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The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a mediterranean scots pine forest[☆]

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Abstract

The relationships between climate variability and canopy dynamics (monthly litter production), chemical composition of the litter, secondary growth and female-cone production were studied in an old growth Scots pine (*Pinus sylvestris*) forest over the 1993–2003 period. The forest was located at a Mediterranean mountain site (Valsaín, Segovia, central Spain). The temporally explicit relationships between the mentioned variables were explored by chronological cluster of their time series. Mean air temperature significantly influenced litter production and its seasonal and intradecadal patterns. Seasonal patterns of litter N and P content were negatively correlated with litter production, exhibiting minima of 5.3 g kg⁻¹ (N) and 0.5 g kg⁻¹ (P) by the end of the summer and maxima of 15 g kg⁻¹ (N) and 1.2 g kg⁻¹ (P) during winter; these results are interpreted as retranslocation before needle shedding in summer and loss of green needles in winter respectively. In general the driest and hottest years (1994 and 1995) were associated with significantly decreased secondary growth in the next year, an increased cone production, and an increased nutrient loss due to the combined effect of an increased litter production and an increased nutrient concentration of the litter. Climatic changes during the early stages of cone formation that take place during the spring led to alterations in masting and in the tri-annual process of cone production. Since each parameter studied was differentially affected by climatic variability, the overall effect of the short-term climatic changes experienced by the Scots pine forest studied was an uncoupling of litter production, secondary growth, and reproduction.

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1. Introduction

The dynamics of litterfall are an important part of the nutrient cycle and energy transfer in forest ecosystems (Vitousek, 1982). Litterfall is closely related to the growth rate both of natural and of managed forests (Kavvadias et al., 2001), and constitutes an important nutrient feedback to the soil (Blanco, 2004). The fact that litter production is closely related to climate is well documented (Arneith et al., 1998; Pausas et al.,

1994), but there is not sufficient information to establish a general pattern due, to a great extent, to the difficulty involved in dealing with climatic variability, particularly in such climatically variable areas such as Mediterranean forests (Pausas et al., 1994). Thus, and despite growing concern regarding the impacts of climate change on forest ecosystems, we are still far from a sound understanding of how climate influences many important forest processes such as leaf turnover, biogeochemical cycles and productivity (Lindner et al., 2002; Sabaté et al., 2002). Moreover, this understanding is vital for anticipating the eventual impacts of climate change on the functioning of forests.

Previous studies have established significant relationships between litterfall production and climate conditions, although they have highlighted a broad year-to-year variability (Pausas et al., 1994). Precipitation is one of the factors most affecting

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litterfall production, principally due to the effect of the wind that tends to accompany storms and which also provokes the fall of living green needles (Cuevas and Lugo, 1998). Precipitation does not only cause leaves to fall (Pausas, 1997), but also influences the nutrient concentration of the litterfall (North et al., 2005; Wood et al., 2005). As was observed by Wood et al. (2005), precipitation washing green leaves can reduce the concentration of nutrients in the litterfall of these leaves during the rainy season in tropical forests. Another factor conditioning the amount of litterfall of a forest is the amount of aerial biomass existing in the canopy, this biomass being in turn related to the size, growth and density of the trees. This is why the elimination of trees by forestry practices or by natural causes can give rise to serious alterations in forest dynamics, influencing different aspects of the biogeochemical cycles and the long-term stability of the forest (Chertov et al., 1999).

The amount of nutrients reaching the soil in a forest ecosystem not only determines the rhythm of the main biogeochemical cycles, but also the productivity of the forest, and is in turn determined by the amount of litterfall and by the concentration of elements and nutrients contained therein (Blanco, 2004). Leaves have a high nutrient demand, particularly for nitrogen (N) and phosphorous (P), which is much greater than the other organs of the trees (Piatek and Allen, 2000). The seasonal variability of leaf N and P has been reported by several authors. For instance, Santa Regina and Tarazona (2001) observed nutrient withdrawal in the leaves prior to the moment of greatest litterfall production, which enables the loss of these elements by the trees to be minimized.

Tree growth results from a series of processes, litterfall playing an important role among these, and climate has a noteworthy influence, both direct and indirect, upon these processes (Albaugh et al., 2004; Fritts, 1976; Manrique and Cancio, 2000). In the Iberian Peninsula, the increase in temperatures and dry periods is currently conditioning the dynamics of forests in Mediterranean climate areas (Andreu et al., 2007; Valladares et al., 2004). Water stress can give rise not only to reduced plant growth but can also cause foliage to fall earlier (Gracia et al., 2001; Wright and Cornejo, 1990). This premature leaf senescence can in turn prevent complete nutrient translocation, which leads to an increase in nutrients in the litterfall in times of drought (Wood et al., 2005).

This paper attempts to evaluate the influence of climate upon the functioning (canopy dynamics, secondary growth, female-cone production) of a *Pinus sylvestris* forest in a Mediterranean site located near the southern edge of the species distribution limit. *Pinus sylvestris* has been well studied in different parts of Europe (Albrektson, 1988; Berg and Meentemeyer, 2001; Blanco, 2004; Cutini, 2002; Helmsaari et al., 2002; Kuoki and Hokkanen, 1992; Santa Regina and Tarazona, 2001), but little is currently known of these forests at the southern limit of the species distribution. In a scenario of climate change, it is precisely these southernmost forests that will undergo the most radical changes. It is the Mediterranean region and southern Europe where the impact of climate change will be greatest on forest growth and regeneration (Blanco et al., 2005; Castro et al.,

2004; Guerrero-Campo et al., 1998). We based our study upon three significant parameters for the functioning of the pine forest such as canopy dynamics (litterfall production), female-cone production and secondary growth of the trees. The main hypotheses expounded in this paper are: (i) litterfall production is affected by the local climatic variables of the area, which causes phenological differences from other Scots-pine forests in more northern regions; (ii) dry periods, typical of the Mediterranean region, not only reduce tree growth, but also increase nutrient loss through litterfall; (iii) climatically unusual events or periods alter the synchronization of key processes related to tree growth (litterfall production, secondary growth), and reproduction (female-cone production).

