Trees (1998) 13:40–53

ORIGINAL ARTICLE

Christian Rolland · Véronique Petitcolas
Richard Michalet

Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750

Received: 30 October 1997 / Accepted: 4 May 1998

Abstract Changes in radial growth of the four coniferous species growing in the French Alps near the upper treeline are investigated. Thirty-seven populations of Norway spruce [*Picea abies* (L.) Karst.], European larch (*Larix decidua* Mill.), Swiss stone pine (*Pinus cembra* L.) and mountain pine (*Pinus uncinata* Mill. ex Mirb.) were sampled by taking 1320 cores and analysing tree-ring widths. Sites were chosen in various climatic conditions (macroclimate and aspect) and on two kinds of bedrock in order to take into account the ecological behaviour of these species. Belledonne, Moyenne-Tarentaise, Haute-Maurienne and Briançonnais areas were sampled along increasing gradients of summer aridity and winter continentality. The calculation of time series after removing the age trend brings strong evidence for an increase in radial growth during the two last centuries, but with different stages and fluctuations for each species. This growth trend is significantly enhanced since 1860 for the spruce, and since 1920 for the two pine species. Furthermore, it also appears on *Larix decidua* with the same pattern despite periodical growth reduction due to attacks of the larch bud moth (*Zeiraphera diniana* Gn.). The analysis of ring-widths at a given cambial age reveals that this enhanced phenomenon is observed especially during the tree's early years (25–75 years). The analysis of four regional climatic series, and three longer series of temperature (in farther single sites) reveals synchronous decadal fluctuations and an evident secular increase in minimum temperatures (especially in January and from July to October), that may be involved in tree-growth enhancement. Thermic amplitudes are significantly reduced during the whole growing period, what is more pronounced in Belledonne, the most oceanic region. Long term growth changes are well described by stepwise regression models, especially for the pine species. These models involved both a linear trend (CO_2 concentration or N-deposition) and low frequency of Turin monthly temperatures. However, they show different patterns than those observed from response functions at a yearly scale.

Key words Global change · Timberline · Dendroclimatology · Tree-ring · Conifers

Introduction

Since the study of La Marche et al. (1984), many other dendroclimatological studies were carried out on the effect of CO_2 and air temperature rise on radial tree growth (Innes 1991; Ceulemans and Mousseau 1994; Becker et al. 1994; Mortier 1995). After removing the age trend, most of them observed important radial increases in ring width in different environments (Ecocraft/ICAT 1994), both for deciduous species such as *Quercus petraea, Q. robur*, and *Fagus sylvatica* L. (Becker et al. 1995), and for coniferous species like *Pinus nigra* (Lebourgeois and Becker 1996), *Abies alba* (Becker et al. 1995), *Pinus cembra* (Nicolussi et al. 1995), *P. uncinata* (Rolland 1996) or *Larix decidua* (Belingard 1996).

However, most of these field works have been done at low elevations where forest management, recent human disturbance, and competition among trees also have strong effects on growth.

Human impact on tree growth is supposed to be less important at high elevation sites, characterized by low stand densities and reduced air pollution (Peterson et al. 1990). Moreover, subalpine forests or timberlines are near the abiotic ecological limits of the tree species that occur there, and they may react more strongly to climatic changes (Gale 1986; Graumlich 1991). For example, cold strongly limits tree growth near timberline, and thus global warming of the air may have a more significant effect.

Furthermore, few studies have examined a large number of timberline species simultaneously and specifically incorporated bioclimatic variation among sites (Petitcolas and Rolland 1996).

C. Rolland · V. Petitcolas · R. Michalet (✉)
Laboratoire des Ecosystèmes Alpins, Centre de Biologie Alpine, Université Joseph Fourier, BP 53 X, F-38 041 Grenoble, France
e-mail: Richard.Michalet@UJF-Grenoble.FR
Tel.: 04 76 51 46 00; Fax: 04 76 51 44 63

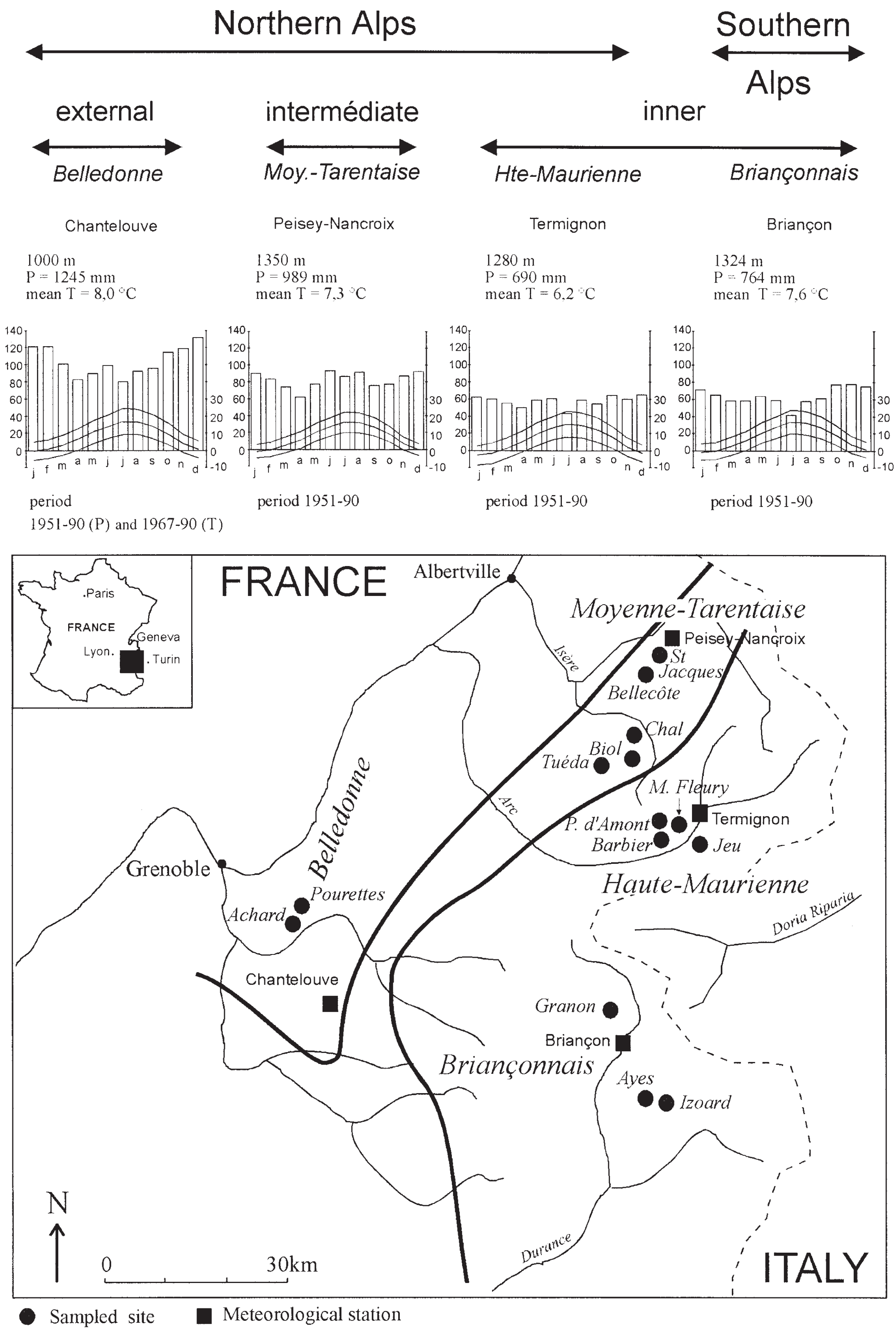


Fig. 1 Map of localisation of the sampled sites in the French Alps, in Belledonne, Moyenne-Tarentaise, Haute-Maurienne and Briançonnais areas. Climatic diagrams from four meteorological stations with mean monthly values of temperature (minimum, mean and maximum) in °C and precipitation in mm per month (1951–1990)

Fig. 2 Yearly variations of July monthly mean temperature in Lyon (1881–1990), low frequency at decadal scale (obtained with a moving average, *bold solid line*), and adjustment of a linear long term trend (*dashed line*)

