# AGE-DEPENDENT TREE-RING GROWTH RESPONSES TO CLIMATE IN *LARIX DECIDUA* AND *PINUS CEMBRA*

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*Abstract.* Dendrochronology generally operates under the assumption that climate–growth relationships are age independent, once growth trends and/or disturbance pulses have been accounted for. However, several studies have demonstrated that tree physiology undergoes changes with age. This may cause growth-related climate signals to vary over time. Using chronology statistics and response functions, we tested the consistency of climate–growth responses in tree-ring series from *Larix decidua* and *Pinus cembra* trees of four age classes. Tree-ring statistics (mean sensitivity, standard deviation, correlation between trees, and first principal component) did not change significantly with age in *P. cembra*, whereas in *L. decidua* they appeared to be correlated with age classes. Response function analysis indicated that climate accounts for a high amount of variance in tree-ring widths in both species. The older the trees are, the higher the variance explained by climate, the significance of the models, and the percentage of trees with significant responses.

Age influence on climate sensitivity is likely to be non-monotonic. In *L. decidua*, the most important response function variables changed with age according to a twofold pattern: increasing for trees younger than 200 years and decreasing or constant for older trees. A similar pattern was observed in both species for the relationship between tree height and age. It is hypothesized that an endogenous parameter linked to hydraulic status becomes increasingly limiting as trees grow and age, inducing more stressful conditions and a higher climate sensitivity in older individuals.

The results of this study confirm that the climate signal is maximized in older trees, but also that a sampling procedure non-stratified by age (especially in multi-aged forests) could lead to biased mean chronologies due to the higher amount of noise present in younger trees. The issue requires more extensive research as there are important ecological implications both at small and large geographic scales. Predictive modeling of forest dynamics and paleo-climate reconstructions may be less robust if the age effect is not accounted for.

*Key words: dendroclimatology; dendroecology; Italy;* Larix decidua; Pinus cembra; *response function; timberline; tree age; tree height; tree ring.*

## Introduction

Tree rings, as natural archives, provide important proxy data for paleo-environmental studies and reconstructions (Bradley and Jones 1992, Luckmann 1996). The use of tree-ring series has also recently spread to climate model validation in the context of global warming assessment. In particular, the last 1000 years are considered as a suitable time interval for the study of the background variability in relation to climate change detection and an appropriate period in relation to the longevity of several tree species (Mann et al. 1998, 1999, IPCC 2001). The major strengths of tree rings as climate change indicators are the capability to perform annually resolved dating, the existence of large geographic-scale patterns of synchronic interannual variability, the increasing availability of extensive networks of tree-ring chronologies covering large parts of the terrestrial regions of the globe, and the possibility of using simple linear models of climate–growth relationships that can easily be verified and calibrated (Hughes 2002). Conversely, weaknesses include the fact that tree-ring series record only certain wavelengths of climate variability and that the climate signal reflects complex biological responses to climate forcing. Problems may occur when removing the non-climate variability present in the series; furthermore, the biological response may change over time (IPCC 2001).

The longevity of trees (from hundreds to a few thousands years) complicates the detection of environmental signals. Long-lived species present a greater potential to record signals over a range of temporal and spatial scales (Schulman 1958, Currey 1965, Lara and Villalba 1993, Luckman 1996), but there is an increased risk of variability over time due to changes in biological response. The environmental signal in a time series of radial growth (e.g., ring width, wood density, and stable isotope concentration) is the result of a com-

PLATE 1. (Top left) Mixed *Larix decidua–Pinus cembra* open forests climb the upper dolomia slopes of the Croda da Lago Ridge. (Top right) Treeline open stands of *Pinus cembra* on porphyric bedrock in the Lagorai Mountains. (Bottom) Winter view of the Lagorai Mountains. Treeline forests of *Pinus cembra* are located around 2100 m a.s.l. Photographs by Marco Carrer.

plex interaction between environmental inputs and the physiological outputs (response) of the organism. Radial growth and related parameters for any given year often integrate the effects of both current and several previous years climate and are further modified by site-specific internal and external factors (Fritts 1976).

In dendroclimatological studies it is generally assumed that climate–growth relationships are age independent, once the biological growth trends and the influence of disturbance pulses have been removed. Actually, this assumption is valid only if the biological trends are due to the geometrical constraint of adding a volume of wood to a stem of increasing radius and/ or to competition and other disturbances effects (Cook et al. 1990). In other cases, especially in multi-aged forest stands, climatic reconstructions and climate–growth relationships may be biased, because at any given time different trees of the chronology are responding differently to climate depending on their age or size (Szeicz and MacDonald 1994, 1995).

Relatively few studies have tested whether climate–growth response is stable across different age classes, and conclusions vary among those that do exist. Gray (1982) discovered discrepancies in response functions computed for stands of different ages at one site in France. In North America, Ettl and Peterson (1995), observed that in younger trees of *Abies lasiocarpa* (Hook.) Nutt., growth is relatively less influenced by climate than in older trees. Szeicz and MacDonald (1994) detected different responses of *Picea glauca* Voss to climate in trees younger and older than 200 years. In contrast, Fritts (1976) obtained no significant differences in growth-climate relationships between chronologies of young and old *Pinus aristata* Engelm. Similarly, Colenutt and Luckman (1991) found no differences in old (age ~300 years) and young (~80 years) trees of *Larix lyalii* Parl. In comparing trees of the stand initiation cohort (older than 250 years) and others regenerated after a disturbance event (younger than 150 years), Parish et al. (1999) observed no dif-

TABLE 1. Comparative mean parameters (temperature [°C] and precipitation [mm]) of the two meteorological stations used for dendroclimatic analysis.

| Station | Elevation (m) | Annual precipitation (mm) | Summer (Jun–Sep) precipitation | Annual temperature | Annual maximum temperature | Annual minimum temperature |
|---|---|---|---|---|---|---|
| Falzarego Pass | 1985 | 1186 | 126 | 2.62 | 6.99 | −1.76 |
| Rolle Pass | 2004 | 1288 | 142 | 2.66 | 6.07 | −0.75 |

*Note:* Time series of temperature and precipitation data extend over the period 1926–1993 for Falzarego Pass (area A) and 1927–1995 for Rolle Pass (area B).

ferences in the response function profiles of *Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmanii* Parry.

