Height and radial growth trends of Corsican pine in western France

François Lebourgeois, Michel Becker, Richard Chevalier, Jean-Luc Dupouey, and Jean-Michel Gilbert

Abstract: Height and radial growth trends were analysed in Corsican pine (*Pinus nigra* Arnold ssp. *laricio* var. *Corsicana*) plantations in western France. Difference in height growth was tested by comparing the site index of stands established before and after 1950 and the height growth development curves of 13 pairs of young and old stands growing side by side on the same soil type. The site index of the young stands was 20–30% greater than the site index of the old stands. From the period 1921–1991, radial growth increased 45, 31, and 50% in earlywood, latewood (LW) and total ring (TR) area, respectively. The amount of increase depended on cambial age. The LW/TR ratio decreased by 8%. The regional climatic data revealed a significant increase in mean annual temperature of 1.1°C, mean annual minimum temperature (1.5°C), mean summer temperature (2.2°C), and minimum summer temperature (2.3°C) for the period 1950–1997. Because of the negative correlation between summer temperature and ring widths, increased temperature cannot explain the observed increases in growth. Effects of nitrogen inputs, which averaged 6.3 and 11 $kg \cdot ha^{-1} \cdot year^{-1}$ for bulk and throughfall depositions, respectively; land use history; improvement in silvicultural practices (wider initial spacing, higher thinning); and CO_2 fertilization are discussed as possible causes of the observed growth trends.

Résumé : Les évolutions de croissance radiale et en hauteur de plantations de pin laricio de Corse (*Pinus nigra* Arnold ssp. *laricio* var. *Corsicana*) échantillonnées dans l'Ouest de la France ont été étudiées. Les différences de croissance en hauteur ont été analysées en comparant l'indice de fertilité de peuplements installés avant et après 1950 et les courbes de croissance en hauteur de 13 couples de jeunes et de vieux peuplements poussant côte à côte sur le même type de station. La croissance en hauteur des jeunes peuplements est de 20 à 30% supérieure à celle des peuplements plus âgés. Pour la période 1921–1991, les surfaces du bois initial, du bois final (BF) et du cerne complet (CC) ont augmenté respectivement de 45, 31 et 50% ; le pourcentage d'augmentation dépendant de l'âge cambial. Le rapport BF/CC a diminué de 8%. Les données climatiques régionales ont montré une augmentation significative des températures minimale et moyenne annuelles de 1,5 et 1,1°C sur la période 1950–1997. Pour la période estivale, les augmentations ont été respectivement de 2,3°C et 2,2°C. En raison de la corrélation négative entre la température et la croissance, un réchauffement ne peut pas expliquer les tendances observées. L'effet des dépôts azotés (valeurs moyennes 6,3 et 11 $kg \cdot ha^{-1} \cdot an^{-1}$), l'origine des plantations, l'amélioration des pratiques sylvicoles (diminution de la densité initiale et éclaircicies plus fortes) et l'effet fertilisant du CO_2 atmosphérique sont discutés comme causes possibles des changements observés.

Introduction

In recent years, evidence of 20th-century increases in atmospheric CO_2, mean annual temperature, and airborne pollutant emissions has prompted interest in the effects of these factors on forest ecosystems (Gates 1990; Amthor 1995; Jacoby and D'Arrigo 1997; Beniston and Innes 1998; Briffa et al. 1998; Cannell et al. 1998).

Dendroecological methods have been widely used to reconstruct past climate and, more recently, to identify and quantify anomalous growth trends over the last century. These studies concerned natural high-altitude coniferous forests in the Northern Hemisphere (Innes 1991; Briffa 1992; Peterson 1994; Nicolussi et al. 1995; Jacoby et al. 1996; Spiecker et al. 1996) and also subalpine stands from New Zealand and Tasmania (Cook et al. 1996; D'Arrigo et al. 1998) and the northern Patagonian rain forest of Chile (Szeicz 1997). In France, measurements of annual rings on increment cores have shown a marked positive long-term radial growth trend during the last century varying between 55% and 160% depending on species and location (Becker 1989; Becker et al. 1994, 1995; Badeau et al. 1995, 1996; Rolland et al. 1998). These previous studies dealt with naturally regenerated coniferous and broad-leaved species growing in mountains or in northeastern plains. None studied growth trends of introduced species used in afforestation in the lowlands. This was one of the aims of the present study carried out on Corsican pine stands (*Pinus nigra* Arnold ssp.

Received August 9, 1999. Accepted January 10, 2000.

