

Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions

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(Received 28 October 2005; accepted 27 January 2006)

Abstract – From 1996 to 2002 the monthly litterfall in a *Quercus suber* forest ecosystem of Montseny (NE Spain) was recorded and its relationship to meteorological variables was statistically analysed. The average annual production ($477 \text{ g m}^{-2} \text{ yr}^{-1}$) was similar to those found in other Mediterranean evergreen forests with relatively high rainfall. The main components were the leaves (55% of the total biomass), followed by acorns (22%) and twigs (16%). Litter production was highest during May and June, when the majority of the old leaves fell. When the meteorological conditions were favourable, a second leaf fall collection was observed. Acorn production in 2001 was about nine times that of the previous years, indicating a mast year. In general, the different litterfall components were highly correlated in time except for the acorns. Interannual covariation was significant for leaves/twigs and leaves/catkins. Catkins were the most variable component with also strong seasonality, acorns were also very variable with low seasonality, while leaves were less variable and with the strongest seasonality. After accounting for seasonal covariation, there were significant effects of rainfall on twig litterfall and of temperature on leaf litterfall, the years with highest leaf litterfall being the hottest.

litterfall / Iberian Peninsula / coark oak / Mediterranean climate / weather

Résumé – Production de litière dans une forêt de *Quercus suber* du Montseny (NE de l'Espagne) et relations avec les conditions météorologiques. De 1996 jusqu'en 2002, la chute mensuelle de litière d'un écosystème forestier de *Quercus suber* du Montseny (NE de l'Espagne) a été enregistrée et mise en relation, au moyen de l'analyse statistique, avec les variables météorologiques. La production annuelle moyenne ($477 \text{ g m}^{-2} \text{ an}^{-1}$) est similaire à celles déjà trouvées dans d'autres forêts sempervirentes avec une pluviosité relativement élevée du pourtour méditerranéen. Les éléments principaux composant la litière ont été : des feuilles (55 % du total de la biomasse), suivies par les glands (22 %) et des rameaux (16 %). La production de litière a été plus importante pendant les mois de mai et de juin, période pendant laquelle sont tombés la plupart des vieilles feuilles. Lorsque les conditions météorologiques ont été favorables une deuxième chute de feuilles a été observée. En 2001, la production de glands a été environ 9 fois plus importante que celle des années précédentes ce qui montre qu'il s'est agi d'une année semencière. En général les différents éléments composant la litière ont présenté une haute corrélation temporelle, sauf pour la chute des glands. La covariation interannuelle a été significative pour feuilles/rameaux et pour feuilles/chatons. Les chatons ont été les éléments les plus variables et ont aussi montré une grande saisonnalité, les glands ont présenté une grande variabilité avec une faible saisonnalité, tandis que les feuilles ont eu moins de variabilité et la plus grande saisonnalité. Prenant en compte les covariations saisonnières, la pluviosité a eu des effets significatifs sur l'importance des rameaux dans les chutes de litière et la température sur l'importance des feuilles dans les chutes de litière ; en effet les années les plus chaudes étant celles qui présentent les chutes de feuilles les plus importantes dans la litière.

chute de litière / péninsule ibérique / chêne liège / climat méditerranéen / conditions météorologiques

1. INTRODUCTION

Leaves and crowns are the active interface of energy, carbon and water exchange between forest canopies and the atmosphere [10]. The use of litterfall as an index of primary production and nutrient cycles in terrestrial ecosystems has been frequently proposed [35]. This approach can be easily applied to deciduous forests but it is more difficult in the case of evergreen species [3].

The productivity of evergreen Mediterranean ecosystems depends on frequent meteorological fluctuations [8, 33]. Amongst the ecological factors, climate generally plays a very important role. Processes like evapotranspiration and photosynthesis are often affected by meteorological conditions,

which can limit the life cycle of forest trees. Forest canopies are more sensitive and react more promptly to biotic and abiotic changes than other components of the ecosystem. The measurement of litter production is a crucial issue for continuous monitoring programs of forest ecosystems [28, 36]. The relation between plant growth and climate can be expressed by several empirical indices, such as those related to temperature and drought stress [6, 15].

Mediterranean oak species have developed mechanisms to avoid excessive loss of cell water. Research on the effects of environmental stress on plant growth in the Mediterranean area has been published [1] but there has been little assessment of the relationship between temporal litter production and temperature and rainfall.

On the other hand, it has been detected that climate warming causes strong phenological changes in evergreen plants.

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All these changes are correlated with temperature and are most noticeable after the mid 1970s [22]. Dendrochronologic studies [13] have found an increasing variability in parameters based on tree rings during the last decades. The results of all these kinds of studies can be applied to cork-oak forest management in response to climatic change.

The aim of our paper is to statistically analyse interannual and seasonal variation of litterfall in a cork oak forest of the Montseny massif (Catalonia, north-eastern Iberian Peninsula) and its relationship with meteorological data.

2. METHODS

2.1. Study area

The Montseny forms part of a mountain range that runs parallel to the Mediterranean Sea about 30 km off the Catalanian coast. The topography is rough, with a difference of 1600 m in altitude between the summit (1713 m) and the lowlands (100 m). Rocks are basically granite and, to a lesser extent, schist and slate. The climate is xerotheric Mediterranean, which is characterised by a dry season lasting approximately two months (July and August) in the lower areas, while on the summits rainfall is more important and there is no dry summer season. At lower altitudes, shallow, stony, greyish brown soils, low in humus and with largely undefined horizons are frequent in the Montseny. At the intermediate altitudes brown soils, rich in humus, are dominant while in the upper ones they are ranker-type soil.

