Response of *Pinus leucodermis* to climate and anthropogenic activity in the National Park of Pollino (Basilicata, Southern Italy)

Luigi Todaro[a], Laia Andreu[b], Carmela Miriam D'Alessandro[a], Emilia Gutiérrez[b], Paolo Cherubini[c], Antonio Saracino[d,*]

[a]Department of Crop Systems, Forestry, and Environmental Sciences, University of Basilicata, Viale dell'Ateneo Lucano 10, 85100 Potenza, Italy
[b]Department of Ecology, University of Barcelona, Avenida Diagonal 645, 08028 Barcelona, Spain
[c]WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zuercherstr. 111, 8903 Birmensdorf, Switzerland
[d]Department of Arboriculture, Botany and Plant Pathology, University of Naples "Federico II", Via Università 100, 80055 Portici, Italy

ARTICLE INFO

ABSTRACT

Pinus leucodermis (=*P. heldreichii* var. *leucodermis*) is widespread in the Balkan Peninsula and is present as a post-glacial relict in Southern Italy. The oldest Italian populations of this species are located at high elevation in the National Park of Pollino, where grazing and logging had endangered their survival, especially during the 20th century. In 1993 the National Park was founded and anthropogenic activities were restricted. To understand the response of *P. leucodermis* at the upper tree-line to climatic and anthropogenic activity variations, we developed a tree-ring width chronology (1464–2003). For the period 1804–2003 separate chronologies for the earlywood and latewood were built, and resin duct density was assessed on total ring, earlywood and latewood. Age structure of saplings was also determined. After 1950 a steep decline in tree-ring width was followed by a recovery since 1981. During the 20th century radial growth response to climate was not strong and not stable. In the period 1953–2000 *P. leucodermis* radial growth seemed to take advantage of high temperatures and low precipitation. Resin duct density chronologies were not a reliable dendroecological variable, but they documented a metabolic trade-off between growth and differentiation processes. The gap in the age structure between long-lived trees (over 200 years old) and saplings around 40 years old, which mainly grow in protected microsites between rocks, could indicate a negative influence of grazing and related human activities. We suggest that the protection strategies introduced by the National Park could play a positive role in the recruitment of new saplings and in the ring growth recovery of old trees of *P. leucodermis*.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Pinus leucodermis (=*P. heldreichii* var. *leucodermis*) is widespread in the Balkan peninsula and has some scattered and isolated populations in Southern Italy, where it grows at the western limit of its geographical range distribution (Jalas and Suominen, 1973). It grows in the Apennines, between Calabria and Basilicata, from 530 up to 2240 m a.s.l. (Avolio, 1996). These

---

populations represent a biogeographical island, interpreted as a relict of Tertiary flora of oro-Mediterranean forests which are genetically isolated from Greek populations (Bucci et al., 1997). According to Farjon (2001) and the IUCN Specialist Group (1998), *P. heldreichii* var. *leucodermis* is at low risk of extinction. However, a limited recruitment of new individuals at the tree-line ecotone (sensu Körner, 1999) was observed in many stands and especially in those located in the National Park of Pollino (site of study). Today these stands are characterised by many large white snags and stumps mixed with scattered living old trees. A comparison of aerial photographs from 1954 to 2000 shows an upslope (re)colonisation by layering of *Fagus sylvatica* (not shown).

Several authors documented a reduction of *P. leucodermis* populations in the study area (Douglas, 1905; Morandini, 1950; Longhi, 1956) as a consequence of a long-lasting anthropo-zoogenic pressure (sensu Cairns and Moen, 2004). Research on recruitment dynamics is considered a priority in the case of populations located at the limit of the species' geographical range and away from the main range, because these stands may be more sensitive to climatic change than those at the core of the range (Brubaker, 1986).

Growth of *P. leucodermis* can be assessed using the information contained in the tree-rings and recruitment by studying the age structure of saplings. Changes in annual tree-ring growth trends could be due to the effect of environmental conditions, climate and anthropogenic disturbances. To analyse the influence of climatic conditions on the growth of conifer species at the tree-line, tree-ring width and wood density chronologies are used (Fritts, 1976; Schweingruber, 1988).

In the genus *Pinus*, constitutive resin ducts in the secondary xylem may give additional information on environmental conditions. The amount and position of vertical resin ducts, considered as a product of secondary metabolism (Loomis, 1932; Lorio, 1986), seem to reflect environmental conditions affecting the metabolic trade-off between growth and differentiation processes during the growing season (Lorio, 1986; Herms and Mattson, 1992). Constitutive secretory structures (i.e. resin ducts) located in the earlywood are built in the spring, which is a period of rapid tree growth. However, latewood resin ducts are produced when the plant experiences stressful environmental conditions, which limit growth and promote differentiation processes (Lorio, 1986; Lorio and Sommers, 1986).

The main aims of our research are: (i) to document temporal variation of total ring width (TRw) from 1464 to 2003, earlywood (EWw) and latewood (LWw) width, and resin duct density (RDd) series in total ring (TRRDd), earlywood (EWRDd) and latewood (LWRDd) from 1804 to 2003; (ii) to search for relationships between these series and climate; (iii) to assess the stability of these relationships through time comparing two overlapping periods (1925–1972 and 1953–2000); and (iv) to assess the recent pattern of *P. leucodermis* recruitment.

2. Materials and methods

2.1. Study site

The study site (Fig. 1) is located at Serra di Crispo (39° 56′ 47″ N, 16° 12′ 22″ E), in the municipality of Terranova del Pollino,
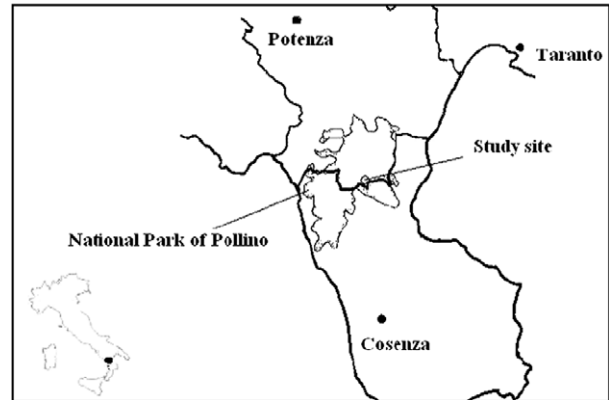

Fig. 1 – Location of the study site in the National Park of Pollino (Southern Italy).

Province of Potenza (Basilicata Region, Southern Italy). Serra di Crispo is a N-S oriented rocky mountain ridge, which peaks at 2054 m a.s.l., with the west-facing slope less steep (40–60%) than the east-facing one (up to 100% and more). Together with Serra delle Ciavole and Serra Dolcedorme (located at its southern and south-western sides, respectively) and Monte Pollino (at the western side), Serra di Crispo forms a natural amphitheatre surrounding a wide Karst plateau, the Piani del Pollino, characterised by glacial Würm morphotypes. The bedrock is a fissured greyish limestone (dolomite) from the Mesozoic. The soil is shallow, rendzina-like with xeromoder humus, basic pH and large outcropping rocks.