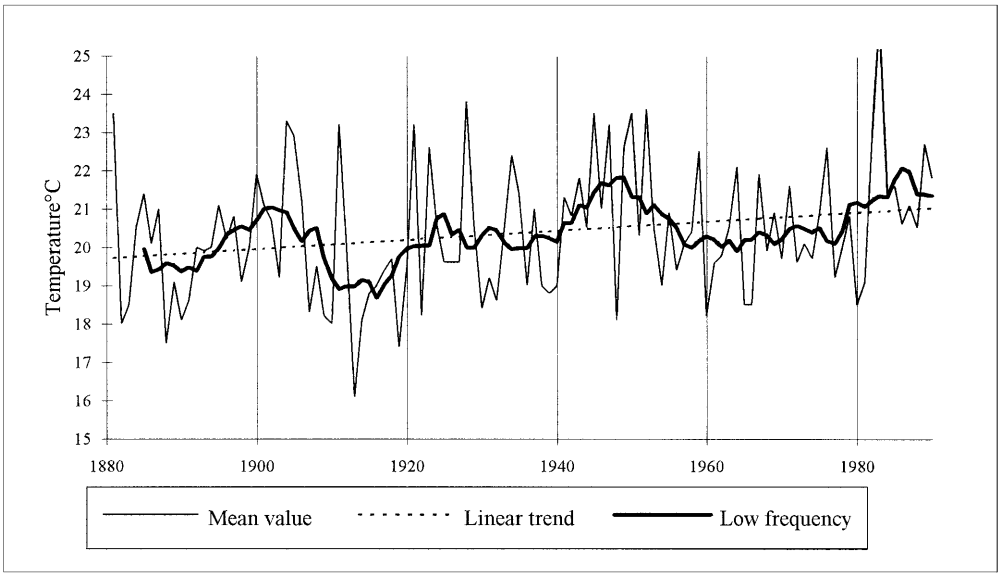


Table 1 Number of populations for four species on different sampling ecological conditions

Number of populations		Bed rock		Aspect	
Species	Sites	Calcareous	Non calcareous	South	North
Picea abies	8	3	5	5	3
Larix decidua	7	4	3	2	5
P. cembra	12	4	8	5	7
P. uncinata	10	6	4	5	5
TOTAL	**37**	**17**	**20**	**17**	**20**

Here we have analysed long term trends in the radial growth of four conifers growing near timberline in the French Alps. These four species, *Picea abies*, *Larix decidua*, *Pinus cembra* and *P. uncinata*, are the dominant large trees at timberline throughout the Alps. These species were analysed over a range of substrate and topographic conditions, and in four different climatic regions along a precipitation gradient. It ranges from areas characterised by oceanicity (high amount of precipitation during the whole year) to regions with summer drought and winter continentality due to a rainshadow effect, that spans the large differences in climates in the western Alps (Pache et al. 1996).

Materials and methods

Sampling species and areas

The four main coniferous species growing near the timberline in the French Alps were each sampled in various ecological conditions at the upper forest line, from 1750 to 2300 m. Each species was sampled in 7–12 different populations. For precise dendrometric features of these populations see Petitcolas et al. (1997).

Eight populations of Norway spruce (*Picea abies* Karst.), seven populations of European larch (*Larix decidua* Mill), 12 populations of Swiss stone pine (*Pinus cembra* L., Swiss stone pine), and 10 populations of mountain pine (*Pinus uncinata* Mill. ex Mirb.) were sampled (Fig. 1). The sites are located on calcareous or non-calcareous bedrock and either on northern or southern slopes (Table 1).

Five populations were sampled in the Belledonne mountains (northern external Alps), 10 in the Moyenne-Tarentaise (northern intermediate Alps), 10 in the Haute-Maurienne (northern inner Alps) and 12 in the Briançonnais (southern inner dry Alps) along two gradients of increasing summer aridity and winter continentality (Pache et al. 1996).

Core sampling and measurements

In each population, 12 dominant trees were sampled at approximately 1.30 m above the ground with a Presler increment borer, taking 3 cores per tree in different directions. All the individual ring-widths were measured with an accuracy of 0.01 mm, and visually cross-dated using a visual method with skeleton plot and checked by cross-correlation calculation and pointer years analysis (Schweingruber 1996). When a core did not reach the centre of the tree, the number of missing rings was estimated and added to the number of measured rings to obtain the corrected tree age. The details for elevations, locations of forests, number of trees, cores, and ring-widths are presented in Table 2. We analysed 1320 cores and a total of 185 667 ring-widths (Table 3).

Calculations and methods

We used two dendroclimatological methods. First, the average growth trend curve as a function of tree age was calculated for each species (Becker 1988). This is done by averaging all measured ring-widths formed at the same cambial age for all different sites for a given species (Petitcolas et al. 1997). These curves are then used for standardising the data, by dividing each measured ring-width at a given age of formation by the corresponding mean growth value at the same age. The growth indices that are obtained are expressed as a percent. Second, the measured values are examined without any standardisation, by plotting the ring-width as a function of the year of ring formation for several cambial ages (25, 50, 75, 100, 125 and 150 years; Becker 1987).

Climatic data

In order to analyse the possible trends in the climatic data, regional series were obtained by averaging several single meteorological

Table 2 Ecological growth conditions of the 37 sampled populations of four coniferous species in four alpine areas. Forest name, slope (°), aspect, elevation (m), latitude (°N) and longitude (°E), and numbers of sampled trees and cores

Regions	Belledonne			Moyenne-Tarentaise				Haute-Maurienne				Briançonnais			TOTAL				
Populations	5			10				10				12			37				
Species	*Picea*	*P.cem*	*P.unc*	*Picea*	*Larix*	*P.cem*	*P.unc*	*Picea*	*Larix*	*P.cem*	*P.unc*	*Larix*	*P.cem*	*P.unc*	*Picea*	*Larix*	*P.cem*	*P.unc*	
Populations	2	2	1	3	2	3	2	3	1	3	3	4	4	4	8	7	12	10	37
Trees	24	24	12	36	24	37	24	36	12	34	36	47	48	48	96	83	143	120	442
Cores	72	69	36	108	72	111	72	108	36	100	108	141	144	143	288	249	424	359	1320
Rings	8535	10675	5246	13935	9167	10143	6567	17369	6515	13580	18226	24416	22248	20030	39839	40098	56646	50069	186652
Calcareous Bedrock (South)																			
Name				TCAE			TCAP	MCAE			MCAP	BCAM	BCAA	BCAP					
Place				Chal			Chal	M. Fleury			M. Fleury	Izoard	Ayes	Izoard	2	1	1	3	7
Exposure				SW			S/SW	S			S	W/SW	SW	W/SW					
Altitude				2050			2050	2050			2150	2250	2300	2250					
Latitude				45°25′			45°25′	45°15′			45°15′	44°49′	44°50′	44°49′					
Longitude				6°41′			6°41′	6°46′			6°46′	6°44′	6°41′	6°44′					
Trees				12			12	12			12	12	12	12	24	12	12	36	84
Cores				36			36	36			36	36	36	36	72	36	36	108	252
Rings				5654			4077	5570			7833	1851	3104	2760	11224	1851	3104	14670	30849
Calcareous Bedrock (North)																			
Name					TCUM	TCUA	TCUP	MCUE	MCUM	MCUA	MCUP	BCUM	BCUA	BCUP					
Place					Bellecôte	Bellecôte	Biol	Le Jeu	Le Jeu	Le Jeu	Le Jeu	Izoard	Izoard	Izoard	1	3	3	3	10
Exposure					N/NE	N/NE	N	NW	NW	NW	NW	N/NE	N/NE	N/NE					
Altitude					2050	2050	1950	2100	2100	2100	2100	2150	2150	2150					
Latitude					45°29′	45°29′	45°23′	45°14′	45°14′	45°14′	45°14′	44°50′	44°50′	44°50′					
Longitude					6°42′	6°42′	6°40′	6°48′	6°48′	6°48′	6°48′	6°44′	6°44′	6°44′					
Trees					12	13	12	12	12	10	12	12	12	12	12	36	35	36	119
Cores					36	39	36	36	36	28	36	36	36	35	36	108	103	107	354
Rings					3097	3631	2490	8278	6515	5739	7160	7866	7609	6626	8278	17478	16979	16276	59011
Non Calcareous Bedrock (South)																			
Name	ESAE	ESAA	ESAP	TSAE		TSAA		MSAE		MSAA		BSAM	BSAA	BSAP					
Place	Achard	Achard	Achard	Tuéda		Tuéda		Barbier		Barbier		Granon	Ayes	Granon	3	1	4	2	10
Exposure	S	S/SW	S/SW	S/SW		S		S/SW		S		SW	W/SW	S					
Altitude	1900	1950	1950	2000		2000		2000		2000		2250	2200	2300					
Latitude	45°07′	45°07′	45°07′	45°22′		45°22′		45°14′		45°14′		44°48′	44°50′	44°57′					
Longitude	5°54′	5°54′	5°54′	6°36′		6°36′		6°43′		6°43′		6°38′	6°41′	6°36′					
Trees	12	12	12	12		12		12		12		12	12	12	36	12	48	24	120
Cores	36	33	36	36		36		36		36		36	36	36	108	36	141	72	357
Rings	4670	5703	5246	3488		2726		3521		3580		7823	6253	3977	11679	7823	18262	9223	46987
Non Calcareous Bedrock (North)																			
Name	ESUE	ESUA		TSUE	TSUM	TSUA				MSUA	MSUP	BSUM	BSUA	BSUP					
Place	Pourettes	Pourettes		St Jacques	St Jacques	St Jacques				P. Amont	P. Amont	Granon	Ayes	Granon	2	2	4	2	10
Exposure	N/NE	N		N	N/NW	N/NW				NE	N/NE	N	N	N/NW					
Altitude	1750	1950		2000	2000	2000				2150	2100	2250	2300	2250					
Latitude	45°08′	45°08′		45°30′	45°30′	45°30′				45°15′	45°15′	44°48′	44°49′	44°57′					
Longitude	5°54′	5°54′		6°42′	6°42′	6°42′				6°43′	6°43′	6°38′	6°40′	6°36′					
Trees	12	12		12	12	12				12	12	11	12	12	24	23	48	24	119
Cores	36	36		36	36	36				36	36	33	36	36	72	69	144	72	357
Rings	3865	4972		4793	6070	3786				4261	3233	6876	5282	6667	8658	12946	18301	9900	49805