On the lower slopes, the dominant vegetation communities are evergreen forests. Bolòs [4] describes the plain situated on the southwest of the range as occupied by *Quercus ilex* communities (*Quercetum ilicis* Br.-Bl. 1915, *Viburno tini-Quercetum ilicis* Br.-Bl. 1936 em. nom. Rivas Mart 1975). Depending on their orientation the slopes between 200 and 600–700 m are dominated by *Q. suber* communities (*Carici depressae-Quercetum suberis* (O. Bolòs 1959), Rivas Mart. 1987); in higher altitudes communities of *Q. ilex* (*Asplenio onopteris-Quercetum ilicis* Br.-Bl. 1936 em. Nom. Rivas Mart. 1975) reappear and in poorly developed soils they go up to 900–1000 m. Still higher, *Fagus sylvatica* communities are dominant (between 900–1100 m and 1100–1600 m).

Two representative cork-oak forest plots of 400 m² near El Polell at 780 m high were selected (41° 44' 8" N, 2° 23' 2" E; UTM 31T $x = 448775$, $y = 4620682$). The tree level had a density of 1720 trees/ha and was constituted by *Quercus suber* (62%), *Quercus ilex* (36%) and *Pinus pinea* (2%). The maximum diameter of cork oaks was 48.6 cm and the average was 17.8 cm. The average height was 8.5 m. The undergrowth was dominated by *Arbutus unedo*, *Crataegus monogyna*, and *Erica arborea* among other species.

2.2. Field measurements

For litterfall measurements, seven 0.25 m² conical traps were placed at random in each plot [31]. Collection took place monthly from July 1995 to December 2002. The samples were sorted into five components: cork-oak leaves, twigs, male catkins, acorns and miscellanea (including all other material). They were then dried at 75 °C for 48 h and weighed. Monthly and annual litterfall amounts were estimated from the monthly collected litterfall in the seven traps on each plot. The closest meteorological data available were from the station of Viladrau, in the border of the Natural Park of Montseny.

2.3. Statistical analyses

To explore patterns of association among meteorological variables and reduce the number of variables, principal component analysis (PCA) was applied to the correlation matrix. Kaiser-Meyer-Olkin's measure of sampling adequacy (KMO) was used to assess the usefulness of a PCA. KMO ranges from 0 to 1 and should be well above 0.5 if variables are interdependent and a PCA is useful.

The analysis of the relationship between time-dependent variables is not a simple task. For instance, to test for a relationship between litterfall and temperature in a long series of monthly data, ordinary regression techniques (though often used) are inappropriate because: (1) the assumption of independent errors is violated if time is not considered as a factor in the model; (2) selecting specific months involves the splitting of the set data, hence less statistical power and possible incoherency of results. Moreover, if the time series displays strong seasonality (as with most meteorological and ecological variables), it is often necessary to account for the seasonal variation prior to testing for the relationship between variables. For instance, a correlation between temperature and litterfall might simply indicate that both increase in summer, while we are generally more interested in testing whether warmer summers produce increased litterfall. Finally, relationships might be obscured because of delays in the response of variables to specific factors.

To overcome these problems, we used several time-series modelling approaches that yielded similar results. We first evaluated the strength of seasonality in the series with the coefficient of determination of the autoregressive regression model, as recently suggested by Moineddin [20]. We used linear regression analysis with 11 dummy variables for months as predictors, and then calculated the coefficient of determination. Moineddin [20] showed that this coefficient of determination is a useful measure of the strength of stable seasonality. No significant overall trend existed in the time-series but it was necessary to log-transform ($\log_{10} x + 1$) all variables except temperature and wind speed to stabilize variances and reduce positive asymmetry.

We then used exponential smoothing with only a multiplicative seasonal model to remove seasonality of all the time-series [30]. Exponential smoothing is a popular, flexible time series forecasting technique that allows for the existence of trends, additive or multiplicative seasonality, and attenuation in times-series data. We used exponential smoothing of the original variables with no trend parameter and multiplicative seasonality because our time-series showed heteroscedasticity and no significant trend. Given the multiplicative model used, the variables were not log-transformed for this analysis. We tested the relationship of the different model errors thus obtained with cross-correlation analysis [17]. A cross-correlation function (CCF) displays the correlation coefficients between two series at different time shifts or lags. Lag 0 means no time shift and is identical to the conventional correlation coefficient between the two time series. Lag 1 means that the first series has been shifted backwards one time unit (one month in our case) and if significant (conventionally beyond ± 2 SE limits) means that the two series are associated with a time-unit delay. We used CCFs to test for any direct (at lag 0) or delayed dependence (at other lags) between variables. The relationship of litterfall components with selected meteorological variables was also analysed with Spearman's correlation and multiple linear regression; the later analyses are not shown because they yielded similar results. All statistical analyses were performed with the SPSS for Windows 11.5.

Table I. Annual fall registered for different litter components in the experimental cork-oak forest in Montseny.

