mountains, Washington. *Canadian Journal of Forest Research*, **36**, 77–91.
- Nemani RR, Keeling CD, Hashimoto H *et al.* (2003) Climate driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, **300**, 1560–1563.
- Olano JM, Palmer MW (2003) Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *Forest Ecology and Management*, **174**, 139–148.
- Palmer WC (1965) *Meteorological Drought*. Research Paper No. 45, U.S. Weather Bureau. NOAA Library and Information Services Division, Washington, DC.
- Phipps RL (1984) Ring-width analysis. In: *Proceedings of the Symposium on Air Pollution and the Productivity of the Forest, 4–5 October 1983* (eds Davis DD, Millen AA, Dochinger LS), pp. 255–271. Izaak Walton League, Washington, DC.
- Piovesan G (1998) *Analisi di problemi assestamentali nella foresta montana dell'Appennino centrale*. PhD Thesis, University of Tuscia, Viterbo, 143pp.
- Piovesan G, Adams JM (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*, **79**, 1039–1047.
- Piovesan G, Bernabei M, Di Filippo A *et al.* (2003) A long-term tree ring beech chronology from a high-elevation old growth forest of Central Italy. *Dendrochronologia*, **21**, 13–22.
- Piovesan G, Biondi F, Bernabei M *et al.* (2005b) Spatial and altitudinal bioclimatic zones of the Italian peninsula identified from a beech (*Fagus sylvatica* L.) tree-ring network. *Acta Oecologica*, **27**, 197–210.
- Piovesan G, Di Filippo A, Alessandrini A *et al.* (2005a) Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. *Journal of Vegetation Science*, **16**, 13–28.
- Piovesan G, Schirone B (2000) Winter North Atlantic Oscillation effects on the tree rings of the Italian beech (*Fagus sylvatica* L.). *International Journal of Biometeorology*, **44**, 121–127.
- Poage J, Tappeiner JC (2002) Long-term patterns of diameter and basal area growth of individual old-growth and young-growth forests in western Oregon. *Canadian Journal of Forest Research*, **32**, 1232–1243.
- Richardson SJ, Allen RB, Whitehead D *et al.* (2005) Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus*. *Ecology*, **86**, 972–981.
- Rubino DL, McCharty BC (2000) Dendroclimatological analysis of White Oak (*Quercus alba* L., *Fagaceae*) from an old-growth forest of Southeastern Ohio, USA. *Journal of the Torrey Botanical Society*, **127**, 240–250.
- Salter PJ, Williams JB (1967) The influence of texture on the moisture characteristics of soils. A method of estimating the available-water capacities of profiles in the field. *European Journal of Soil Science*, **18**, 174–181.
- Schröder D, Cramer W, Leemans R *et al.* (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science*, **5752**, 1333–1337.
- Soil Survey Staff (1992) *Keys to Soil Taxonomy*, 5th edn. SMSS Technical Monograph no. 19, Blacksburg, VA, USA, 556pp.
- Stenseth NC, Mysterud A, Ottersen G *et al.* (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Stenson H, Wilkinson L (2004) Factor analysis. In: *Systat 11, Statistics I* (ed. Systat Software Inc.), pp. 359–377. Systat Software Inc., Richmond, CA.
- Sterba H, Blab A, Katzensteiner K (2002) Adapting an individual tree growth model for Norway spruce (*Picea abies* L. Karst.) in pure and mixed species stands. *Forest Ecology and Management*, **159**, 101–110.
- Thürig E, Kaufmann E, Frisullo R *et al.* (2005) Evaluation of the growth function of an empirical forest scenario model. *Forest Ecology and Management*, **204**, 51–66.
- Van Der Schrier G, Briffa KR, Jones PD, Osborn TJ (2006) Summer moisture variability across Europe. *American Meteorological Society*, **19**, 2818–2834.
- Von Wuehlisch G (2006) *EUFORGEN Technical Guidelines for Genetic Conservation and Use for European Beech (Fagus sylvatica)*. International Plant Genetic Resources Institute, Rome, Italy. http://www.ipgri.cgiar.org/networks/euforgen/Euf_Distribution_Maps.asp
- Vose JM, Swank WT (1994) Effect of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. *Forest Ecology and Management*, **64**, 25–39.
- Weiner J, Damgaard C (2006) Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influence model of plant competition. *Ecological Research*, **21**, 707–712.

- Wells N, Goddard S, Hayes MJ (2004) A self-calibrating Palmer Drought Severity Index. *Journal of Climate*, **17**, 2335–2351.
- Wensel CL, Turnblom EC (1998) Adjustment of estimated tree growth rates in northern California conifers for changes in precipitation levels. *Canadian Journal of Forest Research*, **28**, 1241–1248.
- Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Applied Meteorology*, **23**, 201–213.
- Woollons RC, Snowdon P, Mitchell ND (1997) Augmenting empirical stand projection equations with edaphic and climatic variables. *Forest Ecology and Management*, **98**, 267–275.
- Wyckoff WR, Crookston NL, Stage AR (1982) *User's guide to the stand prognosis model*. General Technical Report INT-133, USDA Forest Service.
- Xiao J, Moody A (2005) Geographic distribution of global greening trends and their climatic correlates: 1982 to 1998. *International Journal of Remote Sensing*, **26**, 2371–2390.

Supplementary material

The following material is available for this article online:

Fig. S1. CIM (a) and VCH (b) mean decadal BAI vs. DBH, for the two periods 1960–1969 and 1987–1996. The BAI–DBH regression lines for the two periods have significantly different intercepts at both sites (see text for details).

Fig. S2. (Above) Hierarchical cluster analysis (HCA) of 50-year splines fit to individual-tree BAI at Monte Cimino (CIM) over the periods 1890–1996 and 1950–1996. For the period 1890–1996, codes assigned to the different clusters are as follows: A = increasing growth trend; B = decreasing growth trend; C = variable growth trend. For the period 1950–1996, these additional codes were used: d = decreasing growth trend; i = increasing growth trend; s = no trend. (below) Growth Type Chronologies (GTCs; dotted lines: ± 1 SE; PC1: percentage of variance explained by the first principal component) obtained by grouping Monte Cimino trees with similar BAI trends over the periods 1890–1996 and 1950–1996. Each GTC is identified by two letters on the basis of codes assigned to different clusters.

Fig. S3. Same as Fig. S2, but for Valle Cervara (VCH).

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2486.2008.01570.x>.

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.