

Nutrients return from leaves and litterfall in a mediterranean cork oak (*Quercus suber* L.) forest in southwestern Spain

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Received: 8 January 2008 / Revised: 4 November 2008 / Accepted: 22 December 2008 / Published online: 21 April 2009
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Abstract The knowledge of the cycle of nutrients is fundamental for the correct comprehension of the tree–soil relationship and for an adequate forest management. In order to analyse the nutrients return from leaves and litterfall in a Mediterranean cork oak forest in southwestern Spain, 12 trees were randomly selected and litterfall collected for 2 years. Samples were taken monthly and separated in different fractions (leaves, twigs, catkins, acorns and miscellaneous), then leaves nutrients were analyzed. Simultaneously, we analyzed the nutrient content of living leaves from the same trees in each season during 1 year. The analyzed nutrients were C, N, P, K, Ca, Mg, Fe, Mn, S, Cu, Zn and Mo. Annual patterns of each nutrient in fallen leaves were characterized and compared with seasonal values of these nutrients in living leaves. Leaves fall has two annual maximum, first and most important in spring around April coinciding with renewal of foliar cover and second around October. Main concentration patterns of N, P and K are related with phenological patterns, in consequence minimum concentration in leaves fall were obtained in periods of growing and maximum litterfall. Concentrations of Ca, Fe and Mn increase with the age of the leaves and maximum concentrations were obtained before periods of maximum litterfall while concentrations of Cu, Mo and Mg stay stable.

Seasonal analysis of nutrients in living leaves collected from the same trees in four different periods of the year allowed to corroborate the patterns of leaves fall and the probable osmotic function of K.

Keywords *Quercus suber* · Litterfall · Nutrients cycling · Nutrients return

Introduction

Cork oak (*Quercus suber* L.) is an important forest species of the Mediterranean region in Spain. According to II National Forest Inventory (DGCONA 1998), it covers 409.025 ha that is 3.9% of the total forest tree cover of the country and the 25% of the species at world level. They are usually forests with a high human intervention, mainly focused in providing food for cattle (acorns and pastures), firewood and cork. It is one of the few Mediterranean forest species that could be preserved just taking into account its economical importance, due to the extraction of cork and the high added value of cork stoppers. It has also a high ecological and landscape value and it makes up an efficient Mediterranean system to couple with a limiting, diverse and highly interannual variable environment (Montero and Cañellas 1998).

Forest litterfall is associated with the transfer of energy and nutrients to the soil and is the starting point for nutrient recycling (Gray and Schlesinger 1981). The knowledge of the cycle of biomass and nutrients between trees and soil through the litterfall is one of the fundamental aspects for an adequate management of forests. This task is more difficult in the Mediterranean region, where the economy of water resources and nutrients is critical (Arianoutsou 1989). Other aspects that make difficult the study of

Communicated by A. Merino.

This article belongs to the special issue “Plant–soil relationships in Southern European forests”.

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nutrients in Mediterranean open woodland forest agroecosystems (called “dehesas” in Spain) are the long-live character of sclerophyllous leaves (Bellot et al. 1992) and the feeding of pasture and litterfall by herbivorous (Escudero et al. 1985).

Some researches about nutrient content of leaves in *Q. suber* L. stands have been published (Escudero and Del Arco 1987; Leonardi et al. 1992; Caritat et al. 1996; Orgeas and Bonin 1996; Orgeas 1997; Orgeas et al. 2002; Oliveira et al. 1996; Robert et al. 1996 and Passarinho et al. 2006), but most of them are focused only in nutrient content of living leaves or fallen leaves. As far as we know, only Robert et al. (1996) studied nutrients in both living and fallen leaves of *Q. suber*, but only with data corresponding to the summer period. Other Mediterranean tree species have been studied with more detail than cork oak (Rapp et al. 1999; Bussotti et al. 2003; Fife et al. 2008) but results of these studies cannot be applied to *Q. suber* due to the different environments and different life periods of leaves. Our work takes into account the annual pattern of nutrients content in fallen and living leaves in order to assess foliar retranslocation and transference to the soil of several macro- and micronutrients.

Materials and methods

Study site

The plot is located in Hinojos (Huelva, southwest of Spain) in a flat area at an altitude of 100 m a.s.l. The total surface of the plot is 1.9 ha where *Q. suber* L. is the dominant species and *Q. ilex* spp *ballota* appears as secondary species. Plot density is 99.6 trees ha⁻¹ and the basal area is 8.1 m² ha⁻¹. Climate is typical Mediterranean with mean annual precipitation of 579 mm, mean annual temperature of 18.9°C and a summer drought period of 5 months with high interannual variability.