2. Materials and methods

2.1. Study area

The study was conducted in a 120-year-old *Pinus sylvestris* L. forest site located in Cuenca de los Acebos, Valsaín, Segovia, Spain, at an elevation of 1500 m a.s.l. (latitude 40°46'50"–40°53'50"N, longitude 3°57'40"W–4°5'35" W). The density is 340 trees ha⁻¹, with a mean height of 25 m and a mean diameter at breast height (1.3 m) of 41 cm. The overstorey is dominated by *Pinus sylvestris* L. and the understorey consists mainly of the shrubs *Genista florida* L., *Cytisus scoparius* (L.) Boiss., *Juniperus communis* L. and *Ilex aquifolium* L. The soil has a pH (H₂O) of 4.9 and is based on gneiss with quartzite inclusions. In this study area, annual precipitation ranges from 750 to 1250 mm (over the 1993–2003 period), which is irregularly distributed over the year, summer being the driest period. Mean monthly temperatures range from 23 °C to –3 °C.

We used three experimental plots (fenced-off since 1991) for this study at different elevations on the northern slope of the forest, facing eastwards and with a mean slope of 20–40% (High plot: 1550 m.a.s.l., 20 m × 19.5 m; Medium plot: 1450 m.a.s.l., 20 m × 25.5 m; Low plot 1300 m.a.s.l., 20 m × 15 m). We also selected a control plot (Cerro Pelado), outside the pine forest, at 1650 m.a.s.l. (5 m × 5 m).

2.2. Meteorological data

In the three experimental plots we installed eight Hellman-type pluviometers and eight water collectors (a polyethylene bottle with a 12.5 cm-diameter, 22.72 cm² area collected), at a height of 1.5 m from the ground, all of these randomly distributed (López Arias, 1999; Puckett, 1991). We also installed two plastic (PVC) buckets to collect snow, with a collection area of 1590 cm². The water was collected every 15 days from 1993 to 2003. In the control plot we installed 2 Hellman pluviometers, two water collectors and two snow buckets. To measure air temperature we used temperature data from the Puerto de Navacerrada meteorological station (1890 m.a.s.l.; latitude 40° 46'50"N, longitude 4° 00'37"W) and installed temperature sensors in each experimental plot at a height of 1.60 m from the ground to fit the data. The sensors were programmed to record the data every 10 min throughout

the year, from August 2003 to August 2004. The data were recorded in a data-logger (HOBO, Onset Computer, USA) and were processed with BoxcarPro software (Onset Computers). To extend the temporal range of the study we used the precipitation and temperature data from the Puerto de Navacerrada meteorological station (1890 m snm; latitude 40° 46'50"N, longitude 4° 00'37"W) and the precipitation data from the Granja de San Ildefonso station (1191 m snm; latitude 40° 54'00"N, longitude 4° 00'17" W).

2.3. Sampling method

The collection of the litterfall involved the installation of 8 square litter traps, measuring 0.25×0.25 m (0.25 m^2) in each experimental plot (ICP Forests, 1998). The collectors were installed at a height of 1.50 m from the ground and were distributed randomly. The litterfall samples deposited in each collector were collected once a month over an 11-year period (1993–2003). Once the litterfall samples were collected, they were taken to the laboratory where they were dried in an oven at 65 °C to constant weight, for approximately 48 h. Once the samples were dried, we weighed them on a precision scale and separated them into different fractions: needles, branches, female cones, bark and others (shoots, seeds and non-pine tree remains). We estimated the nutrient content (N, P, K, C, S, Ca, Mg, Fe, Mn, Cu, B and Zn) of the needle fall using the samples collected from 2000 to 2003. With 2 g of dry sample we performed the chemical analysis. A 3-month average for nutrient concentration data is presented according to seasons: winter (December, January and February), spring (March, April and May), summer (June, July and August) and autumn (September, October and November).

Annual growth of the adult pines: To estimate the annual growth of the adult individuals of *Pinus sylvestris*, we selected the trees in the upper and lower plots, along with some individuals from outside these two plots, at a distance no greater than 50 m from the borders of the plot. From each selected pine we took two cores at breast height in opposite directions and perpendicular to the maximum slope to avoid the reaction wood using a Pressler increment borer, and following standard methodology (Cook and Kairiukstis, 1990). The cores were dried and polished using sand-paper of progressively finer grain. Then, they were crossdated using characteristic tree-rings (Yamaguchi, 1991). We measured the tree-ring width to the nearest 0.01 mm using a semiautomatic TSAP measuring device (Frank Rinn, Heidelberg, Germany). Tree-ring crossdating was evaluated using COFECHA software (Holmes, 1983).

2.4. Time series

To analyze the temporal variation of litterfall production between the years 1993 and 2003, and to study the relationships between litter production and the explanatory variables, temperature and precipitation, we used time series analysis. This methodology is based upon the study of the tendency, seasonal or periodic variation and irregular fluctuations of a time series. To assess the relationship among variables we

performed cross-correlations among them. Temporal correlation violates the assumption of independence required in most statistical tests including cross-correlation analyses. To correct for the presence of temporal autocorrelation we followed a two-step process. First, we analyzed the temporal autocorrelation of the variables. Second, we corrected the significance of the cross-correlations between variables taking into account the autocorrelation of each variable. An effective number of degrees of freedom was calculated to obtain a corrected significance level for the cross-correlations (Pyper and Peterman, 1998). Then we analyzed the maximum temporal correlations (the moment in which the correlation is maximum) with the explanatory variables (precipitation and temperature), to identify the relationships among the variables according to the time scale (Zuur et al., 2003a,b). We identified abrupt changes in the temporal tendencies of needle fall, secondary growth, and cone production, and in the climatic variables (precipitation and temperature) using chronological clustering (Bell and Legendre, 1987; Legendre et al., 1985), with different degrees of significance ($\alpha = 0.01, 0.05, 0.1, 0.2$, etc.). Chronological clustering allows one to partition a multivariate time series into homogeneous subgroups, i.e. this technique detects the main discontinuities along the analyzed series taking into account the temporal constraint. Low values for α ($\alpha = 0.005, 0.01, 0.1$) allow for the visual observation of the sharpest changes in the series. The points of change in the series are shown in the figures resulting from the analysis, the vertical bars indicating the moments of sharp change in the series, and the numbers indicating the different groups in which the series can be partitioned.