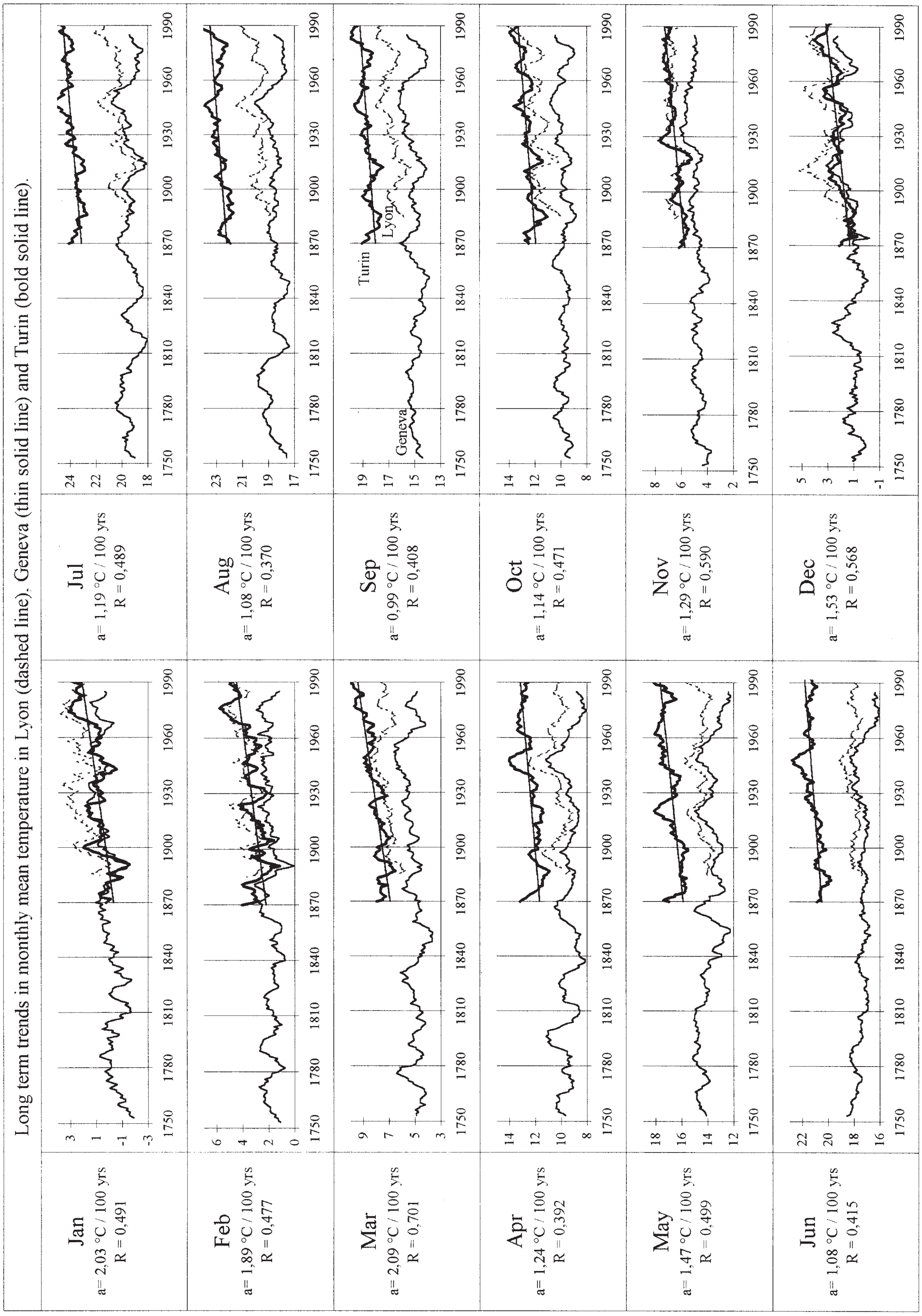


Fig. 3 Decadal scale trends in mean monthly temperatures in the long series of Lyon (1881–1990, France), Geneva (1753–1990, Switzerland) and Turin (1866–1994, Italy) calculated with moving averages. A linear long term trend is calculated for Turin monthly mean temperatures (*N*=125 years), with the slopes (a in °C/100 years) and R^2 values

Table 3 Total number of cores, rings and mean tree age for the four species

Species	Number of cores	Number of rings	Mean tree age (years)
Picea abies	288	39020	135
Larix decidua	249	40014	161
Pinus cembra	424	56646	134
Pinus uncinata	359	49987	139
TOTAL	1320	185667	141

series located in homogeneous climatic areas. This method is used to avoid local peculiarities of single sites and to obtain a regional chronology for a more extended area (Blasing et al. 1981). Five parameters were studied, the maximum (T_n) and minimum (T_x) monthly temperatures, the precipitation (P), the mean temperature (T_m), obtained by 1/2 (T_x+T_n) and the amplitude (T_x–T_n).

Four regional climatic series were calculated for the period 1946–1993 (48 years) in Belledonne (external Alps), Moyenne-Tarentaise (intermediate Alps), Haute-Maurienne and Briançonnais (inner Alps) (Fig. 1) with most of the time four single sites per regional chronology (for more details, see Petitcolas 1998).

Three longer time series were also provided by important stations around the studied area (Fig. 1):

1. Geneva (Switzerland) during the period 1826–1987 (with 162 years) for P, and during 1753–1990 (238 years) for T_m.
2. Turin (Moncalieri, Italy) 1864–1994 (131 years) for P, and 1866–1994 (129 years) for T_n, T_x, T_m (Di Napoli and Mercali 1996).
3. Lyon (France) 1921–1992 for P (72 years), and 1881–1990 (110 years) for T_x, T_n, T_m.

The common period 1866–1990 (125 years) was used to compare these three long series of temperature.

Comparisons of trends in climate and tree-ring

The hypothesis of a climatic trend influence on tree growth is tested using stepwise regression. We used at once low frequencies of Turin monthly minimum (T_n), maximum (T_x) and mean (T_m) temperature (Di Napoli and Mercali 1996) obtained with moving averages, and the year number (as shown on Fig. 3). For each species, only the three first steps of the stepwise regression are retained (Table 4 and Fig. 8).