Soil was characterized opening two soil profiles, with main physical and chemical properties shown in Table 1, and collecting soil samples from 12 points distributed in a net of 40 × 40 m. At each point, a minimum of three samples were collected at different depths from 0 to 90 cm

and superficial and mean profile values of texture, organic matter content (%), N, P, Cation Exchange Capacity and exchangeable Ca, Mg, Na and K were determined. The soil is a complex profile with a sandy-loam to loamy-sand upper layer of 25–40 cm thickness over an argilic horizon (with loam-clay to clay texture) showing stagnic properties. It is classified as Thapto Alfisol Xerorthent (USDA 2003). Climatic and soil moisture variables were gathered through a meteorological weather station installed inside the plot. Data was registered each 15 min and included precipitation, air temperature, relative humidity, PAR radiation, wind speed and direction, leaf wetness, soil temperature at 30 cm depth and soil moisture (C-Probe[®] sensor) at 10, 30, 60, 90 and 120 cm depth.

Litterfall data

All trees of the plot (107) were numerically identified and the following dendrometric variables were measured: circumference at breast height (CBH), total height, height of first living branch and four crown radius. Groups of three trees with similar diameter were made and four of these groups were selected randomly to complete 12 sampling trees in the plot. The CBH of selected trees ranged from 68 to 109 cm with mean value of 87 cm (whole plot CBH range is from 48 to 170 cm with mean value of 89 cm). Hence, selected trees represent the central circumference classes of the plot. Fifty percent of the trees inside the plot ranged between the circumference values of the selected trees.

To collect the litterfall, four 0.16 m² circular traps were placed on each cardinal point of each tree at a distance corresponding to three quarters of the crown radius measured from the stem. Samples were taken monthly from March 2004 to 2006 and separated in different fractions (leaves, twigs, catkins, acorns and miscellaneous). Later, they were oven dried at 105°C during 2 days and weighted.

Nutrient analysis

The analysis was done with the leaves collected from the litterfall traps from March 2004 to 2006. We analyzed also the nutrient content of living leaves from the same trees in

Table 1 Soil analysis

Horizon	Depth	Color	Clay (%)	Sand (%)	pH (H ₂ O)	OM (%)	CEC	V (%)	P (ppm)	K (ppm)
A	0–15	10YR/4/3	6	79	5.1	1.5	12.2	21	2	120
C	15–40	10YR/6/6	6	82	5.6	0.2	5.2	26	2	60
2Btg	40–80	10YR/6/4	29	58	4.9	0.3	28.3	25	1	90
2C	80–125	10YR/5/8	20	61	6.0	0.3	25.6	47	1	70

OM organic matter, CEC cation exchange capacity (cmol + Kg⁻¹), V saturation percent (%), P assimilable phosphorous, K assimilable potassium

April, June and September 2004 and in January 2005 with the objective of having seasonal data. Living leaves were taken from the outermost part of the crown at three meters height approximately. Four samples of living leaves were taken at each tree, one at each cardinal point, and then mixed to get a sample per tree.

After separating the different fractions of the litterfall, the leaves of each tree were taken from the four traps, mixed altogether and grinded with a micro mill (0.8 mm diameter). The dry samples were burned at 550°C during approximately 7 h, followed by an acid digestion by HCl 5N.

The analyzed nutrients were: C, N, P, K, Ca, Mg, Fe, Mn, S, Cu, Zn, Mo. For the carbon and nitrogen analysis an elemental analyzer (Termo Finningan 1112 Series EA) was used. The other nutrients were analyzed with an ICP-OES Yobin Yvon Última 2 analyzer.

Data analysis

Leaves fall data was expressed in $g\ m^{-2}$ of crown dividing the dry weight of leaves collected by the surface of the four litter traps placed under each tree ($0.64\ m^2$). To calculate the amount of falling leaves and nutrient content for each gathering date, the mean value of the 12 trees was calculated. The evolution of nutrient contents and the evolution of leaves fall along the 2 years of study were analyzed graphically.

To analyse the influence of the month and year on the nutrient concentration in fallen leaves, we considered the following general lineal model (model 1):

$$y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + e_{ijk}$$

where y_{ijk} is the arcsin transformation of nutrient concentration (N, P, K...) in fallen leaves of the k th tree the j th month of the i th year, μ is the overall mean, α_i is the fixed year effect, β_j is the fixed month effect, $\alpha\beta_{ij}$ is the month x year interaction and e_{ijk} is the random error term with $e_{ijk} \sim N(0, \sigma_e^2)$. The significance of the model was contrasted with ANOVA and fixed effect coefficients were estimated with Ordinary Least Squares. In case of significative year, month or interaction effects, differences between groups were tested with the Scheffé test.

