Journal of Vegetation Science 8: 643-650, 1997
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Litter fall and litter decomposition in *Pinus sylvestris* forests of the eastern Pyrenees

Pausas, Juli G.

Departament de Biologia Vegetal, Universitat de Barcelona, Av. Diagonal 645, E-08028 Barcelona, Spain;
Current address: Centro de Estudios Ambientales del Mediterráneo (CEAM), Carrer 4, Sector Oest,
Parc Tecnològic, E-46980 Paterna, València, Spain; Fax +34 6 131 8190; E-mail juli@ceam.es

Abstract. Litter fall and litter decomposition were studied in four mature stands of *Pinus sylvestris* (Scots pine) in the eastern Pyrenees. The stands were located in environments differing in bedrock type and exposition and were studied for two years. Mass-loss during the first year of decomposition was compared with other European *P. sylvestris* forests and regressed with environmental variables (temperature and rainfall) and latitude. The results suggested that the mean amount of needle fall (1760 kg·ha^{-1}·yr^{-1}) was within the range reported for northern European stands. There were more differences in the amount of litter fall between the four stands than between the two years studied. However, the needle fall pattern over the year showed significant differences between years in three of the four stands. Litter decomposition was similar in all the stands and only the one in drier conditions showed a lower decomposition rate. On the European scale the decomposition rate was positively related to mean annual temperature and annual rainfall. However, regression analysis suggests that there are other factors, not taken into account in this study, that are important for predicting the decomposition rate.

Keywords: Forest production; Litter production; Mass loss; Needle fall; Temperature.

Introduction

Litter fall and litter decomposition are key processes in nutrient cycling of forest ecosystems. Litter fall provides the main above-ground contribution of carbon and nutrients to the forest floor (Bray & Gorham 1964; Binkley 1986) and has often been related to climate (Bray & Gorham 1964; Meentemeyer et al. 1982; Kouki & Hokkanen 1992; Pausas et al. 1994). Litter decomposition involves the mineralization and humification of lignin, cellulose and other compounds and the leaching of soluble compounds whose carbon and nitrogen are progressively mineralised or immobilised (Aber & Melillo 1980, 1991; Coûteaux et al. 1995).

The process of decomposition is mainly controlled by climate, litter quality (e.g. plant species and the soil where they grow) and soil organisms (Meentemeyer 1978). Litter decomposition is an important source of CO_2 to the atmosphere; mineralization of the annual litter fall contributes to approximately half of the CO_2 output from the soil, and the average global annual CO_2 flux from the soil is estimated to be about 68×10^{15} g of carbon (Raich & Schlesinger 1992). It is important to provide data from a wide range of environmental conditions for possible improvement of predictions on carbon balance and ecosystem responses to global change (Anderson 1991; Berg et al. 1993).

Pinus sylvestris forests are widely distributed in Europe; they reach their southern limit in the Iberian peninsula (Jalas & Suominen 1973). The Iberian distribution of Scots pine is discontinuous and restricted to the mountains, probably due to the dry climate of most of the peninsula. While there is abundant information on organic matter cycling in northern Europe (e.g. Staaf & Berg 1982; Berg et al. 1993 and references therein), little is known on the southern area of the species' distribution (e.g. Carceller et al. 1989; Santa Regina & Gallardo 1985, 1995). In the Pyrenees this type of forest is widely distributed and found in different environmental (climatic and edaphic) conditions having a different structure and understorey composition (Pausas 1994, 1996; Pausas & Fons 1992; Pausas & Carreras 1995). Few data have so far been published on the organic matter cycling of Scots pine in the Pyrenees (Alvera 1980; Pausas 1993). To study ecosystems near the limits of their distribution and the relation to the climate is an important challenge in an environmentally changing world.

The objective of this study is to evaluate the litter fall and litter decomposition in four natural forests of *Pinus sylvestris* in the eastern Pyrenees in the northeast of the Iberian Peninsula and compare the results with those obtained in Spanish, southeast French and northern European stands. The emphasis will be put on the relationship between the processes of litter fall and decomposition and climatic factors.