We explored the relationship between the climatic variables and the variables for litterfall and secondary growth conducting a correlation analysis. We calculated the maximum correlations and the time period in which this correlation was at its maximum. We made all the calculations of time series with the software Brodgar, ver. 2.4.1. (Highland Statistics Ltd. 2000).

3. Results

3.1. Temperature and precipitation

Mean annual precipitation in the 1993–2003 period in the experimental plots was 767 mm and outside the pine forest 967 mm. The driest years were 1994 and 1995 and the rainiest year was 1996 (Fig. 1). The months with the highest precipitation were January, May, October, November and December, and the driest months were July and August (Table 1). The mean annual temperature of the experimental plots was 9 ± 0.6 °C. The coldest years were 1993 and 1996 and the hottest ones 1995 and 1997 (Fig. 1). The minimum temperatures in the experimental plots were reached during the month of March, dropping to -12 °C, and the maximums during July and August, exceeding 37 °C.

Litterfall variation: There were statistically significant differences between the litterfall collected in the upper plot and in the other two plots ($F = 22.10, p < 0.0001$). We observed noticeable year-to-year variations, the biggest amount

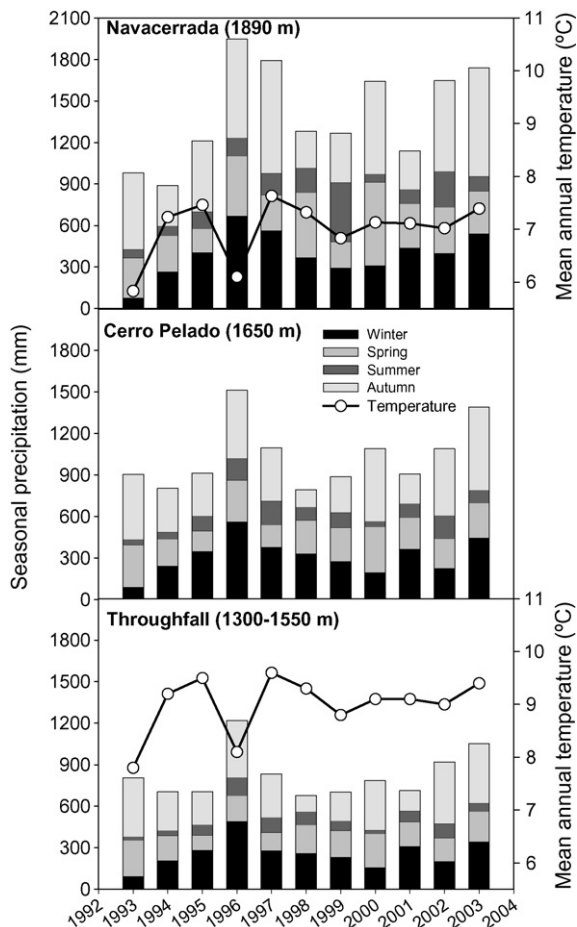


Fig. 1. Seasonal precipitation (Puerto de Navacerrada, 1890 m and Cerro Pelado, 1650 m stations), throughfall (1300–1550 m) in experimental plots and annual mean temperature in Puerto de Navacerrada station and in the experimental plots over the 1993–2003 period.

of litterfall being produced in the years 1995, 2000 and 2003, and the smallest amount in 1997 (Fig. 2). The biggest fraction of litterfall involved needles, accounting for 49% of the total litterfall collected. Each of the remaining fractions accounted for less than 15% of total litterfall. The significant increase in

total litterfall in 2000 coincided with a great increase in fallen cones, which was greater in the upper plot than in the rest of plots (Fig. 2). Needle fall showed a periodic tendency every 12 months in the three experimental plots, and was the only fraction that presented a significant temporal autocorrelation.

Nutrient content in needle fall: there was a very notable seasonal variation in N and P concentrations from 2000 to 2003, maximum values being reached at the end of winter and the start of spring (February and March) and the minimums at the end of summer and the beginning of autumn (September). The mean annual concentration of N was 9.78 g kg^{-1} , with maximum values of 15 g kg^{-1} in February and minima of 5.3 g kg^{-1} in September. The mean annual concentration of P was 0.8 g kg^{-1} , with minimums of 0.5 g kg^{-1} in September and maximums of 1.2 g kg^{-1} in March. We also observed a certain seasonality for S, Ca and K, although this was not as clear as for N and P (Fig. 3). We observed no significant seasonal pattern for the micronutrients Fe, B, Cu, Mn and Zn (Fig. 4).

Annual secondary growth of the pines: the average secondary growth of the pines was $0.90 \pm 0.17 \text{ mm year}^{-1}$ in the upper plot, and $1.16 \pm 0.3 \text{ mm year}^{-1}$ in the lower one, and statistically significant differences were observed between these plots ($F = 5.81, p < 0.03$). The years of least growth were 1996, 1997 and 2000, the minimum values being observed in the year 1996, with an annual average of $0.62 \pm 0.08 \text{ mm yr}^{-1}$. To the contrary, the years 1994, 2001 and 2002 presented the highest growth values in the upper plot, with average growth rates of $1.05 \text{ mm year}^{-1}$ ($F = 1.94, p < 0.04$), and in the lower plot, the years 1994, 1995 and 2001, with growth rates of over $1.25 \text{ mm year}^{-1}$ ($F = 51.46, p < 0.001$; Fig. 5A). The annual secondary growth of both plots did not show any sharp change in tendency for $\alpha = 0.01$; 0.05 and 0.1, but it did for $\alpha \geq 0.2$ where we observed a change in tendency in the years 1996 and 1998 (Fig. 5B). We did not find any significant relationship between the annual production of cones and tree-ring width ($r = -0.14, p < 0.68$).