Annual temperature and precipitation patterns indicate a Mediterranean climate, humid type: high temperature and irradiance in summer and irregular distribution of precipitation throughout the year. Mean annual precipitation is 1570 mm, distributed as follows: 39.5% in winter, 23.7% in spring, 29.2% in autumn and 7.6% in summer. At the study site, mean annual temperature is 4 °C (Avolio, 1996), snow cover lasts from November to the end of May.

Soil water depletion during summer is mitigated by fog and low clouds, carried by western weather systems from the Tyrrhenian Sea, about 36 km distant from the study site. The high atmospheric humidity condenses on the tree crowns and reaches the soil via throughfall.

2.2. Study stands

At the study site *P. leucodermis* is the only tree-line species forming stands with long-lived, slow-growing scattered trees. The tree-line ecotone ranges from 1800 up to 2050 m a.s.l. In this habitat trees can reach an age up to 1000 years (Serre-Bachet, 1985; Biondi and Visani, 1993). Due to the harsh environmental conditions (wind, ice, snow) old trees exhibit asymmetrical growth forms and flagged crowns. Stems show spiral grain and are frequently struck by lightening. Many trees have wounds and fire scars at the base of the stem, as well as a lack of branches caused by axes.

We sampled a *P. leucodermis* stand on Serra di Crispo, where scattered isolated large trees grow among rocks on a

west-facing slope. The main accompanying species are: *Daphne oleoides*, *Rhamnus pumilus*, *Sorbus graeca*, very short shrubs of *Juniperus hemisphaerica* (20–60% cover) and *Gentiana lutea*, surrounded by patches of grassland of the *Caricetum–Seslerietum nitidae* association (Bonin, 1978).

2.3. Meteorological data

There are few meteorological stations in the area and with short operation periods (Capra et al., 2004). We used monthly mean (T_{mean}), minimum (T_{min}) and maximum (T_{max}) temperatures recorded at Castrovillari (353 m a.s.l., 12.5 km distant from the study site) from 1924 to 2003. The few missing values were estimated by linear regression (R^2 is 0.96, 0.93 and 0.94 for T_{mean}, T_{min} and T_{max}, respectively) with temperature series recorded at the meteorological station of Teana (806 m a.s.l., 34.8 km distant from Castrovillari). Monthly precipitation (P) records were taken from Campotenese (965 m a.s.l., 11 km distant from the study site) from 1922 to 2000. The missing values were estimated by linear regression ($R^2 = 0.78$) using data from the meteorological station of Cosenza (242 m a.s.l., 60.8 km distant from Campotenese).

2.4. Tree-ring width chronologies

Three cores were extracted at breast height (1.30 m) from each of 15 *P. leucodermis* trees, but 4 cores were damaged. In total we measured 41 cores, which were mounted and sanded until tracheids were clearly visible under a 40× stereomicroscope. After visual cross-dating (Yamaguchi, 1991), EWw, LWw and TRw were measured with an accuracy of 0.01 mm by means of a semiautomatic measuring device (Aniol, 1983). The resulting series underwent a cross-dating quality control with Cofecha statistical software (Holmes, 1983). Standardization was done in two steps using Arstan software (Cook, 1985). Firstly, individual raw series were detrended by fitting a 70-year cubic smoothing spline, in order to amplify the climatic signal (high frequency) and to remove the non-climatic one (low frequency) (Fritts, 1976). Secondly, an autoregressive model was applied to remove the autocorrelation with the previous year's growth, obtaining uncorrelated values. A robust mean which reduces variance and bias caused by extreme values was computed (Cook and Briffa, 1990). Standard (detrended) and residual (detrended without autocorrelation) chronologies were developed following this procedure. Descriptive statistics of the ring series were calculated for the chronologies to allow comparisons with other dendroclimatic data sets. Residual chronologies were used to evaluate the relationship between radial growth and climate (Cook et al., 1990).

A reliable time span of our chronology was established, based on a minimum EPS value of 0.85 (Wigley et al., 1984), which is a widely used threshold in dendroclimatic studies. The expressed population signal (EPS) quantifies the common variability in all tree-ring series at a particular site, that is the proportion between common variance of trees (signal) and total variance (signal + noise). If all the trees in a stand are affected by the same set of climatic variables, such common information can be regarded as climatic information (Cook and Briffa, 1990).

2.5. Resin duct density

From 41 undamaged cores ten were randomly selected from 10 *P. leucodermis* trees. In a constant tangential window of 5 mm width, vertical resin ducts (RD) of each core were counted for every ring from 1804 to 2003. Under a 40× stereomicroscope we considered the earlywood (EW) and latewood (LW) portion of each ring separately.

TRRDd, EWRDd and LWRDd were assessed by dividing the number of RD by ring portion area. This was calculated by multiplying a given tangential window by the tree-ring portion width of the correspondent year. No traumatic resin ducts were found. Arstan software was used to compute a robust mean of the RDd individual series (without any detrending) and to calculate descriptive statistics. Standard chronology version of ring width (RW) and RDd series were used to perform simple Pearson correlations for three different study periods (1804–2003, 1804–1903 and 1904–2003).

2.6. Correlations and response functions

Correlation and response function analyses (FFRR) were performed using Dendroclim software (Biondi and Waikul, 2004) in order to quantify the climate–growth relationship between residual chronology and meteorological data (monthly T_{mean}, T_{min} and T_{max}, and p) from 1925 to 2000.

The response functions were used to assess climate–growth relationships using a stepwise multiple regression on principal components in order to avoid multi-collinearity usually found in meteorological data sets (Fritts, 1976). Climate–growth relationships were analysed from July of the previous year up to October of the current growth year.

Response functions were performed for the entire period 1925–2000 covered by meteorological data, and for two subperiods (1925–1972 and 1953–2000) to analyse temporal stability of growth–climate relationships throughout time, as well as to detect changes in the climatic response of *P. leucodermis*.

2.7. Age structure of P. leucodermis saplings

In 1990, the age of 118 *P. leucodermis* saplings (root collar diameter: 0.4–10 cm; height: 0.1–2.1 m) was estimated in five transects (from 200 up to 7854 m^2) and of 109 saplings sampled at random outside the transects. The age was determined by counting branch whorls and bud scars. All the saplings (n = 227) were classified according to their microsite establishment: (i) between rocks, (ii) inside *Juniperus* cover, and (iii) in open spaces without rock and shrubs covers.

2.8. Historical records

The temporal variation of the resident population in 4 villages (Terranova del Pollino, San Severino Lucano, Viggianello and Rotonda) surrounding the study site was obtained from the Istituto Nazionale di Statistica (ISTAT) for the period from 1861 (Unity of Italy) to 2000, while data for 1797 were taken from the Municipal archives.

No data are available about the number of animals grazing in the past. In order to fill this gap we interviewed some old native shepherds. Thanks to the memory of these shepherds,

we reconstructed roughly the number of animals and the activities related to grazing before and after the 1970s. The year 1974 marks the decline of transhumance (seasonal movement of livestock between mountain and lowland pastures).

With the institution of the Regional Park of Pollino (1986) *P. leucodermis* began to be a protected species. Its protection status was reinforced in 1993 when the area became the National Park of Pollino.

3. Results

3.1. Ring width and resin duct density chronologies

The 540-year site master chronology, from 1464 to 2003, is depicted in Fig. 2. The descriptive statistics are shown in Table 1A.