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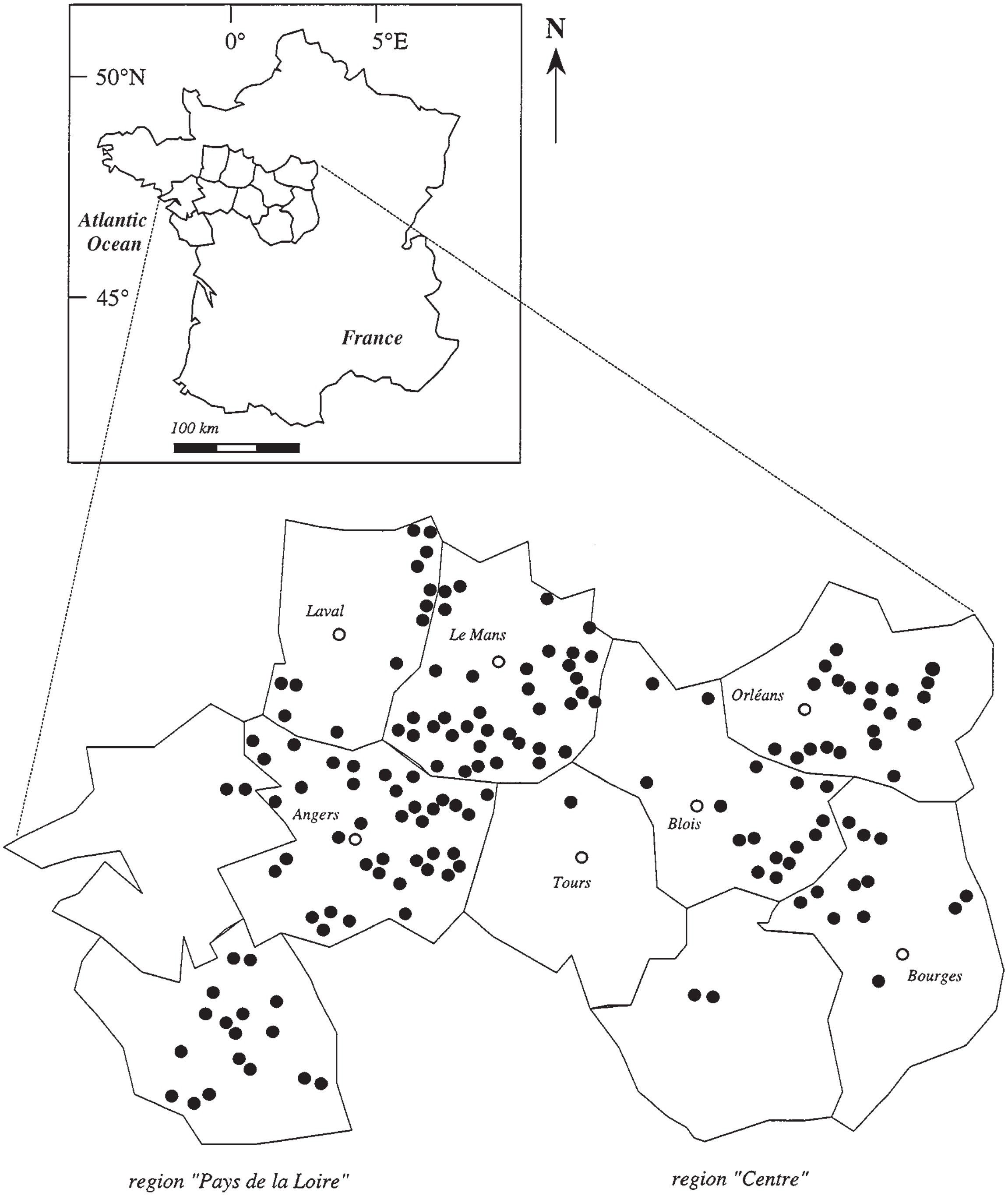
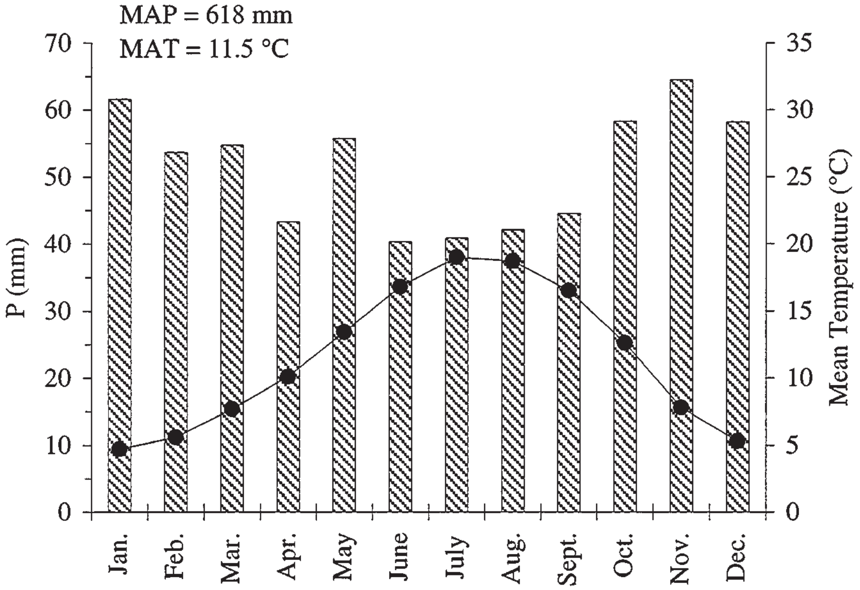
Fig. 1. Location of forests. Open circles represent the towns. Solid circles represent the Corsican pine forests sampled in both regions. The number of sampled plots by forest varied from 1 to 23.



laricio var. *Corsicana*) in western France. Because of its high-quality timber, Corsican pine has been widely used as an introduced afforestation tree species and, in recent decades, is the most widely planted species in western France. In contrast to the previous studied areas, western France is characterized by low elevations (often below 200 m) and is influenced by Atlantic climate, which corresponds to mild winters, early springs, and sunny and warm summers; snow-covered winters and late frosts in spring are very rare. Because of the negative influence of high summer temperature on Corsican pine growth (Lebourgeois 2000), a warmer regional climate (if it does exist) may influence tree growth and the long term dynamic of stands.

Because climatic variations influence earlywood and latewood widths differently (Lebourgeois 2000) and thus modify wood density and quality, the separate analysis of these two compartments can be use to assess possible wood structure changes (latewood/total ring (LW/TR) ratio). Such a study has never been done yet, although earlywood and latewood widths have been already used as indicators of climatic changes (Kienast and Luxemoore 1988; Nicolussi et al. 1995).

Fig. 2. Mean monthly temperature (°C; solid line) and precipitation (*P*; mm) at Angers (47°30′N, 00°35′W, 57 m). Means were calculated for the period 1961–1990. MAP and MAT, mean annual precipitation and temperature, respectively.



The influence of tree competition within stand is a potential confounding factor in studies of long-term growth trends (Becker 1992; Cherubini et al. 1998). This effect could overshadow any effect of environmental change. Thus, when it is not possible to remove, or at least to minimize, the effect of stand structure and stand history on radial growth, stem analysis and height growth measurements are more appropriate for investigating growth changes (LeBlanc et al. 1987; Goelz et al. 1988). Height growth of dominant trees is relatively independent of stand density effects on radial growth and is directly related to stand-level productivity (Goelz and Burk 1998). This approach has been already successfully applied in several case studies of growth trends in Europe (Kenk and Fischer 1988; Eriksson and Johansson 1993; Spiecker 1995; Skovsgaard and Henriksen 1996), but none of these previous studies compared height and radial growth in the same sample.

The aims of this work were (*i*) to quantify possible trends in both height and radial growth in managed Corsican pine stands in western France growing at low elevation; (*ii*) to separately study earlywood and latewood growth trends; and (*iii*) to assess the possible influences of climate, silviculture, and atmospheric deposition on tree growth.

Materials and methods

Study area and climatic data

The forests were located in western France in the regions called “Pays de la Loire” and “Centre” (Fig. 1). The plots were chosen to represent as many diverse ecological situations as possible in the forest areas, i.e., geological, soil, topographical, and silvicultural situations. The sample consisted of 380 single-species managed crops. Plantations were mostly established after broadleaf tree cuttings in forests (80% of the stands). The other forests were located on former agricultural lands, fallow lands, or heathlands. The highest point was 417 m, but the altitude of most of the sites was below 200 m. The site type was identified using soil descriptions and chemical analysis (Gilbert et al. 1996; Lebourgeois et al. 1997). Soils are mainly acidic with a sandy-loam to sandy-clay loam texture and low in available nitrogen (N) and phosphorus (P).

