Original article

Nutrient release dynamics in decomposing leaf litter in two Mediterranean deciduous oak species

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Summary – The release and dynamics of macronutrients from decomposing leaf litter were determined for two deciduous oak species: one in Spain, *Quercus pyrenaica,* growing on a *humic Cambisol (Sol brun forestier)* and the other in France, *Q lanuginosa*, on a *rendsic Leptosol (Rendzine)*. The same processes were studied after leaf-litter exchanges between the French stand and a Spanish stand. Nylon litter bags (1 mm^2 mesh), containing 10 g of leaves, were placed in five stands (four in Spain and one in France) and collected every 2 months when they were weighed and analysed for N, P, Ca, Mg and K. The mean amount of nutrients in the decomposing leaves decreased over the 36-month period. The four *Q pyrenaica* stands were classified into two groups involving different nutrient release processes, without any relation to yearly litterfall. For the *Q lanuginosa* stand, the results obtained were similar to those for one of the *Q pyrenaica* groups. Similar nutrient release processes occurred in the litter-bags collected from native stands and after exchanges between the two species, with a quick release of K, followed by Mg and P. Higher Ca accumulation was noted for the *Q pyrenaica* litter as compared to *Q lanuginosa* litter. For N, the results were very different between the two species and the two locations.

litter decomposition / litter bags / nutrient release / oak coppice / *Quercus pyrenaica* / *Q lanuginosa*

Résumé – Dynamique de libération des bioéléments de feuilles en décomposition de deux taillis méditerranéens à chênes caducifoliés. La dynamique qualitative et quantitative de la perte d'éléments majeurs à partir de litières de feuilles en décomposition a été établie pour deux espèces de chênes caducifoliés, l'une en Espagne : *Quercus pyrenaica*, implantée sur Cambisols humifères (sols brun forestier), l'autre en France : *Quercus lanuginosa*, implantée sur Leptosols rendsiques (Rendzines). Les mêmes mécanismes ont été étudiés après échange de litières entre la station française et une station espagnole. Des sachets de nylon, de maille de 1 mm^2, contenant chacun 10 g de feuilles ont été déposés dans cinq stations (quatre en Espagne et une en France) et des échantillons récoltés tous

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les 2 mois. Sur ces échantillons on a dosé : N, P, Ca, Mg et K. Les teneurs en éléments majeurs des feuilles diminuent au cours des 36 mois d'étude. Les quatre stations à *Q pyrenaica* peuvent être regroupées en deux groupes, indiquant des processus de décomposition différents, sans relation avec les quantités de litière arrivant annuellement au sol. Pour *Q lanuginosa*, les résultats étaient similaires à l'un des deux couples espagnols. Au cours de l'expérience d'échange de litières, des dynamiques semblables ont été observées dans les stations d'origine des litières et après échange. K est libéré le plus rapidement, suivi de Mg et de P. On a trouvé une accumulation relative de Ca dans les litières de *Q pyrenaica*, supérieure à celle des litières de *Q lanuginosa*. Concernant l'azote les résultats sont variables, à la fois entre les deux espèces et entre les deux localités.

décomposition de la litière / perte d'éléments / décomposition en sachets / taillis / *Quercus pyrenaica* / *Quercus lanuginosa*

INTRODUCTION

Release of nutrients from decomposing litter is an important internal pathway for nutrient flux in forested ecosystems. Nutrients may be released from litter by leaching or mineralization (Swift et al, 1979). Nutrient release from decomposing litter affects ecosystem primary productivity (Blair, 1988), since these nutrients thus become available for plant uptake and are not lost from the system.

The rate at which nutrients are released depends on several factors as indicated by Seastedt (1984): chemical composition of the litter, structural nature of the nutrient in the litter matrix, microbial demand for the nutrient, and availability of exogenous sources of nutrients. Litter release factors are: litter quality (Fogel and Cromack, 1977; Aber and Melillo, 1980; Berg and Staaf, 1980, 1981; Melillo et al, 1982), macro- and microclimatic variables (Meentemeyer, 1978), microbial and faunal biotic activity (Reichle, 1977). Several authors have defined litter quality in terms of initial N concentrations, the C/N ratio, initial lignin concentrations, and the lignin/N ratio. Litter quality affects not only the rates of mass loss, but also the patterns and rates of nutrient immobilization or release. Climatic factors influencing litter decomposition rates include soil temperature (Lousier and Parkinson, 1976; Heal, 1979; Edmonds, 1980; Moore, 1986; Witkamp, 1996), and soil moisture (Hayes, 1965). Soil fertility is directly related to the activity of decomposers (Bocock and Gilbert, 1957; Witkamp and Van der Drift, 1961).

In nature, it is often difficult to separate the effects of individual factors. Both inter- and intra-site differences in decomposition rates could reflect variations in several of the above-mentioned types of factors.

Element release is above mass loss if biotic mineralization processes are not necessary or if the nutrients are not structurally bound in the litter; it is below mass loss if the nutrients are in short supply relative to microbial demand and then accumulate in the litter during early phases of decomposition (Berg and Staaf, 1981).

The aim of this study was to compare the release of nutrients from decomposing litter of two species of Mediterranean deciduous oaks (*Q pyrenaica* Willd and *Q lanuginosa* Lamk), characteristic of climax formations. The stands are located on forest plots differing in their geological substrates and microclimates. A reciprocal exchange of leaves from the two species between two stands was also studied in order to determine the effects of climatic and leaf quality factors (Martín et al, 1994).