Raw data of ring width show a clear decreasing trend with age (Fig. 2a), that was removed using standardization (see Section 2.4). As a result, the residual chronology (Fig. 2b) does not present this trend. A clear decrease of the tree-ring width indices appears since 1951, followed by a steep increase from 1981 to 2003. During the 20th century, the highest peaks are reached in 1951 and 2003.

TRw, EWw and LWw standard chronology trends and their corresponding RDd standard series during the 200 years from 1804 to 2003 are shown in Fig. 3. The descriptive statistics of their standard and residual ring width chronologies are reported in Table 1B.

Kurtosis indicates asymmetrical distribution of the mean, especially in LWw. The signal-to-noise ratio (SNR) of TRw in two periods (1600–2003 and 1807–2003) and of EWw in one period (1807–2003) indicates a strong common signal. LWw shows a low first-order autocorrelation coefficient and EPS (<0.85), indicating that this chronology might be less reliable.

The absolute number of resin ducts is significantly ($p < 0.05$) higher in the LW (82.7% of the total) than in the EW (17.3% of the total) portion. TRRDd, EWRDd and LWRDd show higher mean sensitivity values than ring width (Table 1B). Skewness and Kurtosis indicate an asymmetrical distribution of the mean, mainly in LWRDd. A low first-order autocorrelation is shown in all RDd series. EPS of TRRDd, EWRDd and LWRDd is very low, particularly in EWRDd, indicating a lower common variability than in tree-ring width chronologies. These weak common signals did not permit to analyse RDd-climate relationships through time. Our results show that *P. leucodermis* ring width contained more common information that can be regarded as climatic information, compared to resin ducts when using the same number of samples (10 trees).

The pattern of TRRDd and LWRDd (1804–2003) is contrasting to the one of TRw and LWw, respectively. The same pattern is not always present in EWRDd (Fig. 3).

Table 2 shows simple Pearson correlations between RDd and RW series for three different periods (1804–2003, 1804–1903 and 1904–2003). For all the periods there is a significant negative correlation between TRRDd, LWRDd and almost all RW series, showing a major strength in the last century. A significant positive correlation between EWRDd and TRw and between EWRDd and EWw is only found in the whole study period.

3.2. Correlation and response functions between the ring width chronologies and climate

The two chronologies (1464–2003 and 1804–2003) are statistically similar (Table 1). Moreover, the results obtained with correlation and response function analyses are almost identical. Therefore, in order to make easier comparisons with the other ring width chronologies (EWw and LWw), we present only the correlation and FFRR results of TRw built with 10 cores.
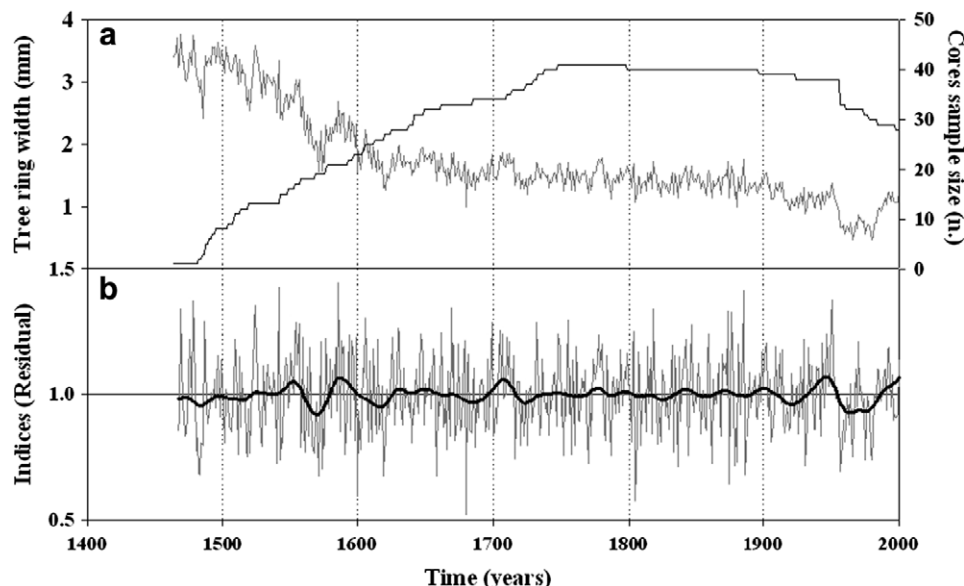

Fig. 2 – Tree-ring width chronology of *Pinus leucodermis*. (a) Raw data and cores sample size. (b) Residual chronologies. Bold line is 32-year smoothing spline.

Table 1 – (A) Descriptive statistics and common interval analysis of total ring width (TRw) chronologies based on 41 cores from 15 trees. (B) Descriptive statistics and common interval analysis of chronologies of width in total ring (TRw), earlywood (EWw) and latewood (LWw), and density of resin duct in total ring (TRRDd), earlywood (EWRDd) and latewood (LWRDd), based on 10 cores from 10 trees