Year	Annual litterfall ($\text{g m}^{-2} \text{yr}^{-1}$)					Total
	Leaves	Twigs	Catkins	Acorns	Miscellaneous	
1996	334.5	71.24	31.36	47.52	12.16	496.8
1997	195.6	66.12	17.32	81.96	21.00	382.0
1998	321.2	126.1	3.660	63.74	19.00	533.8
1999	180.6	78.49	27.12	33.08	8.686	327.9
2000	333.6	42.27	36.68	23.57	6.568	442.7
2001	217.0	63.94	13.73	460.1	15.77	770.5
2002	257.6	75.30	12.18	24.93	18.30	388.3
Average	262.9	74.78	20.29	105.0	14.50	477.4
SD	67.05	25.53	11.78	158.0	5.490	147.2

3. RESULTS

Table I shows the production of litterfall components from 1996 to 2002. The production of litterfall registered during a seven-year period in the cork-oak forest of Montseny gave an average of $477 \pm 147 \text{ g m}^{-2} \text{yr}^{-1}$. The more important litter components were leaves (55%), followed by acorns (22%), and twigs (16%). Leaf production values alternated between $300 \text{ g m}^{-2} \text{yr}^{-1}$ to ca. $200 \text{ g m}^{-2} \text{yr}^{-1}$. The average for acorn production was $105 \text{ g m}^{-2} \text{yr}^{-1}$.

Litter production was highest during May and June, when the majority of the old leaves fell. A second smaller harvest in autumn was often observed (Fig. 2). The highest amount of litterfall was registered in June 1996 and May 2000 with 157 and 145 g m^{-2} respectively. In years of low leaf production, such as 1997, the fall was more gradual throughout the summer and the autumn.

Twig fall presented an average value of $74.78 \pm 25.53 \text{ g m}^{-2} \text{yr}^{-1}$. It was especially high during the spring and throughout the autumn and the winter. The highest twig fall was registered for December 1996 with 21.52 g m^{-2} , December 1998 with 32.46 g m^{-2} , and October 1999 with 27.47 g m^{-2} . Average annual catkin production was $20.29 \pm 11 \text{ g m}^{-2} \text{yr}^{-1}$, and took place mostly during June. The highest production of catkins took place in 2000 with $32.5 \text{ g m}^{-2} \text{yr}^{-1}$, this being the year of lowest acorn fall ($23.56 \text{ g m}^{-2} \text{yr}^{-1}$), whereas the third year of lowest catkin fall (2001 with $13.72 \text{ g m}^{-2} \text{yr}^{-1}$) was the one with maximum acorn production ($460 \text{ g m}^{-2} \text{yr}^{-1}$).

Mature acorn fall took place mostly in autumn and winter, but the quantity and distribution of this component changed considerably depending on the year. In January 1996 there was a collection of the acorns formed the previous year (16.24 g m^{-2}) and another in November with 5.44 g m^{-2} . In 1997 the acorn fall took place gradually from September to January of the following year with a collection in October of 23.6 g m^{-2} . In 1998 there was a premature acorn fall of aborted acorns in June (20 g m^{-2}). During 1999 and 2000, the production was very poor with a maximum observed in December and August respectively. The only mast year during the stud-

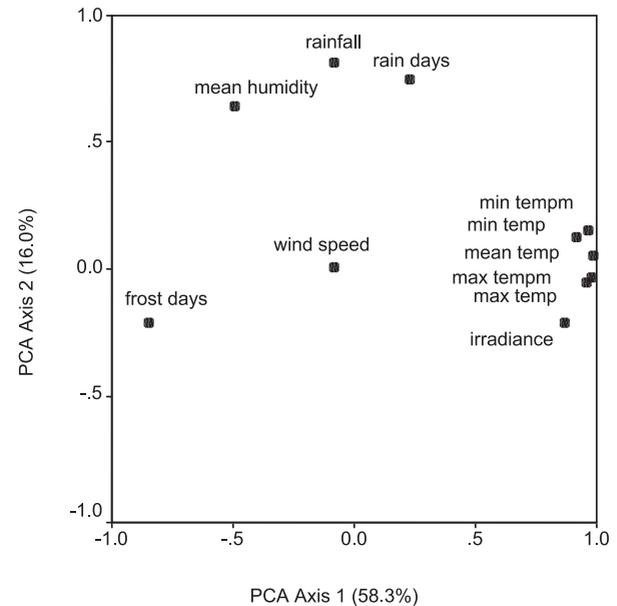


Figure 1. Principal component analysis of the monthly values for eleven meteorological variables from January 1996 to December 2002. The factor loadings of variables for the first two components are shown (the percentages are the variance explained by each axis). “min temp” stands for “daily minimum temperature recorded for a month”, “min tempm” for “monthly mean daily minimum temperature”, and similarly for maximum and mean temperatures.

ied period was, as stated previously, in 2001 and took place in September and November with a collection in November of 174 g m^{-2} . During 2002 acorn production was poor and took place prematurely in July.

3.1. Meteorological variables

The meteorological variables were highly interdependent ($KMO = 0.75$) and two axes of a PCA explained 74.3% of the variation (Fig. 1). The first axis explained most of the variation and corresponded mostly to a winter-summer gradient and the strong correlations between temperature variables, number of frost days, and mean irradiance. E.g., the correlation between mean temperature and number of frost days was $r = -0.79$ ($n = 84$, $P < 0.0005$). The second axis displayed monthly variation in precipitation and humidity. E.g., the correlation between rainfall precipitation and humidity was $r = -0.51$ ($n = 77$, $P < 0.0005$). In contrast, wind speed was not significantly related to any of the remaining ten variables ($P \gg 0.05$) and for this reason it appears in the centre of the factor plot. The largest factor loadings for the two axes were for mean temperature and rainfall precipitation, respectively. For these reasons, we chose to study the relationship between litterfall variables and these three contrasting variables (mean temperature, rainfall precipitation and wind speed) that summarize the most important patterns in meteorological conditions.