MATERIAL AND METHODS

Site description

The four *Q pyrenaica* forest plots are situated on the northern slope of the 'Sierra de Gata' mountains in the southwestern part of Salamanca province (Spain). The *Q lanuginosa* plot is in the Causse Mejean, north-west of Montpellier (France).

The climatic, edaphic and stand data are given in table I. There was a rainfall gradient between Navasfrías and Fuenteguinaldo. The 3 years of the study of decomposition were considered dry, since mean precipitation was 10–40% lower than the general averages. The annual mean precipitation was very similar between La Viale and El Payo (Moreno et al, 1993).

However, although there were no great differences in climatic factors or elevation between the four Spanish plots and the La Vialle plot,

there was a notable lithological difference. The latter stand is located on dolomitic calcareous bedrock, with a *rendzic Leptosol*, whereas the four Spanish forest areas lie on acid bedrock (granite or shale), producing *humic Cambisols* (FAO, 1989).

Tree densities varied from 406 trees ha^{-1}, with a mean diameter of 25 cm at El Payo, to 2 100 trees ha^{-1}, with a mean diameter of 9.5 cm at La Vialle, reflecting different coppice managements.

The following annotation is used for the plots: Navasfrías: NF; El Payo: EP; Villasrubias: VR; Fuenteguinaldo: FG; La Viale: LV.

Local leaf litter

In each of the five plots studied (four in the 'Sierra de Gata', Province of Salamanca and one in LV, near Montpellier), 54 nylon litter bags

Table I. Characteristics of the five stations studied (Martín et al, 1994).

| Plot characteristics | Forest ecosystem | | | | |
| | Q pyrenaica | | | | Q lanuginosa |
	Fuenteguinaldo	Villasrubias	El Payo	Navasfrías	La Vialle
Elevation (m)	870	900	940	960	1 000
Geology	granite	schist	granite	schist	dolomitic limestone
Soil units	—————————— Humic Cambisol ——————————				Rendzina
Humus type	forest *mull*	forest *mull*	forest *mull*	forest *mull*	calcic *mull*
pH	5.3	5.1	5.0	5.0	7.6
OM (%)	7.3	12.0	13.0	18.0	10.0
C/N	15.0	19.0	17.0	19.0	14.5
CEC (cmol kg^{-1})	19.6	24.5	26.0	25.4	28.6
Avail P$_2$O$_5$ (mg kg^{-1})	385	51.1	77.2	50.0	450
Density (tree ha^{-1})	738	1043	406	820	2 100
Tree mean diameter (cm)	16.5	11.0	25.4	15.2	9.5
Tree mean height (m)	12.0	8.5	17.0	13.0	7.0
Long-term mean P (mm yr^{-1})	720	872	1245	1580	900
3 years mean P (mm yr^{-1})	568	767	859	969	843
Mean annual t (°C)	13.3	nd	nd	5.5	4.8

OM: soil organic matter; CEC: total cation exchange capacity; Avail: available; P: rainfall; t: temperature; Nd: no data available.

with 1 mm^2 mesh and a surface area of 400 cm^2 (each containing 10 g of leaves collected from each site) were placed over the litter in three different locations on each plot. The litter contained in the bags had been dried at room temperature, the remaining humidity being determined by drying at 80 °C until constant weight was achieved. Every 2 months, beginning in February 1990, three bags per plot (one from each location) were collected over a period of 3 consecutive years. The leaves were dried (at 80 °C) and weighed in the laboratory. Temperature should have been 105 °C, but above 80 °C there is a risk of loss of organic matter and minerals (Hernández et al, 1995).

Leaf litter exchanged

Beginning in February 1991 and using the same study method for 2 consecutive years, leaves were exchanged between the EP and LV plots (36 litter bags placed in three groups).

Methods

The following methods were used for chemical analysis of the different litter components: total N determined by the Kjeldahl method or with a Macro-N Heraeus analyzer; total P by spectrophotometry using the vanadomolibdophosphoric yellow method; total Ca and Mg by atomic absorption spectroscopy, and total K by flame photometry (Hernández et al, 1995).

In order to establish possible significant differences in mass loss for the different plots studied, a one-factor Anova was applied with repeated measures for times. Hartley's test had been previously implemented to verify the nature of the variances. Wilcoxon's test was applied to the data obtained in relation to the leaf exchange experiments.

RESULTS AND DISCUSSION

Leaf-litter decomposition

Litter weight loss over 3 years of decomposition has been studied previously (Martín et al, 1994). The main results obtained here indicated that decomposition was slowest at VR–EP, and more intense in LV, intermediate results being obtained for the NF–FG sites, although closer to the LV levels.

Regressions for time (t = time in months) and percentage decomposition (% dec) calculated from the mean decomposition rates at VR–EP and also at NF–FG–LV gave the following equations:

VR–EP: %Dec $= 4.29.t^{0.707}$ $r = 0.967$

NV–FG–LV: %Dec $= 4.38.t^{0.746}$ $r = 0.966$

These equations indicated half-decomposition times (50% of the initial matter) of 32 months for the first group (EP, VR) and 26 months for the second (NF, FG and LV).