| Chronology	(A) 1464–2003 TRw		(B) 1804–2003 TRw		EWw		LWw		TRRDd	EWRDd	LWRDd
	Stand	Res	Stand	Res	Stand	Res	Stand	Res	Stand	Stand	Stand
Mean	0.99	1.00	0.99	1.00	0.99	1.00	0.98	0.99	0.64	0.12	4.28
Median	0.98	0.99	0.98	0.99	0.98	0.99	0.97	0.98	0.64	0.10	3.99
Mean sensitivity	0.15	0.17	0.14	0.17	0.15	0.18	0.17	0.18	0.47	0.99	0.52
Standard deviation	0.17	0.15	0.16	0.15	0.17	0.15	0.17	0.16	0.26	0.10	2.12
Skewness	0.22	0.05	0.38	0.03	0.42	0.08	0.62	0.72	0.82	0.79	1.54
Kurtosis	0.02	−0.11	0.27	−0.02	0.26	−0.19	1.46	1.93	1.42	0.13	3.21
Autocorrelation ord1	0.34	0.00	0.36	−0.06	0.36	−0.04	0.14	−0.04	−0.19	0.01	−0.21
Partial AR ord2	0.18	−0.01	0.16	−0.01	0.18	0.02	0.08	0.03	−0.18	−0.10	−0.09
Common interval	1600–2003		1807–2003						1804–2003		
Among all radii	0.41	0.46	0.39	0.42	0.38	0.40	0.17	0.18	0.11	0.01	0.06
Between trees	0.40	0.45	0.39	0.42	0.38	0.40	0.17	0.18	0.11	0.01	0.06
Signal-to-noise ratio	5.33	6.55	6.35	7.29	6.22	6.76	2.07	2.22	1.20	0.11	0.66
EPS	0.84	0.87	0.86	0.88	0.86	0.87	0.68	0.69	0.54	0.10	0.40
1st eigenvector Var (%)	47.55	51.74	45.70	48.45	45.22	46.76	25.78	26.67	20.57	14.23	16.20
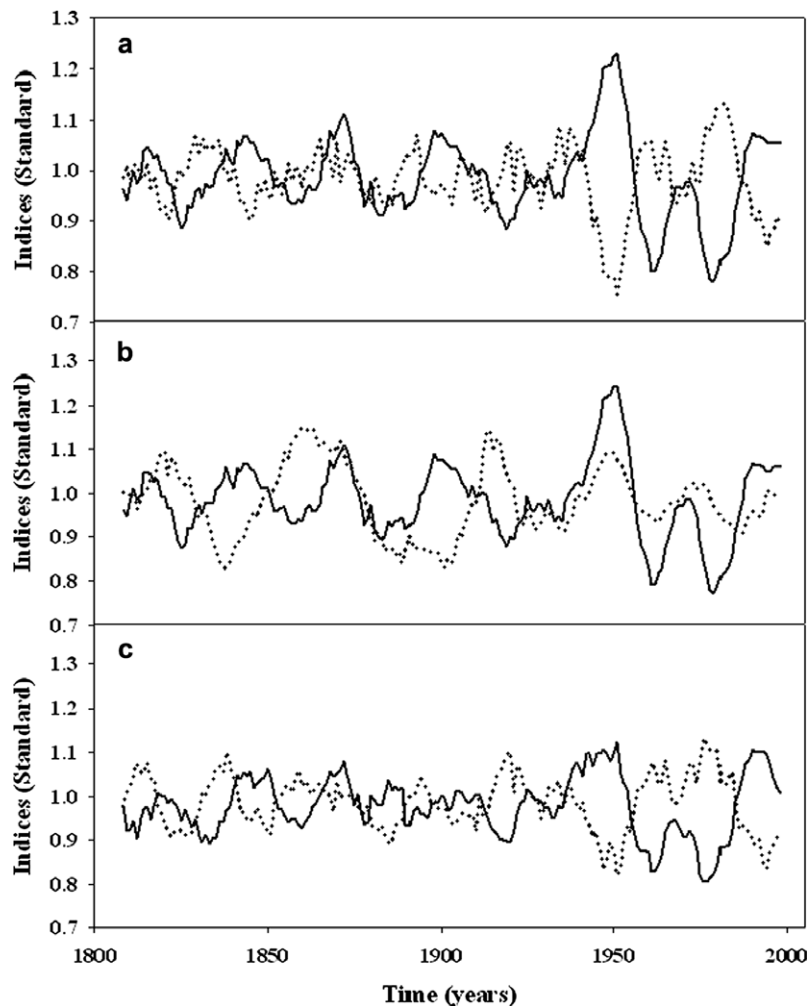
Fig. 3 – (a) Total ring, (b) earlywood and (c) latewood width and corresponding resin duct density for the period 1804–2003. Standard chronologies of RW (bold line, 10-year running average) and RDd (dotted line, 10-year running average) were used.

Table 2 – Simple Pearson correlation between width of total ring (TRw), earlywood (EWw) and latewood (LWw), and density of resin duct in total ring (TRRDd), earlywood (EWRDd) and latewood (LWRDd) for three periods (1804–2003; 1804–1903; 1904–2003)

	TRRDd	EWRDd	LWRDd
1804–2003			
TRw	**−0.26**	**0.13**	**−0.22**
	$p = 0.000$	$p = 0.036$	$p = 0.001$
EWw	**−0.27**	**0.13**	
	$p = 0.000$	$p = 0.039$	
LWw	**−0.12**		**−0.37**
	$p = 0.043$		$p = 0.000$
1804–1903			
TRw	**−0.17**	0.10	−0.11
	$p = 0.044$	ns	ns
EWw	**−0.19**	0.09	
	$p = 0.027$	ns	
LWw	0.01		**−0.36**
	ns		$p = 0.000$
1904–2003			
TRw	**−0.33**	0.16	**−0.31**
	$p = 0.000$	ns	$p = 0.001$
EWw	**−0.32**	0.17	
	$p = 0.000$	ns	
LWw	**−0.26**		**−0.40**
	$p = 0.005$		$p = 0.000$

Standard chronologies of RW and RDd were used. Bold numbers are significant at $p < 0.05$; ns indicates no significant correlation.

In the whole period (1925–2000), TRw shows a significant ($p < 0.05$) positive relationship with October and November T_{max} of the previous year ($t − 1$) and April and July of the current year (t) (Table 3A). Correlation between ring width and T_{mean} is significant and positive in November$_{(t − 1)}$, April$_{(t)}$ and July$_{(t)}$. A significant positive correlation between TRw and T_{min} is detected only in April$_{(t)}$. Concerning precipitations, the ones of July$_{(t − 1)}$ also affect ring growth positively.

A different picture emerges when comparing the periods 1925–1972 and 1953–2000 (Table 3Cb, respectively). T_{max} positive correlations (especially in the previous autumn and in the current spring and summer) seem to be more evident in the second period than in the first one. T_{mean} exerts a significant positive effect mainly in the first period. T_{min} exhibits a greater significant positive effect in several months of the first period, while in the second period there is a significant negative effect in March$_{(t)}$. However, the largest differences between the two periods are due to precipitation. During the first period (Table 3B), April$_{(t)}$ precipitation shows a significant negative relationship with tree growth, while a significant positive relationship is found in August$_{(t − 1)}$ (also significant by FFRR analysis) and in October$_{(t)}$. During the second period (Table 3C) there is a significant positive effect of July$_{(t − 1)}$ precipitation on TRw, while October$_{(t − 1)}$ and October$_{(t)}$ precipitation has a significantly negative effect.

Concerning the temporal trends of meteorological data (Fig. 4), T_{max} tends to decrease during the first period (1925–

1972), while it increases during the second period (1953–2000), and the slopes of the two linear regressions differ significantly ($p < 0.05$). In contrast, T_{min} decreases in both periods and the slope of the two linear regressions are also significantly ($p < 0.05$) different.

For the whole period (1925–2000), the results for EWw are similar to those for TRw (Table 4Aa). LWw does not establish a significant relationship with climate (Table 4Ab), except T_{max} of November$_{(t − 1)}$ and T_{min} of July$_{(t − 1)}$ which show significant positive and negative correlations, respectively.

In the period 1925–1972 (Table 4Ba), EWw is positively affected by T_{max} of October$_{(t − 1)}$ and April$_{(t)}$, and by T_{mean} and T_{min} of various months of the previous and current year. Precipitation effect on the EWw is significantly positive (significant FFRR) in August$_{(t − 1)}$ and significantly negative in April$_{(t)}$.

In the period 1953–2000 (Table 4Ca), T_{max} shows a positive effect in several months on EWw. T_{mean} has a significant positive effect in November$_{(t − 1)}$, May$_{(t)}$ and July$_{(t)}$, while T_{min} does not show any significant effect. Precipitation, for the same period, has a significant positive effect in July$_{(t − 1)}$ and a negative effect in October of the previous and current year.

In the period 1925–1972 (Table 4Bb), LWw exhibits a significant positive relationship with temperature parameters (T_{max}, T_{mean} and T_{min}) of November$_{(t − 1)}$. T_{max} and T_{mean} of July$_{(t)}$, show a significant positive effect, while precipitation affects LWw mainly in August$_{(t − 1)}$ (significant FFRR).

A different picture emerges in the period 1972–2000 for LWw (Table 4B and C). T_{max} of May$_{(t)}$ exhibits a significant positive correlation. T_{mean} of July$_{(t − 1)}$ and February$_{(t)}$ and T_{min} of the previous year and current winter show significant negative correlations. October$_{(t − 1)}$, January$_{(t)}$ and May$_{(t)}$ precipitation affect growth negatively.