The analysis of the influence of the type of leave (living or fallen leave) on nutrient concentration was undertaken considering the model (model 2):

$$y_{ijk} = \mu + \gamma_i + \beta_j + \gamma\beta_{ij} + e_{ijk}$$

where y_{ijk} is the arcsin transformation of nutrient concentration (N, P, K...) of the i th type of leave (fallen or live) the j th month and μ, β_j and e_{ijk} with the same meaning as in previous analysis. Significance of the model, coefficient estimation and differences between groups followed the same process as in previous analysis. Both analysis considered as year 1, the period March 2004–February 2005, and year 2, the period March 2005–February 2006.

Finally, the amount of nutrient returned to the soil through leaf fall was calculated as follows:

$$NR_{ij} = \frac{CS \left(\sum_{k=1}^{12} LF_{jk} N_{ijk} / 100 \right)}{S}$$

where NR_{ij} amount of nutrient i returned to soil in year j ($kg\ ha^{-1}\ year^{-1}$), CS total crown surface in the plot calculated as sum of elliptical crown surfaces of all trees in the plot (m^2), $9,892\ m^2$, LF_{jk} mean value of leaf fall in month k of year j ($kg\ m^{-2}$ of crown), N_{ijk} concentration of nutrient i in the fallen leaves of month k of year j (%), S plot area (ha), $1.9\ ha$.

Results

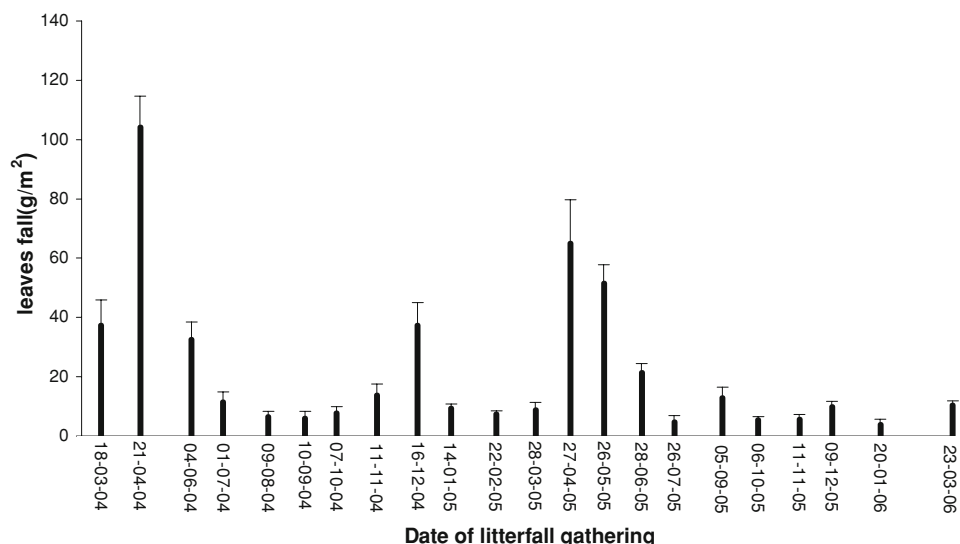
Litterfall

Annual values of litterfall and their components are presented in Table 2. The amount of leaves fall between March 2004 and February 2005 was $274.40\ g\ m^{-2}$ (10.90% of total litterfall) while on the second year was $189.56\ g\ m^{-2}$ (69.60% of total litterfall). The high difference in percentages is due to the high difference in the acorn production between the 2 years, as in 2004 acorn production ($2,113.68\ g\ m^{-2}$) was much more higher than in 2005 ($2.68\ g\ m^{-2}$). Without taking into account acorns, leaves fall on the first year was 67.86% while on the second year was 70.29% of total litterfall.

Table 2 Annual values for different litterfall components in $g\ m^{-2}$ (standard error) and percentage of total litterfall of the year

Year	Twigs	Leaves	Catkins	Acorns	Miscellaneous	Total
Mar 2004–Feb 2005	70.12 (24.44) 2.78%	274.40 (55.52) 10.90%	24.24 (13.92) 0.96%	2,113.68 (1,578.40) 83.94%	35.64 (7.92) 1.42%	2,518.08
Mar 2005–Feb 2006	49.88 (18.84) 18.32%	189.56 (68.12) 69.60%	14.68 (15.56) 5.39%	2.68 (3.12) 0.98%	15.56 (6.84) 5.71%	272.36
Average	60.00 (14.28) 4.30%	231.96 (60.00) 16.64%	19.44 (6.76) 1.40%	1,057.32 (1,491.52) 75.83%	25.60 (14.20) 1.84%	1,394.40 (396.69)

Fig. 1 Leaves fall (g m^{-2}) (\pm standard error) from March 2004 to March 2006



Monthly values of leaf fall are shown in Fig. 1. Higher values of leaves fall were in spring (March–June) with approximately 60% of total leaves fall of both years. Also there were a peak of leaves fall between October and December, although this value was lower in comparison with spring.