The climatic data set collected at Angers (1950–1997, 47°30′N, 00°35′W, 57 m elevation) included air temperature (°C) and total precipitation (mm). The Angers station is the only source of long-term weather data for the Pays de la Loire region. The climate data collected at this station are also the most representative for this region. Mean annual precipitation is 618 mm, and the number of rainy days averages 161 (Fig. 2). Annual temperature averages 11.5°C with an average minimum of 4.7°C and an average maximum of 19°C. Average growing season rainfall is 224 mm with 60% of rainless days and 30% of days with a maximum temperature above 25°C. The bootstrapped response-function analysis of trees sampled from near the weather station has shown that previous October water balance, current May temperature, and current summer water balance negatively influenced interannual radial growth variation; mean July temperature was the most significant climate variable (negative effect) (Lebourgeois 2000).

To analyse the possible trends in the local climatic data, five parameters were studied: maximum (T_x), minimum (T_n), amplitude ($T_x - T_n$), and mean temperatures ($T_m = 0.5(T_x + T_n)$) and the precipitation (*P*). From these monthly data, mean values were calculated for the year and the growing season. Climatic changes were investigated by observation of linear increasing trends over the period 1950–1997.

Dendroecological approach

To assess radial growth, a total of 1808 dominant trees were sampled in 183 plots located in the Pays de la Loire region (10 trees per plot). Each tree was measured (total height (*H*) and diameter at breast height outside bark (DBH)) and cored to the pith at breast height (one core per tree). The 10 trees per plot were cored at a right angle to the slope direction so as to avoid tension wood. Any geometrical abnormalities of the trunk were avoided as well. Furthermore, the trunk of this species being very spherical (Debazac 1964) the influence of eccentricity of stem growth was low. Because Corsican pine has been widely used for reforestation only since the 1950s, most of the managed crops were less than 40 years old. Thus, the current age of trees varied from 15 to 70 years, and 75% of the sampled trees were less than 35 years old.

Each ring was measured microscopically for earlywood, latewood,

Table 1. Data structure for the analysis of variance of annual BAIs and ring widths.

	Cambial age-class					
Year	1–10	11–20	21–30	31–40	>40	Total
1920–1955	1 854	1 725	392	26	0	3 971
	4.81%	4.52%	1.03%	0.07%	0.00%	10.41%
1956–1965	1 148	645	1333	366	26	3 518
	3.01%	1.69%	3.49%	0.96%	0.07%	9.22%
1966–1975	8 723	1 930	645	1333	392	13 023
	22.87%	5.06%	1.69%	3.49%	1.03%	34.14%
1976–1985	3 750	9 980	1930	645	1725	18 030
	9.83%	26.16%	5.06%	1.69%	4.52%	47.26%
Total	15 475	14 280	4300	2370	2143	38 568
	40.56%	37.43%	11.27%	6.21%	5.62%	100.00%

Note: The table gives the number and the percentage of rings analysed. The corresponding cambial age and calendar classes are indicated for each column and row, respectively.

and total ring width to the nearest 0.01 mm. Early and latewood transitions within the annual rings were defined according to qualitative aspects (darkening). To reduce bias in the tree-ring measurements, earlywood and latewood data were collected by one only person. After measurements, the individual ring-width series were cross-dated to ensure absolute dating accuracy after progressive detecting of so-called “pointer years” (Becker 1989). The initial ring-width values (mm) were converted mathematically into annual basal area increments (BAIs; cm^2). Although this conversion has been already successfully applied to detect radial growth trend (Briffa 1992; Becker et al. 1994; Badeau et al. 1996), the respective values of ring widths and BAIs for such a study are still debated (LeBlanc 1990, 1996), and BAI estimations from cores could be sometimes biased (Visser 1995). Thus, both ring widths and BAIs were used in this study and corresponding results were compared.

The two following methods were used to standardize both ring widths and BAIs, i.e., to remove age effects.

Constant cambial age method

In this approach, ring measurements within a specific cambial age range (age of the tree when the ring was formed) were averaged for each date when at least four rings were available and then plotted versus calendar date. This gave regional tree-growth estimates within which the age of trees was held roughly constant through time. Eight age-classes were considered here: 1–5, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, and >35 years. Linear regressions were performed for each age-class to identify trends for both ring widths (mm) and BAIs (cm^2).

Analysis of variance

To take into account cambial age and date effects on radial growth simultaneously, we used the method of Dupouey et al. (1992) and Badeau et al. (1995). Ring widths and BAIs can be organized in a two-way table with cambial age in rows and calendar date in columns. Thus, it is possible to analyse this table using an analysis of variance procedure to extract age and date effects and their interaction simultaneously. The age and date factors were divided into a limited number of classes (Table 1). In each cell of the table, individual annual rings belonging to a given tree were averaged to give each tree the same weight in the analysis. Parameters of this unbalanced model were fitted using the general linear models procedure of SAS Institute Inc. (1988). Age and date were considered as fixed effects. Least-square estimates of marginal means were computed for each age and date class and their interactions.

Site index comparisons

To assess height growth, the previous sample was supplemented with 197 plots. In agreement with the standard procedure for forest yield experiments used at the French National Forest Office (Duplat 1989), the first, third, and fifth largest trees in diameter in a circular 600-m^2 plot were cored to the pith at 1.30 m and measured to determine the site index (i.e., the average height of dominant trees at a reference age) of the stand. According to yield tables, there was a close relationship between site index and site productivity in terms of the mean annual increment (MAI, $m^3 \cdot ha^{-1} \cdot year^{-1}$) of stemwood. The site index was determined by using the age from seed and the mean height of these three dominant trees. The age from seed was obtained by adding (*i*) the number of counted rings at 1.30 m, (*ii*) the number of nodes from 1.30 to 0.30, and (*iii*) the mean age of seedlings of 0.30 m in height (4 years). The dominant height was adjusted to the age of 30 years (H_{30}) (average age of the sampled stands) using height development curves for Corsican pine. Because potential biases in site index curves are of great importance for the interpretation of results (Goelz and Burk 1996), the applicability of different yield tables available in western France was tested. The table of Hamilton and Christie (1971) for England proved to be the most suitable (Gilbert and Chevalier 1994; Gilbert et al. 1996). This method was also applied to the plots sampled for the dendroecological study. Thus, the total number of trees analysed was 1140, and the mean age (from seed) varied from 21 to 80 years old in 1992. The existence of a difference was tested by comparing the site index of old stands, mainly established before 1950, to the site index of young stands established after 1950.