Results

Trends in climatic data

Several authors have found an increase in temperature for western Europe (Hansen and Lebedeff 1987; Di Napoli and Mercali 1996) especially at high elevations (Bücher and Dessens 1991; Beniston et al. 1997) and for minimum temperatures (Diaz and Bradley 1997).

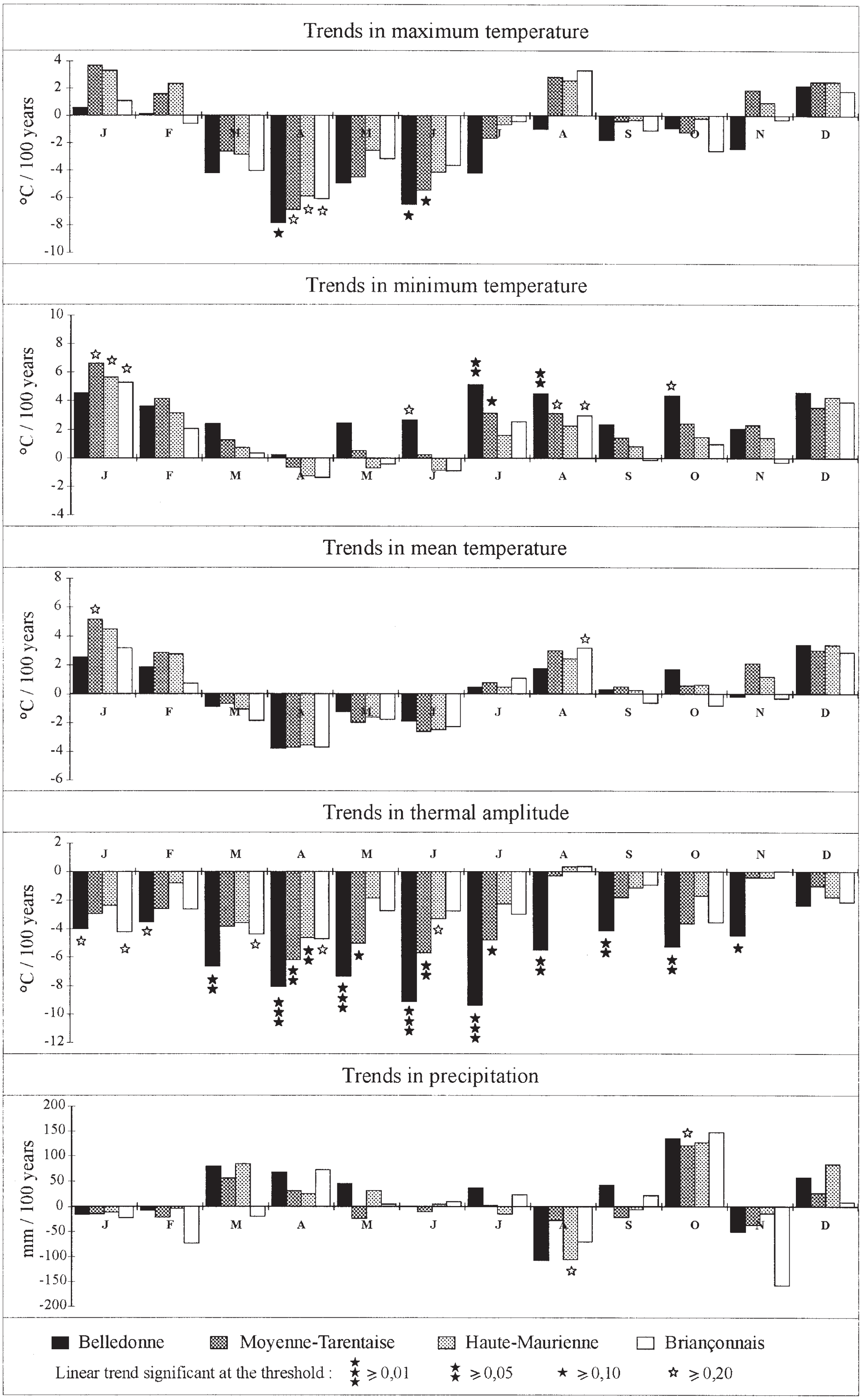
Trends in long series of climatic data (in Lyon, Geneva and Turin) are investigated by observation of the low frequencies of yearly variations, and by calculation of a linear trend between yearly data and time (in Turin). Figure 2 provides an example in Lyon for July mean monthly temperatures. A secular increasing trend appears with the linear adjustment with a slope of 1.18°C/100 years, but oscillations at decadal scale are revealed by the moving average (Di Napoli and Mercali 1996). For whole months, results are gathered in Fig. 3 in Lyon, as well as for two other meteorological stations (Turin and Geneva). All the months show secular positive trends in mean temperature, more pronounced from January to March. The increase in mean temperature is a global phenomenon since it appears for the three stations. Moreover, the decadal scale fluctuations are synchronous (in October for instance) despite the distances between the sites.

For the studied area, trends in minimum and maximum temperatures (T_n and T_x) are studied separately in the four regions during 1946–1993 (Fig. 4). Minimum temperatures increase for all the months, especially in July, whereas the maximum ones decrease from April to June. Consequently, the increase in the mean temperatures previously observed in long series is less pronounced. On the contrary, thermal amplitudes (T_x–T_n)

Fig. 4 Monthly increases in temperature expressed in °C/100 years, calculated by linear correlation between temperatures and time for the same period 1946–1993 (48 years) in four alpine valleys Belledonne, Moyenne-Tarentaise, Haute-Maurienne and Briançonnais. Significant results at different thresholds (*P* values) are indicated by different symbols. Results are given for minimum, maximum and mean temperatures, thermal amplitude and precipitation ▶

Table 4 Stepwise regression of long term changes in tree-rings using low frequency monthly climatic predictors. The year number and the temperatures of Turin were used, with minimum, maximum and mean values (Tn, Tx, Tm). The R^2-value of each model per species is given, with the number of steps, and coefficients of each model. (*N*=124 years, 1870–1993)

	Stepwise regression with 3 steps											
	Picea abies			*Larix decidua*			*Pinus cembra*			*Pinus uncinata*		
	R^2=0.75			R^2=0.66			R^2=0.90			R^2=0.84		
		Coeff	*T*-ratio		Coeff	*T*-ratio		Coeff	*T*-ratio		Coeff	*T*-ratio
Constant		–750			–601			–503			–206	
Step 1	Tx_Feb	0.5	13.3	Tm_Sep	20.2	7.7	Year	0.3	10.1	Tn_year	16.7	8.6
Step 2	Tx_Nov	–6.1	–5.5	Tx_Aug	15.5	7.3	Tx_May	–4.5	–6.5	Tx_Feb	–4.7	–6.8
Step 3	Tn_May	–6.9	–3.2	Tx_May	–4.9	–3.2	Tn_year	12.2	6.0	Year	0.1	4.7



Trends in maximum temperature
°C / 100 years
Trends in minimum temperature
°C / 100 years
Trends in mean temperature
°C / 100 years
Trends in thermal amplitude
°C / 100 years
Trends in precipitation
mm / 100 years
J F M A M J J A S O N D
Belledonne
Moyenne-Tarentaise
Haute-Maurienne
Briançonnais
Linear trend significant at the threshold : ≥ 0,01 ≥ 0,05 ≥ 0,10 ≥ 0,20