Relationship between climatic variability, annual tree growth rate and litterfall: there was a high positive correlation between the monthly needle fall and the mean temperature of the same

Table 1
Mean and standard deviation of monthly throughfall, precipitation (in experimental plots, and in Puerto de Navacerrada and La Granja meteorological stations) over the 1993–2003 period

	Throughfall	Precipitation	Navacerrada	La Granja	Test	g.l.	p
January	98 ± 66 a	121 ± 83 a	125 ± 85 a	93 ± 79 a	1.55	3	0.6710
February	63 ± 61 a	72 ± 68 a	79 ± 59 a	47 ± 36 a	1.76	3	0.6228
March	45 ± 27 a	54 ± 34 a	86 ± 55 a	48 ± 27 a	4.77	3	0.1896
April	63 ± 39 a	78 ± 49 a	110 ± 101 a	67 ± 45 a	7.5	3	0.0760
May	79 ± 33 a	105 ± 36 a	134 ± 67 a	89 ± 37 a	5.75	3	0.1244
June	39 ± 30 a	56 ± 36 a	46 ± 39 a	43 ± 31 a	1.37	3	0.7128
July	18 ± 20 a	22 ± 29 a	33 ± 36 a	23 ± 24 a	2.02	3	0.5678
August	23 ± 22 a	33 ± 28 a	47 ± 63 a	29 ± 28 a	1.18	3	0.7587
September *	34 ± 17 a	49 ± 19 ab	73 ± 36 b	40 ± 19 a	5.48	3	0.0031
October	105 ± 69 a	136 ± 86 a	151 ± 97 a	94 ± 61 a	1.24	3	0.3089
November *	100 ± 58 a	119 ± 70 ab	191 ± 112 b	113 ± 69 ab	2.86	3	0.0486
December	101 ± 65 a	123 ± 76 a	192 ± 128 a	98 ± 50 a	3.44	3	0.3286
Total	767 ± 112	967 ± 152	1266 ± 254	781 ± 174			

Letter codes indicate significant differences (ANOVA, $p < 0.05$, *Kruskal Wallis test for no normal values $p < 0.05$) between the different sites (g.l. degrees of freedom).

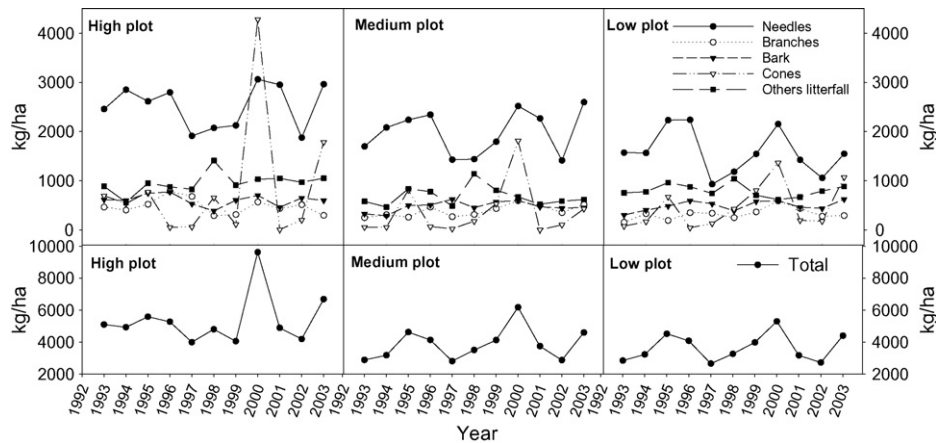


Fig. 2. Canopy dynamics (total and monthly litter production of needles, branches, bark, cones and others fractions) over the 1993–2003 period in the experimental plots.

month recorded in the experimental plots ($r = 0.71$). This correlation was negative and much lower between monthly needle fall and precipitation ($r = -0.39$; Table 2). In the case of cone production and temperature, the maximum correlation was observed with the temperatures in the month of May ($r = 0.65$, $p < 0.05$) in the three experimental plots. Years with low radial growth such as 1996, 1997 and 2000 corresponded with low precipitation records in June or July. Specifically, June precipitation was positively related to radial growth in the low

plot, whereas July temperature was negatively associated with growth in the high plot. Furthermore, previous August–September precipitation was positively related to growth. The secondary growth was negatively related to December precipitation of the year prior to tree-ring formation ($r = -0.56$ and $r = -0.71$, upper and lower plots, respectively), but positively to the mean temperature of this month ($r = 0.59$ and $r = 0.69$, upper and lower plots, respectively). A similar but not significant result was obtained with January data of the year of tree-ring formation.

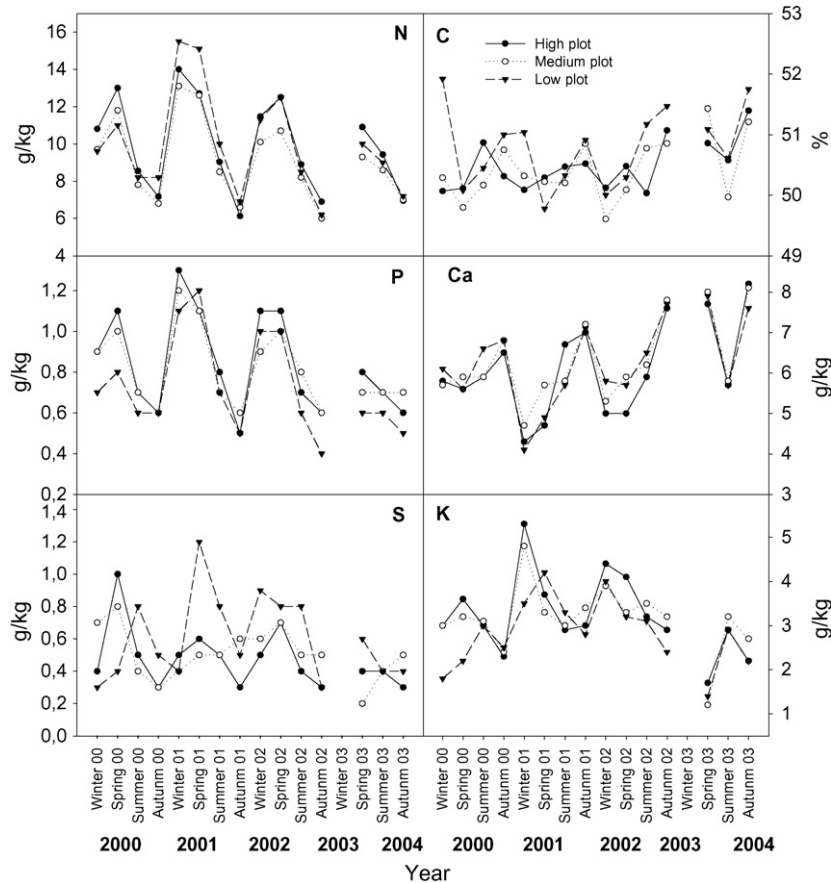


Fig. 3. Mean seasonal values of N, P, S, C, Ca and K content in needles litterfall over the 2000–2004 period.