Methods

Sites

Four stands of mature *Pinus sylvestris* forests were selected in two valleys in the eastern Pyrenees (NE Iberian peninsula). These experimental stands were chosen along the montane belt, where *P. sylvestris* forests are the natural vegetation. The two main environmental factors of variation in the study area (aspect and bedrock type) were combined to select the four study sites. Two stands were located in Vall de Tosses (Ripollès), with a bedrock of schists; one of these was on the south-facing slope (Ps1) and the other on the north-facing slope (Ps2). The other two stands were located in Vall de Pi (Cerdanya, in the *Parc Natural Cadí-Moixeró*), on calcareous bedrock, again with one on the south-facing (Ps3) and the other on the north-facing slope (Ps4). This selection covered the main environmental conditions in which natural *P. sylvestris* forests occur in the eastern Pyrenees (Pausas 1994, 1996; Pausas & Carreras 1995). The main characteristics of these stands are shown in Table 1. Texture and pH are related to bedrock type. Stoniness tends to be higher and soil depths shallower in the stands facing south (Ps1 and Ps3), although a large variation within the plots was observed. Tree density was higher in the two stands facing north (with low annual radiation). Stand age ranged from 60 to 106 yr. The highest basal area was found in the north-facing slopes in Vall de Tosses (Ps2). Additional information on these sites can be found in Pausas & Fons (1992), Pausas (1993) and Pausas et al. (1994).

Climatic conditions at the nearest meteorological station (La Molina, Spanish Meteorological Service, 1704 m altitude, observation period: 1967 - 1989) fits in the non-xeric cold bioclimate (Banyols & Gaussen 1957). Mean annual temperature was ca. 5.4 °C and mean annual precipitation was 1280 mm.

Sampling

At each site, diameter at breast height (DBH) was measured for all trees in a circular plot of 10 m radius. Four soil samples of the top 10 cm were collected to measure stoniness, pH and texture. Soil depth was estimated by driving a 1-m needle at 10 points systematically located within the plot. Annual incoming radiation was estimated following Pausas (1994), based on the aspect, cloudiness and percentage of visible sky.

Four plaster blocks were located in each stand, two at 10 cm and the other two at 30 cm of soil depth. Changes in conductivity on these plaster blocks were assumed to be related to changes in soil moisture. Conductivity of the four blocks was measured monthly (during 1990 and part of 1991) and means calculated for each soil depth. The method is used here simply as a comparison between stands rather than to quantify the availability of water.

Table 1. Characteristics of the four study plots. Ps1 and Ps2:Vall de Toses; Ps3 and Ps4: Vall de Pi. Results of Analysis of Variance and Multiple Mean Comparison (letters) are shown for some soil parameters. In rows, means with the same letter are not significantly different ($p > 0.05$); * $p < 0.05$; *** $p < 0.001$.

Locality	Ps1	Ps2	Ps3	Ps4	
Latitude	42° 20'	42° 19'	42° 19'	42° 20'	
Longitude	2° 03'	2° 05'	1° 46'	1° 45'	
Bedrock type	Schists	Schists	Calcareous	Calcareous	
Slope exposure	SSE	N	SW	N	
Altitude (m a.s.l.)	1540	1380	1420	1410	
Radiation (kcal/cm^2)	138.0	84.9	113.8	81.9	
Soil:					
Slope (°)	32	28	30	28	
Depth (cm)	68 b	94 ab	89 ab	98 a	*
Stoniness (%)	60.7	46.5	60.9	46.9	ns
pH mineral soil	4.8 b	4.4 b	7.2 a	7.6 a	***
pH humus	4.4 b	4.0 b	5.4 a	4.4 b	**
Texture	loam	silt	clay	clay	
Forest structure:					
Mean DBH (cm)	24.0	27.4	30.3	24.3	
Density (tree/ha)	592	854	605	828	
Basal area (m^2/ha)	31.6	53.4	45.3	44.4	

Litter fall was collected using five randomly located litter traps (Newbould 1967) each with an area of 0.5 m^2 each. The traps were emptied monthly for two years (from March 1990 to February 1992). The litter trapped was dried at 60 °C, separated into components and weighed. The components separated were needles, cones, twigs, bark, male flowers, buxus (i.e. any component of the shrub *Buxus sempervirens*, which is abundant in some of the stands) and remaining litter.

In each stand recently fallen needles were collected from meshes hung between trees during autumn (the maximum litter fall). These needles were air-dried and later included in 20 cm × 20 cm mesh bags with a mesh size of about 0.5 mm^2. Four to five grams of needles previously weighed at mg precision were included in each litter-bag. All bags were numbered and fixed to the ground of the corresponding forest with metal pegs. Four of these bags (randomly selected) in each stand were collected every three months for two-three years and the needles were oven-dried at 60 °C until constant weight. The sampling was not simultaneous in all four stands; that is, needles of Ps1 and Ps4 were collected in autumn 1989 and the litter-bags positioned on the ground at the end of 1989; needles for stands Ps2 and Ps3 were collected in autumn 1990 and the litter bags positioned at the beginning of 1991.