Nutrient concentration phenology in fallen leaves

Table 3 shows the significance of the year, month and interaction effects in model 1 (fallen leaves) for the different nutrients. N, P, K and Ca concentration in fallen leaves are shown in Fig. 2. The P concentration had higher values on February and March, significantly higher than those found in dates of new tissue production (April 2004, 2005 and surroundings October 2004) where lower P concentration values were observed. Similar to P, the N concentration was higher in March and significantly lower

values were observed in dates of maximum litterfall. Concerning K, an increase of concentration from early summer until late summer was observed, with values from July to October being significantly higher than those found in the dates of new tissue production (April, October). Ca had a first higher value in spring 2004 (March–June) and later, the concentration reduced until winter (December–January). It increased again in spring 2005, showing a second maximum in winter 2005 (December), hence showing a different behavior in the 2 years of study.

Figure 3 shows concentrations of Mg, Fe, Mn, S, Zn, Cu, Mo in leaves fall. Mo and Mg had an even tendency all year long showing a non significant year, month or interaction effect (Table 3). For Fe relative maximum values in August 2004, November 2004 and October–November 2005 were observed. Sequence of Zn was similar to Fe, with higher values in March and November. For S, a higher concentration was observed in March and

Table 3 Significance of effects in model 1 (fallen leaves) and model 2 (living vs. fallen leaves) for the different nutrients

Nutrient	Model 1 (fallen leaves)			Model 2 (living leaves vs. fallen leaves)		
	Year	Month	Interaction	Leaf type	Month	Interaction
N	*	***	***	***	***	***
P	*	**	**	***	***	***
K	n.s.	***	***	***	***	***
Ca	***	n.s.	***	***	*	***
Mg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C	n.s.	***	**	*		n.s.
Fe	***	***	***	***	***	**
Mn	**	n.s.	**	***	n.s.	**
S	***	***	***	n.s.	***	n.s.
Cu	***	***	***	***	**	*
Zn	n.s.	***	n.s.	**	**	n.s.
Mo	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

n.s. non significant

* $p < 0.05$; ** $p < 0.01$;