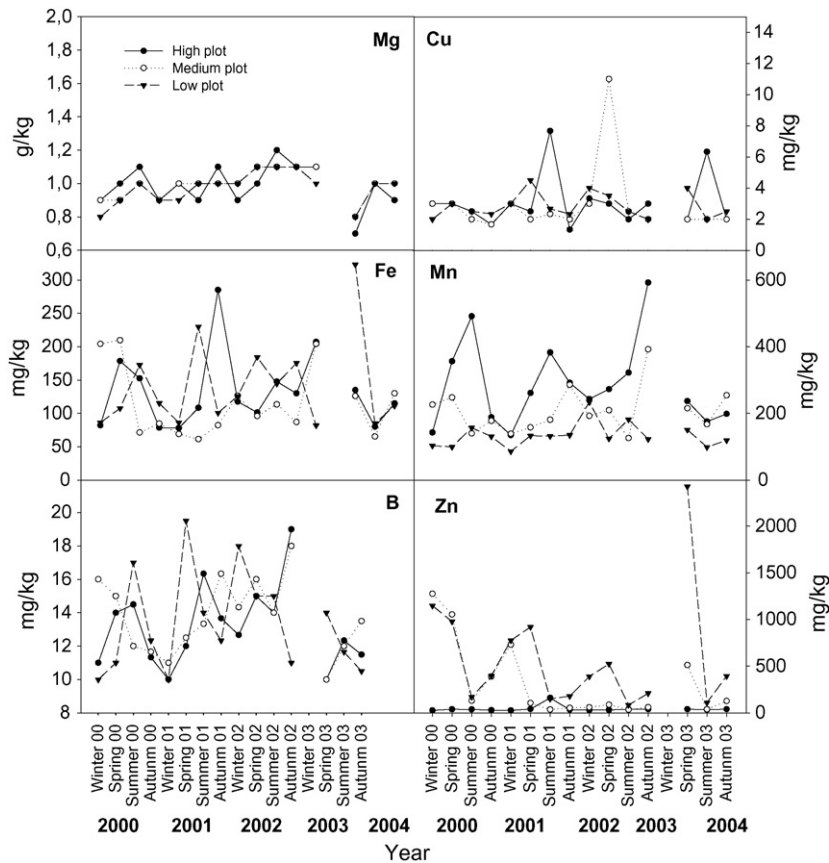


Fig. 4. Mean seasonal values of Mg, Fe, B, Cu, Mn and Zn content over the 2000–2004 period.

We did not find any significant relationship between the annual amount of needle fall and tree-ring width ($r = -0.02, p < 0.96$). For the level of significance of $\alpha = 0.01$ needle fall presented 6 abrupt changes throughout the time period studied. These changes occurred during the months: 8 (August, 1993), 11 (December, 1993), 43 (July, 1996), 47 (November, 1996), 56 (August, 1997), and 59 (December, 1997). These events correspond to the summer and winter periods of the years 1993, 1996 and 1997 (Figs. 6 and 7). Cone production also presented 6 sharp changes for a level of significance of $\alpha = 0.01$,

but in periods different from those of the needles. The cone-series discontinuities occurred in the months: 28 (April, 1995), 31 (July, 1995), 60 (December, 1997), 87 (March, 2000), 95 (November, 2000) and 124 (April, 2003) (Figs. 6 and 7). For monthly precipitation we observed three episodes of sudden change with a level of significance of $\alpha = 0.01$, in the months: 48 (December, 1996), 50 (February, 1997), and 130 (October, 2003), corresponding to the autumn and the winter of the years 1996, 1997 and 2003. For monthly temperature, however, we observed no sharp changes in the tendency for $\alpha = 0.01$.

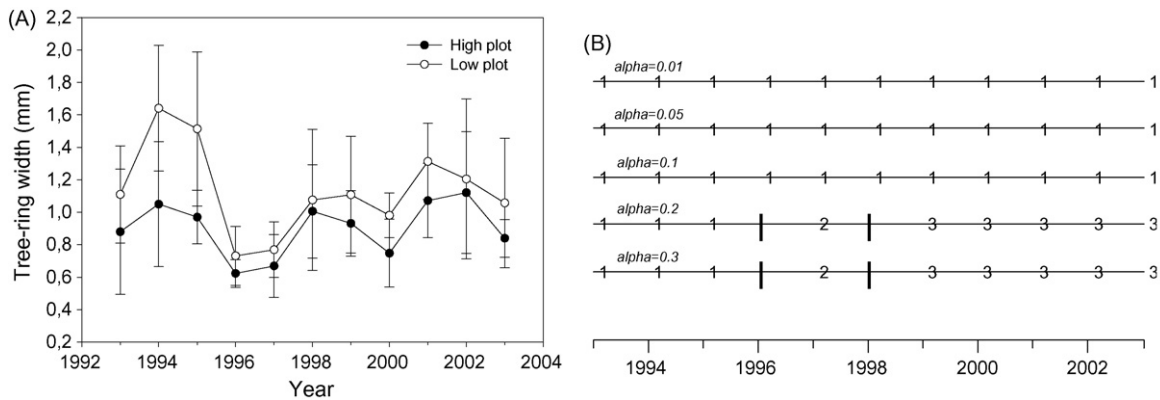


Fig. 5. (A) Mean and standard deviation of tree-ring width in the high and low plots over the 1993–2003 period. (B) Results of chronological clustering applied to the tree-ring width time series. A vertical line corresponds to the start of a new group. Numbers refer to groups. A small alpha (0.01) corresponds to low-frequency variability and shows the most important breakpoints in the data. Larger alpha values visualize smaller high-frequency variability.