The results in the literature are sometimes conflictive since they are based on both field (in situ) and laboratory (in vitro) studies. Bockheim et al (1991) obtained a decomposition rate of 50% for 25 months in *Q ellipsoidalis*, while Rapp (1967), under controlled moisture conditions, recorded half-decomposition times in *Q ilex*, *Q coccifera* and for other *Q lanuginosa* leaves after 22 months of decomposition.

These observations indicated that leaf decomposition patterns were similar for both oak species, but occurred at different rates. Seasonal variations played a major role, with a deceleration or interruption of decomposition in summer (due to drought and typical Mediterranean high temperatures; Martín et al, 1994) and more active decomposition from autumn to spring.

Apart from the intra-annual role of climate, it also appears to be important at a global scale. Thus, LV the northernmost stand studied, showed the highest decomposition rate. However, it could not be determined whether the less intense summer drought, or the geological and soil properties (soils with abundant calcium), were responsible for the differences relative to the four

plots of Sierra de Gata; probably, both factors were involved (Martín et al, 1994).

On the basis of these litter weight loss data and its chemical composition, the following were successively investigated:

1) variations in litter nutrient concentrations at various decomposition times and relative to the initial nutrient content;

2) variations in absolute nutrient mass during decomposition relative to nutrients in yearly litterfall.

Relative release of nutrients from litter bags

Nutrient concentrations, expressed as a percentage of initial concentrations, are shown in figures 1–5. The same data after 1, 2 and 3 years of decomposition and the mean chemical composition of leaves at the same time are summarized in table II.

The mean concentration of N in the leaves relative to the initial concentration decreased over the 36-month period (fig 1).

However, for two stands (LV and EP) an initial increase was observed, with a maximum concentration of 140% in the LV stand after almost 2 months.

Net N release began after 2 months in LV, after 6 months in EP, and from the outset in the other stands (fig 1). The greatest N loss was seen in the FG stand after 25 months. At VR and LV 85% of the original N from the litter bags still remained at the end of the experiments (table II). An increase in N was noted at NF and FG at the end of the experiments with respect to the other years (table II).

Many workers (Bocock, 1963; Gosz et al, 1973; Will, 1967; Edmonds, 1979) have noted increased N concentrations in leaves during the decomposition process. Gosz et al (1973) have suggested that this increase probably arises from external sources such as precipitation, atmospheric dust and invasion of litter bags by fungal hyphae.

Initial P loss was very rapid in all stands during the first 2 months (fig 2). The concentration then remained at a steady level for 6 months in VR, FG and EP while it
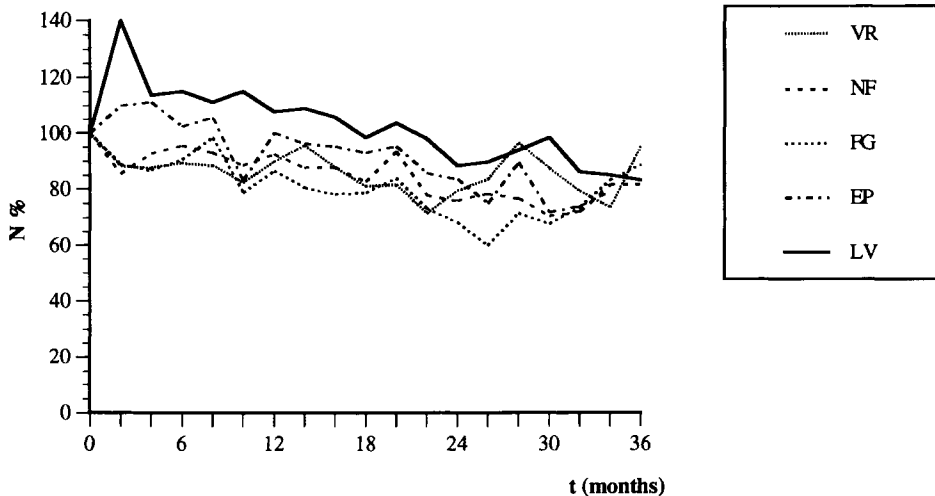

Fig 1. Mean nitrogen contents in decomposing leaves at the five studied sites over 3 years.

Table II. Chemical composition of fresh and decomposed leaf litter in the five stands and percentage of nutrients remaining after 1, 2 and 3 years of decomposition.