Numerical analysis

Statistical comparisons between stands were performed by analysis of variance (ANOVA) and the LSD test was applied for multiple comparisons. The amount of litter fall was log-transformed before any test was applied. Monthly needle fall was summed to form a cumulative curve of seasonal leaf fall. The cumulative percentage of needle fall was fitted using logistic regressions and the significance tested by analysis of deviance (Nelder & Wedderburn 1972; McCullagh & Nelder 1989). Statistical comparisons between curves for the different stands and between curves of different years were also performed by means of Analysis of Deviance. The statistical method of leaf fall pattern analysis described here is conceptually similar to Dixon's (1976) method, but statistically more robust. The advantage of Dixon's method is the fact that the parameters estimated are meaningful (see original reference). Dixon's method may be appropriate for the description of leaf-fall patterns, but the method proposed above seems more appropriate when statistical comparisons are required.

The mass-loss over time was fitted to a negative exponential curve (Olson 1963):

$$\ln (x_t / x_0) = -kt, \qquad (1)$$

where x_0 is the original mass of needle litter, x_t is the amount of needle litter remaining after time t, t is the time (in yr) and k is the decomposition rate (per yr). Half-decomposition time (t_{50}, yr) was calculated as the time necessary to reach 50% mass-loss. Comparisons between curves were carried out by analysis of covariance (ANCOVA) using time as a covariant.

Climate gradient

In order to test the relationship between climate and decomposition and to establish the position of our plots on the temperature gradient, first year mass losses of different European Scots pine forests were compiled. These data were obtained from Berg et al. (1993) by scanning their Fig. 1 and selecting the data on *Pinus sylvestris* forests, as well as from our own sites as reported here. A stepwise logistic regression analysis was used to test the relationship of percent mass-loss to mean annual temperature, annual rainfall, latitude, longitude and altitude. For our sites annual temperature was taken from 22 yr of observation at La Molina meteorological station (1704 m altitude) and adjusted for each stand by the altitudinal gradient recorded in the eastern Pyrenees (Xercavins 1981). The temperature values for the European data were based on mean climatic data records published elsewhere and adjusted for the altitude of the sites (see details in Berg et al. 1993).

Results

Soil moisture

Soil moisture decreased in summer; in terms of conductivity, the summer level dropped from 1 - 10 mS to < 0.01 mS, particularly in the north-facing sites; in the south-facing sites the dry period is extended to spring and autumn. Ps1 was driest over the whole period.

Litter fall

Most of the fractions of the mean annual litter fall showed differences between stands but similarities between years (Tables 2 and 3). The total amount of litter fall ranged from 2700 kg/ha (Ps2) to 4400 kg/ha (Ps1).

The needle fraction corresponds to 40 - 60 % of the total litter fall (Table 3). This fraction is also the fraction with the least spatial variation, showing a variation coefficient of between 5 and 20 % (Table 3).

Litter fall pattern

In both 1990 and 1991 needle litter fall showed a clear seasonality in all stands (Fig. 1). The period of maximum needle fall was from August to October. The production of flowers showed a peak phase in June-July (60 - 90 %), while bark, cones and twigs did not show a clear pattern throughout the year (not shown).

Cumulative percentage of annual needle fall for the two years studied is shown in Fig. 1. For all stands and in both years the model fitted was statistically significant ($p < 0.0001$). The curves were different between years

Table 2. Mean annual litter fall (kg/ha^{-1}dry weight) of the different fractions in the study stands. 'buxus' refers to the litter components from *Buxus sempervirens*, the most abundant shrub in two of the stands. In rows, means followed by the same letter are not significantly different ($p < 0.05$). Significant differences between years is shown below each value. Significant differences between stands (ANOVA) are shown in the right column. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Locality	Ps1	Ps2	Ps3	Ps4	
Needles	2539.7 a **	1193.3 c *	1772.8 b *	1552.4 b ns	***
Twigs	367.9 ns	352.6 ns	414.9 ns	475.8 **	ns
Bark	572.2 ns	405.1 ns	412. ns	480.8 ns	ns
Flowers	425.9 a ns	273.0 b ns	164.0 c ns	231.4 b ns	***
Cones	279.5 c ns	316.7 c *	205.7 b ns	751.3 a ns	**
Buxus	0.0 c ns	0.0 c ns	552.0 a ns	10.9 b ns	***
Others	248.7 a ns	143.9 c ns	184.2 bc *	203.3 ab ***	***
Total	4433.9 a ns	2684.8 b **	3705.4 a ns	3705.9 a **	***