Table 2

Results of maximum cross-correlations over several time lags between monthly needle fall and cone production, maximum monthly temperature in the experimental plots, and precipitation

	Needles	Cones	Precipitation	Temperature
Needles	0	0.39	-0.39	0.71
Cones	10	0	0.10	-0.23
Precipitation	1	2	0	-0.50
Temperature	1	5	0	0

Values in bold are significant ($p < 0.05$). Values above the zero diagonal correspond to the maximum correlation and values below the zero diagonal show the time lag when the correlation is maximum (time units are months).

The macronutrient concentration (N, C, S, P, K, Ca and Mg) of the needle fall was significantly correlated with the production thereof ($r > 0.70$ y $r = 0.53$ for K), but this relationship was not observed for the micronutrients, except for Fe. The decrease observed in the N and P concentrations at the end of the summer was associated with an increase in needle fall. Temperature was also correlated with the concentration of macronutrients, except for K, but in this case, the relationship was negative and was maximum for 1 seasonal period (-1), equivalent to 3 months (Table 3). Precipitation was positively

related with the concentration of N, C, P and Ca. Springtime precipitations were significantly related with the concentration of macronutrients in the needles during summer (Table 3).

4. Discussion

The annual mean amount of total litterfall observed in the experimental plots, $4116 \pm 932 \text{ kg ha}^{-1}$, is within the production range of *Pinus sylvestris* forests (Blanco et al., 2006; Pausas, 1997; Puigdefábregas and Alvera, 1977). These amounts are greater, however, than others studied in the North of the Iberian Peninsula, where the amounts of litterfall ranged from 1200 to 3200 kg ha^{-1} in the Pyrenees, in the Moncayo Sierra (Alvera, 1980; Pausas et al., 1994; Pausas, 1997), or in Salamanca (Santa Regina et al., 1989). Studies conducted in northern Europe also show litterfall amounts lower than those obtained in Valsaín, such as 800 and 1600 kg ha^{-1} observed in Sweden (Albrektson, 1988; Flower-Ellis, 1985), values of 1400 kg ha^{-1} in Poland (Brey Meyer, 1991), and 800 kg ha^{-1} in Finland (Mälkonen, 1974). On the contrary, litterfall production of different species of the genus *Pinus* is much higher in tropical climates, up to 10,000 kg ha^{-1} in some experiments performed in Brazil for *Pinus caribea* (Smith et al., 1998).

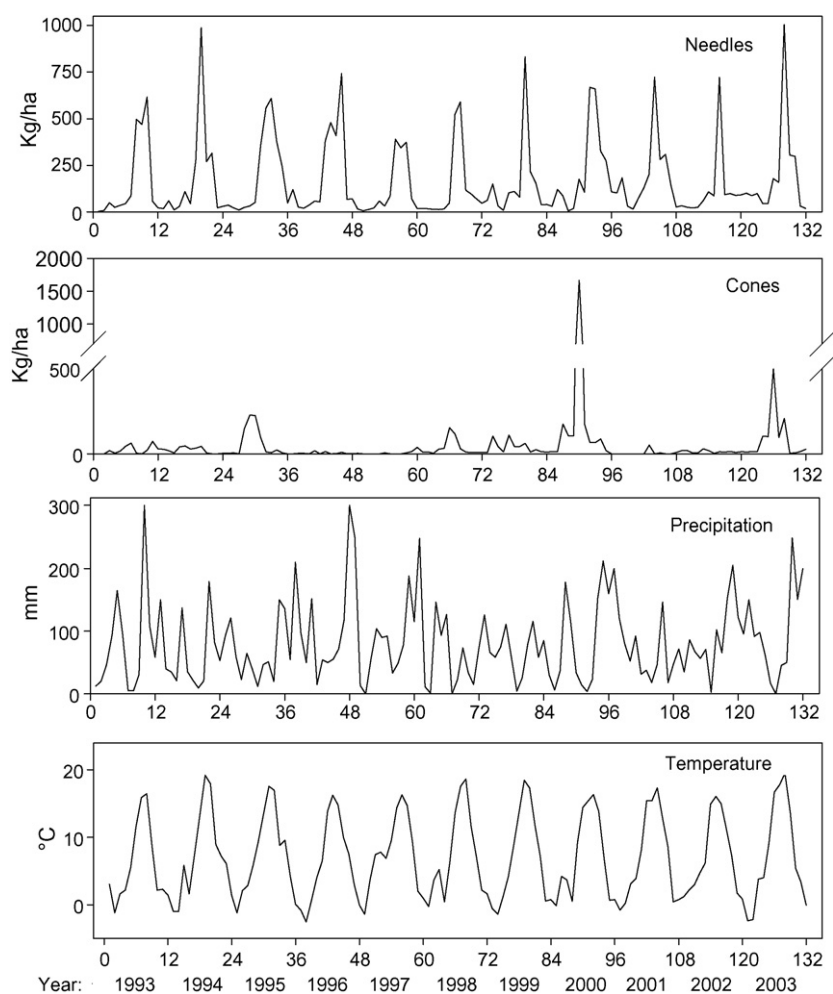


Fig. 6. Monthly mean variation of needles litterfall and cones production, precipitation and maximum temperature (in experimental plots) over the 1993–2003 period. Study period: 132 months (month 1: January 1993 and month 132: December 2003).