|	Year	Chemical composition (mg g^{-1})					Remaining nutrients (%)				
		N	P	K	Ca	Mg	N	P	K	Ca	Mg
NF	0	14.0 ± 0.9	0.7 ± 0.1	2.7 ± 0.2	6.3 ± 0.3	4.0 ± 0.3	100	100	100	100	100
	1	9.8 ± 0.6	0.5 ± 0.1	0.4 ± 0.1	6.3 ± 0.3	0.7 ± 0.1	70	71	15	91	33
	2	8.6 ± 0.5	0.4 ± 0.1	0.4 ± 0.1	5.3 ± 0.2	0.8 ± 0.1	57	57	15	77	38
	3	8.0 ± 0.5	0.4 ± 0.1	0.4 ± 0.1	4.4 ± 0.2	0.6 ± 0.1	61	57	15	64	28
EP	0	15.0 ± 0.8	0.9 ± 0.2	2.7 ± 0.3	5.7 ± 0.4	1.9 ± 0.2	100	100	100	100	100
	1	14.4 ± 0.7	0.9 ± 0.2	0.7 ± 0.1	6.0 ± 0.5	0.3 ± 0.1	96	100	28	105	47
	2	12.0 ± 0.7	0.5 ± 0.1	0.5 ± 0.1	5.4 ± 0.4	1.1 ± 0.2	80	55	18	95	58
	3	11.4 ± 0.4	0.5 ± 0.1	0.5 ± 0.1	4.8 ± 0.4	0.9 ± 0.1	76	55	18	84	47
VR	0	10.1 ± 0.6	0.7 ± 0.2	2.2 ± 0.3	5.2 ± 0.4	2.4 ± 0.3	100	100	100	100	100
	1	10.4 ± 0.5	0.7 ± 0.2	0.5 ± 0.1	6.0 ± 0.5	1.2 ± 0.2	103	100	23	115	50
	2	9.2 ± 0.5	0.5 ± 0.1	0.5 ± 0.1	5.1 ± 0.4	1.3 ± 0.2	91	71	23	98	54
	3	8.5 ± 0.5	0.5 ± 0.2	0.6 ± 0.1	4.2 ± 0.4	0.9 ± 0.1	84	71	27	81	37
FG	0	13.1 ± 0.7	1.2 ± 0.2	2.6 ± 0.2	8.3 ± 0.5	2.2 ± 0.3	100	100	100	100	100
	1	11.6 ± 0.7	0.8 ± 0.2	0.8 ± 0.1	9.1 ± 0.5	1.4 ± 0.2	88	67	31	110	64
	2	9.2 ± 0.6	0.5 ± 0.1	0.5 ± 0.1	7.0 ± 0.5	1.2 ± 0.2	70	42	23	84	54
	3	11.2 ± 0.7	0.5 ± 0.1	0.5 ± 0.1	6.2 ± 0.4	1.1 ± 0.2	85	42	23	75	50
LV	0	10.2 ± 0.5	0.5 ± 0.1	4.4 ± 0.4	18.3 ± 1.0	1.4 ± 0.2	100	100	100	100	100
	1	10.2 ± 0.5	0.4 ± 0.1	1.0 ± 0.2	15.2 ± 0.9	0.5 ± 0.2	100	88	23	83	39
	2	9.2 ± 0.4	0.4 ± 0.1	0.1 ± 0.1	16.1 ± 0.9	0.6 ± 0.1	90	91	3	88	43
	3	8.5 ± 0.4	0.4 ± 0.1	0.2 ± 0.1	11.0 ± 0.6	0.5 ± 0.1	83	91	5	60	35
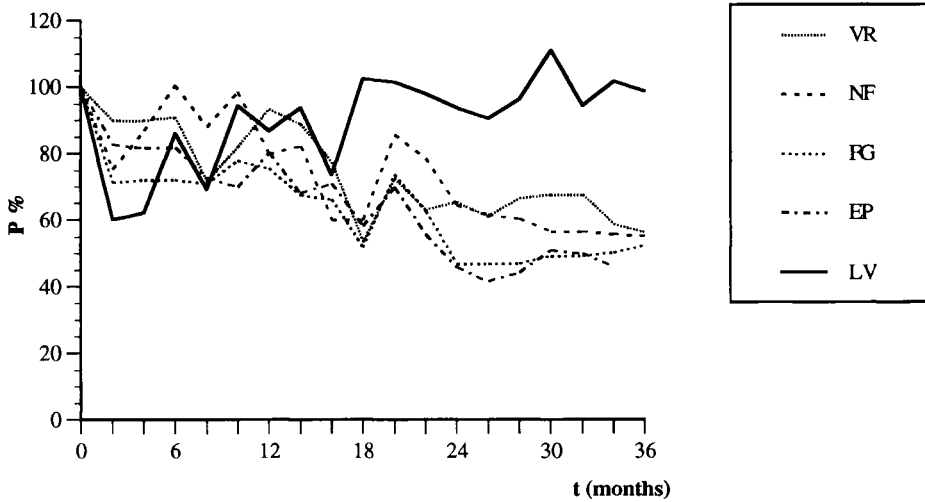
Fig 2. Mean phosphorus contents in decomposing leaves at the five studied sites over 3 years.
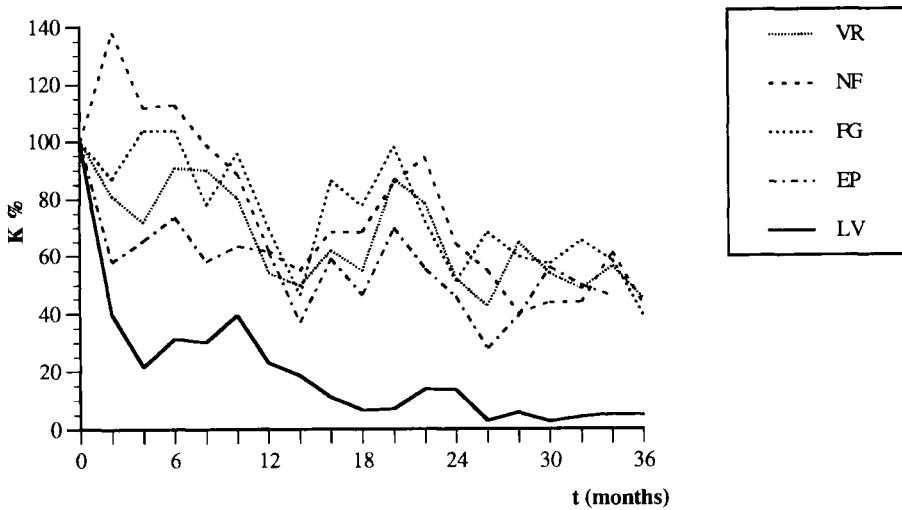

Fig 3. Mean potassium contents in decomposing leaves at the five studied sites over 3 years.

increased in NF and LV. Strong phosphorus release also occurred at 14 and 20 months.