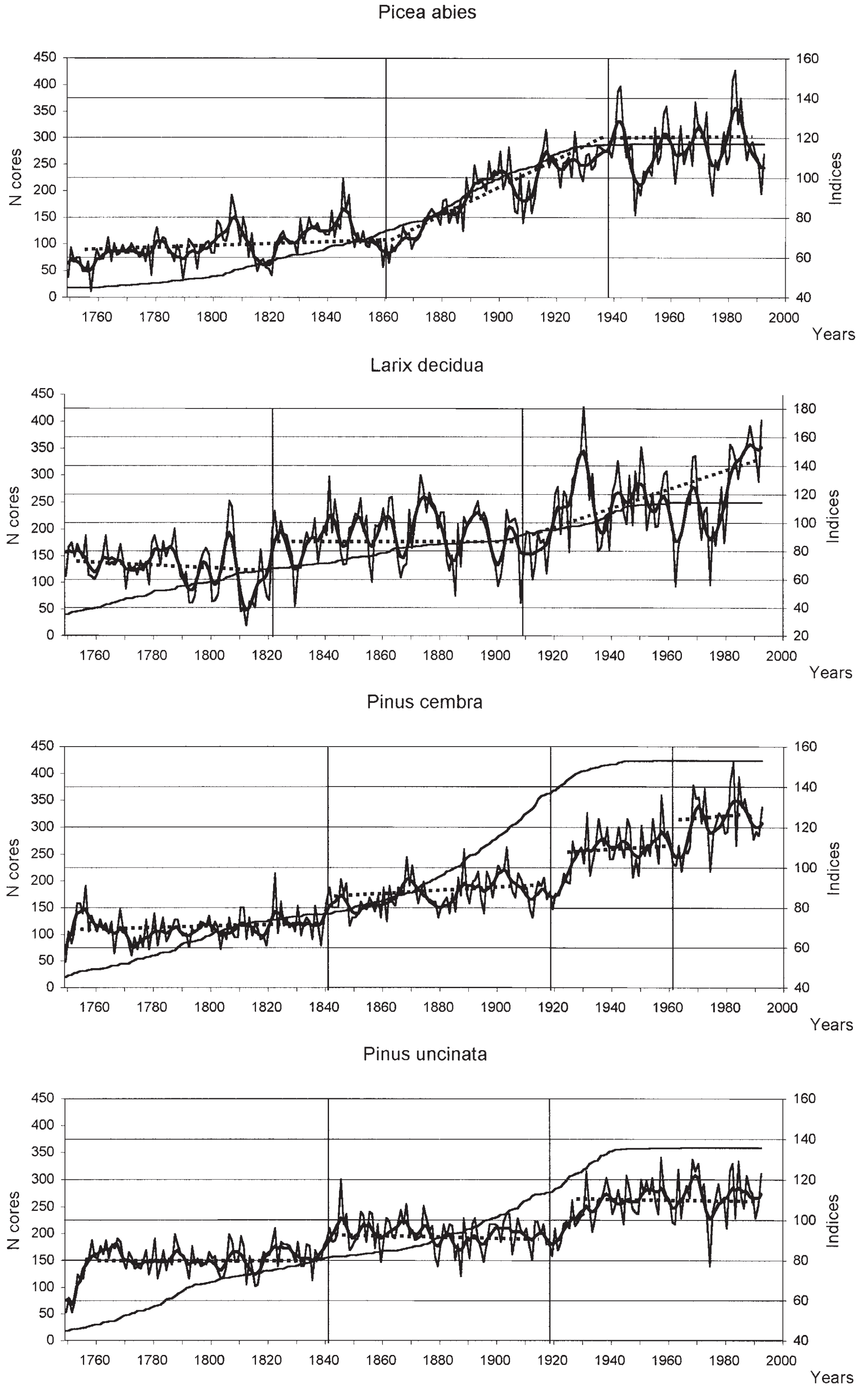
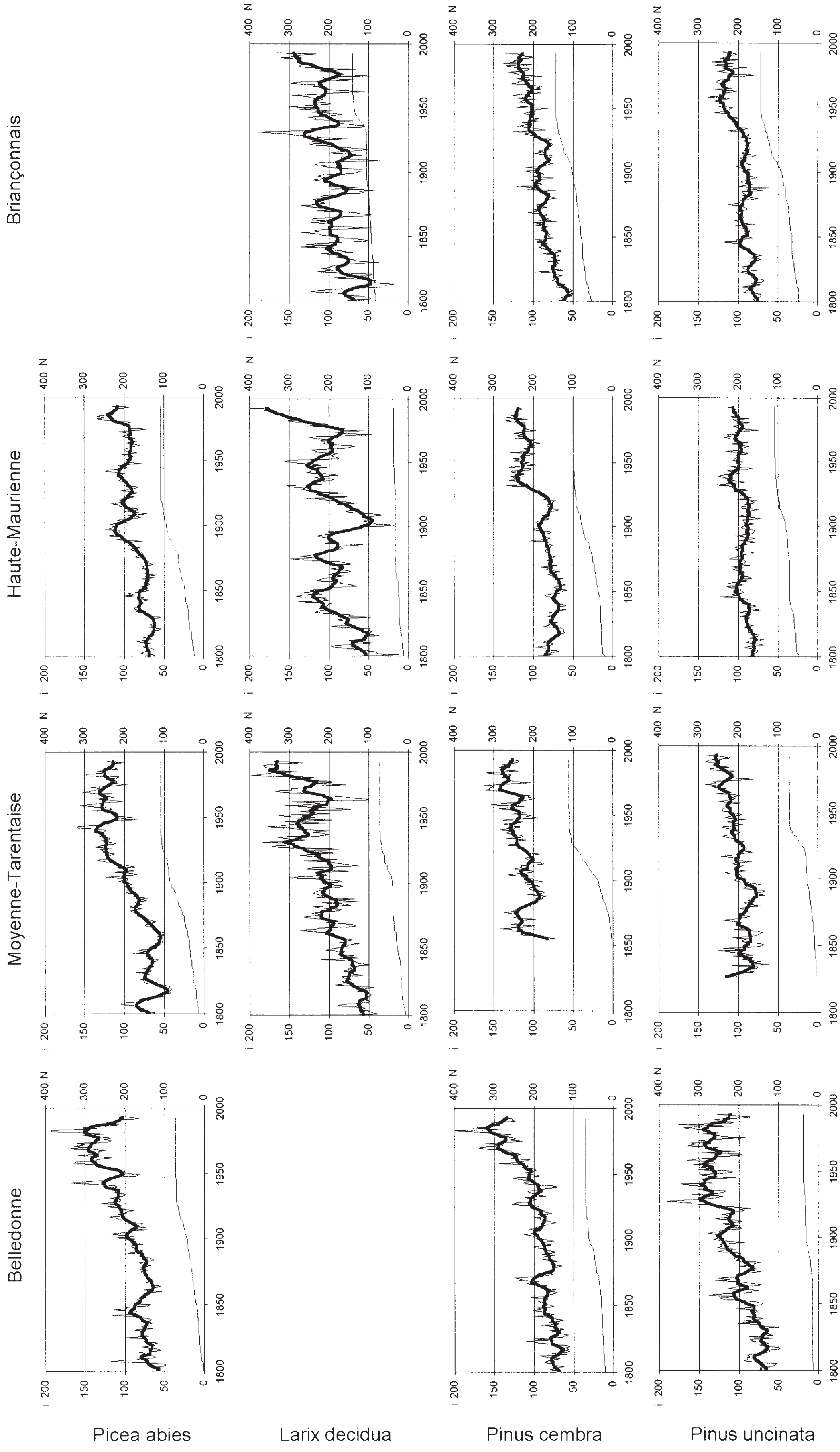
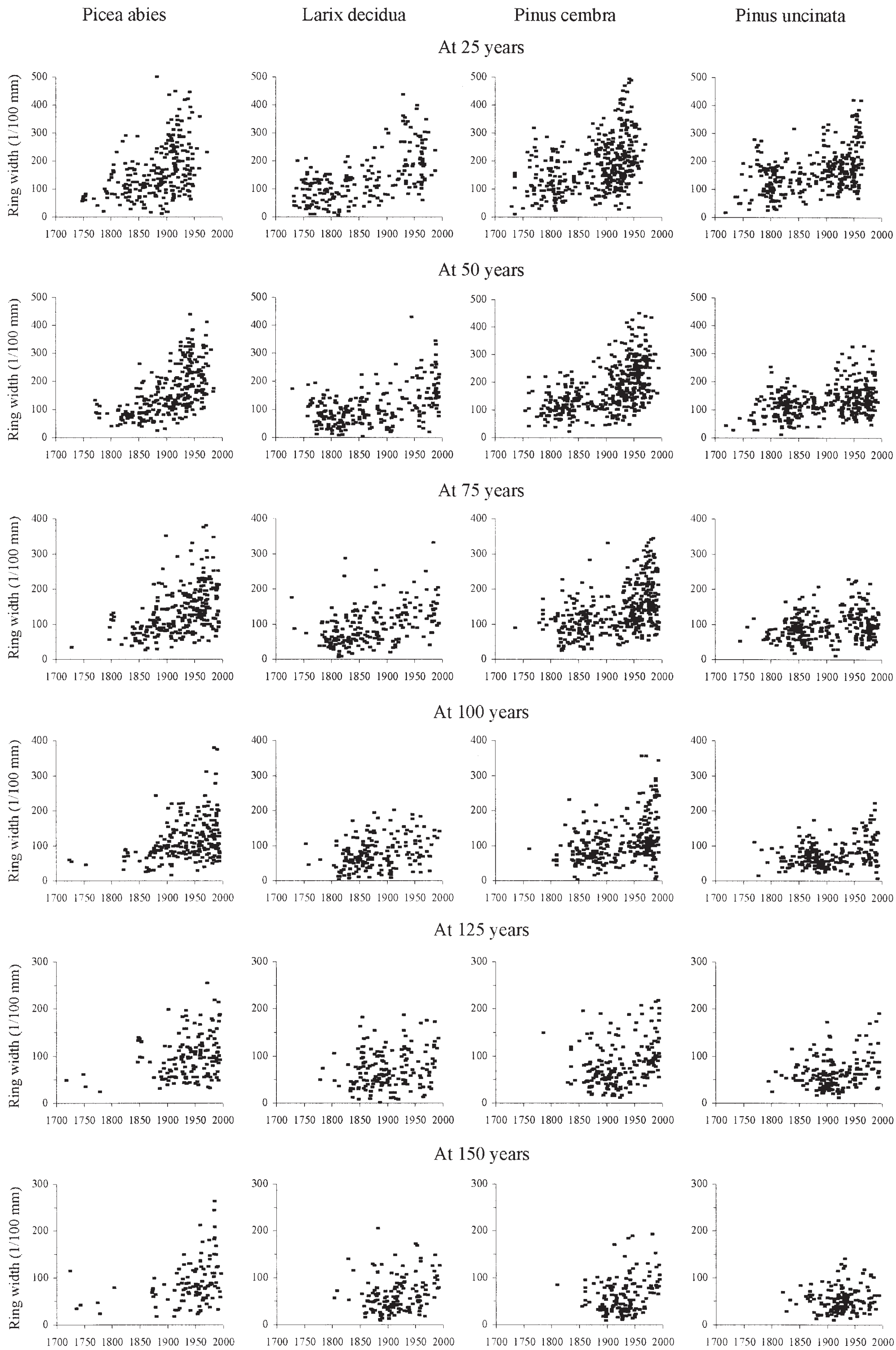