3.3. *P. leucodermis* recruitment and anthropogenic activity

Fig. 5 shows the age structure frequency of saplings in 1990, standard chronology and human population variations (from 1797 to 2003).

For the last 50 years it is interesting to observe that the recruitment of *P. leucodermis* saplings increased with a decreasing of the inhabitants, which is an indirect index of human pressure in our case. About 90% of *P. leucodermis* saplings were recruited in the 30 years previous to 1990 with a mode in 1970 accounting for 15% of the total saplings recruited. Regarding microsite seedlings establishment, 95% were found between rocks, 5% inside *Juniperus* cover and no saplings in open space.

4. Discussions and conclusions

For the *P. leucodermis* population growing at the tree-line on a Mediterranean mountain, the main results obtained using dendroecological tools documented:

– a recent recovery of radial growth in old *P. leucodermis* trees;
– that the radial growth response to climate is not strong and not stable during the 20th century;
– a metabolic trade-off between growth and differentiation processes (of which resin ducts are a product);

Table 3 – Simple Pearson correlation and response function (FFRR) coefficients between total ring width (TRw) and monthly temperatures (T_{max}, T_{mean}, T_{min}) and precipitation for (A) 1925–2000, (B) 1925–1972 and (C) 1953–2000

TRw	TEMPERATURE																PRECIPITATION																
	Previous year						Current year										Previous year						Current year									
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
A. (1925-2000)																																
T max	·	·	○	0.21	0.26	·	○	·	·	0.28	○	○	0.23	○	·	·	0.23	○	·	·	·	·	·	·	○	·	○	·	·	·	·	○
T mean	·	·	○	○	0.23	·	·	·	·	0.29	○	○	0.24	○	·	·	0.23	○	·	·	·	·	·	○	·	·	○	○	·	·	·	○
T min	·	·	○	○	○	○	·	·	·	0.24	○	○	○	○	·	·	0.23	○	·	·	·	·	·	○	·	·	○	○	·	·	·	○
B. (1925-1972)																																
T max	·	·	○	○	○	·	○	○	○	0.26	○	○	○	○	○	·	○	(0.33)	·	○	·	·	·	○	○	-0.26	·	○	○	○	·	0.25
T mean	·	·	0.28	○	0.26	○	○	○	○	0.34	○	·	0.28	○	○	·	○	(0.33)	·	○	·	·	·	○	○	-0.26	·	○	○	○	·	0.25
T min	·	·	0.34	○	0.27	○	○	○	○	0.33	0.25	·	0.30	○	○	·	○	(0.33)	·	○	·	·	·	○	○	(-0.26)	○	○	○	○	·	0.25
C. (1953-2000)																																
T max	·	·	○	0.27	0.38	·	0.27	·	○	0.36	0.35	○	0.32	○	○	·	0.31	○	·	(-0.32)	·	·	·	·	○	·	·	○	·	·	·	-0.31
T mean	·	○	·	○	○	·	○	·	·	○	0.27	○	○	○	·	·	0.31	○	·	(-0.32)	·	·	·	·	○	·	·	○	·	·	·	-0.31
T min	·	○	○	○	○	·	·	·	-0.24	○	○	○	○	○	·	·	0.31	○	·	-0.32	·	○	·	·	○	·	·	○	·	·	·	-0.31

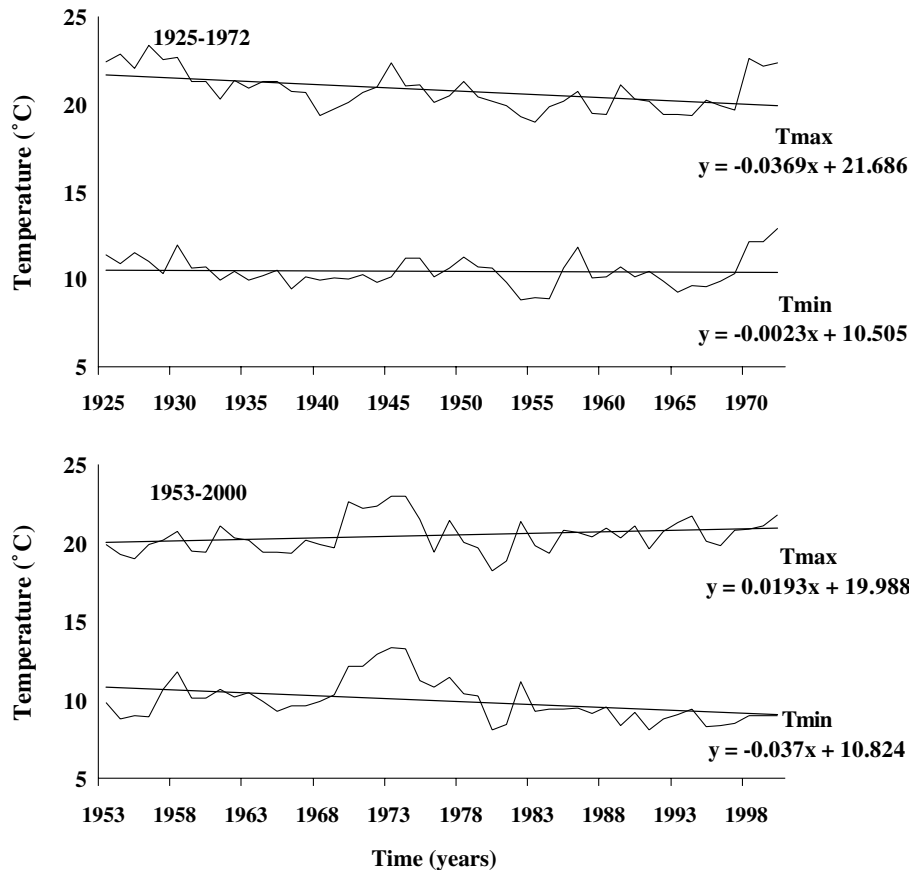|		
☐ Positive correlation	n	significant correlation
▨ Negative correlation	(n.)	significant correlation and significant FFRR coefficients
○ Positive FFRR coefficient	*(n.)*	only significant FFRR coefficients
· Negative FFRR coefficient		

Fig. 4 – Annual variation of T_{max} and T_{min} recorded at the meteorological station of Castrovillari for the periods 1925–1972 and 1953–2000.

– a restart of regeneration recruitment with a gap between long-lived trees (more than 200 years old) and young saplings.

Finally meteorological records document a significant increase of T_{max} and a significant decrease of T_{min} during the last 48 years.

4.1. Ring width and resin duct density

It is well known that growth declines due to biological age trends. At the study site growth recovery in old trees seems not be affected by atmospheric nitrogen deposition (ICP Forests, 2005).

The strong ring width decline documented after 1950 was attributed hypothetically by Biondi and Visani (1993) to the wounds found at the base of the stems. Growth recovery registered since 1981 could be due to stopping of injuring *P. leucodermis* trees and to the strong reduction of grazing pressure. Moreover the significant trend of increasing differences between T_{min} and T_{max}, during the last decades, could have favoured this pioneer species which grows in open spaces, where great differences between minimum and maximum meteorological parameters are common.