At the end of the 3 years (table II) the greatest differences were noted between LV and FG. At LV, the phosphorus concentra-

tion remained practically constant: 91% of the initial amount was still present. Hernández et al (1995) reported a relative increase during decomposition, but only 55% of the initial P remained at the end of the experi-
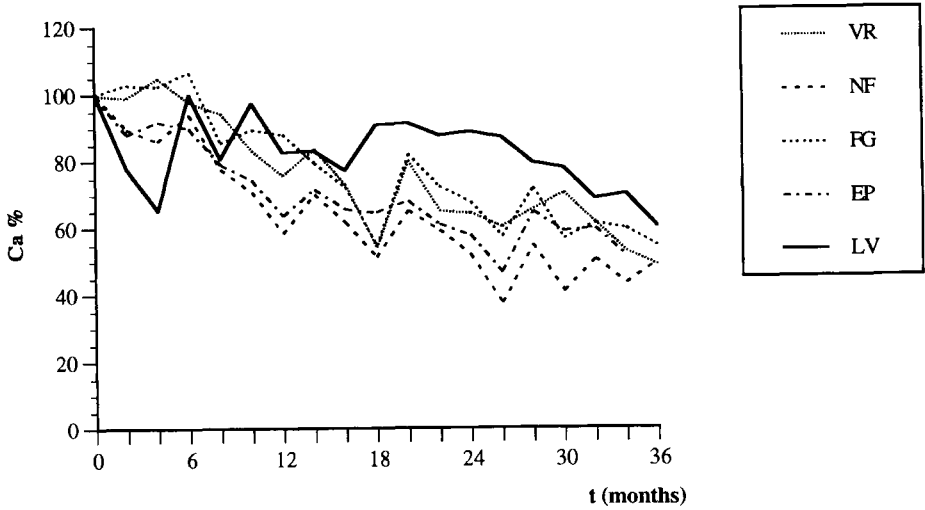
Fig 4. Mean calcium contents in decomposing leaves at the five studied sites over 3 years.
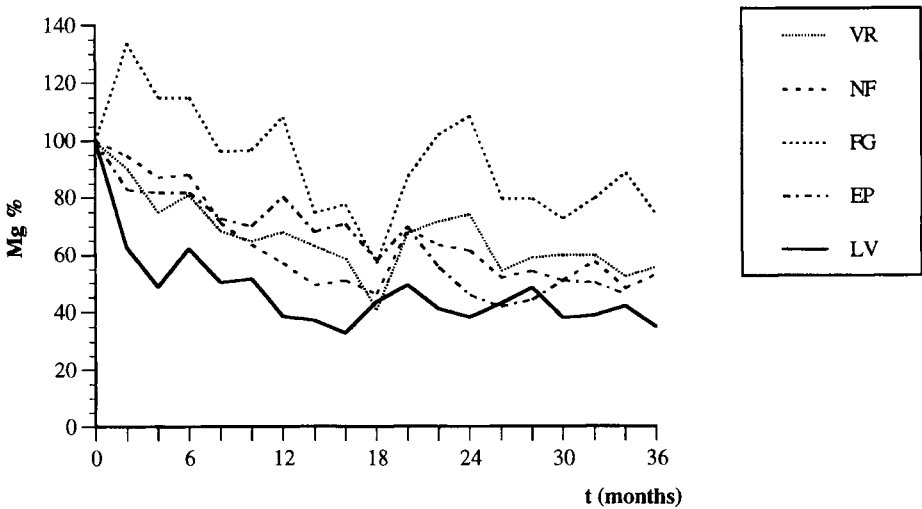

Fig 5. Mean magnesium contents in decomposing leaves at the five studied sites over 3 years.

ments. For Berg and Staaf (1980), the phosphorus release pattern was similar to that of N.

Initial Ca concentrations were ranked as follows:

$$LV \gg FG > NV \approx EP > VR$$

Calcium concentrations increased slightly over the first 6 months in the VR and FG stands (fig 4) and decreased in NV, EP and, more markedly, in the LV stand with respect

to the soil contents of this element. Similar results were obtained by Bockheim et al (1991).

As shown in table II, after a relative accumulation during the first years in litter bags, calcium showed lower rates of decrease as compared to the other nutrients. After 3 years of experiments 84% in EP, 81% in VR, 75% in FG, and 64 and 60% of the initial Ca in the NF and LV plots, respectively, still remained. This could result from the association of Ca with resistant compounds such as cellulose (Schlesinger, 1985), or Ca inclusion within cell walls.