Fig. 5 Growth indices for four species (Norway spruce, Swiss stone pine, mountain pine, European larch) growing at the French alpine timberline in various sites and conditions, from 1750 to 1993. *N*=Number of cores, *I*=growth indices with moving averages in bold. The moving averages are calculated and the slopes or stages are hand drawn

show strong reduction especially during the whole growing period, as observed by Bücher and Dessens (1991) in the French Pyrenees. This pattern is more pronounced in Belledonne (P>0.01) and secondary in Moyenne-Tarentaise; these are the two most external studied regions, with the most oceanic and cold climates. At the same

Fig. 6 Comparison of the regional growth trends of four subalpine species since 1800 in four regions of the French Alps. *N*=Number of cores, *I*=growth indices with moving averages in bold ▶


Belledonne
Moyenne-Tarentaise
Haute-Maurienne
Briançonnais
Picea abies
Larix decidua
Pinus cembra
Pinus uncinata


Picea abies
Larix decidua
Pinus cembra
Pinus uncinata
At 25 years
At 50 years
At 75 years
At 100 years
At 125 years
At 150 years
Ring width (1/100 mm)
1700 1750 1800 1850 1900 1950 2000

time, precipitation does not show significant trends (P<0.1). Notice that linear regressions for modelling the trends show only weak significance levels due to decadal fluctuations of climate.

These regional results confirm the global feature of the climatic change, and reveal that the reduction of thermal amplitude is due mainly to the increase of minimum temperatures.

Trends in tree-rings

The oldest tree found was a spruce sampled in the Haute-Maurienne, with 449 years providing a chronology from 1546 to 1994. However, the mean chronological curves are only shown since 1750 because the number of cores is insufficient before this year (Fig. 5).

Annual values are shown in Fig. 5, with moving average in bold. The stages and slopes are hand drawn in order to show the long term trends. All four mean curves obtained for the different species reveal an increase of growth during the two last centuries. However, the curves show different patterns for each species. Results are quite similar for the two pine species. Their radial growth shows successive stages that are almost constant and separated by short periods of increase starting around 1840 and 1920 (and 1970 for the Swiss stone pine). The spruce shows the longest and also highest continuous period of growth increase, from approximately 1860 to 1940.

Tree-rings of larch also show a general increase since 1810, despite periodic strong growth reductions at decadal time scale correlated with outbreaks of the larch bud moth (*Zeiraphera diniana* Gn.). This effect is particularly intense at high altitudes (Baltensweiler 1985; Weber 1997). These growth reductions occurred in cycles of approximately 8–9 years length.

Some regional differences also appear (Fig. 6). For the spruce, the positive trend is more pronounced in Belledone and Moyenne-Tarentaise. It is also higher in Moyenne-Tarentaise for the larch, and in Belledonne for the two pine species. Thus, the highest trends are observed in the more external and northern part of the Alps (Belledone and Moyenne-Tarentaise), which are wetter and colder, and where the climatic trends are the most obvious, whereas they are weaker in the inner Alps (Briançonnais and Haute-Maurienne), which are drier and with less pronounced climatic trends.

Ring-widths at selected cambial ages were drawn as a function of their years of formation (Fig. 7). These age-related scatter plots also confirm a growth increase for all the species, especially for young cambial ages. However, the four species show different behaviours. *Picea abies* shows the strongest increasing trend with an exponential shape, for every cambial age until 150 years. The trend is less pronounced and disappears after 75 years for *Larix decidua*, whereas it disappears after 100 years for *P. cembra* and after 50 years for *P. uncinata*.

◀ **Fig. 7** Ring-width as a function of their year of formation at different cambial ages (25, 50, 75, 100, 125 and 150 years) for the same three species

Comparisons of trends in climate and tree-rings

The stepwise regression models of each species are shown in Table 4, and visually compared with long term changes in growth in Fig. 8.

The best fits are obtained for *P. cembra* (R^2=0.90) and *P. uncinata* (R^2=0.84). For both, the linear trend (″year″ in Table 4) is one of the predictors of the models, the first one for *P. cembra* and the third one for *P. uncinata*. Notice that the enhanced growth increase period around 1925 is well modelled. *Low frequency* variations in May maximum temperatures and ring-widths of *P. cembra* are negatively correlated (Table 4), while response functions showed (Petitcolas and Rolland 1996) that *high frequency* variations of these parameters were positively correlated. Such complex influences appear just at the beginning of the photosynthesis period (Wieser 1997).

The model obtained for *P. uncinata* involves mainly the rise of yearly minimum temperatures (that was the third step for *P. cembra*). Such correlation suggests an enhanced growth at subalpine level during years with clement minimum temperatures.

For *Picea abies* and *Larix decidua*, the fittings of the stepwise models are lower. The periodical attacks of the Larch bud moth [*Zeiraphera diniana* (Gn.)] in *Larix decidua* populations may explain some divergences between observed and predicted values. *Picea abies* and *Larix decidua* models show mainly positive links between *low frequency* variations of ring-widths and temperatures, involving respectively February and the late summer (August and September). As for *P. cembra*, these results differ from those obtained by analysing the *high frequency* variations of the growth and local climate (Petitcolas and Rolland 1996).

Discussion and conclusion

This is the only study of long term radial growth changes that has been conducted in the French Alps, and to our knowledge of all the Alps, that includes all the four dominant coniferous species of the timberline with a large sample (1320 cores). Moreover, it covered various ecological conditions, and four areas that cover the different climatic gradients in the western Alps.