Ecophysiological studies have shown that functional processes strongly coupled to tree growth undergo changes with increasing tree age. This suggests that growth-related environmental signals are likely to be age dependent. For example, Ryan et al. (1997) observed a shift of carbon resources to different parts of the plant with ageing. Reductions in foliar efficiency, leaf size, and gas exchange attributes have been observed in trees of increasing age (Kull and Koppel 1987, Richardson et al. 2000, Day et al. 2001). Lower photosynthetic rates in older trees have been measured in various conifer species (see Bond 2000 for a review). With increasing age, trees may also undergo a change in genetic expression acting at the meristem level that could affect height, tree-ring growth, and various wood-cell features (Greenwood 1995). Tracheid length, diameter and cell wall thickness as well as latewood percentage generally increase in older trees (Zobel and van Buijtenen 1989, Lindström 1997), whereas ray volume proportion has an opposite trend (Sellin 1996, Spicer and Gartner 2001).

Finally, size is generally positively correlated with age, but the individual responses of size and age to environmental factors cannot be completely separated. The increasing size of a tree creates conditions for improved growth by lowering sensitivity to competition and expanding the crown for a better coupling with the atmosphere. However, larger size and structural complexity increase maintenance respiration costs (Hunt et al. 1999) and reduce the efficiency of water transport; these both tend to reduce growth (Ryan et al. 1997, Bond 2000).

This study focuses on the two main tree species growing near the treeline in the Italian Alps: *Larix decidua* Mill. and *Pinus cembra* L. The aim was to test if climate–growth responses remain constant as age increases after removal of size trends and disturbance signals. Samples were grouped by age class and chronology features, and response functions were used to assess climate–growth relationships.

STUDY SITES

The study sites are located in high-altitude forest areas of the eastern Italian Alps (see Plate 1). These are ecotonal forest ecosystems, located at a maximum altitude of 2000–2200 m above sea level (a.s.l.), featuring irregular spatial distribution of trees with low canopy density (5–20% on average). The first area, area A (46°27′ N, 12°08′ E), is situated at Croda da Lago (Ampezzo Dolomites), on dolomite and limestone bedrock with shallow rendzic leptosols soils. It is a mixed *L. decidua*–*P. cembra* forest at an elevation of 2100 m a.s.l., extending for >3 km along the treeline, with a N–NE aspect and a 30% slope. The species composition is principally made up of *L. decidua* (72%), *P. cembra* (23%), and *Picea abies* (L.) Karst. (5%) (Carrer and Urbinati 2001).

Area B (46°15′ N, 11°30′ E) includes five different sites within 20 km of each other in the Lagorai Mountains (Trentino Region), 60 km southwest of the previous site. Bedrock consists of volcanic and metamorphic silicates, such as porphyry, gneiss, and phyllite. Soils can be deeper and wetter than in the Dolomites and are generally classified as podzols (Ronchetti 1965). All the sampled sites are located within pure *P. cembra* treeline forests, at ~2100 m a.s.l., with a NE aspect and 20–30% slopes.

The climate in both areas has the typical features of the southeastern Alpine region. Winters are dry, with most of the precipitation occurring during summer and early autumn. In area A, the summers are slightly warmer and the winters are colder than in area B. Precipitation is ~100 mm/yr higher in area B (Table 1).

MATERIALS AND METHODS

From areas A and B, a total of ~250 undamaged standing trees were selected in treeline locations. From each tree, two cores were extracted with an increment borer at breast height on the cross-slope sides of the trunk. In the sampling of younger trees, in order to avoid the possible effects of external influences such as competition, crown suppression, and related factors, only isolated individuals were selected. A small number of cores that were found to contain heart rot, mainly from *P. cembra*, were later rejected. All cores were mounted, planed with progressively finer grade sandpaper, and ring width measured to the nearest 0.01 mm with a semiautomatic measuring system connected to a computer (Aniol 1987). Dating and measurement errors were checked with the COFECHA computer program (Holmes 1983).

TABLE 2.   Age-class tree-ring features for the two study species.

| Species | Age class (yr) | No. trees | Mean ring width (mm) | Class chronology | | Tree chronology | | AC | Correlation between trees | PC1 |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | MS | SD | MS | SD | | | |
| *Larix decidua* | <100 | 35 | 0.833 | 0.242 | 0.227 | 0.315 | 0.346 | 0.320 | 0.470 | 53.1 |
| | 101–200 | 32 | 0.700 | 0.280 | 0.248 | 0.353 | 0.349 | 0.269 | 0.599 | 63.8 |
| | 201–300 | 49 | 0.497 | 0.338 | 0.281 | 0.369 | 0.379 | 0.062 | 0.741 | 74.8 |
| | >300 | 19 | 0.375 | 0.342 | 0.270 | 0.375 | 0.329 | 0.002 | 0.755 | 77.5 |
| *Pinus cembra* | <150 | 17 | 1.603 | 0.106 | 0.092 | 0.149 | 0.138 | −0.032 | 0.425 | 47.9 |
| | 151–250 | 60 | 1.108 | 0.113 | 0.095 | 0.157 | 0.147 | −0.054 | 0.409 | 43.4 |
| | 251–350 | 29 | 0.824 | 0.113 | 0.094 | 0.157 | 0.144 | −0.006 | 0.407 | 43.7 |
| | >350 | 7 | 0.690 | 0.114 | 0.100 | 0.150 | 0.141 | 0.030 | 0.426 | 51.9 |

*Notes:* Abbreviations are: MS, mean sensitivity; SD, standard deviation; AC, first order autocorrelation; PC1, percentage of variance accounted for the first principal component. Class chronology statistics are computed on the mean chronology of each age class. Tree chronology statistics are the averages of all the tree chronology values related to each age class.