for all the stands except Ps2 (Table 4) suggesting the maximum needle fall in three of the stands was significantly earlier in 1991 than in 1990 (Fig. 1). The maximum needle fall occurred one to two months earlier in 1991 than in 1990. There were no significant differences between the curves of the four stands in the same year (neither 1990 nor 1991). The interaction between years (1990 and 1991) and time throughout the year was only significant for Ps1. This means that the shape of the curve in Ps1 was slightly different between years, while in Ps3 and Ps4 it showed parallel logit curves (displacement of the peak only). Ps2 did not show a significantly different pattern between years.

Litter decomposition

Needle mass-loss over time fitted a negative exponential function (Fig. 2). The pattern of decomposition over time was very similar between all the stands and only for the stand Ps1 was decomposition found to be significantly slower than in the others (ANCOVA, p = 0.02). Ps1 showed the lowest decomposition rate and Ps3 the highest (Table 5). Pooling together all stands, the decomposition rate was 0.24 and the half-decomposition time was 3.56 yr. The functions fitted do not precisely follow the data points, suggesting that the decomposition rate was not constant. Decomposition was shown to be lower in winter and higher in spring and autumn.

Climate gradient

The latitudinal area of the data studied ranged from 42° 19' N (Pyrenees, Spain) to 69° 45' N (Finland). Mean annual temperature values ranged from – 1.7 to 11 °C and the first year mass-loss ranged from 12.7 % to 46.5 % (Fig. 3). See Berg et al. (1993) for details.

The relationship between first-year mass loss and mean annual temperature was significant (Table 6) and explained ca. 41 % of the deviance. However, a significant improvement on explained deviance (ca. 78 %) was achieved when latitude and rainfall were also included in the regression model. The regression coefficients were all positive, i.e. although first-year mass loss was initially negatively related with latitude, when temperature and rainfall were taken into account, the relationship was positive (Fig. 3). For a given mean annual temperature, decomposition rates increase with latitude. If we do not consider variation in latitude, our stands fall below the general trend expected from the regression with temperature (Fig. 3), suggesting that the decomposition is lower for the temperature condition than most European stands. Sites in central Europe (Poland) are found in a similar position with characteristics of an inland climate.

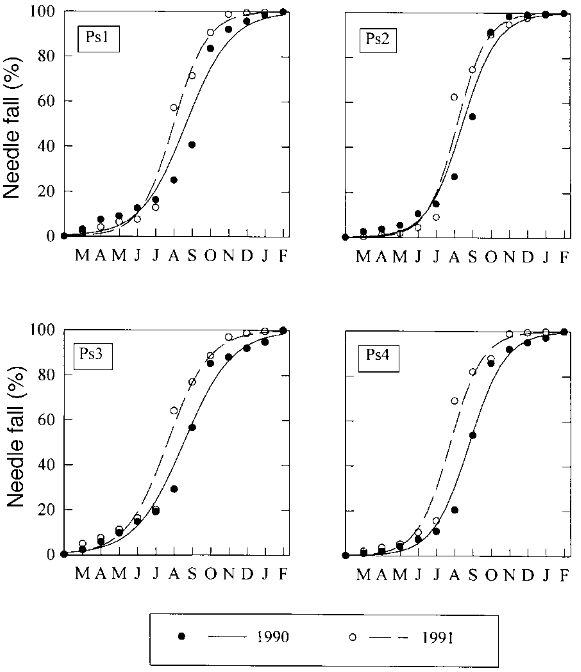

Fig. 1. Cumulative percentage of needle fall during 1990 (closed circles, solid line) and 1991 (open circles, broken line). All fitted models are statistically significant ($p < 0.0001$).