The significant negative and positive correlation found between RW and RDd series might indicate the presence

and absence, respectively, of a metabolic trade-off between growth and differentiation processes. In the secondary xylem of genus *Pinus*, the amount of constitutive resin ducts is more a phenotypic than a genotypic response (Fahn, 1990). According to Lorio (1986), the phenotypic pattern of oleoresin and related storage structures in pines is well explained by the growth/differentiation balance hypothesis (GDBH), which was first proposed by Loomis (1932) and reviewed by Herms and Mattson (1992). According to this hypothesis, the growth of new tissues (primary metabolism) competes with differentiation (secondary metabolism), because the carbon-source is the same (photosynthesis) for both pathways.

Concerning the annual growth pattern of *P. leucodermis*, it must be considered that maximum cambial activity peaks around the summer solstice at the study site (Rossi et al., 2006). In addition, when resin ducts are formed in EW, shoots and cambium are active sinks. Formation of RD in the LW starts presumably in July, when growth processes are less prominent, shoots and cambium are moderate carbon sinks, and the tree is under moderate water stress conditions.

Growth is more sensitive to this resource limitation than photosynthesis and the surplus of carbon not invested for growth is employed for secondary metabolism (Lorio and Sommers, 1986; Herms and Mattson, 1992; Luxmoore et al., 1995). Higher LWRDd and amount of stored oleoresins,

Table 4 – Simple Pearson correlation and response function (FFRR) coefficients between earlywood (EWw) and latewood (LWw) width and monthly temperatures (T_{max}, T_{mean}, T_{min}) and precipitation for (A) 1925–2000, (B) 1925–1972 and (C) 1953–2000.

Column groups — Temperature: Previous year (Jul–Dec) and Current year (Jan–Oct); Precipitation: Previous year (Jul–Dec) and Current year (Jan–Oct). Precipitation columns are suffixed "(p)". Circled values shown in parentheses.

EWw-LWw	Var	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Jul(p)	Aug(p)	Sep(p)	Oct(p)	Nov(p)	Dec(p)	Jan(p)	Feb(p)	Mar(p)	Apr(p)	May(p)	Jun(p)	Jul(p)	Aug(p)	Sep(p)	Oct(p)
A. (1925-2000)																																	
a.EW	T max				0.24	0.27					(0.29)			0.24				0.23															
a.EW	T mean					0.25					(0.31)			0.26				0.23															
a.EW	T min									0.26				0.23	0.21			0.23															
b.LW	T max					0.24																											
b.LW	T mean																																
b.LW	T min	-0.22																															
B. (1925-1972)																																	
a.EW	T max				0.24						0.27								(0.31)									-0.26					
a.EW	T mean			0.29	0.27			0.22			0.36		0.28						(0.31)									-0.26					
a.EW	T min			0.36		0.27					0.35	0.27		0.31					(0.31)									(-0.26)					
b.LW	T max				(0.31)									0.35					(0.38)														
b.LW	T mean				(0.32)									0.33					(0.38)														
b.LW	T min					0.30													(0.38)									(-0.24)					
C. (1953-2000)																																	
a.EW	T max				0.31	(0.43)		0.30			(0.40)	0.35		0.33				0.31			(-0.31)												-0.32
a.EW	T mean					0.27						0.27		0.26				0.31			-0.31												-0.32
a.EW	T min																	0.31			-0.31												-0.32
b.LW	T max												0.21								(-0.33)			(-0.36)			-0.27						
b.LW	T mean	-0.29							-0.31												(-0.33)			(-0.36)			-0.27						
b.LW	T min	-0.34		-0.29		-0.33			-0.42	-0.38											-0.33			(-0.36)			-0.27						

Legend:
- □ Positive correlation
- ▨ Negative correlation
- ○ Positive FFRR coefficient
- · Negative FFRR coefficient
- n. significant correlation
- (n.) significant correlation and significant FFRR coefficients
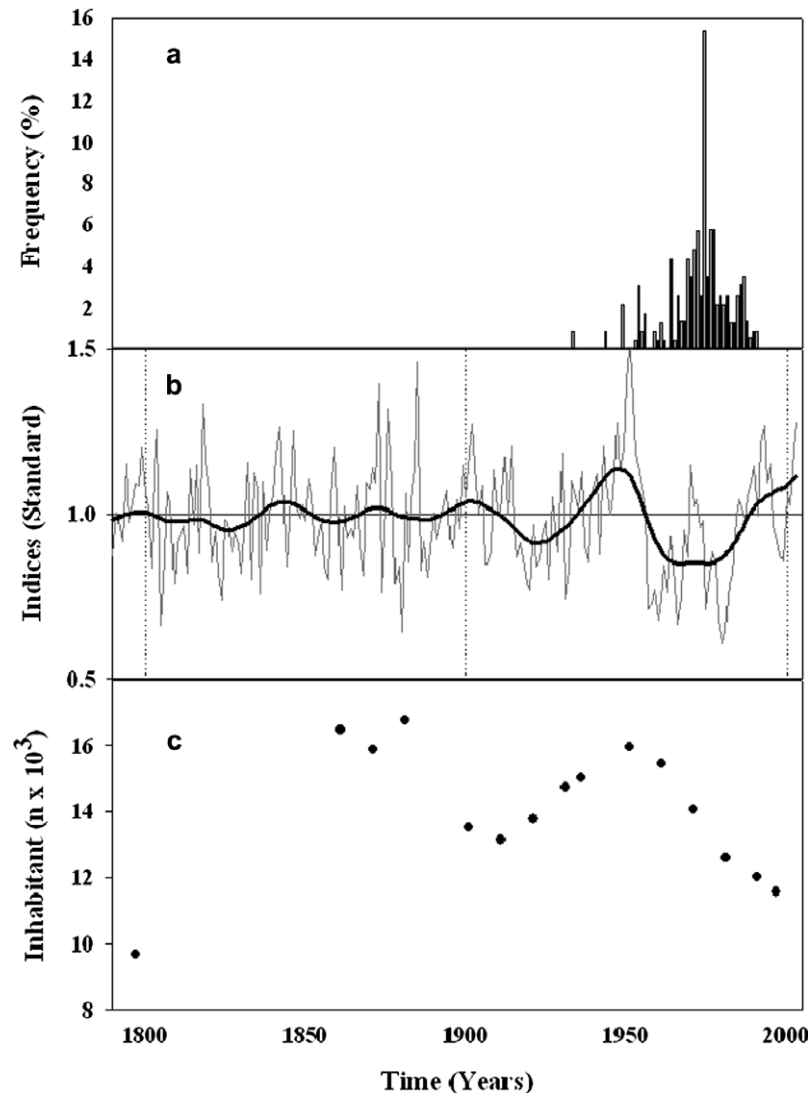- (*n.*) only significant FFRR coefficients

Fig. 5 – (a) Age structure of *Pinus leucodermis* saplings (n = 227) in 1990, (b) total ring width indices of *Pinus leucodermis* and (c) inhabitants of the four neighbouring villages.

together with thicker secondary tracheid walls (Esau, 1977), determine the plant's major investment in secondary metabolites (lignin, resin ducts, oleoresins). In the trees studied, the apposition of lignin in the secondary wall of tracheids starts on June 14th and ends on October 4th (Rossi, personal communication). In the same period plant metabolic efforts to build storage structures are higher than those needed to build oleoresins contained in them (Lerdau and Gershenzon, 1997).