During leaf decomposition the relative concentration of Mg decreased during the first season in the VR, NV, EP and LV stands, but increased in the FG plot (fig 5). Thereafter, Mg remained more or less stable in all stands, except in the FG plot midway through the experiments. Here, there was marked release of Mg followed by a sharp increase (fig 5). At FG, 50% of the initial Mg concentration remained after 3 years of decomposition; this was similar to EP (47%). Mg release was higher for VR and LV with 37 and 35% remaining, respectively, and for NF, where only 28% Mg remained at the end of 3 years of leaf decomposition in litter bags (table II). Berg and Staaf (1981) indicated that this is not a limiting bioelement, and Hernández et al (1995) confirmed that there is a parallel with the loss of dry matter and carbon. It should be stressed that the imbalance of Ca/Mg in NF (Martín et al, 1994) gives higher values of Mg and lower values of Mg in LV; this could explain such patterns.

Potassium was most readily lost from litter bags from all stands, except for NF which showed a substantial increase over the initial 3 months (fig 3). The greatest K loss was noted at the end of the experiments, especially at LV. The remaining amounts of K were very similar at EP, VR and FG: 18, 27 and 23%, respectively, and then at NF and LV: 15 and 5% (table II).

The concentration of K decreased for both species considered. All studies published report a similar loss of K (Bockheim et al, 1991; Hernández et al, 1995). Contrary to N and P, K is not bound as a structural component in plants and is highly water soluble (Gosz et al, 1973). In *Q rotundifolia* leaves, Hernández et al (1995) found losses of 30–40% with respect to the initial content during the first 4 months of decomposition. This is in accordance with the abundance and solubility of this bioelement. Later losses were smaller, 10% of the initial amount remaining at the end of the second year. Berg and Staaf (1980) attributed this second phase to the retention of K to fulfill the needs of decomposers.

Amounts of nutrients released from the yearly litter in the five sites studied

From the results of nutrient release in the litter bags it was possible to estimate nutrient fluxes at the different sites and for the two species in relation to yearly litterfall (table III). The yearly amounts of nutrients released were also determined (table IV).

Table III summarizes the amounts of nutrients (N, P, Ca, Mg and K) returned each year during the 3 years of decomposition and which are again available for uptake by the trees.

Similar nutrient release balances during litter decomposition were observed by Bockheim et al (1991) for *Q ellipsoidalis* and Hanchi (1994) for *Fagus sylvatica*.

The four *Q pyrenaica* stands can be subdivided into two groups, clearly indicating different nutrient release processes for decomposing litter: NV and FG is the first group, EP and VR is the other. As a result, no relation between the amount of annual litterfall and annual nutrient release was found. Additionally, these two groups were not affected by geology or climate.

Litter decomposition and nutrient release processes seem to be independent of the amount of available litter and climatic patterns.

Concerning the *Q lanuginosa* stand, the results were similar to those obtained for NV and FG.

Nutrient release after leaf litter exchange between *Q pyrenaica* and *Q lanuginosa*

Leaf litter samples from EP (*Q pyrenaica*) and LV (*Q lanuginosa*) were studied for 2 years in native stands after exchange between the two stands, using the litter bag

methodology (36 litter bags placed in three groups beginning in February 1991, three bags per plot every 2 months). Figures 6 to 9 indicate the dynamics of the nutrients released during 2 years of leaf litter decomposition in litter bags.

Similar nutrient release processes occurred in both situations: litter bags in native stands and after exchange between the two stands, with rapid release of K, followed by Mg and P. There was high Ca accumulation in the EP litter as compared to that of LV. For N, the results were very different between the two species and the two locations. Leaf litter from LV indicated only a slight N accumulation during the first months of decomposition. For EP, leaf litter

Table III. Litterfall and nutrient content remaining after 1, 2 and 3 years of decomposition (in kg ha^{-1}; DM: dry matter).

Plot	Years	DM	N	P	K	Ca	Mg
NF	0	2088 ± 224	29.2 ± 4	1.5 ± 0.3	5.6 ± 0.7	14.4 ± 2	4.4 ± 0.5
	1	1294 ± 108	20.4 ± 3	1.2 ± 0.3	0.9 ± 0.2	12.5 ± 2	1.5 ± 0.3
	2	1044 ± 97	16.6 ± 2	0.9 ± 0.2	0.9 ± 0.2	11.2 ± 2	1.7 ± 0.3
	3	814 ± 86	16.4 ± 2	0.7 ± 0.2	0.6 ± 0.2	9.7 ± 2	1.3 ± 0.2
EP	0	2346 ± 231	35.2 ± 4	2.1 ± 0.4	6.3 ± 0.8	13.4 ± 3	4.4 ± 0.6
	1	1595 ± 131	33.8 ± 4	2.1 ± 0.4	1.6 ± 0.4	14.0 ± 3	2.2 ± 0.4
	2	1314 ± 118	28.2 ± 3	1.2 ± 0.2	1.2 ± 0.3	12.7 ± 3	2.6 ± 0.4
	3	1079 ± 101	26.7 ± 3	1.2 ± 0.2	1.2 ± 0.3	11.3 ± 2	2.0 ± 0.4
VR	0	2208 ± 217	22.3 ± 3	1.5 ± 0.3	4.9 ± 0.7	11.5 ± 2	5.3 ± 0.6
	1	1501 ± 126	23.0 ± 3	1.6 ± 0.3	1.2 ± 0.3	13.2 ± 3	2.7 ± 0.4
	2	1281 ± 110	20.4 ± 5	1.1 ± 0.2	1.1 ± 0.2	11.3 ± 2	2.9 ± 0.5
	3	1038 ± 92	23.0 ± 4	0.9 ± 0.2	0.9 ± 0.2	8.0 ± 2	2.1 ± 0.4
FG	0	2829 ± 246	37.0 ± 5	3.4 ± 0.4	7.4 ± 0.9	23.5 ± 4	6.2 ± 0.7
	1	1811 ± 123	32.8 ± 4	2.3 ± 0.3	2.2 ± 0.3	25.9 ± 4	4.0 ± 0.6
	2	1320 ± 97	25.7 ± 3	1.4 ± 0.2	1.6 ± 0.2	19.8 ± 3	4.0 ± 0.6
	3	1301 ± 86	32.3 ± 4	1.6 ± 0.3	1.8 ± 0.3	15.3 ± 3	2.6 ± 0.4
LV	0	2466 ± 201	24.2 ± 3	1.0 ± 0.2	11.0 ± 2.0	43.2 ± 6	3.7 ± 0.5
	1	1615 ± 120	26.1 ± 3	0.9 ± 0.2	2.6 ± 2.0	35.7 ± 5	1.4 ± 0.3
	2	1198 ± 86	21.7 ± 2	0.9 ± 0.2	0.5 ± 0.1	37.5 ± 5	1.6 ± 0.3
	3	0858 ± 48	20.1 ± 3	0.0	0.5 ± 0.1	26.0 ± 4	1.3 ± 0.2