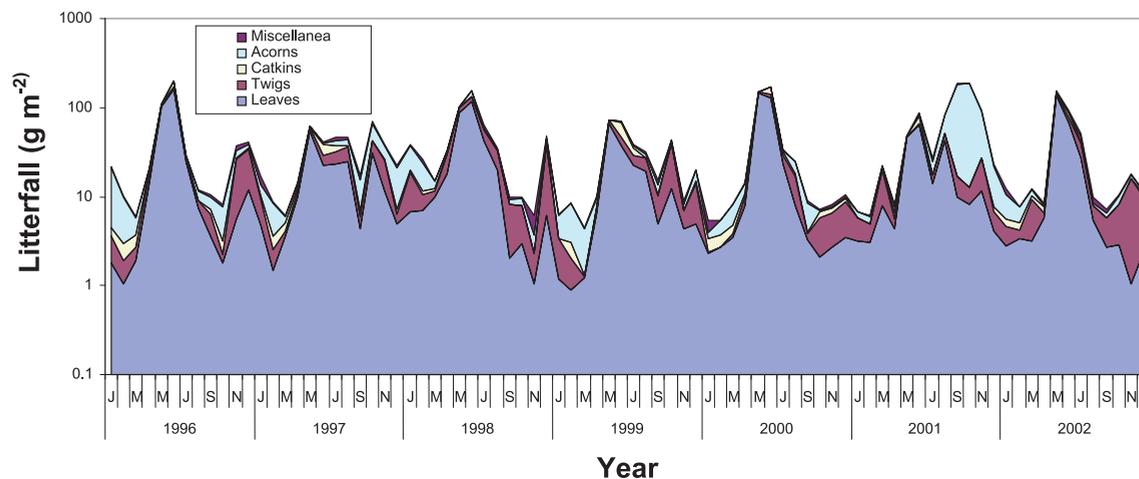


Figure 2. Time series of the litterfall components from January 1996 to December 2002. (A color version of this figure is available at www.edpsciences.org/forest.)

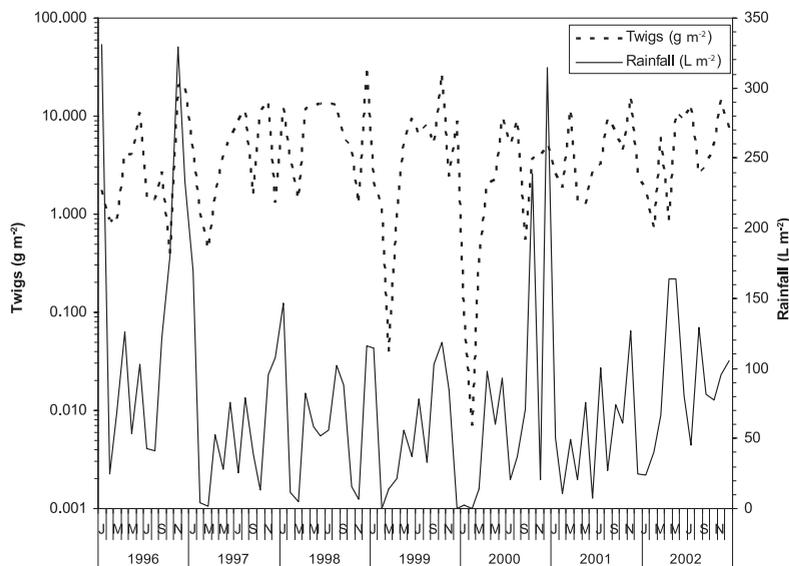


Figure 3. Time series of the twig litterfall and rainfall precipitation from January 1996 to December 2002.

3.2. Degree of variation and strength of seasonal pattern

The time-series of the five litterfall components and the three selected meteorological variables are shown in Figures 2–5. Regression analysis with months as dummy variables indicated that all of the eight variables displayed seasonal variation ($P < 0.05$) except acorn litterfall ($P = 0.51$) and (marginally) wind speed ($P = 0.07$). Catkin litterfall took place mostly in June and then in July (Figs. 2 and 8) and leaf litterfall mostly in May and June (Figs. 2 and 4). The other litterfall components showed much less seasonal variation and twigs peaked in early summer and autumn. Rainfall precipitation was more variable and less seasonal than temperature but rainfall generally peaked in December–January and then in April–May.

Figure 6 shows that the degree of overall variation (coefficient of variation) and seasonal pattern were not significantly

related ($r = 0.19$, $P = 0.65$), since catkins were the most variable component and had a marked seasonal pattern. Rainfall and acorns were also very variable, but with a less marked seasonal pattern, while leaves and temperature were less variable, though with the strongest seasonal pattern. Catkin litterfall displayed the highest coefficient of variation because it generally gave zero values except in June and July, when it increased sharply (Fig. 8). Acorn litterfall was the least seasonal variable and showed a strong peak in 2001 (Fig. 2). In contrast, leaves and twigs were the least variable litterfall components because they yielded most of the necromass and were present throughout the year (Figs. 2–4).