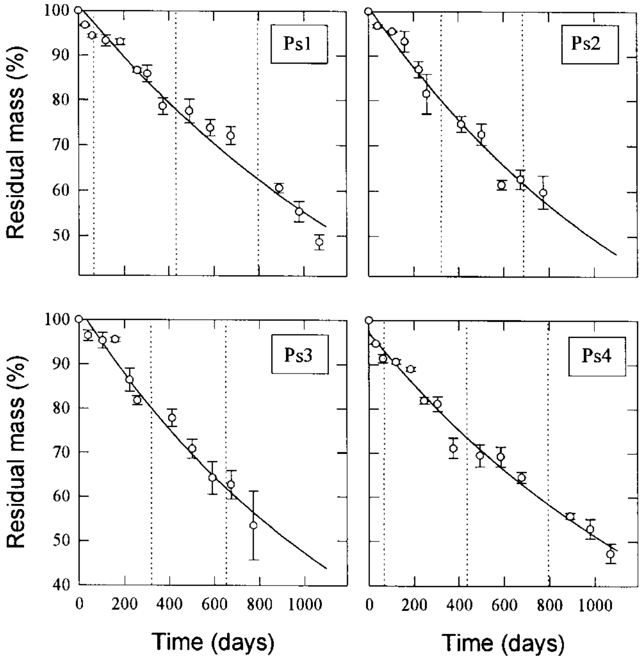

Fig. 2. Remaining mass (in percentage) in the decomposition bags throughout the decomposition process. The fitted lines are significant at $p < 0.00001$.

Table 3. Mean annual needle fall (kg/ha dry weight), standard deviation (Sd), coefficient of variation (Cv), and percentage of needle fall from the total litter fall collected (%) over two years (1990 and 1991) in the study sites. Results of Analysis of Variance (ANOVA) (last column) and multiple mean comparison (letters) are also shown. In rows, means with the same letter are not significantly different ($p < 0.05$). The significance of the difference between years is indicated at the bottom of the columns. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Locality	Ps1	Ps2	Ps3	Ps4
1990				
Mean	2771.9 a	1015.4 c	1425.9 b	1393.4 b ***
Sd	243.5	100.7	310.1	140.7
Cv	8.8	9.9	21.8	10.1
%	59.9	44.9	41.8	43.6
1991				
Mean	2307.5 a	1371.3 c	2119.8 ab	1711.4 bc**
Sd	119.2	269.5	441.4	257.1
Cv	5.2	19.7	20.8	15.0
%	54.4	44.1	53.1	40.6
1990-1991				
Mean	2539.7 a	1193.3 c	1772.8 b	1552.4 b ***
Sd	142.2	173.7	376.7	186.7
Cv	5.6	14.6	20.7	12.0
%	57.3	44.4	47.8	41.9
	*	**	ns	*

Discussion

Litter fall

Needle litter fall observed during the sampling period is close to that reported for *Pinus sylvestris* in the central Pyrenees (1600 kg·ha^{-1}·yr^{-1}; Alvera 1980) and the Iberian range (1800-2000 kg; Carceller et al. 1989), but much lower than in the Central Range of Spain (4100 kg; Santa Regina & Gallardo 1985) and SE France (4100 - 6200 kg; Aussenac 1969; Aussenac et al. 1972). Our values are also similar to mean amount values in 16 Swedish *P. sylvestris* forests (1600 kg; Albrektson 1988), and higher than a 24-yr mean in Finnish stands (1040 kg·ha^{-1}·yr^{-1}; Kouki & Hokkanen 1992). Pausas et al. (1994) showed a significant (negative) relationship between needle fall of *P. sylvestris* and latitude on a European scale. They suggested that the variation in the amount of litter fall is higher at low latitudes than at high latitudes due to larger spatial and temporal heterogeneity (e.g. topography, climate) at low latitudes in Europe.

There were significant differences in the amount of needle litter fall between the four stands studied, as was reported previously in a one-year study of the same stands (Pausas 1993). These differences are mainly related to the aspect of the sites, i.e. stands facing south showed higher litter fall rates than those facing north (see also Pausas 1993). However, needle litter fall showed

Table 4. Analysis of deviance of the needle fall pattern in the four sites studied (Ps1, Ps2, Ps3 and Ps4). The parameters tested are: time (throughout the year), year (1990 vs 1991) and the interaction between both time and year.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

Source of variation	Ps1	Ps2	Ps3	Ps4
time	***	***	***	***
+year	*	ns	**	***
+year*time	*	ns	ns	ns

Table 5. Decomposition rate k (/yr) and half-decomposition time (t_{50}, yr) for the four different stands and for all stands together.