decomposition remained steady for both situations: litter in the native stand or litter transferred to LV.

The release of nutrients after 2 years of decomposition, expressed as a percentage of the initial amount available in the yearly litterfall, is indicated in table V.

For N, the nutrient release dynamics were confirmed after 2 years of decomposition. The same amount of N was released from the EP leaves, with no differences in relation to the localization of litter bags. For *Q lanuginosa* leaves, N release rates seemed to be higher in the native LV stand than after transfer to EP. Although ammonification and nitrification processes occurred at all sites, the biochemical composition of the leaves, probably varying between *Q pyrenaica* and *Q lanuginosa*, could interfere with the decomposition processes and be an explanation for the same mineralization for EP leaves irrespective of stand conditions (Martín et al, 1994).

P release was more important in the leaves of LV placed in EP, whereas no appreciable variation was observed. When the leaves from EP were placed in the two plots (EP, LV). The scarcity of this element may govern retention due to microbial activity.

The transfer of *Q pyrenaica* litter from EP to LV increased K and Ca release from the decomposing litter, whereas litter transfer from LV to EP increased the release of Ca and P from *Q lanuginosa* leaves. A possible explanation is that microorganisms may retain bioelements, which would also explain the reduced retention of Ca in the leaves on their own plot. Concerning K release, factors such as high soluble mineral and climatic patterns (eg, yearly precipitation distributions) were important. Rainfall events were more frequent at LV than at EP.

The stronger release of Mg always occurred in the native stand litter, even though the amount of leaf litter decomposition was higher after litter exchange between the two stands (Martín et al, 1994). Mg may be restricted in LV because it is a limiting factor for excess of Ca.

CONCLUSIONS

The mean amount of nutrients in the decomposing leaves decreased over the 36-month period. The four *Q pyrenaica* stands were classified into two groups involving different nutrient release processes, with no relationship to yearly litterfall. For the *Q lanuginosa* stand, the results obtained were similar to those for one of the *Q pyrenaica* groups. Similar nutrient release processes occurred in the litter bags collected from native stands and after exchanges between the two

Table IV. Amounts of the five nutrients returning to the soil each year.

Plots	After 1 year (kg ha⁻¹)	After 2 years (kg ha⁻¹)	After 3 years (kg ha⁻¹)
NF	18.6	5.4	2.6
FG	12.3	12.3	8.1
EP	8.3	7.6	3.5
VR	6.3	2.6	4.5
LV	18.3	4.6	14.3

Table V. Release of nutrients after 2 years of decomposition.

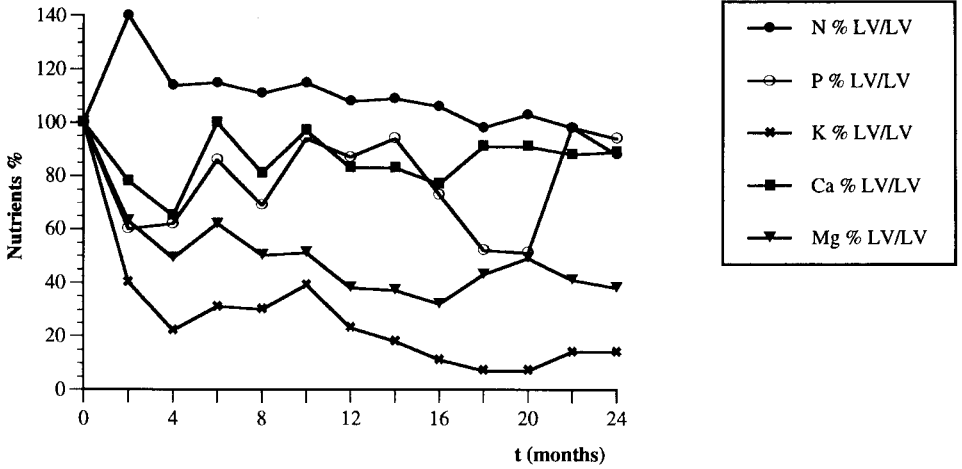| Leaves from:	La Vialle (%)		El Payo (%)	
Plots at:	LV	EP	EP	LV
N	11	0	17	17
P	9	17	52	48
Ca	13	27	0	21
Mg	57	43	41	28
K	97	77	81	95