Our study demonstrates for all species a clear increase in tree growth near the timberline. The radial growth of the two pines shows almost constant successive stages, separated by short periods of increase that start around 1840 and 1920, whereas the spruce shows the longest and also the highest continuous growth increase period, from approximately 1860 to 1940. Larch results are more ambiguous due to evident *Zeirapheira diniana* at-

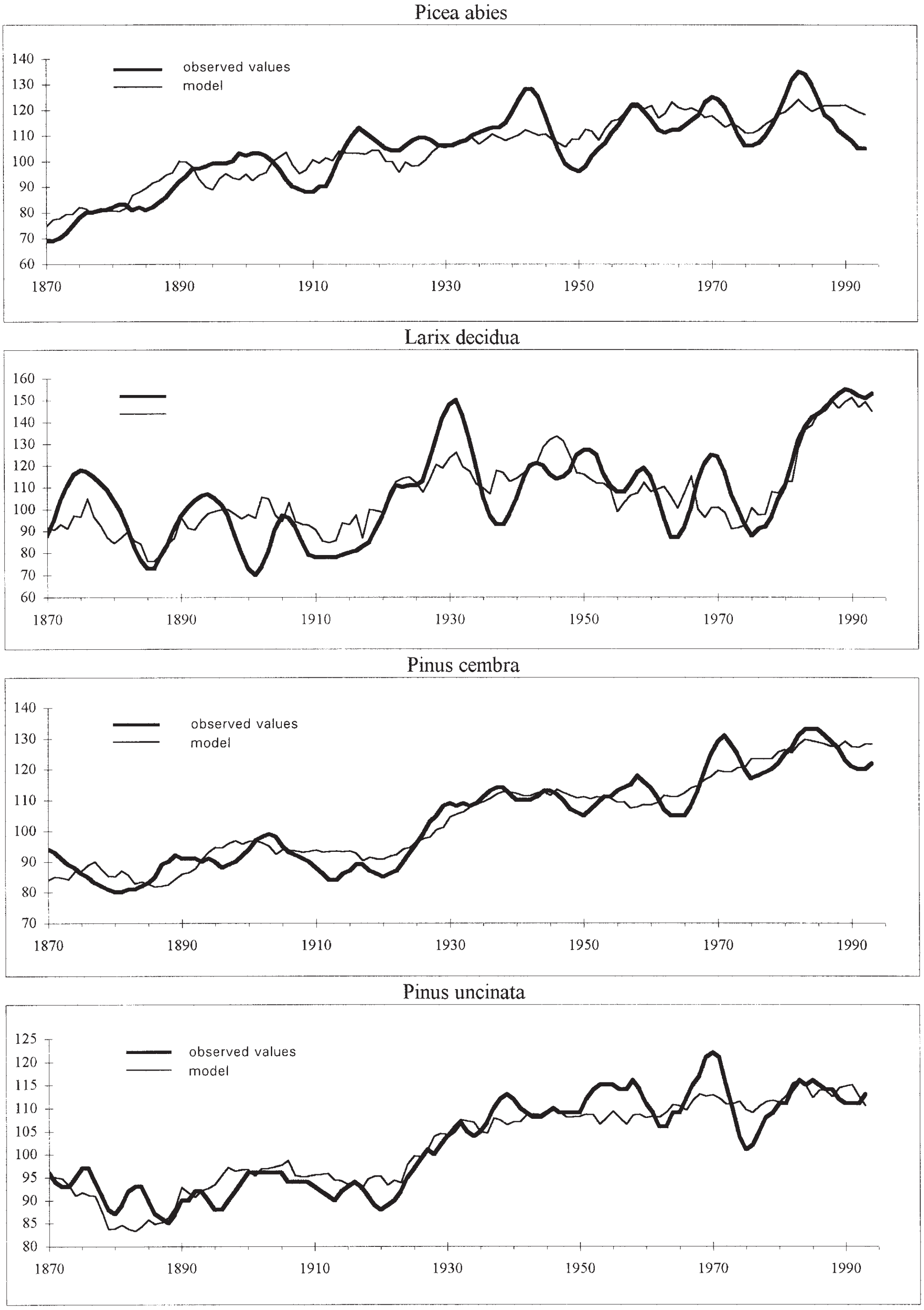


Fig. 8 Model of long term radial growth trends in tree-rings for four species using low frequency of temperature data in Turin for the period 1870–1993 (N=124 years), (see details in Table 4). *Bold line*=observed values, *fine line*=model with climatic data

tacks. Furthermore, both low frequency tree-ring time series and ring-widths as a function of year of formation at different cambial ages lead to the same conclusion.

These results clearly confirm those obtained by other authors for different species in different environments (Hari and Arovaara 1988). For example, *Quercus petraea*, *Q. robur*, *Fagus sylvatica*, *Abies alba* and *Picea ab-*

ies in north-eastern France show strong increases in radial growth (Becker et al. 1995). For *Pinus nigra* ssp *laricio* var *corsicana*, the radial growth mean curves from 1935 to 1991 also showed an increasing general trend of the growth indices +50, +60 and +35% for, respectively, the total ring, the earlywood and the latewood (Lebourgeois and Becker 1996). Nicolussi et al. (1995) found a steady and significant increase of *Pinus cembra* mean ring-width from 1 mm per year in the middle of the last century and about 1.4 mm per year at present in the Tyrolian Central Alps. The mountain pine *P. uncinata* shows the same trend in the Briançonnais at high altitude (Rolland 1996), as the larch in the southern Alps (Belingard 1996). Others, however, have failed to find evidence for a growth increase during the last 100–150 years. For example, Kienast and Luxmoore (1988) identified only 8 out of 34 sites in Europe where ring-width increased after 1950, and Kullman (1991) observed a growth *decline* of a *P. sylvestris* natural forest in northern Sweden, but associated this with recent cooling trends in local climate.

Four main hypotheses may be involved to explain such positive trends: an increasing air CO_2 concentration, N-deposition from air pollution by NO_2, forest management influences or climatic changes. The two first hypotheses (increasing CO_2 or N-deposition) may partly explain the usually observed growth increase (Nicolussi et al. 1995; Hättenschwiler et al. 1996). Hättenschwiler and Körner (1997) found a clear increase in annual net ecosystem carbon gain for model spruce ecosystems exposed to elevated CO_2, with an effect on growth still uncertain and dependant on soil (Egli and Körner 1997). However, CO_2 continuous increase or N-deposition hypothesis failed to explain both the stages observed in tree growth with decadal fluctuations and the regional differences observed in tree growth trends.

Tree growth changes may also be caused by possible influences of forest management. Indeed, it can be hypothesised that trees that grew exceptionally fast may have been selectively cut when they were young, so that only trees with a slow growth rate during the first years were left (Lebourgeois and Becker 1996). However, this pattern was found in low elevation forests, and forests near the timberline are much less likely to have experienced such selective harvesting. Moreover, many jumps are synchronous with those found in other dendroclimatological studies on the same species but in different forests (Nicolussi et al. 1995; Belingard 1996; Rolland 1996). Thus, the effect of tree cuts does not seem to be responsible for these jumps.

Finally, the role of the climatic change may be more clearly involved to explain the low frequency jumps in tree ring growth trends. It is well known that global warming can explain the recent glacial retreat or fluctuations in the French and Swiss Alps (LaMarche and Fritts 1971). Thus, glacial advance and ring-width growth are known to react to air temperature at high altitudes (Serre-Bachet and Tessier 1985; Tessier 1986).

The analysis of climatic trends revealed a clear and general warming at all sites during the last two centuries especially for the minimum temperatures, with synchronous fluctuations between the different series, and a clear reduction of thermic amplitudes during the growing period. These trends are sharp in July when most of the ring is formed at subalpine levels (Müller 1981). Notice that the stronger growth increase is found in the two coldest regions (external and intermediate Alps), where cold in summer may be a more limiting factor (Petitcolas 1998). Another argument that supports this climatic interpretation is that the two pine species show rather similar long term trends, and their response to climate (Petitcolas and Rolland 1996; Petitcolas 1998) is similar.