Stand	k	t_{50}
Ps1	0.221	3.84
Ps2	0.262	3.24
Ps3	0.283	2.99
Ps4	0.234	3.31
Mean	0.239	3.56

Table 6. Analysis of deviance for the stepwise logistic regression of first-year mass loss in 27 European *Pinus sylvestris* forests. Significance: *** = $p < 0.0001$: ** = $p < 0.01$.

Source of variation	Deviance	DF	% Expl.Dev.	p
Null model	86.90	26		
Annual mean temperature	51.00	25	41.31	***
+ Latitude	26.35	24	69.68	***
+ Mean annual precipitation	19.51	23	77.55	**

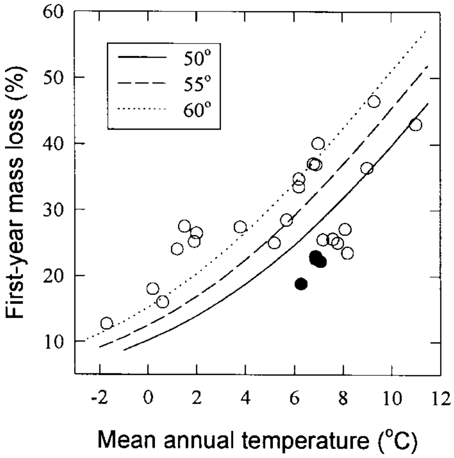

Fig. 3. First-year mass loss (%) in relation to mean annual temperature (°C) and latitude in European stands of *Pinus sylvestris*, based on Berg et al. (1993; hollow circles) and the present study (filled circles). Fitted lines represent the statistical model (Table 6) at three different latitudes (50, 55 and 60° N) without taking precipitation into account.

a relatively similar temporal pattern in all stands.

The spatial variation of the needle fall is relatively low (5 - 20 %), and thus the estimation is acceptable. However, other fractions have shown coefficients of variation between 10 and 45 % (Pausas 1993), suggesting that more traps should be used to obtain an accurate estimation of the litter production of these fractions.

Flower-Ellis (1985), in a 10-yr of study of Swedish mature stands of *Pinus sylvestris*, found that the proportion of needles ranges between 40 - 70 % in a mature 120-yr-old stand, which is similar to our range (40 - 60 %). He also reported that the proportion of needles ranges between 75 - 95 % in a 18-yr-old stand and between 60 - 80 % in a 55-yr-old stand. The period of maximum needle fall (August to October) also agreed with other studies on *P. sylvestris* forests (Flower-Ellis 1985; Cousens 1988; Carceller et al. 1989).

The fact that the peak of maximum needle fall was earlier in 1991 than in 1990 may be related to the difference in weather conditions between these two years. There were no great differences between the years sampled (1990 and 1991) in annual climatic characteristics, e.g. mean annual temperature and total annual rainfall. However, there was a clear difference in rainfall distribution. In 1990 rainfall peaked in June (223 mm), and during that summer, monthly rainfall was between 80 and 223 mm. The period of minimum rainfall was observed in autumn-winter (< 35 mm). However, in 1991, the maximum rainfall was recorded in March (206 mm), and the minimum rainfall was in summer (37, 28 and 66 mm during June, July and August, respectively). In terms of water stress (Walter 1985), i.e. rainfall (mm) < 2 × mean temperature (°C); there was no stress in 1990, whereas June and July 1991 had water stress. This may explain the increase in needle fall; however, a longer period of study is needed to verify this (Kouki & Hokkanen 1992). Microclimatic parameters of the stands will also be necessary to understand the non-significant effect between years in site Ps2. Different studies have reported a relationship between dry conditions during the growth period and the timing of needle fall in different coniferous forests (Cromer et al. 1984; Kumar Das & Ramakrishnan 1985; Hennessey et al. 1992). Hennessey et al. (1992) found that in dry years the maximum needle fall occurred two months earlier than in wet years (a similar time lag to that found in the present study). Reich & Borchert (1984) showed how drought constrains different plant phenologies in tropical forests. These results are consistent with the suggestions that the needle fall pattern is a function of the environmental conditions during the current year (Vose & Allen 1991). This seems a general pattern, at least in temperate forests. In tropical ecosystems it is often difficult to distinguish the environmental effect in plant phenologies from the role of insect pests (Lieberman 1982; Aide 1988; Wright & van Schaik 1994).