*** $p < 0.001$

Fig. 2 Nutrient concentration sequence for N, P, K and Ca in the fallen leaves

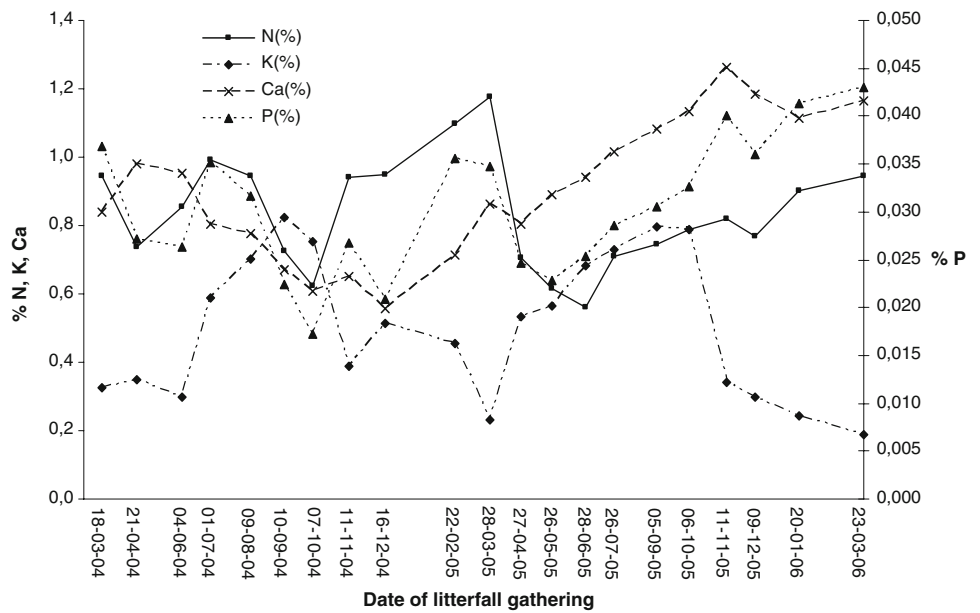
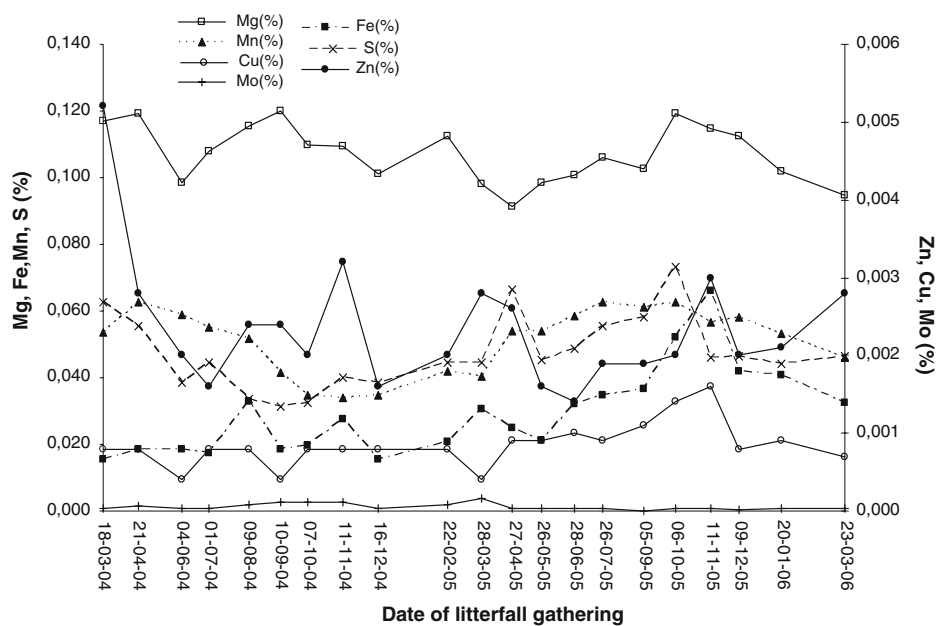


Fig. 3 Nutrient concentration sequence for Mg, Fe, Mn, S, Zn, Cu and Mo in the fallen leaves



April 2004 and an increase tendency since October 2004 until March 2005, while in 2005 the highest value was in October. Concerning Mn higher values of concentration were observed in March and April 2004, then showing a decreasing tendency until November 2004; later values of concentration increased showing the highest values in October 2005.

The nutrients N, P, K, Ca, Fe, Mn, S and Cu, show a significant different phenology between the first and the second year of study, indicated by a significant year x month interaction effect (Table 3).

Nutrient concentration phenology in living leaves

Table 4 shows the values of the nutrients concentrations in living leaves. N, P, S, Cu and Zn had their highest values in April, while the rest of the year concentrations were lower and similar. Other nutrients like Ca, Fe and Mn showed the opposite behavior as they had lower value in April and higher the rest of the year. K had the higher value on April but this value decrease continuously until to the lower value in January. Finally, Mg shows similar values the whole year.

Table 4 Nutrient Content in living leaves (%) for different seasons

Date	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (%)	Mn (%)	S (%)	Cu (%)	Zn (%)
April 2004	2.2967	0.1973	1.2220	0.2800	0.1387	0.0083	0.0137	0.0600	0.0010	0.0027
June 2004	1.3200	0.0673	0.9120	0.5513	0.1147	0.0103	0.0320	0.0360	0.0008	0.0017
September 2004	1.2000	0.0547	0.8180	0.6653	0.1313	0.0157	0.0360	0.0387	0.0007	0.0015
January 2005	1.2000	0.0590	0.5070	0.6350	0.1250	0.0170	0.0343	0.0360	0.0008	0.0013

The comparison of nutrient concentration between live and fallen leaves (Table 3, model 2) showed significant differences in most of the nutrients (N, P, K, Ca, C, Fe, Mn, Cu and Zn). Concentration of N, P, K and Cu were higher in live leaves and the contrary occurred for the rest of the nutrients. N, P, K, Ca, Fe, Mn, Cu showed also a significant leaf type \times month interaction, indicating a different phenology of these nutrients in fallen and living leaves.

Nutrient return from leaves

Total amount of nutrients return to the soil from leaves in the second year of study was 30% lower than nutrients return in the first. Highest amount values of each nutrient were in April 2004, which coincide with the highest value of litterfall.

The total amount of each nutrient returned to the soil showed the following ranking ($C > Ca > N > K > Mg > Mn > S > P > Fe > Zn > Cu > Mo$), being the mean values of the 2 years ($\text{kg ha}^{-1} \text{ year}^{-1}$): N (9.55), P (0.34), K (5.60), Ca (10.45), C (587.25), Mg (1.23), Fe (0.28), Mn (0.65), S (0.62), Cu (0.01), Zn (0.03) and Mo (0.0005).