All samples of the two species were grouped into four 100-year age classes based on tree age at breast height in 1993 for area A and in 1994 for area B. The 100-year interval was considered a reasonable compromise between sufficient sample size and sufficient disaggregation of the data.

Standardization was applied to remove trends in mean ring width that typically occur due to increasing circumference of the tree. Mean indexed chronologies of each tree and age class were developed from the cross-dated ring-width series using the program AR-STAN (Holmes 1992). Every tree-ring width series was fitted with a curve, and then each measured value was divided by the correspondent estimated value of the fitted curve. For fitting, a spline function was used with a 50% frequency response of 20 years, which was sufficiently flexible to remove trends in ring width of >7 years. Flexible cubic spline curves (Cook and Peters 1981) are more efficient in removing both the long-term trend and the effect of localized disturbance events, but at the risk of removing possible low-frequency climatic information (Cook et al. 1990, Peterson and Peterson 1994). A standard arithmetic mean function was used to construct a standardized growth curve for each tree, and a robust estimation of the mean value function was adopted in age-class averaging. This function should enhance the common signal and reduce the effect of outliers (Cook 1985).

Several descriptive statistics commonly used in dendrochronology were used to compare the age-class mean chronologies (AGC) over a common time period of 70 years, which was determined by the availability of the meteorological data set (Table 1). These statistics included the mean sensitivity (MS) and standard deviation (SD) to assess the high-frequency variations (Fritts 1976), the first order serial autocorrelation (AC) to detect eventual persistence retained after the standardization and the mean correlation between trees (CBT), and the variance explained by the first principal component (PC1) to estimate the amount of year-to-year growth variations shared among trees of the same chronology.

Climate–growth relationships were assessed by means of response function (RF) analysis (Fritts 1976, Briffa and Cook 1990) using the software program CALROB of the PPPBASE package (Guiot and Goeury 1996). This program applies a bootstrap scheme to evaluate statistical significance and stability of the response function (Guiot 1991). In total 10,000 bootstrap replications were undertaken.

Mean monthly maximum temperatures and total monthly precipitation data from two meteorological stations were collected. Maximum temperatures ($T_{max}$) were used as they produced more significant results than mean or minimum temperatures (Carrer 1997). The weather stations are situated very near to the sample areas. For area A, the station is located 3 km away at Falzarego Pass, 1985 m a.s.l., and for area B, 15 km distant at Rolle Pass, 2004 m a.s.l. (Table 1). In the RF, 24 independent variables were used and sequenced according to a ''biological'' year frequently adopted for studies of alpine species (Ettl and Peterson 1995, Tessier et al. 1995, Nola 1996), which starts from October of the year prior to growth ($t - 1$) and continues to September of the year of growth ($t$). A minor difference in reference periods (1926–1993 for area A, 1927–1994 for area B) meant that the matching of climate and tree-ring data was not identical for the two areas. Response functions were computed for each age-class mean chronology and for each tree independently to verify possible bias due to sample stratification.

A parametric ANOVA $F$ test was used to assess age-class differences among the most significant climate–growth relationships. A nonparametric Kruskal-Wallis test was performed when the basic assumptions of normal distribution and homogeneity of variances were not met through the Shapiro-Wilk's $W$ test and the Bartlett's chi-square (Zar 1999). A generalization of the Tukey's HSD test (Spjotvoll and Stoline 1973) and the nonparametric $Q$ test (Dunn 1964, Zar 1999), both designed for unequal samples size, were adopted for post hoc testing.

## RESULTS

Chronology statistics are summarized in Table 2. The mean ring-width values (MRW) show that both species

TABLE 3. Age-class response functions parameters.

| Species | Age class (yr) | $r^2$ | Mean $r^2$ | $r/s$ ($P$) | %ST ($n$) |
|---|---|---|---|---|---|
| *Larix decidua* | <100 | 0.48 | 0.46 | 0.81 (0.42) | 8 (5) |
| | 101–200 | 0.62 | 0.54 | 1.90 (0.058) | 20 (7) |
| | 201–300 | 0.66 | 0.60 | 2.66 (0.008) | 55 (27) |
| | >300 | 0.68 | 0.61 | 3.36 (0.0008) | 63 (12) |
| *Pinus cembra* | <150 | 0.63 | 0.53 | 2.22 (0.026) | 6 (1) |
| | 151–250 | 0.64 | 0.53 | 2.89 (0.004) | 29 (17) |
| | 251–350 | 0.66 | 0.53 | 3.16 (0.002) | 39 (9) |
| | >350 | 0.70 | 0.55 | 3.54 (0.0004) | 43 (3) |

*Notes:* Abbreviations are: $r^2$, coefficient of determination; mean $r^2$, mean coefficient of determination obtained averaging all the corresponding values of single-tree response functions; $r/s$ ($P$), mean multiple correlation coefficient divided by its standard deviation and the corresponding $P$ value of the 10 000 bootstrap replications response function; %ST ($n$), percentage and the corresponding number of trees with a significant response function.

have a biological–geometrical trend decreasing with age. The reduction (up to 57% in *P. cembra* and 55% in *L. decidua*) is almost the same, although the growing rate of *P. cembra* is nearly double that of *L. decidua*.