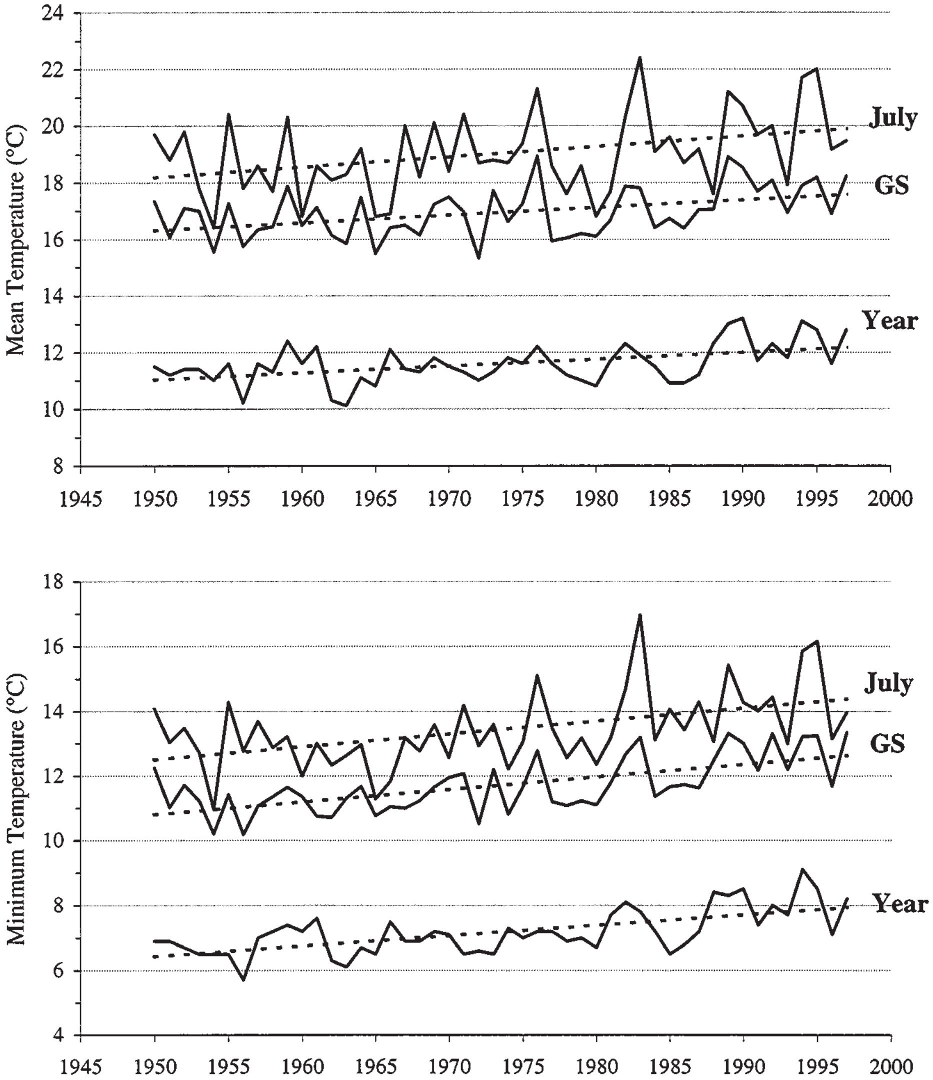
Finally, we compared growth curves of 13 pairs of old and young stands growing side by side on the same sandy acidic soils and under identical silvicultural managements (density, thinnings). Three stems of each of the two paired stands were measured to reconstruct the dominant height growth of the stand. The sampled trees corresponded to the first, third, and fifth largest trees in diameter in a circular 600-m^2 plot. The height-growth curve was established by measuring the height every three nodes from 1.30 m to the top of the crown. The corresponding ages were obtained by counting the number of nodes. The age at 1.3 m determined by counting the total number of nodes was verified by counting the number of rings observed on cores. The age from seed, the site index and the mean annual height increment were obtained by the method previously used.

Results

Variations in climatic parameters

A linear positive trend was observed in minimum temperature during the period 1950–1997 with a slope of 0.032°C/year and 0.039°C/year for the total year and the

Fig. 3. Yearly variations of minimum and mean temperature (°C) for the year, the growing season (May to September, GS), and July in Angers (period 1950–1997). The broken lines show the positive linear regression trends (significant at the $p < 0.05$ level).



growing season, respectively ($r = 0.64$ for both periods; $p < 0.001$) (Fig. 3). The positive trend was observed for each month from May to October (excluding September) but was more pronounced for July (0.04°C/year) and August (0.054°C/year) ($r = 0.48$ and 0.59, $p < 0.001$). During the same period, the increase in maximum temperature was less pronounced and only significant for August (0.058°C/year, $r = 0.41$, $p < 0.01$). Consequently, the mean temperature significantly increased in July (0.036°C/year, $r = 0.36$, $p < 0.01$) and August (0.057°C/year, $r = 0.51$, $p < 0.001$) and for the total year (0.024°C/year, $r = 0.48$, $p < 0.001$) and the growing season (0.027°C/year, $r = 0.43$, $p < 0.001$). On the contrary, thermal amplitudes and precipitation did not show significant linear trends.