Discussion

Leaves fall

Values of leaves fall collected in the 2 years of study are similar to other values found in literature about litterfall in *Q. suber* L. (Caritat et al. 1996; 2006). Higher values of leaves fall are in spring and the highest value is in April. The main cause of this leaves fall is the renewal of foliar cover (Sa et al. 2001). This renewal of foliar cover is typical of Mediterranean species (Escudero and Del Arco 1987) and can be interpreted as an evolutionary adaptation to the water deficit that occurs during the summer dry period (Escudero and Del Arco 1987; Caritat et al. 2006).

A high value of leaves fall has also been observed between October and December. This fact has been interpreted by other authors (Leonardi et al. 1992; Bussotti et al. 2003; Caritat et al. 2006) as due to a second sprout after summer drought, supported by favorable environmental conditions (temperature, precipitation) in early autumn.

A marked difference between the 2 years of study in the amount of leaves fall was observed. Values of most of the months in 2004 were higher than values in 2005. 2005 was a very dry year with a precipitation of 314 mm (67.8 mm in spring and 0.4 mm in summer) while in 2004 precipitation was higher (475 mm with 153 mm in spring and 5.4 mm in summer). The amount of water in soil in the layer 0–120 cm was 173 mm (C-Probe data) in April 2004 while in April 2005 was only 81 mm, that was similar to the lowest value registered in the whole year 2004 (September with 79 mm). In spring 2005, there was not enough water in soil and most of the trees did not renovate the foliar cover. This fact could explain values of nutrient concentration founded in the second year of study. Nevertheless, in December 2004 leaf fall was much higher than in December 2005. This could be explained by storms and the low temperatures and early frosts in November and December 2004 (minimum temperatures of -0.4°C in November 2004 and -5.4°C in December 2004), that produced damages to still non-acclimated leaves (Fernández et al. 2005) and caused an anticipated fall of the damaged leaves.

Leaf nutrient concentration phenology

Values of N, P, K, Ca and Mg in living leaves are similar than values found in other studies (Oliveira et al. 1996; Passarinho et al. 2006). In young living leaves (April), concentration of N, P and K were elevated due to the high mobilization of this nutrients, coming from the absorption from soil and the retranslocation from old leaves and other organs toward growth zones (Marschner 1995; Oliveira et al. 1996; Robert et al. 1996). In full expanded leaves (June), concentration of N and P had decreased due to dilution and became stabilized in a constant value that was maintained until the end of winter, when the foliar senescence process begins and the nutrients retranslocate to the new tissue production (Fife et al. 2008). Concerning K, concentration in living leaves decreased from spring until summer, but it maintained high values during summer due to its osmotic regulation function, to tolerate water stress. In autumn, concentration of K decreased until the end of winter due to the increase of request for accumulation and translocation of carbohydrates during acorn maturation

(Oliveira et al. 1996). For these reason, concentrations of N, P and K in fall leaves are lower than in living leaves, especially when senescent leaves fall is produced following a phenological pattern.

Concentrations of Ca, Fe and Mn in living leaves increased from April to September probably due to the ontogeny development of leaves. At the end of summer and during winter, values remained approximately constant because they are immobilized into the tree once they are assimilated (Marschner 1995); Ca is accumulated in vacuoles, membranes and cell wall, while Fe and Mn are immobilized in proteins and stable proteins complex. For that reason, concentration of these nutrients in old leaves fall between April and June and are higher than in living leaves. Since September, when leaves are developed and hardened, values of concentration in living and fall leaves are similar.

Concentration of Mo and Mg did not have a clear seasonal pattern (Fig. 3, Table 3). For Mg due to its mobility inside the tree, lower concentrations in fallen leaves than in living leaves could be expected (Passarinho et al. 2006; Robert et al. 1996; Oliveira et al. 1996). Values recorded for exchangeable Mg in the plot varies between 1.4 cmol(+) kg⁻¹ and 3.5 cmol(+) kg⁻¹ with mean value of 2.3 for the 0–90 cm layer, which can be classified as moderate and not low. Therefore, the similar values in the two types of leaves could be due to a non-limiting soil for Mg in this site. Concerning Cu, Robert et al. (1996) obtained indications of retranslocation, although Cu is a relatively immobile nutrient inside of tree because it takes part of stable proteins complex. This aspect could be explained because the capacity of remobilization and retranslocation depends on nitrogen deficiency-induced leaf senescence, relation that is also evident for S and Zn (Marschner 1995). Because of this, in young living leaves (April) concentrations of S, Zn and Cu were elevated but they decreased in June stabilizing this value until their maturation.