Other statistics confirm behavioral differences between the two species: *P. cembra* displays highly homogeneous values in the four age classes, whereas *L. decidua* shows a more coherent increasing pattern with age in the majority of the calculated parameters, except for the first-order serial autocorrelation (AC) and the standard deviation obtained by averaging each single-tree series (SDT). The low AC values denote an efficient removal of the low-frequency persistence present in raw tree-ring series in all age classes of *P. cembra* and in the two oldest classes of *L. decidua*. A significant amount of autocorrelation was still retained in the indexed chronologies of the first two classes of *L. decidua*. For a more suitable comparison, autoregressive modeling was not applied to those series and the residual autocorrelation was preserved.

Response function analysis indicates that climate accounts for a high amount of variance in tree-ring width (Table 3). For *L. decidua*, both parameters ($r^2$ and mean $r^2$ [mean coefficient of determination obtained averaging all the corresponding values of single-tree response functions]) have similar trends, and their values increase substantially from younger to older age classes (from 0.48 and 0.46 to 0.68 and 0.61, respectively). Significance values ($r/s$ [mean multiple correlation coefficient divided by its standard deviation] and $P$) confirm this tendency: in the youngest AGC response function is not significant, but almost reaches the 95% threshold in the second class and is highly significant in the two oldest classes. The situation does not change with the single-tree responses; the percentage of individuals with a globally significant response function (%ST) is below 10% for the youngest class, but drastically increases in the older classes up to 63%.

The results for *P. cembra* confirm the presence of an overall age-related trend, but some differences can be observed in the variables (Table 3). For example, $r^2$ ranges between 0.63 and 0.70, whereas mean $r^2$

reaches 0.53 in all AGC. In the older age classes, the significance of response functions is increasingly high, and all classes have values greater than the 95% level. The %ST also increases from younger to older AGC, as for *L. decidua*, but at lower rates.

The RF profiles of *L. decidua* (Fig. 1A) show that the influence of climate on growth is mainly concentrated in late winter/early spring (negative effects on growth were observed especially in April) and summer (positive effects occurred particularly in June) (Carrer 1997, Carrer et al. 1998). For these periods, climate sensitivity increases with age, whereas for nonsignificant parameters, responses are similar among the different classes. However, if the %ST profile is considered (Fig. 1B), a relevant age-dependent relationship is detected for maximum April and (particularly) June temperature. In the latter case, the percentage of trees with significant RF increases from <50% in the first age class to 100% in the third and fourth age classes. In *P. cembra*, RF profiles are uniform among age classes (Fig. 2A), but there is a higher sensitivity to precipitation (negative effect of June) and a slightly delayed temperature influence (positive effect of July) with respect to *L. decidua*. The age effect is again very clear, but %ST values in pine are somewhat lower than in *L. decidua* (Fig. 2B).

In order to more efficiently test the climate influence within the different age classes, ANOVA and post hoc analyses was applied, using the monthly variables in which %ST attained values >50% in at least one age class (Figs. 1B and 2B) and $r^2$, which concisely expresses the amount of climate variability retained in tree-ring width. For example, the four variables analyzed for *L. decidua* (maximum temperature of April, June, July, and $r^2$) show very significant differences ($P < 0.01$ and 0.005) between the age classes, with the highest values being for June temperatures.