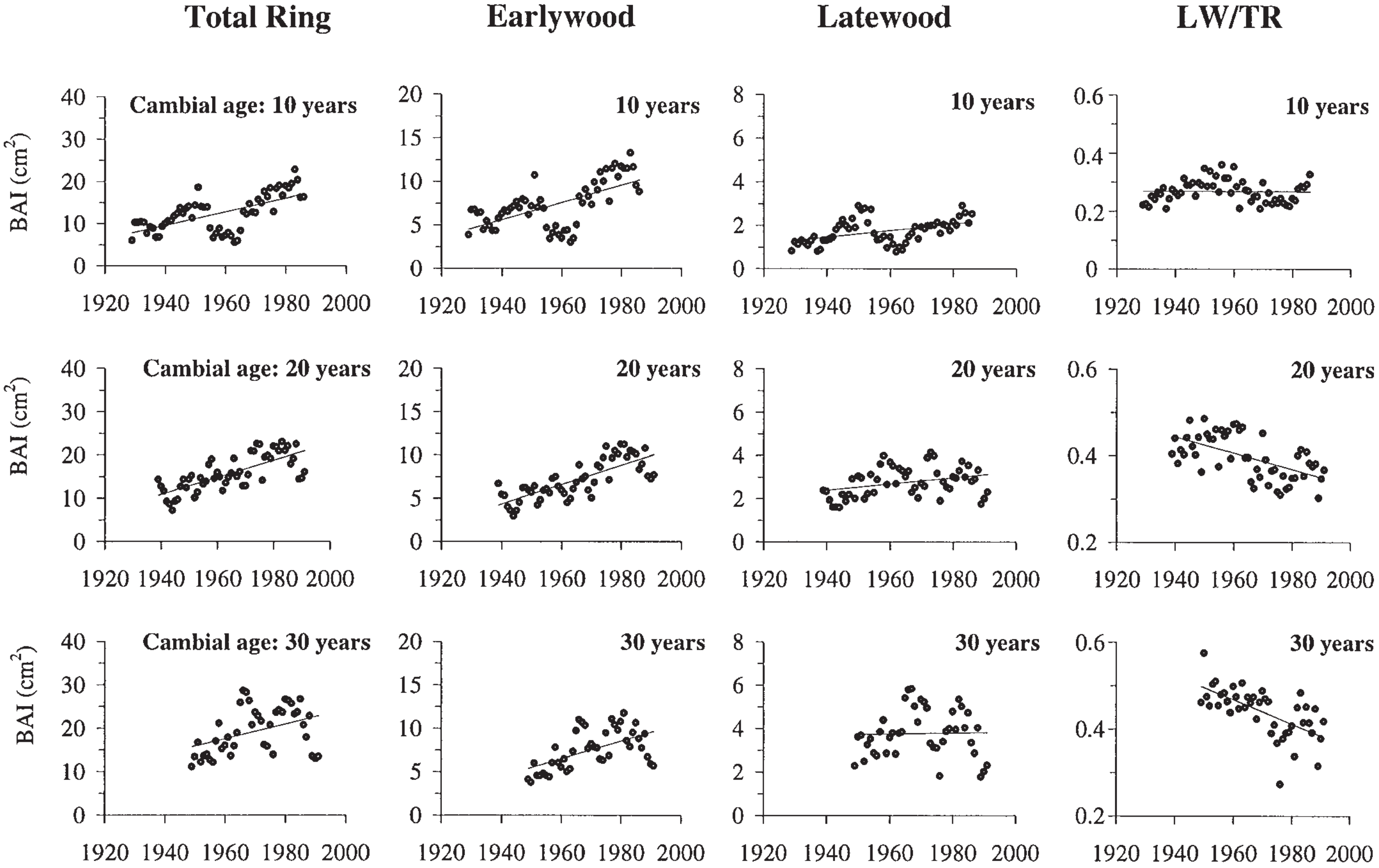
Radial growth trends: constant cambial age method

Recent earlywood rings were larger than rings produced earlier for both BAIs and ring widths (Fig. 4, Table 2). The mean increase was about 0.1 cm^2/year and 0.016 mm/year for rings under 35 years old. The mean relative increase in BAI was lower for latewood (0.013 cm^2/year) and only significant for the youngest cambial ages (6–20 years). For the same compartment, only the class 6–10 years presented a significant increase in ring width. Thus, the increase of the total ring, which averaged about 0.17 cm^2/year and 0.019 mm/year, appeared to be mostly linked to the earlywood increase. The LW/TR ratio significantly decreased by about 0.20% per year for the rings aged from 11 to 35 years old, with the steepest change between 26 and 30 years

Radial growth trends: analysis of variance approach

For both BAIs and ring widths and for each ring compartment, the global variance model was significant (Table 3, Fig. 5). The cambial age and the calendar date integrated between 3 and 42% of the total variance. Latewood and LW/TR variations were mainly controlled by cambial age for both BAIs and widths. The date effect appeared more influential than the age effect for the earlywood expressed in BAIs, whereas earlywood widths were mainly controlled by the age. Although low, the part of variance explained by the interaction between both factors was also significant, which meant that the observed trends of growth since 1920

Fig. 4. Annual basal area increment vs. calendar years according to the cambial age of the total ring, the earlywood, and the latewood. Each point represents the average value of at least four rings. The class 10 years corresponds to the rings aged from 6 to 10 years old; the class 20 years corresponds to the rings aged from 16 to 20; etc. The thin line represents the linear regression fit (SAS Institute Inc. 1988). The results of the regression analysis are presented in Table 2.



depended on age. The rise in BAIs averaged 50 (range 37–62), 45 (range 37–57), and 31% (range 19–63%) for the total ring, earlywood, and latewood, respectively. The LW/TR decreased from 1 to 16% (mean 8%) according to the cambial age class.

Height growth differences: site index comparisons

In the whole data set, the site index varied from 7.8 to 19.3 m at 30 years, corresponding to mean annual volume increments (MAI) varying from 6 to 25 m^3·ha^{-1}·year^{-1} according to yield table predictions (Table 4). Mean MAI decreased with increasing age-classes. The youngest stands (20–30 years) had a site index from 7.8 to 19.3 m (mean MAI 16.4 m^3·ha^{-1}·year^{-1}). The old stands, established before 1950 (age > 40 years), presented a site index from 7.8 to 15.3 m (mean MAI 13.2 m^3·ha^{-1}·year^{-1}). These values suggested a relative volume yield difference of about 20%.

Height growth differences: stem analysis

A significant difference in MAI appeared between young and old stands growing side by side when old stands were at least 50 years old (stands established before 1950) (Fig. 6). The MAI differences ranged from –2 to 7 m^3·ha^{-1}·year^{-1} (mean ΔMAI 2 m^3·ha^{-1}·year^{-1}; df = 12; t = 2.865; p = 0.02; paired t test) and were greater when site conditions were less favourable (estimated from MAIs of old stands). Young stand curves were significantly steeper than the old ones (Fig. 7). Height growth differences appeared from planting (pairs 13 and 10) or after the phase of juvenile growth (pairs 1 and 9). For pair 8, smaller increment value was observed for the young stand. However, although young stand was smaller at the reference age of 25 years, the reverse was thereafter observed. For the other pairs (3, 4, 5, and 7), all established after 1950, MAI values were high and ranged from 18 to 20 m^3·ha^{-1}·year^{-1}.

Discussion

Whatever the method used, a significant radial and height growth increase of Corsican pine stands was found over recent decades. Our site index difference is consistent with the rise of 40% observed by Nouals and Boisseau (1992) in 62 Corsican pine stands sampled in the French Mediterranean region (reference age of 50 years). Our data demonstrated that the radial growth increase was most apparent in earlywood and total ring and lower in latewood, causing a significant decrease in the LW/TR ratio. One conclusion that could be drawn from the study of radial growth is that the different growth rate of earlywood and latewood vessels may have an effect on the technical quality of the stem, especially density. We used previously published values of earlywood and

Table 2. Changing in basal area increments (cm^2) and ring widths (mm) of each ring component and in the LW/TR ratio according to the cambial age-class.