For *Pinus nigra*, Levanič (1999) considered the resin duct not a reliable dendroecological variable, but for *P. sylvestris* Rigling et al. (2003) and for *Picea abies* Wimmer and Grabner (1997) documented a climatic influence. One possible explanation of these different results might be that the resin duct pool counted along the entire annual wood ring does not document sufficiently the influence of the different environmental factors and physiological processes which affect RD production in EW and LW.

4.2. Correlation and response functions between the ring width chronologies and climate

Over the whole period 1925–2000, TRw and EWw seem to be more affected by temperatures than by precipitation. This is supported by other authors' works on tree-line (e.g. Splechtna et al., 2000; Körner, 1999; Xiong et al., 1998). Nevertheless, precipitation seems to be an indirect limiting resource only in case of its excess (Tuovinen, 2005).

As it is well documented in literature, temperatures (especially T_{max}) experienced during the previous autumn affect the metabolic carbohydrate pool (Tardif et al., 2003), while during spring and early summer they affect TRw and EWw in a major way (Schweingruber, 1988; Körner, 1999).

At the study site *P. leucodermis* cambial activity starts in mid May and stops at the end of July. Cell growth starts also in mid May, but ends within the first half of August (Rossi, personal communication). In our study (data not shown),

the single flushing episode of the shoots (from bud opening to the new winter bud) occurred between June 21st and July 19th and reproductive structures were developed around mid June. All these life-cycle stages are active carbohydrate sinks (Luxmoore et al., 1995). The fixed shoot growth pattern is common to many boreal and cold-temperate conifer species (Gower et al., 1995). Root growth pattern data are not available, although they would be a very useful tool for a better interpretation of our data.

A different picture emerges when considering LW formation: in this case opposite effects of temperatures and precipitations are recorded in the two periods. In agreement with these results, an annual thermal increase (from 10.1 °C in 1925 to 10.9 °C in 2000) was recorded during the study period. Quite a uniform temperature trend was observed by Brunetti et al. (2006), with an increase of 1 °C per century all over Italy. For the last 50 years, the authors documented that the maximum temperature trend increase was stronger than that of the minimum temperature.

The combined negative effect of precipitation and minimum temperatures before LW development in the second period (1953–2000), could be related to the mobilisation of the previous year's reserves (Schweingruber, 1988) and to the risk of late frost. The minimum temperatures experienced by trees might alter the growth pattern in terms of loss of mobile carbohydrates for repairing frost damages (Körner, 1999).

4.3. P. leucodermis recruitment and anthropogenic activity

Marked abrupt variations of tree ring parameters do not seem to be modulated only by environmental factors, but also by other controlling factors (i.e. human impact). This is corroborated by the time-limited recruitment of new saplings. The gap in the age structure of the saplings population, from age 40 upward, could be explained with grazing disturbance. This is supported by the saplings' establishment only in protected microsites (mainly between rocks).

A strong association between climate change and recruitment was documented by Wang et al. (2006) for *Picea schrenkiana*. Temperature at the time of germination and the climate after the establishment of the seedlings were also crucial for *Pinus uncinata* (Camarero and Gutiérrez, 1999) and *P. leucodermis* (Borghetti et al., 1989).

Since the 16th century the about 3000 ha area was used for grazing. Goats, sheep, cows and mares arrived by transhumance from the 25 km distant Ionian sea coast and stationed from the beginning of June to the end of October in this area. All related activities were performed in situ: timber from *P. leucodermis* and *Fagus sylvatica* was the main resource for heating, lighting, housing and dairying (Douglas, 1905; Schilizzi and Viola, 1981; Troccoli, 1993).

At the end of the 19th century, a great part of the resident population left the native villages to emigrate to North and South America (Fig. 5). Timber of *P. leucodermis*, rich in oleoresin, was employed to build wood chests for shipping the emigrants' goods. At the beginning of the 20th century, a German company began to cut mainly *F. sylvatica* stands: a decauville (a small railway) was built on the eastern slope of Serra di Crispo (up to 1800 m a.s.l.) to carry the logs to the valley. Also *P. leucodermis* trees were bought and har-

vested by the German company, as reported by Douglas (1905). In the 1920s autarchic fascist laws favoured the increment of the resident population and their agricultural and pastoral activities. According to the old shepherds interviewed, after the Second World War (1945) the number of browsing animals in the area increased up to 2500 sheep, 500 goats, 400 cows and 100 horses. In the same period wild ungulates were extinguished by hunting. During the 1960s, the neighbouring villages were involved in a second emigration wave towards Northern Italy and Central Europe. From 1961 to 1971, the number of families employed in agriculture decreased by about 50%. Since the beginning of the 1970s grazing pressure started to decrease and a further decline of the pastoral activities coincided with the institution of the National Park of Pollino in 1993, even if the protection of *P. leucodermis* had already started in 1986.

In conclusion, the patterns of tree-ring width chronologies (TRw, EWw, LWw), the density of constitutive resin ducts series (TRRDd, EWRDd, LWRDd) and the age structure of *P. leucodermis* saplings were used as indicators to interpret the impact of climate changes and anthropogenic activities on *P. leucodermis* stands.

P. leucodermis population at the upper tree-line of our study site might be affected by temperature variation, which is also documented by Tardif et al. (2003) for other Mediterranean mountains, and by reduced anthropo-zoogenic pressure (Tranquillini, 1979; Tessier et al., 1997; Cairns and Moen, 2004; Holtmeier and Broll, 2005).

We suggest that the recent socio-economic changes and protection strategies introduced by the National Park Institution are playing a positive role in preserving *P. leucodermis* stands at high elevation, although grazing and tourist activities must be still better managed. The recruitment and recovery of radial growth of *P. leucodermis* indicate that today the population studied is not as threatened as in the past.

Acknowledgements

REFERENCES

Aniol, R.W., 1983. Procedures and statistics in dendrochronology. In: Eckstein, D., Wrobel, S., Aniol R.W. (Eds.), Dendrochronology and Archaeology in Europe, Mitteilungen der Bundesforschungsanstalt für Forst-und Holzwirtschaft, Hamburg, pp. 21–32.

Avolio, S. 1996. Il Pino Loricato (*Pinus leucodermis* Ant.), Prometeo Edizioni, Castrovillari (CS), Italy.

Biondi, F., Visani, S., 1993. Cronologie dendroanulari per la Penisola Italiana. Annali della Facoltà di Agraria, Università Cattolica di Milano, Italy, vol. 1, pp. 3–23.

Biondi, F., Waikul, K., 2004. DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers & Geosciences 30, 303–311.

Bonin, G., 1978. Contribution à la connaissance de la végétation des montagnes de l'Apennin centro-méridional. PhD Thesis. Faculté des Sciences et Techniques St Jérôme, Aix – Marseille III.

Borghetti, M., Vendramin, G.G., Giannini, R., Schettino, A., 1989. Effects of stratification, temperature and light on germination of *Pinus leucodermis*. Acta Oecologica/Oecologia Plantarum 10, 45–56.