The most significant differences between classes occur when trees older and younger than 200 years are compared. Significant results were occasionally found for the first two classes (June $T_{max}$ and $r^2$) but none for the two oldest (Table 4). In *P. cembra*, there are sig-
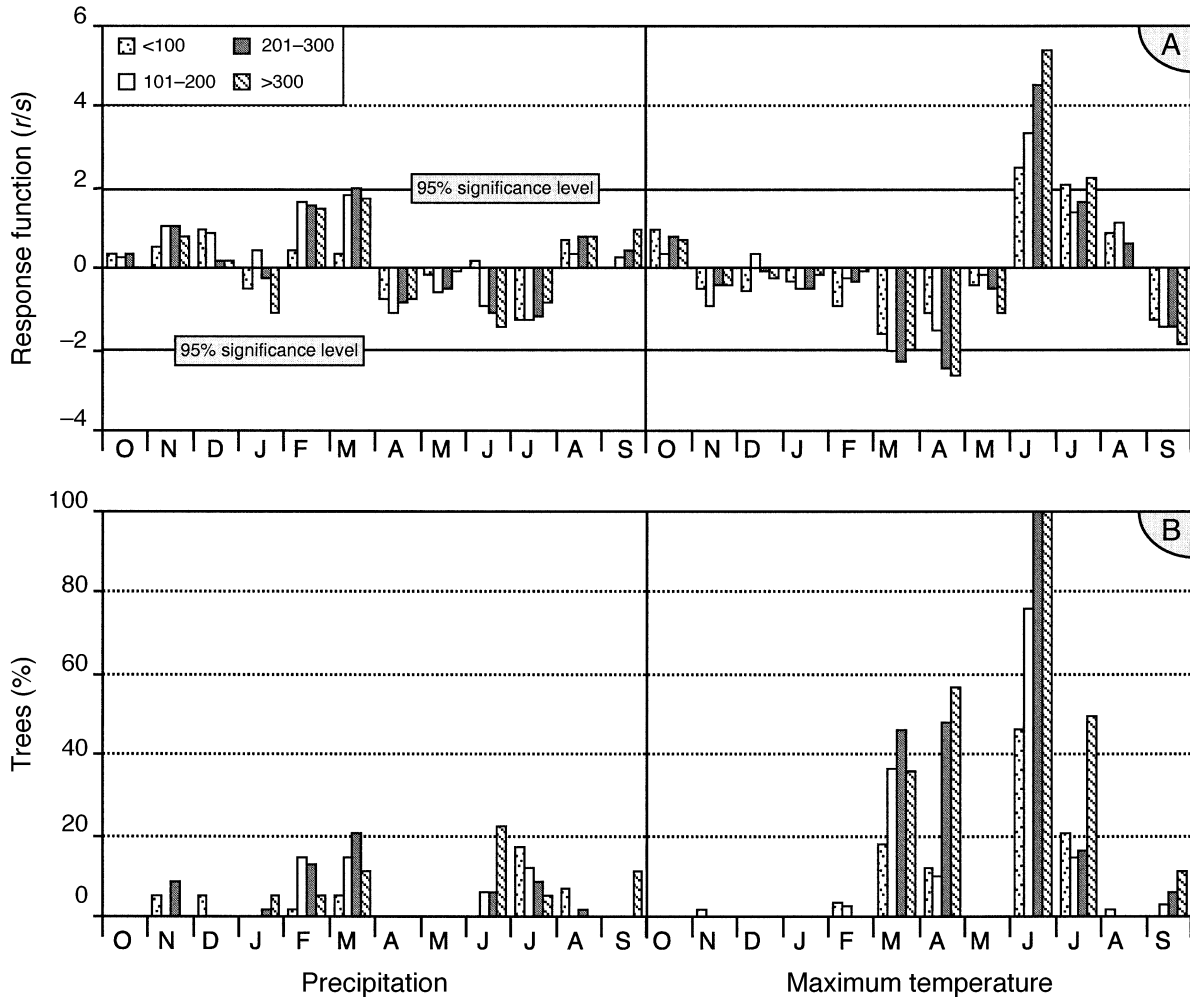
Fig. 1. (A) *Larix decidua* age-class response functions, *r/s*, the partial regression coefficients divided by their standard deviations obtained after the bootstrap replications. These values express the significance of monthly parameters. (B) Percentage of trees with significant monthly regression coefficients for each age class.

nificant differences for July, August, and September maximum temperatures (Table 4). Post hoc tests for *P. cembra* denote much lower differences between groups, but the pattern, although less evident, seems quite similar to that of *L. decidua*, the only significant values being those between non-neighbor groups (i.e., 1 vs. 3 and 1 vs. 4; Table 4).

These results are illustrated in scatter plots in which the main variables used for previous tests are plotted against tree age (Figs. 3 and 4). The overall trends of June $T_{max}$ and $r^2$ in *L. decidua* are positive. However, for the first two age classes (up to 200 years) the trend is clearly increasing, whereas for the third and fourth classes (over 200 years), it is much weaker or even nonexistent. Similar patterns can also be observed between total tree height and age (Fig. 3C). In *P. cembra* only July $T_{max}$ out of three variables used shows a slightly significant trend (Fig. 4C).

## DISCUSSION

The data illustrate two main points: that the growth responses of both species to climate are related to tree age and that the patterns of influence are not fully consistent in *L. decidua* and *P. cembra*. These inferences should be considered in the context of the common biophysical environment, but different growth strategies, of the two species.