3.3. Similar seasonal patterns or inter-annual variation of litterfall components?

The different litterfall components were in general highly correlated in time (without accounting for seasonality), except

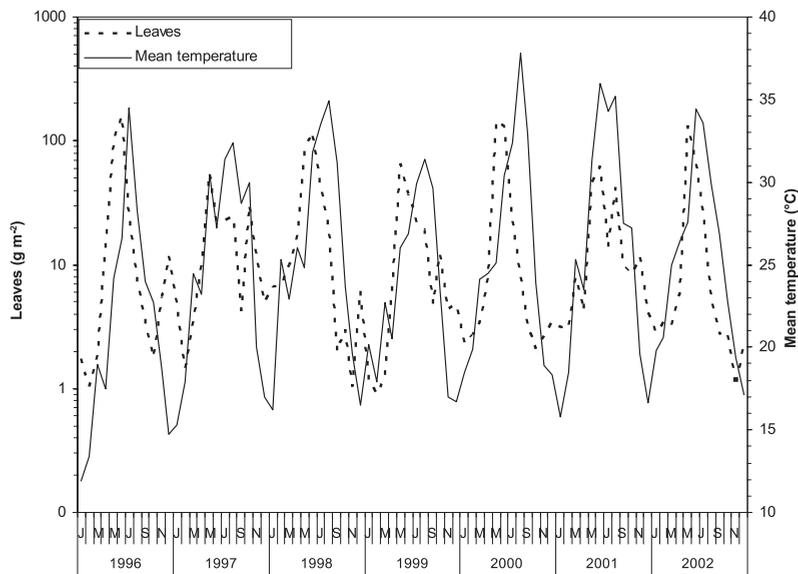


Figure 4. Time series of the leaf litterfall and monthly mean temperature from January 1996 to December 2002.

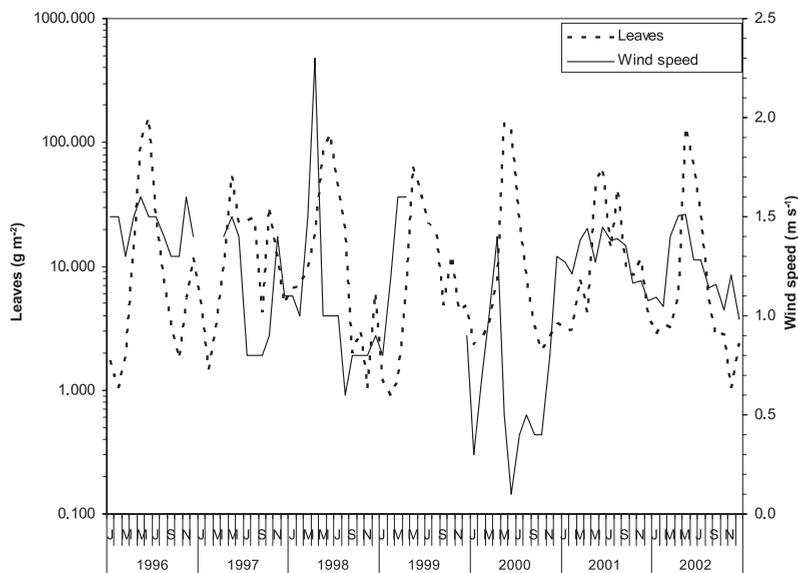


Figure 5. Time series of the leaf litterfall and monthly mean wind speed (the discontinuities correspond to some data not recorded) from January 1996 to December 2002.

for acorns that were only significantly related to miscellanea (Tab. II). Six of the ten correlations were significant but the most important corresponded to leaves/catkins. These correlations imply that the litterfall components were quite synchronised, but may be due to two different complementary mechanisms: similar seasonal patterns of variation in litterfall components or inter-annual variation of litterfall components. To discern between these two mechanisms, it is necessary to test for correlation after partialling out the different seasonal effects of the variables.

This second analysis (Tab. II, above diagonal) showed a quite different correlation matrix. Although the leaf/catkin pairs continued to be the most correlated, the correlation coefficient in general decreased. This means, for instance, that al-

though the time-series of catkins and twigs vary (Tab. II, below diagonal), there was no significant covariation beyond similar seasonal patterns (Tab. II, above diagonal). This is illustrated in Figure 7: the raw data show significant covariation of catkins and twigs and even some significant cross-correlation at lag 4. However, after taking out the seasonal pattern (Fig. 7, bottom) there were no significant coefficients in the cross-correlation function. Therefore, the correlation between catkin and twig litterfall occurs simply because they both peak in June.

In contrast, the correlation between leaves and twigs remains significant after accounting for seasonal variation (Fig. 8, bottom). Therefore, although both variables peak in June there is some additional, interannual covariation: the

Table II. Correlation between different components (leaf, twigs, catkins, acorns, and miscellanea) of the litterfall (variables $\log(x+1)$ transformed). Below diagonal, correlation coefficients of the variables $\log(x+1)$ transformed; above diagonal, correlation coefficients of the variables after accounting for seasonality with time-series modelling. $n = 84$; * $P < 0.05$; ** $P < 0.01$; *** = $P < 0.001$.

	Leaves	Twigs	Catkins	Acorns	Miscellanea
Leaves	–	0.244*	0.314**	0.076	0.166
Twigs	0.467***	–	0.033	0.049	0.406***
Catkins	0.568***	0.295**	–	–0.053	–0.070
Acorns	0.004	0.168	–0.124	–	0.157
Miscellanea	0.256	0.477***	0.232*	0.337**	–

years with more leaf production (1996 and 2000) also had more twig litterfall while other years had simultaneously less leaf and twig production (1997, 1999 and 2001). Moreover, there is an even stronger, significant cross-correlation at lag 6 because those years with more leaf production in May–June (1996, 2000 and then in 1998 and 2002) also show a peak of twigs 6 months later (November–December) and vice-versa (low leaf litterfall in spring and twig production 6 months later in 1997, 1999 and 2001). These patterns can be also clearly seen in Figure 2.