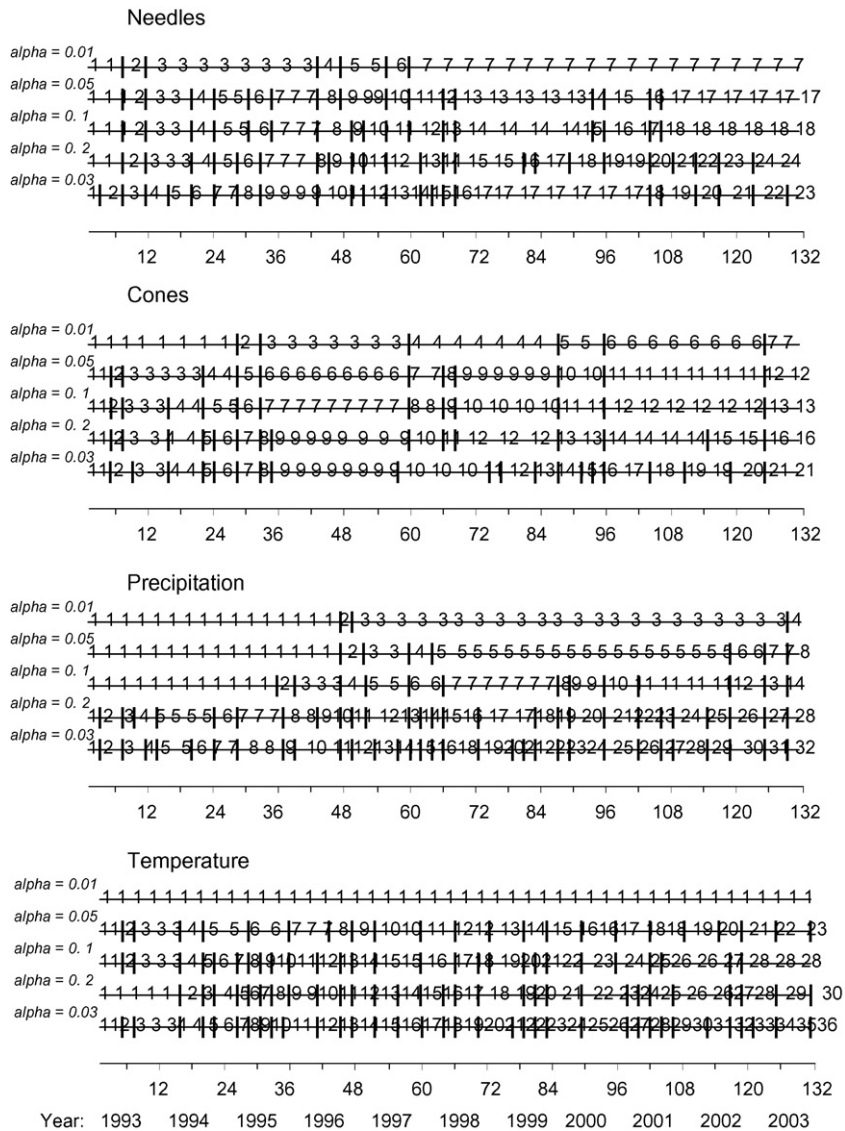


Fig. 7. Results of chronological clustering applied to needles monthly litterfall and cones production, monthly precipitation (Cerro Pelado station) and maximum monthly temperature (in the experimental plots) over the 1993–2003 period. A vertical line corresponds to the start of a new group. Numbers refer to groups. A small alpha (0.01) corresponds to low-frequency variability and shows the most important breakpoints in the data. Larger alpha values visualize high-frequency variability.

These differences found between different latitudes confirm the hypothesis of the influence of climate on litterfall dynamics (Berg and Meentemeyer, 2001). The seasonal variability of needle fall in the Valsaín forest followed a different pattern to that established by other authors in more northern regions (Berg et al., 1999; Guerrero-Campo et al., 1998). In Valsaín, the months with the highest needle fall were in summer (August and September), and not in autumn (October and November) as described in other papers (Blanco, 2004; Puigdefábregas and Alvera, 1977; Santa Regina and Tarazona, 2001). This advance in needle production was probably the result of greater water stress during the summer period, which prevents the tree from maintaining all its leaf biomass and accelerates the fall of the older needles (Pausas, 1997). This is confirmed by the high correlation between needle fall and temperature (Kuoki and Hokkanen, 1992; Martínez-Alonso et al., 2003). The increase in temperatures and in solar radiation during summer, together with reduced precipitation, are considered to be the most

relevant factors in the advance of needle fall (Guerrero-Campo et al., 1998; Pausas et al., 1994; Pausas, 1997). These results confirm the hypothesis of the large influence of short-term climatic variability on litterfall production. These phenology differences in litterfall are also observed in radial growth. In the Pyrenees the ring development of Scot pine has its maximum growth rate in June (Camarero et al., 1998; Guerrero-Campo et al., 1998). However, in Valsaín the tree-ring growth is mostly formed before July (70% of total ring width), which suggests that the maximum growth-rate may occur in May. The most important climatic factors controlling radial growth were July temperature (negative) and June precipitation (positive), being this last variable more influential in the low plot.

The biggest fraction of litterfall corresponded to the needles, which represented 50% of the total ($1971 \pm 459 \text{ kg ha}^{-1}$). These values are within the range observed by other authors: 2772 kg ha^{-1} (at 1540 m asl) and 1015 kg ha^{-1} (at 1380 m asl) in the Pyrenees (Pausas, 1993), and 1024 kg ha^{-1} in Finland

Table 3

Maximum cross-correlations between explanatory variables (temperature, precipitation, and litterfall) and nutrients (N, C, S, P, K, Ca, Mg, Fe, Mn, Zn, Cu and B)

	Pre	Temp	Needles	N	C	S	P	K	Ca	Mg	Fe	Mn	Zn	Cu	B
Pre	0	0.51	0.74	0.62	0.6	−0.42	0.6	−0.39	0.55	0.47	−0.56	0.34	−0.43	0.44	0.24
Temp	1	0	0.83	−0.78	−0.73	−0.74	−0.72	−0.42	−0.66	−0.56	0.55	0.28	0.4	−0.41	0.25
Needles	1	0	0	0.86	0.86	0.77	0.88	0.53	0.81	0.7	0.51	−0.28	0.43	−0.46	−0.44
N	−1	−1	−2	0	0.94	0.57	0.97	0.45	0.84	0.67	−0.43	−0.51	−0.44	0.49	−0.5
C	−1	−1	−2	0	0	0.58	0.98	0.72	0.98	0.88	−0.42	−0.42	−0.37	0.39	0.51
S	1	−1	−2	0	0	0	0.59	0.38	0.56	0.49	−0.78	0.46	−0.58	0.43	0.57
P	−1	−1	−2	0	0	0	0	0.58	0.92	0.78	−0.47	−0.46	−0.38	0.5	0.44
K	−2	−1	−2	0	0	0	0	0	0.86	0.96	−0.41	0.32	−0.37	−0.16	0.62
Ca	−1	−1	−2	0	0	0	0	0	0	0.96	−0.38	0.39	−0.3	0.3	0.58
Mg	−1	−1	−2	0	0	0	0	0	0	0	−0.36	0.37	−0.22	−0.17	0.62
Fe	1	1	1	1	1	2	1	0	1	2	0	0.56	0.48	−0.25	−0.47
Mn	2	−1	−2	0	0	−1	0	−2	−2	−2	0	0	−0.3	−0.33	0.77
Zn	1	1	2	2	2	−2	2	0	2	2	0	−1	0	−0.27	−0.4
Cu	−1	0	0	0	0	0	0	2	0	2	−2	−2	2	0	−0.34
B	2	0	−1	1	−1	−1	−1	−1	−1	−1	−2	0	0	2	0