The stepwise regression models calculated between *low frequency* variations in ring-width and both climate and the year number revealed that changes in temperatures may explain a part of long term variations in tree-rings. Indeed, these models provide a rather precise fit for the two pine species (R^2 above 0.84), and jump events in growth patterns, such as the increase observed around 1925 in pines and larch curves, are well described especially before 1960 (Fig. 8). However, the ″year″ step retained (i.e. linear trend) in the stepwise regression models of pines requires caution in making climatic interpretations. Moreover, the discrepancy of predictors according to the analysed signal [*low frequency*, studied here, and *high frequency* studied with response functions (Petitcolas and Rolland 1996)] shows that relevant climatic predictors involved in yearly growth variations do not explain long term changes in growth. This suggests that the causes of growth variations are complex, and that some other factors that have not be taking into account in our models (CO_2 air concentrations increase, N-deposition or human impact), may also be involved.

Acknowledgements Financial support was provided by the Ecologie et Gestion du Patrimoine Naturel (EGPN) program. We thank R.M. Callaway (University of Montana, USA) for manuscript revision, G. Pache for providing meteorological data, J. Lucas for technical assistance, and all the workers who helped us during the field work.

References

Baltensweiler W (1985) On the extent and the mechanisms of the outbreaks of the Larch Bud moth (*Zeiraphera diniana* Gn., Lepidoptera, Tortricidae) and its impact on the subalpine Larch-Cembran Pine ecosystem. ″ Establishment and trending of subalpine forest. Research and management″. In: Turner H, Tranquillini W (eds) Proceedings 3rd IUFRO Workshop 1984. Eidg Anst Forstl Versuchwes Ber 270, pp 215–219

Becker M (1987) Bilan de santé actuel et rétrospectif du Sapin (*Abies alba* Mill.) dans les Vosges. Etude écologique et dendrochronologique. Ann Sci For 44: 379–402

Becker M (1988) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of north-eastern France. Can J For Res 19: 1110–1117

Becker M, Bert GD, Bouchon J, Picard JF, Ulrich E (1994) Tendances à long terme observées dans la croissance de divers feuillus et résineux du nord-est de la France depuis le XIX siècle. R F F XLVI: 325–341

Becker M, Bert GD, Bouchon J, Dupouey JL, Picard JF, Ulrich E (1995) Long term changes in forest productivity in north-eastern France: the dendroecological approach. In: Landmann G, Bonneau M (eds) Forest decline and atmospheric depositions effects in the French mountains, pp 143, 153

Belingard C (1996) Etude dendroécologique de la dynamique de la limite supérieure de la forêt dans les Alpes du Sud, en relation avec les facteurs climatique et anthropique.Thesis Doct Aix Marseille, Ecologie

Beniston M, Diaz FH, Bradley RS (1997) Climatic change at high elevation sites : an overview. Climatic Change 36: 233–251

Blasing TJ, Duvick DM, West DC (1981) Dendroclimatic calibration and verification using regionaly averaged and single station precipitation data. Tree Ring Bull 41: 37–43

Bücher A, Dessens J (1991) Secular trends of surface temperature at an elevated observatory in the Pyrenees. J Climate: 4: 859–868

Ceulemans R, Mousseau M (1994) Effects of elevated atmospheric CO_2 on woody plants: a review. New Phytol 71: 58

Diaz FH, Bradley R (1997). Temperature variations during the last century at high elevation. Climatic Change 36: 253–297

Di Napoli G, Mercali L (1996) Moncalieri, 130 anni di meteorologia 1865–1994. Societa Meteorologica Subalpina, Torino

ECOCRAFT/ICAT (1994) Responses of trees and forests to global change. International Symposium, Dourdan, France, Oct 19–22. Université de Paris Sud, Ecologie végétale, Orsay

Egli P, Körner C (1997) Growth responses to elevated CO_2 and soil quality in beech-spruce model ecosystems. Acta Oecol 18: 343–349

Gale F (1986) Carbon dioxide enhancement of tree growth at high elevations. Science 231: 850–860

Graumlich LJ (1991) Subalpine tree growth, climate and increasing CO_2: an assessment of recent growth trends. Ecology 72: 1–11

Hansen J, Lebedeff S (1987) Global trends of measured surface air temperature 1856–1981. J Geophys Res 92: 345–372

Hari P, Arovaara H (1988) Detecting CO_2 induced enhancement in the radial increment of trees. Evidence from northern timber line. Scand J For Res 3: 67–74

Hättenschwiler S, Körner C (1997) Annual CO_2 budget of spruce model ecosystems in the third year of exposure to elevated CO_2. Acta Oecol 18: 319–325

Hättenschwiler S, Schweingruber FH, Körner Ch (1996) Tree-ring response to elevated CO_2 and increased N deposition in *Picea abies*. Plant Cell Environ 19: 1369–1378

Innes JL (1991) High altitude and high latitude tree growth in relation to past, present and future global climate change. The Holocene 1–2: 168–173

Kienast F, Luxmoore RJ (1988) Tree-ring analysis and conifer growth responses to increased atmospheric CO_2 levels. Oecologia 76: 487–495

Kullman L (1991) Cataclysmic response to recent cooling of a natural boreal pine (*Pinus sylvestris* L.) forest in northern Sweden. New Phytol 117: 351–360

LaMarche VC, Fritts HC (1971) Tree rings, glacial advance and climate in the Alps. Z Gletscherk Glazialgeol 7: 125–132

LaMarche VC, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: tree ring evidence for enhancement in natural vegetation. Science 225: 1019–1021

Lebourgeois F, Becker M (1996) Dendroécologie du Pin laricio de Corse dans l'Ouest de la France. Evolution du potentiel de croissance au cours des dernières décennies. Ann Sci For 53: 931–946

Mortier F (1995) Le CO_2 et la forêt. Bulletin Technique de l'Office National des Forêts, Paris, n° 29, Oct 1995

Müller HN (1981) Messungen zur Beziehung Klimafaktoren – Jahrringwachstum von Nadelbaumarten verschiedener Waldgrenznaher Standorte. In: Dickenwachstum der Bäume. Symposium Innsbruck 1980. Mitt Forstl BundesVersuchsanst Wien 142: 327–355

Nicolussi K, Bortenschlager S, Körner C (1995) Increase in treering width in subalpine *Pinus cembra* from the central Alps that may be CO_2-related. Trees 9:181–189

Pache G, Michalet R, Aimé S (1996) A seasonal application of the Gams (1932) modified Michalet (1991) method : the example of the distribution of some important forest species in the Alps. Vol jubilaire JL Richard, Diss Bot, 258. J Cramer, Stuttgart, pp 31–54

Peterson DL, Arbaugh MJ, Robinson LJ, Derderian BR (1990) Growth trend of whitebark pine and lodgepole pine in subalpine Sierra Nevada forest, California, USA. Arctic Alp Res 22: 233–243

Petitcolas V (1998) Dendroécologie comparée de l'épicéa, du mélèze, du pin cembro et du pin à crochets en limite supérieure de la forêt dans les Alpes françaises: influence de la variabilité macroécologique. Doctoral Thesis, University J.Fourier, Grenoble

Petitcolas V, Rolland C (1996) Dendroecological study of three subalpine conifers in the region of Briançon. Dendrochronologia 14: 247–253

Petitcolas V, Rolland C, Michalet R (1997) Croissance de l'épicéa, du mélèze, du pin cembro et du pin à crochets en limite supérieure de la forêt dans quatre régions des Alpes françaises. Ann Sci For 54: 731–745

Rolland C (1996) Long term changes in the radial growth of the mountain pine (*Pinus uncinata*) in the French Alps as influenced by climate. Dendrochronologia 14: 255–262

Schweingruber FH (1996) Tree-ring and environment. Dendroecology. Birmensdorf, Swiss Federal Institute for Forests, Snow and Landscape research, Berne

Serre-Bachet F, Tessier L (1985) Dendroclimatologie, dendrochronologie et Mélèze. Soc Hydrotech Fr, Section Glaciol, 11–12 March 1985, pp 1–14

Tessier L (1986) Chronologie des Mélèzes des Alpes et petit âge glaciaire. Dendrochronologia 4: 97–113

Weber UM (1997) Dendroecological reconstruction and interpretation of Larch budmoth (*Zeiraphera diniana*) outbreaks in two central alpine valleys of Switzerland from 1470–1990. Trees 11: 277–290

Wieser G (1997) Carbon dioxide gas exchange of Cambrian pine (*Pinus cembra*) at the alpine timberline during winter. Tree Physiol 17: 473–477