*L. decidua* and *P. cembra* frequently form mixed forests. *L. decidua* is a deciduous, shade-intolerant species, and it is able to maintain a high photosynthetic rate throughout the whole growing season due to summer osmoregulation (Badalotti et al. 2000). *P. cembra* is evergreen, relatively shade-tolerant, and appears to reduce water loss by maintaining lower stomatal conductance than *L. decidua* at constant weather conditions (Tranquillini 1979, Anfodillo et al. 1998). Both species, as expected and regardless of ecological or site differ-
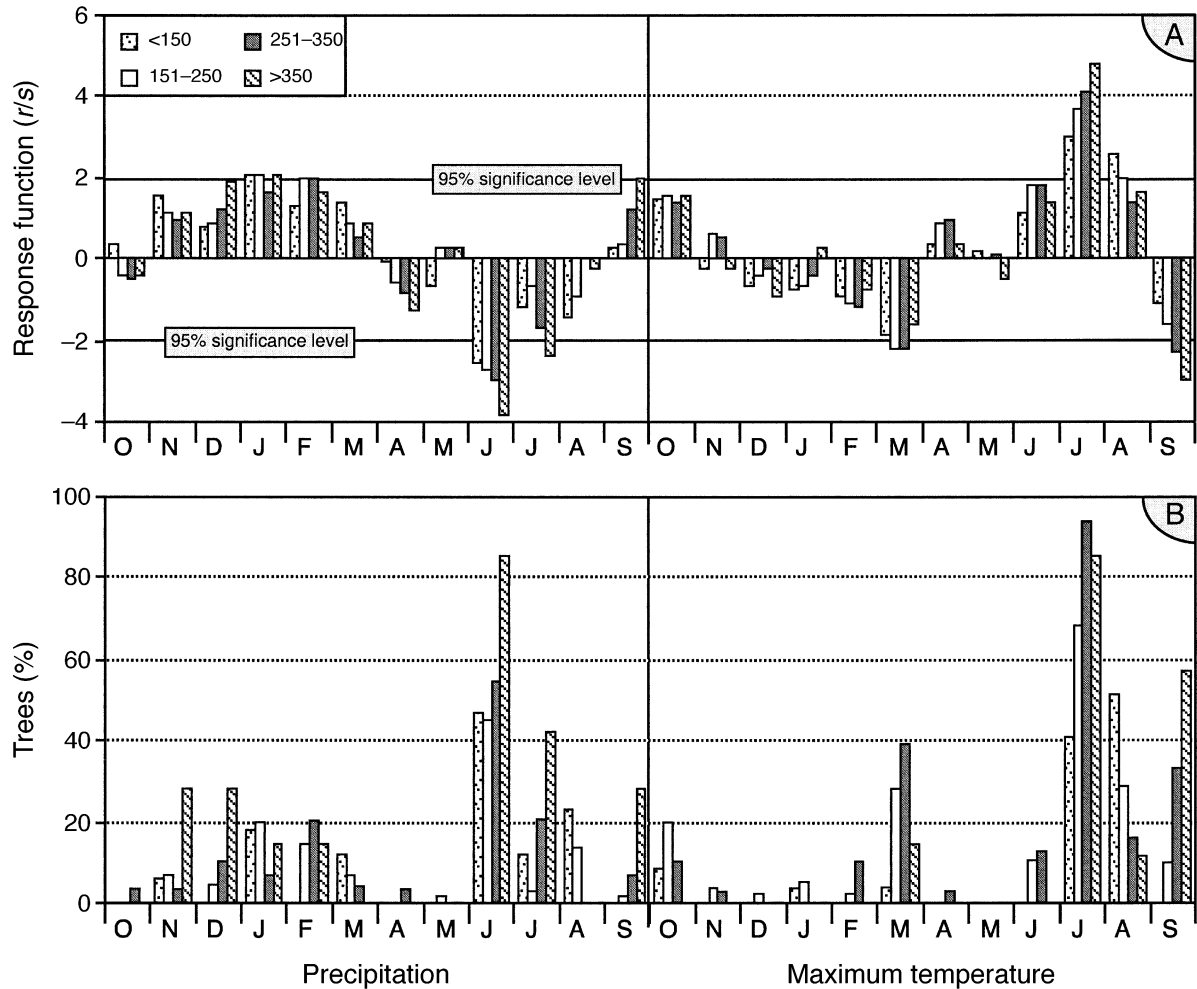
FIG. 2. (A) *Pinus cembra* age-class response functions, *r/s,* the partial regression coefficients divided by their standard deviations obtained after the bootstrap replications. These values express the significance of monthly parameters. (B) Percentage of trees with significant monthly regression coefficients for each age class.

TABLE 4. Results of parametric (*F*) or nonparametric (*H*) ANOVA and corresponding post hoc tests for the selected variables.

| Species and variable | *F* or *H* | 1 vs. 2 | 3 vs. 4 | 1 vs. 3 | 2 vs. 3 | 1 vs. 4 | 2 vs. 4 |
|---|---|---|---|---|---|---|---|
| *Larix decidua* | | | | | | | |
| Temperature April | 16.1*** | | | *** | *** | *** | *** |
| Temperature June | 41.5*** | ** | | *** | *** | *** | *** |
| Temperature July | 6.1** | | | | | * | *** |
| *r*² | 28.2*** | *** | | *** | *** | *** | * |
| *Pinus cembra* | | | | | | | |
| Precipitation June | *5.7* | | | | | | |
| Temperature July | *13.2*** | | | * | | ** | |
| Temperature August | *7.9* | | | | | | |
| Temperature September | *14.8** | | | * | | ** | |
| *r*² | *1.4* | | | | | | |

*Notes:* For both species, age classes are coded from 1 (youngest) to 4 (oldest). The degrees of freedom of the among-groups and within-groups comparisons for *Larix decidua* and *Pinus cembra* are 3, 131 and 3, 113, respectively. Nonparametric (*H*) ANOVA results are in italics.
    * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

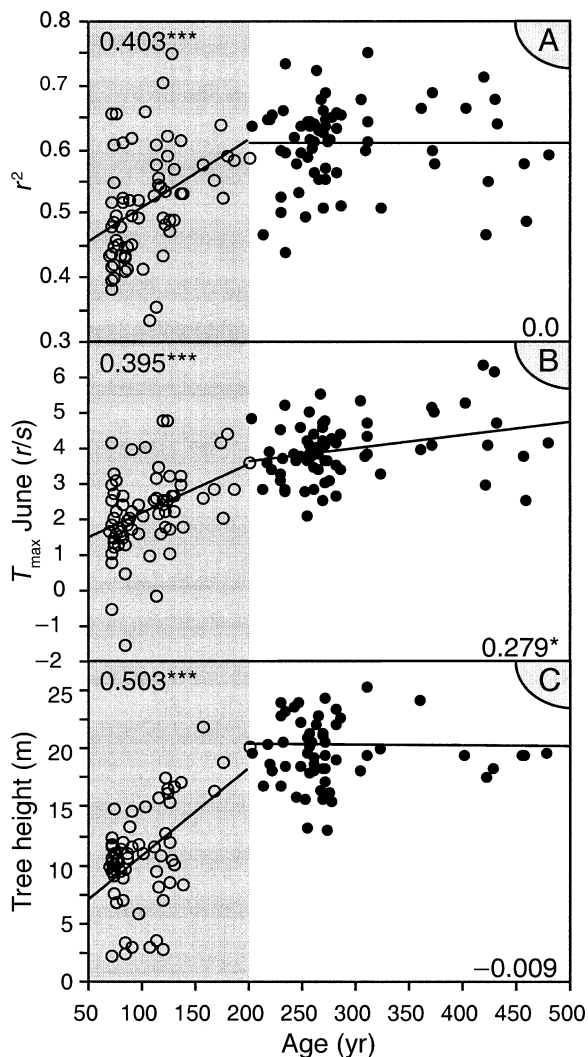FIG. 3. *Larix decidua* tree age relationships with (A) response function $r^2$, (B) partial regression coefficient of June maximum temperature, and (C) tree height. Correlation coefficients for trees younger and older than 200 years (*$P < 0.05$; *** $P < 0.001$) are indicated at top left and bottom right corners of each panel, respectively.