Fig 6. Nutrient release (%) over 2 years from decomposing leaf litter. Litter from La Vialle at La Vialle (in % of initial contents).
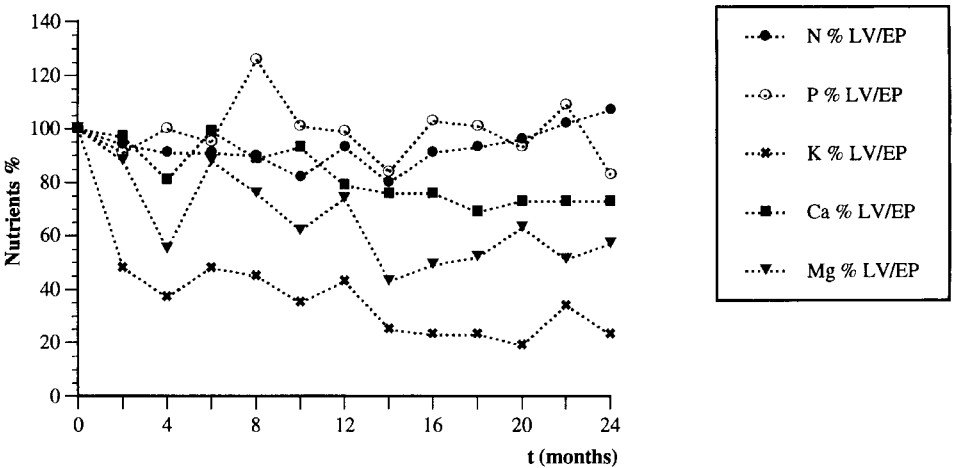

Fig 7. Nutrient release (%) over 2 years from decomposing leaf litter. Litter from La Vialle at El Payo (in % of initial contents).

species, with rapid release of K, followed by Mg and P. A stronger Ca accumulation was noted for the *Q pyrenaica* litter as compared to that of *Q lanuginosa*. For N, the results differed considerably between the two species and two locations.
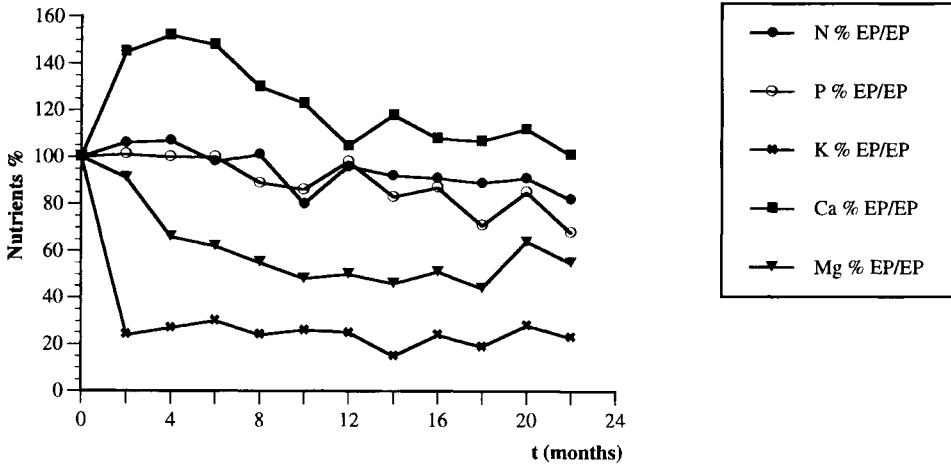
Fig 8. Nutrient release (%) over 2 years from decomposing leaf litter. Litter from El Payo at El Payo (in % of initial contents).
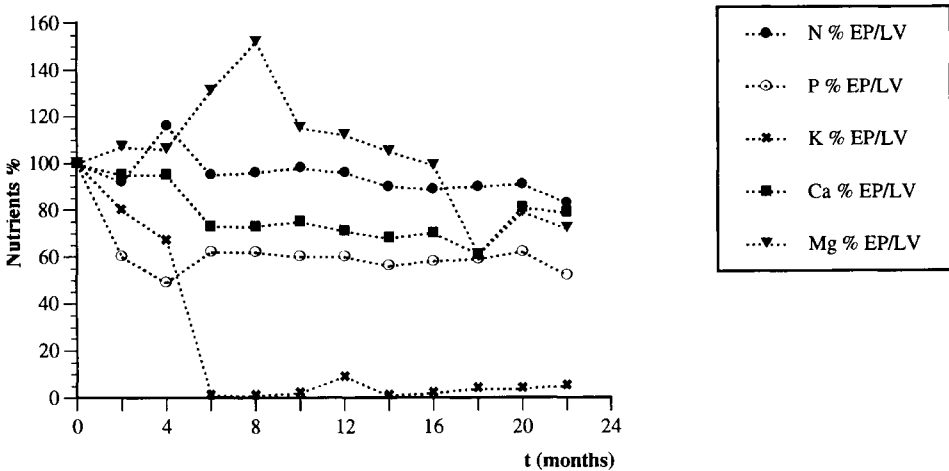

Fig 9. Nutrient release (%) over 2 years from decomposing leaf litter. Litter from El Payo at La Vialle (in % of initial contents).

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