Cambial age (years)	Period	Mean no. of rings per date	Total ring (TR)			Earlywood (EW)			Latewood (LW)			LW/TR		
			r	Slope	*t*	*r*	Slope	*t*	*r*	Slope	*t*	*r*	Slope	*t*
Basal area increment (cm^2)														
1–5	1925–1981	114	0.36	0.07	2.9**	0.39	0.05	3.0**	0.17	0.006	1.3ns	0.03	0.00	0.6ns
6–10	1929–1986	155	0.64	0.16	6.2***	0.63	0.10	5.9***	0.45	0.015	3.8***	0.02	0.00	0.6ns
11–15	1934–1991	156	0.6	0.16	5.7***	0.63	0.10	5.9***	0.30	0.012	2.4*	0.48	–0.13	4.7***
16–20	1939–1991	163	0.73	0.20	7.6***	0.77	0.11	8.6***	0.33	0.014	2.5*	0.58	–0.19	5.6***
21–25	1944–1991	136	0.57	0.19	4.8***	0.75	0.11	7.4***	0.14	0.010	0.9ns	0.62	–0.23	5.8***
26–30	1949–1991	81	0.41	0.17	2.9**	0.57	0.10	4.3***	0.08	0.002	0.2ns	0.63	–0.29	5.6***
31–35	1954–1991	39	0.53	0.23	3.8**	0.65	0.12	5.1***	0.18	0.016	1.2ns	0.62	–0.24	5.1***
>35	1959–1991	144	0.18	0.09	1.0ns	0.14	0.02	0.8ns	0.14	0.019	0.8ns	0.18	–0.03	1.3ns
Ring width (mm)														
1–5	1925–1981	114	0.30	0.019	2.3*	0.31	0.016	2.4*	0.18	0.0029	1.4ns	0.00	0.00	0.2ns
6–10	1929–1986	155	0.51	0.027	4.5***	0.47	0.020	4.0***	0.47	0.0066	4.0***	0.00	0.00	0.2ns
11–15	1934–1991	156	0.42	0.020	3.4**	0.48	0.017	4.1***	0.18	0.0029	1.4ns	0.48	–0.13	4.1***
16–20	1939–1991	163	0.42	0.021	3.3**	0.50	0.019	4.2***	0.17	0.0030	1.2ns	0.58	–0.19	5.0***
21–25	1944–1991	136	0.30	0.015	2.1*	0.46	0.015	3.5***	0.00	0.0000	0.0ns	0.62	–0.23	5.3***
26–30	1949–1991	81	0.21	0.011	1.3	0.38	0.013	2.7**	0.09	–0.0023	0.6ns	0.63	–0.28	5.2***
31–35	1954–1991	39	0.27	0.012	1.7†	0.45	0.013	3.1**	0.05	–0.0011	0.3ns	0.62	–0.24	4.7***
>35	1959–1991	144	0.44	–0.027	2.8**	0.44	–0.013	2.7*	0.41	–0.0129	–2.5*	0.18	–0.07	1.0ns

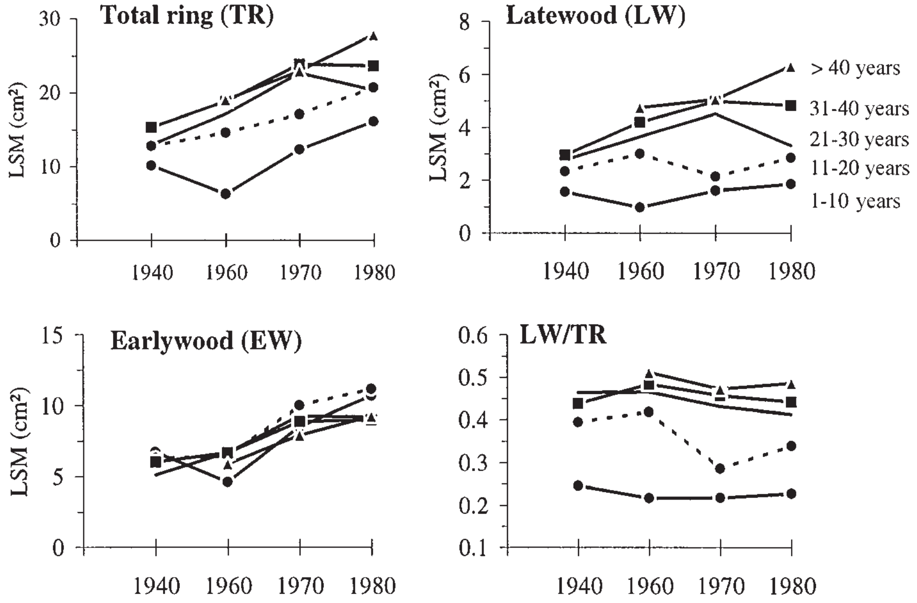
Note: Regression analyses were computed with the regression procedure of SAS Institute Inc. (1988). *r*, correlation coefficient. The *t* statistics and corresponding significance probabilities indicate if the slope (in cm^2/year, mm/year or in % for LW/TR) is significantly different from zero. ns, not significant; †, $p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Table 3. Analysis of variance of cambial age and calendar date effects on annual BAIs and ring widths, computed with the general linear models procedure of SAS Institute Inc. (1988), for each ring compartment and for the LW/TR ratio.

		F value			
Source	df	Total ring	Earlywood	Latewood	LW/TR
Basal area increment (cm^2)					
Model	18	578.3	228.6	932.3	1582.2
Age effect	3	490.0	24.5	950.6	3027.3
Date effect	4	146.6	124.6	39.8	36.9
Age × date	11	42.1	28.1	69.6	68.6
Adjusted r^2		0.21	0.10	0.30	0.42
Ring width (mm)					
Model	18	819.2	1331.2	72.6	1582.2
Age effect	3	1287.9	2270.2	111.9	3027.3
Date effect	4	43.9	47.4	8.1	36.9
Age × date	11	12.2	15.9	26.1	68.6
Adjusted r^2		0.28	0.39	0.03	0.42

Note: All *F* values are significant at the $p < 0.001$ level.

Fig. 5. Least squares mean estimates (LSM) of annual BAIs for all combinations of cambial age (years) and date classes for each ring compartment and for the latewood/total ring ratio. The lines join the different date classes for each age-class. The dates indicate the centre of each date class.



latewood density of Corsican pine (Cown 1974) to calculate an estimate of total wood density variations in our study, assuming that there was no change with time of earlywood and latewood values. We obtained a significant decrease of about 10% of total ring density between 1920 and 1990.

Although we do not have direct information on past sylvicultural regime in the stands we studied, plant breeding does not seem to be a possible hypothesis to explain the growth increase, which appears to have started earlier than the onset of harvesting of improved seeds (Guibert 1997). In the “Centre” area, the initial tree spacing has decreased in recent decades: 3000–3500 plants/ha in the stands aged over 20 years old to 1500–2000 plants/ha in the present young crops. Different experimental observations showed that decreasing initial tree spacing (Thonon 1963; Andre et al. 1975; Jinks and Mason 1998) and higher thinning (Berben and Geebelen 1977; Berben and Dufrane 1980) enhanced girth growth (between 15 and 50%) but had no effect or significantly reduced height growth (about 20%). Thus, changes in sylvicultural management could partially explain the trends in radial increment but not those in height growth.