ences, experience a reduction of >50% in mean ring-widths from younger to older trees (MRW; Table 2), showing a common response of tree-ring growth to the age effect. Their high frequency statistics (MS and SD) reach typical values for these species at high altitude sites (Rolland et al. 1998, Motta and Nola 2001), with *L. decidua* greater than *P. cembra*.

Mean sensitivity also increases with age, especially in *L. decidua*, as does the mean correlation between tree chronologies (CBT) and the variance accounted for the first principal component (PC1). This suggests that the single series of *L. decidua* cross-dates more successfully and retains a higher amount of common signal with increasing age. Supporting evidence comes from a previous study on spatial distribution of tree-
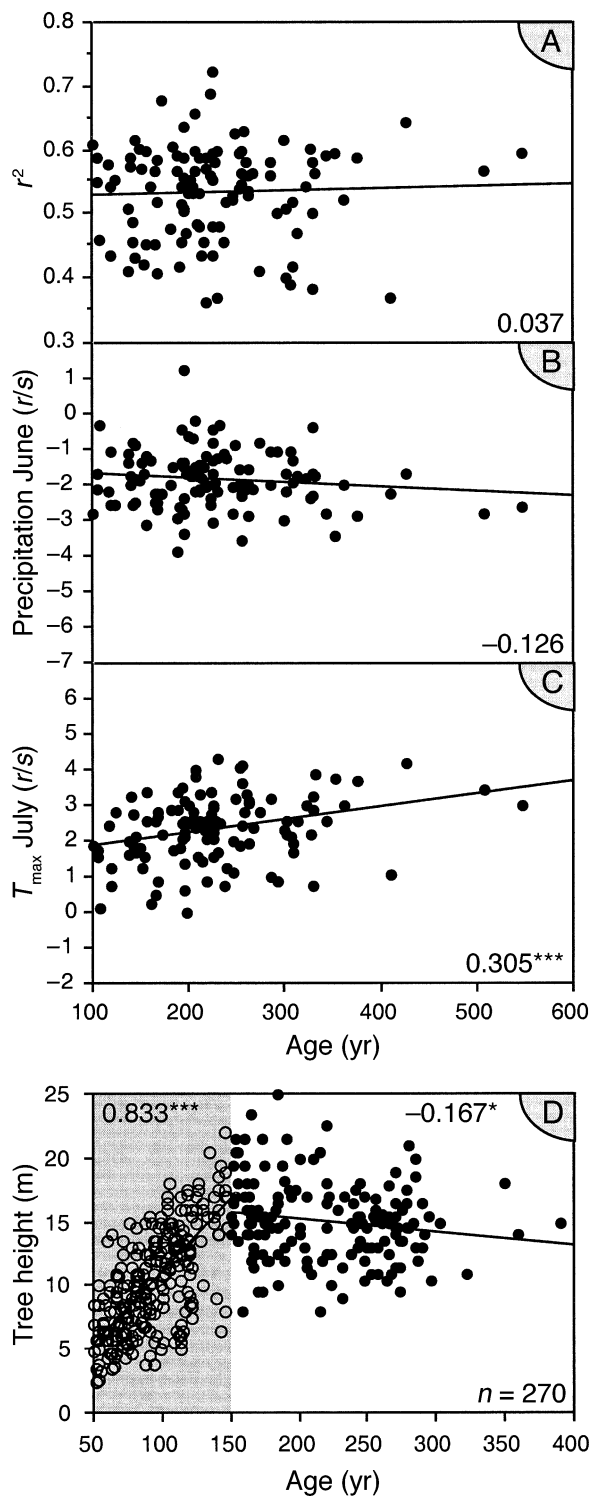


FIG. 4. *Pinus cembra* tree age relationships with (A) response function $r^2$, (B) partial regression coefficient of June precipitation, (C) July maximum temperature, and (D) tree height. In panels A, B, and C, correlation coefficients are indicated at the bottom right corner. In panel D, the correlation coefficients for trees younger and older than 150 years (* $P < 0.05$; *** $P < 0.001$) are at the top left and top right corner, respectively. The number of trees used is indicated at bottom right corner.

ring parameters in the same environment, which determined that young (<100 years) *L. decidua* trees are weakly influenced by climate variability (Carrer and Urbinati 2001). In North America, on *Abies lasiocarpa* (Hook.) Nutt., Ettl and Peterson (1995) found similar results with a CBT of 0.325 to 0.518 and PC1 of 36 and 54, respectively, in younger and older trees.

In *P. cembra*, tree-ring parameters are generally similar throughout the four classes, and the age effect is not as clearly expressed as in *L. decidua*. This could be partly explained by the absence at site B of trees younger than 100 years old and also by the different patterns observed in tree height and age relationships, in which the maximum height value occurs some decades before that of *L. decidua*. Data from several studies on similar treeline sites of the Italian Alps (D. Favero, *unpublished data,* and R. Motta, *unpublished data*) indicate that the height growth trend of *P. cembra* is similar to that of *L. decidua*, but reaches its maximum some 50 years before (Fig. 4D).