Values in bold are significant ($p < 0.05$). Values above the zero diagonal show the maximum correlation and values below the zero diagonal show the time lag when the correlation is maximum (time units are 3 months).

(Helmisaari et al., 2002). Other studies, however, have observed that the percentage of needles in relation to total litterfall represents almost 70% (Blanco, 2004; Puigdefábregas and Alvera, 1977). The needles/litterfall relationship is associated with the state of development and age of the trees, the highest percentage being reached approximately half-way through the life of the tree, coinciding with maximum respiration and photosynthesis rates, and decreasing with maturity (Puigdefábregas and Alvera, 1977). The trees in the study area are generally over 100 years of age, and have therefore passed the period of maximum production, the percentage of needles therefore being around 50%. The pine cones represented less than 10% of total litterfall, except in the year 2000, when it exceeded 25%, reaching 40% in the upper plot. The cones collected in the year 2000 resulted from the induction of buds during the spring of 1997, which flowered in 1998 (Cremer, 1992; Helmisaari et al., 2002). The irregular behavior in the year 2000 might be related to an anomalous period during the spring and summer of 1997, as in this year the spring was very warm and was followed by a rainy, cold period between May and August. That warm spring might have given rise to anomalous bud production, which generated greater cone production during 2000 (Cremer, 1992; Mutke et al., 2005). These variations in temperature and precipitation caused an alteration in the three-yearly rhythm of cone production. Our results suggest that warm springs advance the masting process by 1 year. Our results also agree with previous studies in other pine species which did not detect that a greater reproductive effort (e.g., very high cone production or masting events) was linked to a decrease in secondary growth (Cremer, 1992). In *Pinus contorta*, a higher photosynthetic rate on reproductive branches compensates for the additional sinks, such that annual stem increment is not affected by female cone production (Dick et al., 1990). Indeed, Despland and Houle (1997) found that radial growth and cone production covary with climate in a *Pinus banksiana* population at the limit of the species distribution. We did not find a negative association between cone production and radial growth, even under the stressful conditions of Mediterranean climate. Thus, resource allocation trade-offs may, in fact, be

absent in “marginal” environments where growth and reproduction are mainly constrained by climate.

The relationships observed between precipitation and temperature and nutrient concentration in needle production, were significant for macronutrients but not for micronutrients, except in the case of Fe. The low summertime concentrations can be interpreted as a consequence of the retranslocation processes prior to the needles falling from the trees, in accordance with what was observed by Nambiar and Fife (1991) with a negative relationship ($r = -0.7$, $p < 0.05$) between temperature and N and P concentration in the needle fall. This was observed mainly for N and P, which presented maximums in winter and minimums in summer. Indeed, the N and P concentrations during winter were similar to those of the living needles (12 g kg^{−1} versus 14.8 g kg^{−1} for N and 1.2 g kg^{−1} versus 1.4 g kg^{−1} for P; González Cascón, data unpublished). The needles collected during the winter period must have been principally those of the same year, which would have fallen as a result of mechanical processes induced by strong winds and storms, as has been observed in other systems (Cuevas and Lugo, 1998). To the contrary, the needles collected during the summer period were old ones in which most of the N and P had probably been translocated (Vitousek, 1982). The Ca and Mg, unlike other elements, are not withdrawn from the needles prior to senescence (Chapin, 1980; Finér, 1996; Ryan and Bormann, 1981), and accumulate in the leaf with age, as they are not susceptible either to washing or translocation. For this reason the correlations observed with temperature and precipitation were lower than for other nutrients such as N, and were not even significant in the case of Mg or precipitation, or for K.

The year-to-year climatic variations observed during the 1993–2003 period were clearly related not only to litterfall but also to the secondary growth of the trees. Following a period of summer droughts and cold winters, as in 1994 and 1995–1996, a sudden increase was observed in needle fall, along with a significant reduction of secondary growth, in particular in the following year. Several authors have emphasized the positive relationship between June and July precipitation and secondary

growth in Mediterranean populations of *Pinus sylvestris* (e.g., Génova, 2000; Richter et al., 1991; Tardif et al., 2003). In addition, the previous December conditions also influence Scots-pine growth in the studied plots through a positive effect of temperature and a negative effect of precipitation as in other mountain Mediterranean sites (Gutiérrez, 1989). This effect may be due to the accumulation of photosynthates in winter, which will be used in the development of the tree-ring the following year. Furthermore, the negative relationship of growth with previous December precipitation explains the negative relationship found between tree-ring width and annual precipitation since December is one of the wettest months of the year.

In short, the climatic variability observed during the decade studied gave rise to profound alterations in canopy dynamics and growth rate. The seasonal variability of needle fall, advanced in relation to more northern latitudes, was mainly associated with temperature and was also affected by precipitation. Warm, dry years were linked to a reduced secondary growth, which was also affected by the previous winter, altered the three-yearly cone production cycle and gave rise to greater nutrient loss due to the combined effect of increased litterfall production and a higher nutrient concentration therein. The integrated response of the forest canopy, as a complex result of the interaction of individual variables, showed the clear influence of climatic variability on the development and dynamics of these pine forests. Since each parameter studied was differentially affected by climatic variability, the overall effect of short-term climatic changes involved an uncoupling of growth with reproduction and litter production. More in-depth knowledge in this sense is vital to adapt the management of Mediterranean forests to the new scenarios posed by ongoing climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2007.06.043.

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