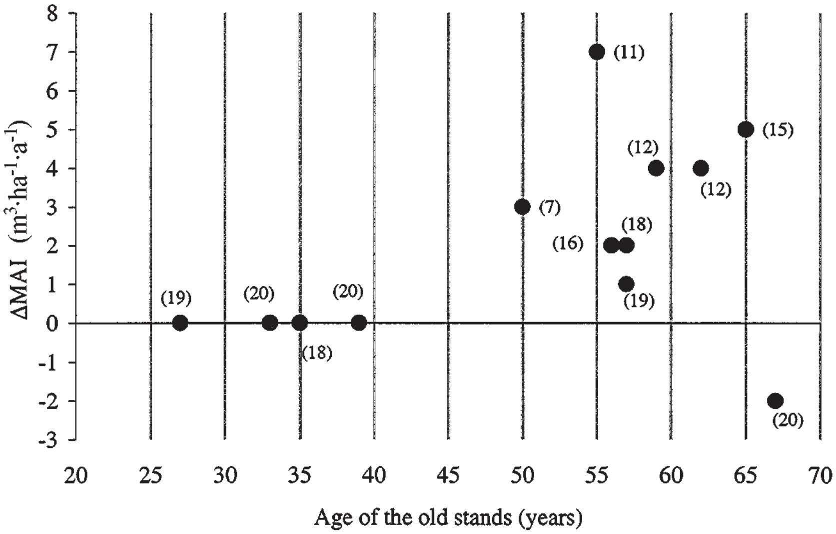
In accordance with other observations in France (Dessens 1995; Rolland et al. 1998; Loustau et al. 1999), the analysis of the regional meteorological data has revealed a significant increase in temperature for the period 1950–1997, especially in mean minimum temperature and for the summer months. A previously established climatic model of radial growth, based on bootstrapped response-function analysis has shown that BAIs were strongly and negatively affected by high mean monthly July temperature. Above the threshold of 18°C, radial

Table 4. Analysis of variance of age effect on site index, computed with the general linear models procedure of SAS Institute Inc. (1988) for the 380 plots.

Age-class (from seed in 1992)	Mean age (years)	No. of stands	MAI ($m^3 \cdot ha^{-1} \cdot year^{-1}$)			Site index (H_{30} in m)		
			Minimum	Maximum	Mean	Minimum	Maximum	Mean
20–25	24	53	9.0	25.0	16.6	9.6	19.3	14.8*a*
25–30	28	123	6.0	24.0	16.2	7.8	19.2	14.6*a*
30–35	33	97	9.0	22.0	16.0	9.6	17.8	14.5*ab*
35–40	37	61	8	22	15.0	9.3	18.0	13.9*bc*
40–50	44	14	10.0	17	14.5	10.9	14.9	13.6*bcd*
50–60	56	15	10.0	17.0	14.2	10.6	15.3	13.2*cd*
> 60	67	17	6.0	17.0	13.0	7.8	15	12.7*d*

Note: For the site index, means followed by the same letter are not significantly different at the $p < 0.05$ level. For each age-class, MAI values correspond to the mean annual volume increment from English yield tables (Hamilton and Christie 1971).

Fig. 6. Difference in MAI (ΔMAI, $m^3 \cdot ha^{-1} \cdot year^{-1}$) between young and old stands growing side by side according to the age of the old stands. The values in parentheses are the MAIs ($m^3 \cdot ha^{-1} \cdot year^{-1}$) of the old stands. For each stand, MAI values correspond to the mean annual volume increment from English yield tables (Hamilton and Christie 1971). Mean ΔMAI = 2 $m^3 \cdot ha^{-1} \cdot year^{-1}$; df = 12; t = 2.865; p = 0.02 (paired t test).