Tree-ring statistics can only indirectly estimate the influence of climate, whereas a better assessment of species behavior can be achieved by calculating specific climate–growth relationship parameters. Response function profiles and statistics (Table 3, Figs. 1 and 2) confirm that *P. cembra* and especially *L. decidua* are sensitive to climate influence, which increases with age ($r^2$, $r/s$, and %ST). The climate–growth relationships did not change with age, in contrast to the findings of Szeicz and MacDonald (1994, 1995) in a subarctic environment. This indicates that, throughout most of their life-span, the trees in this study are reacting to the same climate variables and that these variables become more limiting as trees become older. This pattern is observed clearly for $T_{max}$ in the months of June for *L. decidua* and July for *P. cembra*. The influence of age on climate sensitivity is not a constant, as shown by ANOVA post hoc tests. The nonsignificant differences between responses for the two oldest age classes (3 and 4; Table 4) suggest there are different phases in the long-term dynamics of the climate–growth relationships.

Among the different functional processes linked to tree growth, the role of hydraulic limitation (Ryan and Yoder 1997) could at least partially explain how age may control the climate sensitivity of trees. The total resistance of the hydraulic pathway increases as the tree approaches its maximum height due to a combination of factors including gravity, a longer and more complex hydraulic path length through stems and branches, and reduced allocation to roots. Increases in hydraulic resistance could also lower the supply of water for transpiration inducing earlier stomatal closure to prevent loss of xylem function through cavitation (Ryan et al. 1997, Ryan and Yoder 1997), which in turn limits stomatal conductance and gaseous exchange (Yoder et al. 1994, Hubbard et al. 1999, Kolb and Stone 2000).

Hydraulic constraints are increasingly limiting as trees age, thus inducing stressful conditions in older individuals. Near the treeline, the consequences include higher climate sensitivity in stressed trees and a more prominent growth-climate signal retained in tree rings (Fritts 1976, Travis et al. 1990, Shiyatov et al. 1996). Conversely, younger trees are more able to face adverse weather conditions due to the longer lasting stomatal opening inducing higher assimilation. In severe environmental conditions, their ''overspending'' strategy, with regard to photosynthesis and transpiration, could ensure the growth potential necessary for tree establishment and for overcoming competition, but at the cost of a greater mortality risk (Bond 2000) and, from the dendroecological point of view, of a weaker recording of the climatic signal in tree rings. This may explain the analogous distributions of $r^2$, June $T_{max}$ ($r/s$), and tree height data vs. tree age observed for *L. decidua*. Trends are very similar for the three variables and they all shift, after the age of 200 years, from an increasing to a constant pattern (Fig. 3). The same model works less well for *P. cembra*, possibly because the diverse chronological structure of the sample may give rise to a weaker pattern (Fig. 4). Most of the sampled *P. cembra* trees are older than 150 years and feature a steady height growth trend.

The response function statistical results are similar throughout the different age classes. However, the most important RF parameters in both species (June and July $T_{max}$ for *L. decidua* and *P. cembra*, respectively; Figs. 3B and 4C) express, at different levels of strength, a positive and significant correlation with age. Indeed, even if height growth is maximized at an early stage of development, diameter growth and crown expansion persist in older trees, increasing their atmospheric coupling and climate sensitivity (Carrer 1997).

## Conclusions

The results of this study suggest that climate–growth relationships of the two investigated species are partially controlled by age. The interpretation of the patterns shown by *L. decidua* and *P. cembra* is not straightforward, as there are differences in the life history of the two species and in the age structures of the sampled stands. As these findings relate to a limited geographical area and a specific biological dataset, they should not be applied to other regions or species. However, such patterns may well occur elsewhere, and they may influence both the estimation of climate change impact on forest dynamics and biomass accumulation and the reconstruction of past climate variability.

It is now well known that changes in climatic conditions can affect forest productivity, with remarkable differences (gains or losses) at biome or regional level (IPCC 2001). A forest dynamics modeling approach at high spatial–temporal resolution could fail to provide reliable predictions of climate controlled tree-ring growth if its potential variability over time has not been

assessed. The transfer of climate–growth functions for reconstructions of past conditions could be similarly biased. Tree-ring series are by far the most accessible proxy data and have provided much of the baseline information in climate change studies (Beniston 2002). Due to the inherent complexity of tree ring-based climate reconstruction, tree-ring data are often considered most useful when integrated with other types of information in ''multi-proxy'' estimates of past temperature changes (IPCC 2001). For example, tree-ring records are significant (but not unique) evidence that the 1990s warming of the northern hemisphere is exceptional when compared with the last 1000 years (Hughes 2002).

The value of dendroclimatology could increase further in the near future if a clearer understanding of the mechanisms that induce tree-ring variability could be achieved. Minor adjustments to current dendroclimatological sampling procedures could also reduce the possible bias and provide more reliable results. Standard sampling protocols usually imply that selection occurs among the dominant (and probably older) trees of the investigated stands (Fritts 1976, Schweingruber et al. 1990). This is based on the assumption that trees with reduced competition are more coupled with atmosphere and should provide a higher and clearer amount of common signal recorded. The results of this study confirm that the climate signal is maximized in older trees, but also that a sampling procedure non-stratified by age (especially in multi-aged forests) could lead to biased mean chronologies due to the higher amount of noise present in younger trees. The consequent ecological interpretations of climate–growth relationships or climate reconstructions will be less robust.

The phenomenon of age-controlled climate response is complex, as the heterogeneous outcomes of a small number of similar studies have demonstrated. Because there are important ecological and climatological implications at a range of temporal and spatial scales, the issue should be further assessed through detailed studies of other species and regions.

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