In short, although most litterfall components were correlated (because most peak in May–July and October–December), interannual co-variation was only significant for leaf/twigs and leaf/catkins (both had maximum falls in spring 1996 and spring 2000).

3.4. Effects of meteorological variables on litterfall components

The time-series of meteorological variables also showed numerous significant correlations (both at lag 0 and cross-correlation) with the litterfall components. After accounting for seasonal pattern, however, there were only two significant correlations (Tab. III). The strongest correlation was of rainfall precipitation with twig litterfall and Figure 3 showed good concordance of peaks and lows (note also the low seasonal pattern of both variables). There was also some significant effect of temperature on leaf litterfall and the years with highest leaf litterfall (1996, 2000 and 1998) were the hottest (Fig. 4). The leaf litterfall mimicked the mean temperature well and in less hot summers where temperature fluctuated (1997 and 2001) so did the leaf litterfall. There was no significant cross-correlation of the three selected meteorological variables with litterfall components after removing the seasonality of the time series.

4. DISCUSSION

4.1. Total litterfall

The average annual litterfall production registered in cork-oak forest of Montseny (4.8 Mg ha^{-1}) is similar to other cork-

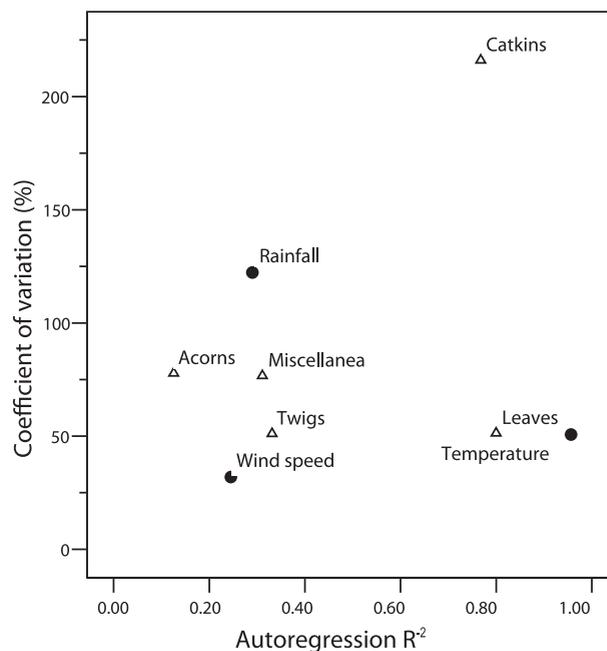


Figure 6. Coefficient of variation and strength of seasonality (autoregression R^2 , see methods) in the meteorological and litterfall variables. All variables were log transformed for the computation of the autoregression R^2 except temperature and wind speed. $n = 84$ except for wind speed ($n = 74$). Different symbols are used for meteorological and litterfall variables.

oak forests and Mediterranean oaks from relatively productive areas (Tab. IV). Usually these areas are far from the coast and with high rainfall. In a previous study for the same species in Sant Hilari, close to Montseny, from 1989 to 1992 we found a similar litter production.

4.2. Seasonal patterns of leaves and twigs

In the cork-oak forest of Montseny, almost all litterfall fractions have a strongly seasonal fall pattern, especially leaves and flowers, and it is similar to those found in other Mediterranean evergreen woodlands.

The regular fall of leaves takes place at the end of spring, in May or June, after the bud flush, as is normal in Mediterranean oaks, but with some variations depending on the place. The phenological study of Sa et al. [28] about cork oaks in Portugal indicated that leaf average longevity was 12 months, and the process of leaf shedding and leaf birth occurs simultaneously, unlike our zone in which it occurs after the new leaves appear (personal observation). More studies are needed.

The peak of leaf of May and June changed depending on the year [3, 7, 19]. This may be because in Mediterranean areas, leaves that fall at the end of spring can be interpreted as an evolutionary adaptation to a hydric deficit that can occur during the summer dry period of July and August [12]. When the conditions are favourable in autumn, we may observe a second leaf fall peak, much smaller than the spring one and this