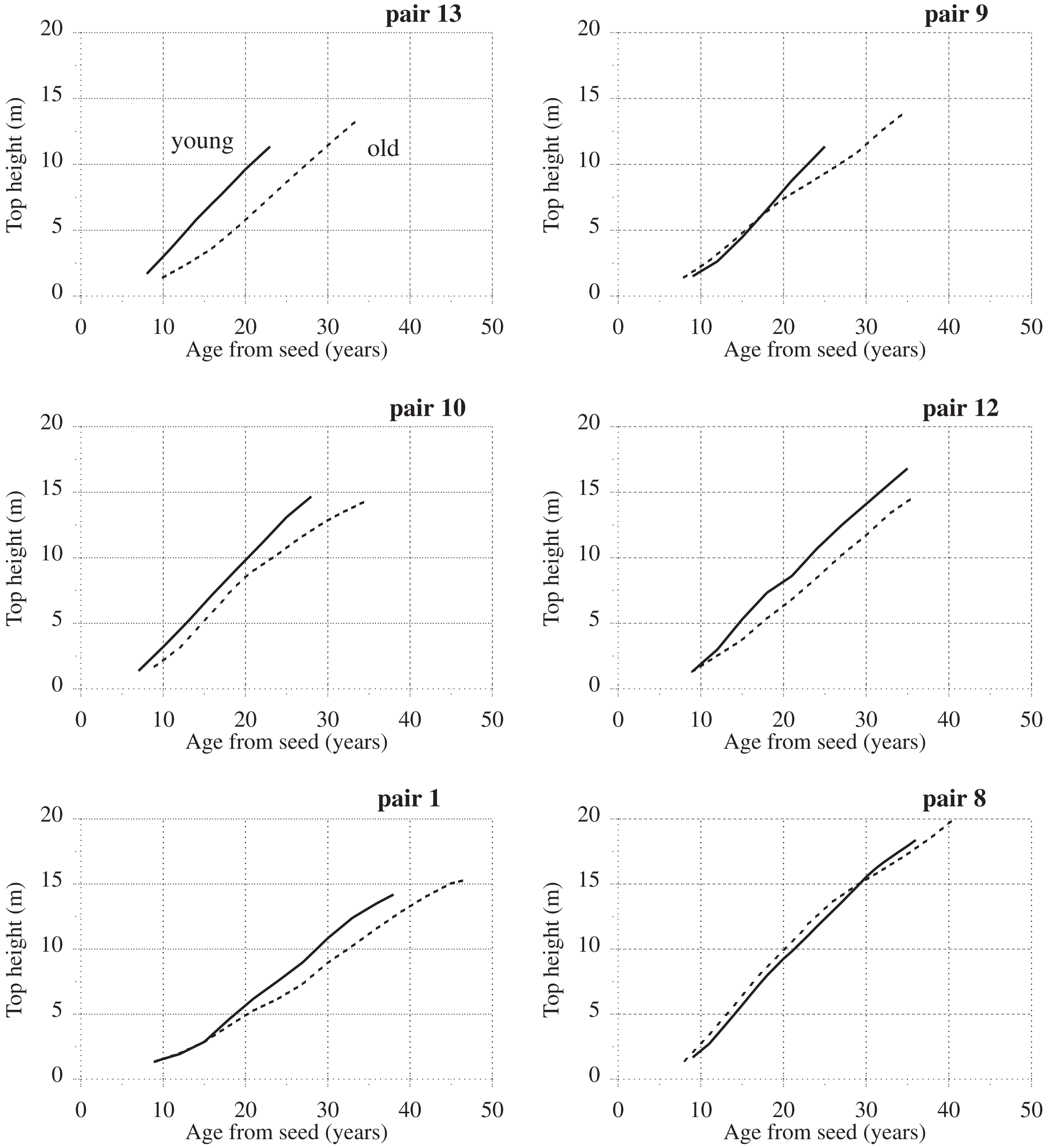


growth dramatically decreased down to 40% of values observed at cooler temperatures (Lebourgeois 2000). Thus, because of this negative relationship between temperature and growth, the observed warm climate does not explain the coincident increase in growth. Observations from controlled environment study have also shown that Corsican pine seedlings avoided stress (high temperature and soil drying) by an efficient stomatal control of transpirational water loss and that summer drought reduced significantly annual aboveground biomass (Lebourgeois et al. 1998). Thus, both observations on mature trees and ecophysiological measurements on seedlings dismiss the hypothesis that warm summer can induce growth enhancement.

Free-air CO_2 enrichment rings (doubling ambient CO_2) in a 13-year-old loblolly pine plantation (*Pinus taeda* L.) showed that, after 2 years, the growth rate of the dominant pine trees increased by about 26% relative to trees under ambient conditions (DeLucia et al. 1999). Although it is unclear if the response will be sustained over many years, such a study of fast-growing pines planted on formely agricultural land with low available N and P supply (similar in some regards to the studied Corsican pine plantations) suggests an important forest growth simulation under CO_2 enrichment. For Corsican pine, the response of mature trees remains to be established. Nevertheless, Kaushal et al. (1989) showed an increase of 10% of both height and diameter growth after one season for seedlings grown at double CO_2 concentration.

The hypothesis that, in the last few decades, the restructuring of broadleaved wood stands to conifer stands has been carried out firstly on poor sites and later on better sites is insufficient to explain growth changes. In a previous study carried out on young stands only (120 stands; mean age 25 years), foliage and chemical soil analysis indicated that growth levels depended on the balance between N and P nutrition (Lebourgeois et al. 1997). Among the 380 stands studied here, 280 stands are characterized by the critical levels of N and P previously defined (<0.05 $g \cdot kg^{-1}$ for P soil content; mean 0.027 $g \cdot kg^{-1}$). For these 280 poor sites, the differences in site index and MAI according to age-classes appeared still highly significant. Between the extreme age classes (20–25 and >60 years; n = 38 and 16 stands, respectively), the mean

Fig. 7. Height growth development curves of six old and young Corsican pine stands growing side by side. Each curve represents the mean of three trees.



MAI difference averages 30% (16.3 and 12.9 $m^3 \cdot ha^{-1} \cdot year^{-1}$). Thus, even if land-use history can differ between some younger and older stands, the changes in site productivity cannot be explained by systematically more favourable soil conditions in the youngest stands.

Growth increases following application of a nitrogenous fertilizer have been widely observed in Corsican pine stands not only on height and diameter growth (Miller and Cooper 1973; Miller et al. 1976; Proe et al. 1992) but also in production of earlywood cells (Smith et al. 1977). More recently, Neirynck et al. (1998) reported that the productivity of a Corsican pine stand growing on a dry sandy soil with low exchangeable nutrient pools in Belgium was 20–40% higher than the increments expected for stands belonging to same age and yield class (observed current annual volume increment between 1988 and 1995: 20.3 $m^3 \cdot ha^{-1} \cdot year^{-1}$; expected: 15–17 $m^3 \cdot ha^{-1} \cdot year^{-1}$). These authors ascribed this difference to atmospheric N inputs estimated at 46 $kg \cdot ha^{-1} \cdot year^{-1}$. In five forests near the area studied here, the total N input levels were estimated between 2.8 and 9.8 $kg \cdot ha^{-1} \cdot year^{-1}$ for bulk deposition (mean value over the period 1993–1996: 6.3 $kg \cdot ha^{-1} \cdot year^{-1}$), and between 5.4 and 19.8 $kg \cdot ha^{-1} \cdot year^{-1}$ for throughfall deposition (mean 11 $kg \cdot ha^{-1} \cdot year^{-1}$) (Ulrich et al. 1998). Northwestern France, which is an important farming area, appeared a relatively polluted area compared with others in France (Ulrich et al. 1998). In our study, the fact that some young–old stand pairs indicate recent growth increases, while other pairs do not, suggests a causal mechanism that interacts with local site conditions. Nitrogen deposition would increase growth of trees on N-deficient soils, but would have no effect on growth of trees on soil where N is not limiting. Atmospheric deposition of N is more of a persistent, long-term process then the acute, single-application methods typical of forestry research. Thus, suggesting that N was an important growth-limiting factor in the past, it is conceivable that relief from N deficiency by atmospheric inputs favours current growth.

Conclusions

The growth trends presented in this paper are the first to be published for a plantation species growing at low elevation in the French atlantic area. The results of this study also give new insights into the recent phenomenon of increased tree growth of French forest ecosystems by associating radial- and height-growth measurements and ring-compartment analysis. Because of the relatively important N inputs in the studied area and the growth response observed subsequently to fertilization, N depositions probably play an important role in the observed trend. Based on experimental results, the single effect of sylvicultural improvements (wider initial spacing and higher thinning) could partly explain the radial growth increase but not the height difference. Difference in land use history is insufficient to explain the changes. The inverse correlation between radial growth and temperature dismisses the role of warmer climate as stimulating growth factor in the studied region. Further investigations could be undertaken to establish the possible role of increasing atmospheric CO_2 among mature trees.

Acknowledgements

The authors are grateful to the French National Forest Office, to the Regional Forestry Administrations of Nantes and Orléans, and to several forest owners who provided resources for this project. The authors also express their gratitude to Yann Dumas, François Gérémia, Christian Kieffer, Roger Schipfer, and Bernadette Vallée for their helpful technical assistance.

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