Brubaker, L.B., 1986. Responses of tree populations to climatic change. Vegetatio 67, 119–130.

Brunetti, M., Maugeri, M., Monti, F., Nanni, T., 2006. Temperature and precipitation variability in Italy in the last two centuries from homogenised instruments time series. International Journal of Climatology 26, 345–381.

Bucci, G., Vendramin, G.G., Lelli, L., Vicario, F., 1997. Assessing the genetic divergence of *Pinus leucodermis* Ant. endangered populations: use of molecular markers for conservation purposes. Theoretical and Applied Genetics 7, 1138–1146.

Cairns, D.M., Moen, J., 2004. Herbivory influences tree lines. Journal of Ecology 92, 1019–1024.

Camarero, J.J., Gutiérrez, E., 1999. Structure and recent recruitment at alpine forest–pasture ecotones in the Spanish central Pyrenees. Écoscience 6, 451–464.

Capra, A., Malara, L.S., Scicolone, B., 2004. Analisi delle temperature e delle piogge mensili in Calabria nell'ultimo cinquantennio. Economia Montana 36, 31–36.

Cook, E.R., 1985. A Time Series Analysis Approach to Tree-ring Standardization. DS Thesis, University of Arizona, Tucson.

Cook, E.R., Briffa, K.R., 1990. Data Analysis. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, pp. 97–162.

Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. Tree-ring standardization and growth trend estimation. In: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of Dendrochronology. Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, pp. 104–123.

Douglas, N., 1905. Old Calabria, Edizione Italiana Aldo Monzella, Milano.

Esau, K., 1977. Anatomy of Seed Plants, second ed. John Wiley & Sons, New York.

Fahn, A., 1990. Plant Anatomy, fourth ed. Butterworth-Heinemann Ltd., Oxford. pp. 135–140, 337–346.

Farjon, A., 2001. World Checklist and Bibliography of Conifers, second ed. The Royal Botanic Gardens, The Bath Press, Kew, UK.

Fritts, H.C., 1976. Tree Ring and Climate. Academic Press, New York.

Gower, S.T., Isebrands, J.G., Sheriff, D.W., 1995. Carbon allocation and accumulation in conifers. In: Smith, W.K., Hinckley, T.M. (Eds.), Resource Physiology of Conifers: Acquisition, Allocation, and Utilization. Academic Press Inc., San Diego, California, pp. 217–254.

Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or defend. The Quarterly Review of Biology 3, 283–335.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69–78.

Holtmeier, F.-K., Broll, G., 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14, 395–410.

ICP Forests, 2005. International Co-operative Programme on Assessment and Monitoring of Air Pollution effects on Forests. Institute for World Forestry. Federal Research Centre for Forestry and Forest Products (BFH), Hamburg, Germany. <http://www.icp-forests.org/pdf/ICPForests05.ppt> at July 2006.

IUCN Specialist Group, 1998. *Pinus heldreichii*. In: IUCN 2004. 2004 IUCN Red List of Threatened Species.

Jalas, J., Suominen, J., 1973. Atlas Florae Europaeae, 2. Gymnospermae (Pinaceae to Ephedraceae). Cambridge University Press, Cambridge.

Körner, C., 1999. Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems. Springer-Verlag, Berlin.

Lerdau, M., Gershenzon, J., 1997. Allocation theory and chemical defense. In: Bazzaz, F.A., Grace, J. (Eds.), Plant Resource Allocation. Academic Press Inc., San Diego, CA, pp. 265–277.

Levanič, T., 1999. Vertical resin ducts in wood of Black Pine (*Pinus nigra* Arnold) as possible dendroecological variable. Phyton 39, 123–127.

Longhi, G., 1956. Alcune osservazioni fitogeografiche e biologiche sul pino loricato. Italia Forestale e Montana 5, 227–228.

Loomis, W.E., 1932. Growth-differentiation balance vs. carbohydrate–nitrogen ratio. Proceedings of American Society for Horticultural Science 29, 240–245.

Lorio Jr., P.L., 1986. Growth-differentiation balance: a basis for understanding southern pine beetle–tree interactions. Forest Ecology and Management 14, 259–273.

Lorio Jr., P.L., Sommers, R.A., 1986. Evidence of competition for photosynthates between growth process and oleoresin synthesis in *Pinus taeda* L.. Tree Physiology 2, 301–306.

Luxmoore, R.J., Oren, R., Sheriff, D.W., Thomas, R.B., 1995. Source–sink–storage relationships of conifers. In: Smith, W.K., Hinckley, T.M. (Eds.), Resource Physiology of Conifers: Acquisition, Allocation, and Utilization. Academic Press Inc., San Diego, CA, pp. 179–216.

Morandini, R., 1950. Tra i boschi di M. Pollino. Monti e Boschi 8, 361–365.

Rigling, A., Brühlhart, H., Bräker, O.U., Forster, T., Schweingruber, F.H., 2003. Effects of irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L. on dry sites in the central Alps, Switzerland. Forest Ecology and Management 175, 285–296.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., Borghetti, M., 2006. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytologist 170, 301–310.

Schilizzi, M.S., Viola, G., 1981. Terranova di Pollino. Storia e volto di una terra, Adriatica Editrice Salentina, Lecce, Italy.

Schweingruber, F.H., 1988. Tree Rings. Basics and Applications of Dendrochronology. Kluwer, Academic Press, Dordrecht.

Serre-Bachet, F., 1985. Une chronologie pluriséculaire du Sud de l'Italie. Dendrochronologia 3, 45–66.

Splechtna, B.E., Dobrý, J., Klinka, K., 2000. Tree-ring characteristics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in relation to elevation and climatic fluctuations. Annals of Forest Science 57, 89–100.

Tardif, J., Camarero, J.J., Ribas, M., Gutiérrez, E., 2003. Spatiotemporal variability in tree growth in the central Pyrenees: climatic and site influences. Ecological Monographs 73, 241–257.

Tessier, L., Guibal, F., Schweingruber, F.H., 1997. Research strategies in dendroecology and dendroclimatology in mountain environments. Climatic Change 36, 499–517.

Tranquillini, W., 1979. Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. Ecological Studies 31. Springer-Verlag, Berlin.

Troccoli, L. 1993. Due secoli di escursioni sul Pollino. Esploratori e studiosi verso il cuore del Parco. Prometeo Edizioni, Castrovillari (CS), Italy.

Tuovinen, M., 2005. Response of tree-ring width and density of *Pinus sylvestris* to climate beyond the continuous northern forest line in Finland. Dendrochronologia 22, 83–91.

Wang, T., Zhang, Q.-B., Ma, K., 2006. Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. Global Ecology and Biogeography 15, 406–415.

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average of correlated time series, with applications in dendroclimatology and hydrometeorology. Journal of Climate and Applied Meteorology 23, 201–213.

Wimmer, R., Grabner, M., 1997. Effects of climate on vertical resin duct density and radial growth of Norway spruce (*Picea abies* (L.) Karst.). Trees 11, 271–276.

Xiong, L., Okada, N., Fujiwara, T., Ohta, S., Palmer, J.G., 1998. Chronology development and climate response analysis of different New Zealand pink pine (*Halocarpus biformis*) tree-ring parameters. Canadian Journal of Forest Research 28, 566–573.

Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21, 414–416.