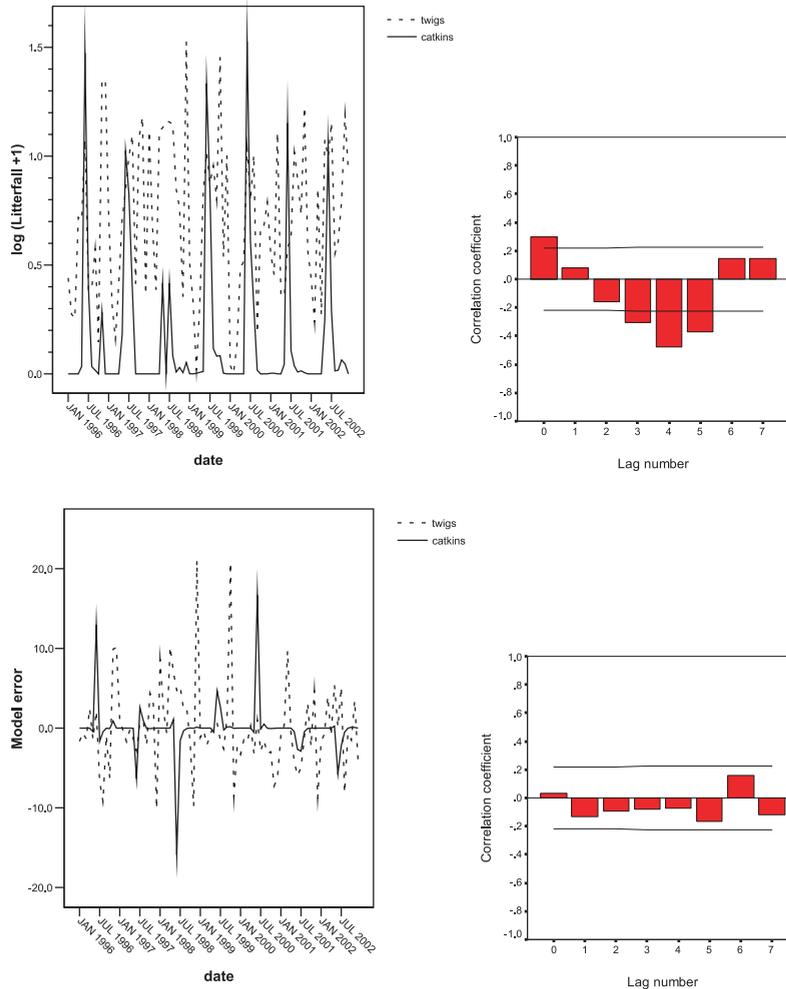


Figure 7. Time series of the twig and catkin litterfall: top, original time series; bottom, seasonally-adjusted residuals. On the right, the corresponding cross-correlation functions are shown (line indicates significant correlations at the conventional 2 standard error limits).

has also been observed by other authors like Leonardi et al. [18] and Bussotti et al. [5]. This last leaf fall may be related to a second sprouting that happens after the summer drought and before the lowering of temperatures in winter. During the winter, photosynthetic activities are limited to days with not very low temperatures [21].

Twig fall is quite erratic and depends significantly on wind and storms. The fall period takes place mostly at the beginning of springtime and the end of the autumn and varies a lot depending on the year as observed for the same species in Sicily [18]. A good correlation may be observed between the leaves and the flowers on the one hand and twigs on the other, but with some months of delay according to the fall rhythms. During the years in which weather conditions allow intensive meristem activity, the water and nutrients are used in a more efficient way for shoot development. On the other hand, drought may favour twig fall.

4.3. Seasonal patterns of reproductive fractions

Catkins fall during June and July. In 1996, 1999 and 2000 the highest catkin fall rate was registered. On the other hand acorn fall does not necessarily follow a seasonal pattern and

does not correlate with other litterfall components with the exception of miscellaneous ones. It presents a different inter-annual rhythm from the other crown organs. We have observed an apparent inverse relation between leaf and acorn production but no significant differences have been found.

Acorn production in 2001 was the highest, round about nine times that of previous years, therefore we surmise that this was a mast year, a year of much higher production than the normal in terms of acorns and these take place periodically. High inter-annual variation in fruit production is a well-known model for many forest species and particularly oaks [26, 29]. One may interpret this as a reproductive strategy of the species which may be favoured by the climatic and pollination conditions. The years in which lowest acorn production has been observed are those anterior to and posterior to the mast year. We may suppose that the internal cycle of acorn production at the cork-oak forest of Polell takes at least five years.

4.4. The relationship of litterfall and meteorological variables

The strong positive effect of temperature on leaf fall, especially at the end of the spring, is explained by the effects