Litter decomposition

In all four sites studied the pattern of mass-loss during the two years was very similar. Only one site (Ps1) may be considered to have a slightly lower decomposition rate. This was the site with the most extreme conditions. Ps1 was the site with the lowest soil moisture, steepest slope, highest solar radiation, shallowest soil depth and was located at the highest altitude (Table 1). Ps1 was also the stand with lowest cover of trees, shrubs and herbs. Escudero et al. (1988) also found lower decomposition rates in more open than in shaded environments, while Pausas & Fons (1992) found that trees in stand Ps1 had a lower growth rate than trees in Ps2.

There was no clear difference in the two-year decomposition rate between sites with different bedrock types. Different litter qualities may be expected from different bedrock types, but chemical analyses are needed to quantify these differences. The possible differences in litter quality of our stands were not sufficient to differentiate the decomposition rate. Meentemeyer (1978), Meentemeyer & Berg (1986), Berg et al. (1993) and Virzo de Santo et al. (1993) also found during the first year a larger span in decomposition rates over a region due to climate variables than to variables related to leaf quality .

Our values for decomposition rates are typical of the lower end of the range according to Gosz (1981) for coniferous forests ($k = 0.25 - 0.35$), but similar to the rates observed in Swedish *Pinus sylvestris* forests, e.g. 0.263 for a 5-yr period (Staaf & Berg 1982). However, some Mediterranean coniferous forests have shown much lower decomposition rates (e.g. 0.07 - 0.19; Hart et al. 1992).

Climate gradient

On a European scale, there was a clear pattern of increasing first year decomposition with the increase of mean annual temperature as has been reported elsewhere (Berg et al. 1993). The fact that latitude was also significant in our regression model suggests that there were some ecological factors other than temperature that contribute to the decomposition rate. These factors may be seasonality of rainfall, different quality of leaves due to different varieties of *Pinus sylvestris*, different solar radiation or different soil nutrient characteristics. Chemical analysis of the litter and estimation of other climatic parameters are needed to test this hypothesis. Meentemeyer (1978) showed that mass-loss rates in five sites of different tree species is positively related to actual evapotranspiration (AET) and to the AET/lignin concentration ratio (an index of litter quality). Following this approach Meentemeyer & Berg (1986) and Berg et al. (1993) showed a positive relationship of first-year mass loss with AET in different pine forests. The regression analysis of Meentemeyer (1978) and Meentemeyer & Berg (1986) shows an increase in explained variance when including variables related to leaf quality (concentration of lignin, nitrogen or phosphorus) after the climatic variables. However, this increase is relatively low compared with the influence of climate. A similar conclusion was reached by Berg et al. (1993).

Berg et al. (1993) emphasized the importance of AET rather than temperature; however, their estimate of AET is highly correlated with mean annual temperature ($r = 0.98$) and therefore we preferred to use temperature because it is a simpler variable. Due to this high correlation, our results using temperature are very similar to those obtained by Berg et al. (1993) using AET. However, the estimation of AET has built-in assumptions, all introducing uncertainty and degrees of freedom. Note, for example, that they compute AET assuming that all the soils (in all sites) have the same hydrological characteristics; and thus, differences in the estimated AET are more related to differences in temperature and potential evapotranspiration than we would expect. A better estimation of the AET could improve the models developed by Berg et al. (1993). The fact that our model includes latitude suggests that a certain ecological factor, which may be related to latitude, is not being taken into account. Berg et al. (1993) also showed the importance of litter quality in the decomposition process.

Some considerations must be taken into account when interpreting Fig. 3. Values of first-year mass loss refer to only a few years of observation (e.g. one year for the Pyrenean sites), while the temperature values refer to long-term mean values from meteorological stations. Furthermore, the decomposition studies were performed in different years. Specific climatic data from the sampled years could improve the prediction. The same can be said for the relationships presented by Berg et al. (1993).

Acknowledgements. This study was financed by the Ministerio de Educación y Ciencia (the Spanish Government) and by a grant from Fundació 'La Caixa' (Caixa de Pensions de Barcelona). I thank V.R. Vallejo for his supervision of the work, T. Sauras for kindly helping in the sampling and the analysis and M. Sicart for his help in the sampling and his hospitality. Valuable comments on the manuscript were provided by B. Berg, J. Cortina and T. Sauras.

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Received 15 April 1996;
Revision received 15 October 1996;
Accepted 22 April 1997.