All these comments are referred mainly to the period March 2004–February 2005. Since March 2005, due to a particularly cold winter and severe drought in winter and spring, trees suffered an important stress that could cause important changes in trees phenology and litterfall (scarce production of new leaves, keeping of old leaves during spring and summer and production of new leaves in autumn). Hence, the behavior of nutrients like Ca and Mn was different in this year as nutrient concentration was measured mainly in old leaves developed during 2004, therefore with more than 12 months old.

Nutrient return from leaves

The annual pattern of the amount of nutrient return to the soil from leaves depended mainly on leaves fall. Peak

values coincided with periods of higher litterfall (April and October 2004 and 2005). We observed also a difference between the 2 years due to different litterfall among both years. This aspect confirm that nutrient and litterfall are influenced by many variables, including climatic factors, being precipitation a major factor to take into account in Mediterranean environments.

Values of each nutrient concentration were lower than values obtained in other studies (Caritat et al. 1996; Rapp et al. 1999; Bussotti et al. 2003). For all nutrients except N, the values in others works are approximately twice higher than values shown in this work. We think that this difference could be due to a higher tree density in the other study sites.

Conclusions

Cycling of litterfall has two annuals maximum, the first and most important is in spring around April and coincides with the renewal of foliar cover. The second, and less important, is around October, when the precipitations after summer drought and the mild temperatures produce a second sprout. Differences in leave fall among 2004 and 2005 could be explained by different precipitation in both years: available amount of water in soil could act as a major limiting factor that influenced the litterfall at the moment of the renewal of foliar cover in spring 2005. Available water in soil was scarce at this date and the renewal of foliar cover was delayed until water conditions were adequate. Also extraordinary frosts occurred in late autumn 2004 that could influence litterfall because this caused an anticipated fall of the damaged leaves.

Main concentration patterns of N, P and K are related with phenological patterns. In periods of growing or maximum litterfall tree retranslocate nutrients from leaves before they fall, hence minimum concentration in leaves fall were obtained in these periods. For Ca, Fe and Mn pattern is different than in previous nutrients: concentration increase with the maturity of the leaves and maximum concentrations were obtained before periods of maximum litterfall. Cu and Mo concentrations stay stable because they are relatively immobile nutrients inside the tree. In other studies, a relative mobility for Cu was found. We think that Cu, like S and Zn, is influenced by nitrogen deficiency-induced leaf senescence. Seasonal analysis of nutrients in living leaves allowed to corroborate patterns of leaves fall and the probable osmotic function of K.

Acknowledgments This work has been partially financed by the projects SUBERWOOD (V EU Framework Program, QLK5-CT-2001-007001), MEDCRE (Plan Nacional I+D+I, 2005, AGL2005-04971) and SUM2006-00026 (Plan Nacional de I+D, Sumideros Agroforestales de efecto invernadero, 2007–2009). We gratefully

acknowledge the collaboration of the Environmental Agency of Huelva and the municipality of Hinojos (Huelva) and the support in field and laboratory work of Celia, Raúl, Nico, Dani and Felipe. First author is benefiting from a doctoral grant from the University of Huelva.