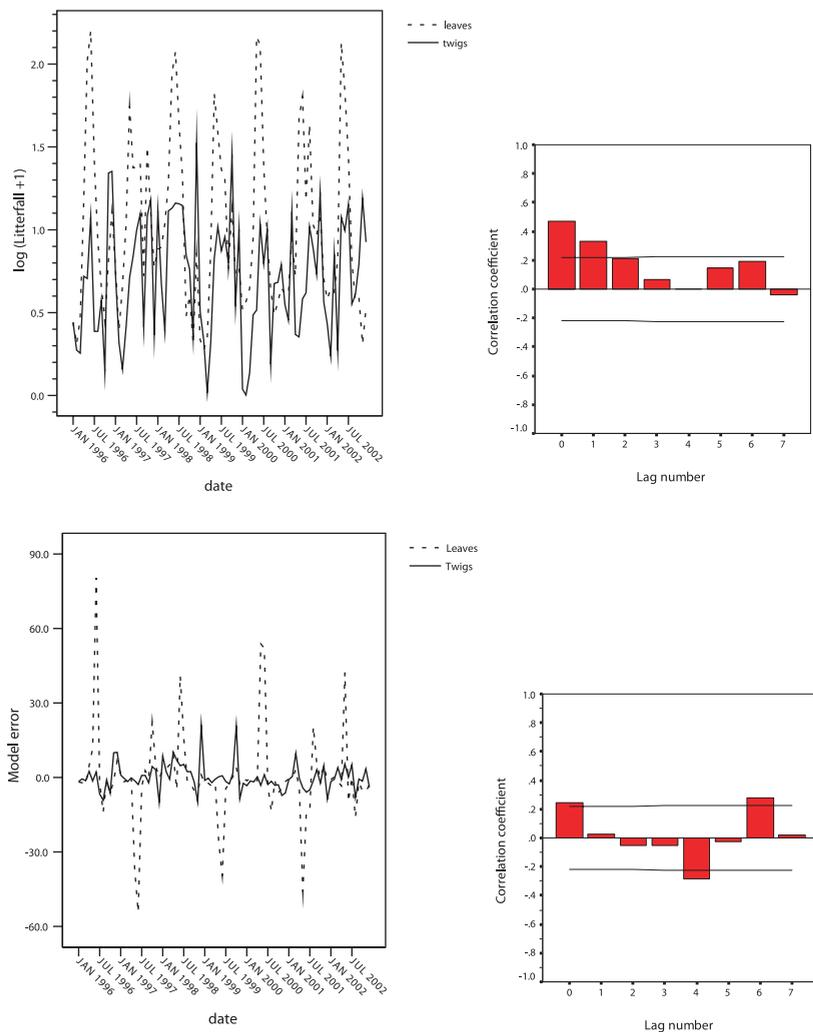


Figure 8. Time series of the leaf and twig litterfall: top, original time series; bottom, seasonally-adjusted residuals. On the right, the corresponding cross-correlation functions are shown (line indicates significant correlations at the conventional 2 standard error limits).

Table III. Correlation between different components (leaf, twigs, catkins, acorns, and miscellanea) of the litterfall and meteorological variables, after accounting for seasonality of all variables with time-series modelling. Spearman's correlation coefficients are shown. $n = 84$; * $P < 0.1$; ** $P < 0.01$.

	Temperature	Rainfall	Wind speed
Leaves	0.188*	0.147	0.033
Twigs	0.152	0.338**	0.091
Catkins	-0.130	0.054	-0.100
Acorns	0.148	-0.072	0.149
Miscellanea	0.133	0.169	0.072

of drying-out of the old leaves. As a consequence, if an increase in temperature is produced, more intense leaf fall may be predicted. In Mediterranean climates water tends to be the most limiting factor and the density of the crown is found to be balanced with the level of rainfall and soil reserves [14]. This is clearly reflected in the positive correlation between rainfall and the production of litterfall components. In spite of this,

it was not possible to detect the delayed effects of rainfall and leaf fall (and other organs), because a longer time series would be necessary.

Owing to the fluctuating conditions of the Mediterranean climate such as the existence of a dry period during the summer, the plant takes advantage of the most favourable periods of temperature and humidity in order to carry out the maximum photosynthesis, and this tends to be during the spring and part of the autumn. During and after the appearance of shoots, the plant discards the old leaves, once the translocation of the nutrients has taken place [24]. In this way the nutrients and hydro-resources are destined to the new leaves which are photosynthetically more active [16]. For this reason Oliveira [21] found that the maximum stomatal conductance and transpiration of the *Quercus suber* is registered in March and June.

During the dry months the stomata normally close at midday to avoid evapotranspiration [21,32]. This closure provokes the interruption of photosynthetic activity. When drought conditions are very extreme premature leaf and acorn falling may take place.

Table IV. Review of litterfall data of different Mediterranean oaks.

Species	Site	Reference	Acorn litterfall (Mg ha ⁻¹ yr ⁻¹)	Total litterfall (Mg ha ⁻¹ yr ⁻¹)
<i>Quercus ilex</i>	Madeleine, France	[23]	2.7	6.9
<i>Quercus ilex</i>	Montseny, Spain	[34]	0.58	4.8
<i>Quercus ilex</i>	Le Rouquet, France	[9]	–	3.8
<i>Quercus ilex</i>	Prades, Spain	[3]	0.14	2.3
<i>Quercus ilex</i>	Puéchabon, France	[25]	–	3.5
<i>Quercus ilex</i>	Le Rouquet, France	[9]	–	5.3
<i>Quercus ilex</i>	Marganai, Italy	[10]	1.11	5.8
<i>Quercus ilex</i>	Calognole, Italy	[5]	0.52	6.9
<i>Quercus ilex</i> / <i>Q. coccifera</i>	Northern Greece	[2]	0.2–1.6	5.3
<i>Quercus suber</i>	Santo Pietro, Italy	[18]	–	3.8
<i>Quercus suber</i>	Quart, Spain	[7]	0.07–1.23	3.9
<i>Quercus suber</i>	St. Hilari, Spain	[7]	0.2–0.5	4.6
<i>Quercus suber</i>	Evora, Portugal	[27]	–	5.1
<i>Quercus suber</i>	Montseny, Spain	Present study	1	4.8
<i>Quercus rotundifolia</i>	Salamanca, Spain	[11]	1.3	5.7
<i>Quercus rotundifolia</i>	Muñovela, Spain	[19]	0.21	1.9
<i>Quercus pyrenaica</i>	Salamanca, Spain	[11]	0.6	3.6
<i>Quercus pyrenaica</i>	El Payo, Spain	[25]	–	3.2
<i>Quercus pubescens</i>	La Vialle, France	[25]	–	3.1
<i>Quercus cerris</i>	Roti, Italy	[10]	0.52	5.2

5. CONCLUSIONS

The degrees of overall variation in the time series of the different litterfall components are not significantly related to their strength of seasonality. Catkins are the most variable component with also strong seasonality, but acorns are also very variable with low seasonality while leaves are less variable and with the strongest seasonality. Twig litterfall was significantly mediated by rainfall. Acorn fall has a pattern that needs to be studied for a longer period. The strong correlation between leaf fall and temperature shows sensitivity towards temperature conditions.

Litterfall production in the Montseny cork-oak forest and its seasonal variations reflect its adaptation to the Mediterranean climate and also the relatively good precipitation conditions of this site. *Quercus suber* uses a favourable and sometimes short growing period to carry out photosynthesis. The predictable increase in temperature due to climate change may have notable repercussions in the phenology of the species resulting in lower production.

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