References

- Arianoutsou M (1989) Timing of litter production in a maquis ecosystem of north-eastern Greece. *Oecol Plant* 10(4):371–378
- Bellot J, Sánchez JR, Lledó MJ, Martínez P, Escarré A (1992) Litterfall as a measure of primary production in mediterranean holm oak forest. *Vegetatio* 99–100:69–76. doi:[10.1007/BF00118211](https://doi.org/10.1007/BF00118211)
- Bussotti F, Borghini F, Celesti C, Leonzio C, Cozzi A, Bettini D, Ferretti M (2003) Leaf shedding, crown condition and element return in two mixed holm oak forests in Tuscany, central Italy. *For Ecol Manage* 176:273–285. doi:[10.1016/S0378-1127\(02\)00283-9](https://doi.org/10.1016/S0378-1127(02)00283-9)
- Caritat A, Bertoni G, Molinas M, Oliva M, Domínguez-Planella A (1996) Litterfall and mineral return in two cork oak forests in northeast Spain. *Ann Sci For* 53:1049–1058. doi:[10.1051/forest:19960601](https://doi.org/10.1051/forest:19960601)
- Caritat A, García-Berthou E, Lapeña R, Vilar L (2006) Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. *Ann For Sci* 63(7):791–800. doi:[10.1051/forest:2006061](https://doi.org/10.1051/forest:2006061)
- DGCONA (1998) Segundo Inventario Forestal Nacional 1986–1996. Ministerio de Medio Ambiente, Madrid
- Escudero A, Del Arco JM (1987) Ecological significance of the phenology of leaf abscission. *Oikos* 49:11–14. doi:[10.2307/3565549](https://doi.org/10.2307/3565549)
- Escudero A, García B, Gómez JM, Luis E (1985) The nutrient cycling in *Quercus rotundifolia* and *Quercus pyrenaica* ecosystems (dehesas) of Spain. *Oecologia Plantarum* 6(20–1):73–86
- Fernández M, Carvajal F, Alejano R, Domínguez L, Tapias R, Alesso SP (2005) Evolución temporal del grado de endurecimiento de plantas de vivero de 4 especies forestales españolas cultivadas en localidades con condiciones climáticas distintas. Actas del IV congreso Forestal Español (CD-ROM), Sociedad Española de Ciencias Forestales, Zaragoza (Spain), 26–30 Sept 2005
- Fife DN, Nambiar EKS, Saur E (2008) Retranslocation of foliar nutrients in evergreen tree species planted in a Mediterranean environment. *Tree Physiol* 28:187–196
- Gray JT, Schlesinger WH (1981) Nutrient cycling in mediterranean type ecosystems. In: Miller PC (ed) Resource use by chaparral and matorral. A comparison of vegetation function in two mediterranean type ecosystems, vol 39. Springer, Ecological Studies, New York, pp 259–286
- Leonardi S, Rapp M, Failla M, Komaromy E (1992) Biomasse, minéralomasse, productivité et gestion de certains elements biogènes dans une forêt de *Quercus suber* L. en Sicile (Italie). *Ecologia Mediterranea* 18:89–98
- Marschner H (1995) Mineral nutrition of higher plants. Academic Press, London
- Montero G, Cañellas I (1998) El alcornoque: manual de reforestación y cultivo. Ed. Mundi-Prensa, Madrid
- Montoya JM (1988) Los alcornocales: revisión del estado de conocimientos en 1987. Ministerio Agricultura, Pesca y Alimentación, Madrid
- Natividade JV (1950) Subercultura. Ministério da Economia. Direcção Geral dos Serviços Florestais e Aquícolas, Lisbon
- Oliveira G, Martins-Louçao MA, Correia O, Catarino F (1996) Nutrient dynamics in crown tissues of cork-oak (*Quercus suber* L.). *Trees (Berl)* 10(24):7–254
- Orgeas J (1997) Dynamique des nutriments de *Quercus suber* L. et production de liège en relation avec les variables environnementales—Le cas du massif des Maures (Var)., Marseille, France
- Orgeas J, Bonin G (1996) Variabilité des nutriments foliaires de *Quercus suber* L. dans différentes situations écologiques dans le Massif des Maures (Var, France) et relations avec la production de liège. *Ann Sci For* 53:615–624. doi:[10.1051/forest:19960240](https://doi.org/10.1051/forest:19960240)
- Orgeas J, Ourcival JM, Bonin G (2002) Seasonal and spatial patterns of foliar nutrients in cork-oak (*Quercus suber* L.) growing on siliceous soils in Provence (France). *Plant Ecol* 164:201–211. doi:[10.1023/A:1021278421821](https://doi.org/10.1023/A:1021278421821)
- Passarinho J, Lamosa P, Baeta JP, Santos H, Candido P (2006) Annual changes in the concentration of minerals and organic compounds of *Quercus suber* leaves. *Physiol Plant* 127:100–110. doi:[10.1111/j.1399-3054.2006.00655.x](https://doi.org/10.1111/j.1399-3054.2006.00655.x)
- Rapp M, Santa-Regina I, Rico M, Gallego HA (1999) Biomass, nutrient content, litterfall and nutrient return to the soil in Mediterranean oak forest. *For Ecol Manage* 119:39–49. doi:[10.1016/S0378-1127\(98\)00508-8](https://doi.org/10.1016/S0378-1127(98)00508-8)
- Robert B, Caritat A, Bertoni G, Vilar L, Molinas M (1996) Nutrient content and seasonal fluctuations in the leaf component of cork-oak (*Quercus suber* L.) litterfall. *Vegetatio* 122:29–35. doi:[10.1007/BF00052813](https://doi.org/10.1007/BF00052813)
- Sa C, Madeira M, Gazarini L (2001) Produção e decomposição da folhada de *Quercus suber* L. *Rev Cie Agr* 24:245–256
- USDA (2003) Keys to soil taxonomy, 9th edn. United States Department of Agriculture