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RESEARCH ARTICLE

Dynamics of macronutrients during the first stages of litter decomposition from forest species in a temperate area (Galicia, NW Spain)

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Abstract The decomposition and dynamics of nutrient elements was studied for leaves and twigs from *Quercus robur*, *Pinus radiata* and *Eucalyptus nitens* in soils developed from granodiorite, slate and limestone in Galicia, NW Spain. Two 1-ha plots were selected for each material-vegetation combination, making a total of 18 plots. Litter decomposition and nutrient dynamics during the first six months were investigated using litterbags. Mass loss was higher for leaves than twigs and not significantly different for different tree species. Mass loss correlated significantly with carbon loss ($r = 0.96$ for leaves, $r = 0.90$ for twigs). As a general trend, nutrient release from leaves and twigs was greater for the broadleaved species (eucalyptus and oak). K and S were rapidly released from all litters, while Ca and Mg showed the highest tendency to be immobilised. N and P behave similarly, with a final balance of net release. Soil parent material did not significantly influence decomposition or nutrient dynamics.

Keywords Litterbags · Decomposition · Leaves · Twigs · Forest soil · *Quercus robur* · *Pinus radiata* · *Eucalyptus nitens*

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Introduction

Litter decomposition determines the nutrient cycling, one of the most important processes in forest soils (Spurm and Barnes 1980). More than half of the nutrients taken up by plants return to the soil in several ways (Cole 1986), among which decay of litter and organic debris plays a major role. Nutrient release from litter may occur through leaching or mineralisation (Berg and Staaf 1981). The rate of nutrient release depends on factors such as physical and chemical properties of litter, moisture and temperature conditions, vegetation cover and soil fauna activity (Seastadt 1984; Moore 1986; Moore et al. 1999; Berg et al. 2000; Trofymov et al. 2002; Thimonier et al. 2001; Heim and Frey 2004).

Tree species is a major factor in determining biological and chemical fertility of soils. Different species have different nutrient release patterns, which are related to litter quality and seasonal environmental factors (Khietwtam and Ramakrishnan 1993). As for *Pinus radiata* needles, several studies carried out in temperate and cold regions show that decomposition depends on their chemical composition (Taylor et al. 1989; Girisa et al. 2003). During the first stages, decomposition is controlled by nutrient contents, and later by lignin content, especially in lignin-rich debris.

Most studies indicate that leaf decomposition is faster for broadleaved than for coniferous species (Kavvadias et al. 2001), especially in the first stages, because of the lower nutrient content in coniferous needles. As for eucalyptus, different studies lead to contradictory results: according to some authors, eucalyptus litter decomposition is slow (Adams and Attiwill 1986; Louzada et al. 1997), while others attribute a non-recalcitrant character to their litter (Briones and Ineson 1996).

Soil fauna and microorganisms act together during litter decay, increasing nutrient cycling and the ability of the soil to sustain plant growth, in natural as well as cropped systems (Levelle et al. 1993; Thirukkumaran et al. 2002).

Some authors point out that homogeneous agro-ecosystems may negatively affect litter decomposition compared to native vegetation (Louzada et al. 1997). These negative effects are related to decrease of litter heterogeneity and nutritional quality, forest microclimate and effects on activity and abundance of soil fauna. Despite the well-known influence of tree species on the decomposition of organic matter in soils, few studies have compared the mineralisation of litter from native and introduced species under the same environmental conditions, particularly in the temperate climate in southern Europe.

In Galicia, NW Spain, the main climax formation is a mixed deciduous forest in which *Quercus robur* is the dominant species. *Eucalyptus* and *Pinus* have been used as species for afforestation, especially during the 20th century. In particular *Pinus radiata* has spread remarkably in Galicia during recent decades, while *Eucalyptus nitens* was introduced some 20 years ago.

Natural soils in this region are acid and commonly poor in nutrients. For this reason, the input of nutrients from litter decomposition is crucial to maintain the productivity of Galician forest soils. The scant studies carried out in Spain comparing native and introduced tree species are somewhat contradictory. Some authors (Bará 1984) report a higher contribution of some macronutrients (K, Ca, Mg) to soil from eucalyptus litter compared to deciduous species or a faster turnover of eucalyptus leaves. In contrast, others (Lozano and Velasco 1981) report a higher nutrient deficit under eucalyptus vegetation compared to native species. Therefore, a further study of the mineralisation of litter from native and introduced tree species would help to clarify some of these contradictory findings, particularly in the early stages of this process, since, according to several authors (Sundarapandian and Swamy 1999; Thirukkumaran et al. 2000), nutrient release takes place mainly during the early stages of litter decomposition, when the tree species plays an essential role (Adams and Atiwill 1986; Zimmer 2002).

The objective of the present work is to study the first stages of decomposition and nutrient release from litter of various forest tree species, both native (*Q. robur*) and introduced (*Pinus radiata* and *Eucaliptus nitens*) in a temperate region. In addition, the possible influence of soil parent material on the decomposition process will be studied.

Materials and methods

The study sites were located in the province of Lugo (Galicia, Spain), between 43°00′ and 43°15′ N and 7°16′ and 7°50′ E, at an altitude between 440 and 640 m above sea level.

The area can be considered to have a cool Mediterranean climate, according to Papadakis (1966), with mild temperature and humid Mediterranean water regimes. The monthly mean temperatures range between 5.5°C and 18.6°C, with an average of 12°C. Annual rainfall is over 1,000 mm, with a minimum in summer. During the period in which this study was carried out (December 1997–June 1998), December was on average the coldest (7.5°C) and rainiest (179 mm) month, whereas June was the warmest (16°C) and driest (18 mm).

The study sites were chosen to include some representative forest species (*Quercus robur* L., *Pinus radiata* D. Don and *Eucalyptus nitens* Maiden) and soils derived from various parent materials (granodiorite, slate and limestone). Two 1-ha plots were selected for each species and parent material, amounting to a total of 18 study plots.

The selected soils developed from limestone were classified as Typic Hapludults and those from granodiorite or slate areas as Dystrudepts or Udorthents (Soil Survey Staff 1998). The soil moisture regime is udic and the soil temperature regime mesic (Soil Survey Staff 1998). The altitude was 500 m for the limestone plots, 440 m for the granodiorite plots, and 640 m for the slate plots. The slope of the various sites was always less than 15%.

The age of the stands ranged between 17 and 25 years for pine, 7 and 15 years for eucalyptus and older than 35 years in the case of the oak plantation. The *Pinus* and *Eucalyptus* sites were previously heath lands. In all cases, the understorey vegetation was formed of *Rubus* sp., *Erica arborea*, *Ulex europaeus*, *Cytisus scoparius* and *Pteridium aquilinum*.

Old leaves and twigs from pine (*Pinus radiata*), eucalyptus (*Eucalyptus nitens*) and oak (*Quercus robur*), were collected in autumn 1997 directly from the lower third of trees and oven-dried at 60°C for 48 h in order to prepare litterbags used to assess decomposition of organic debris and macronutrient dynamics (Fogel and Cromack 1977). Twigs were less than 1 cm in diameter and leaves had an average length of 12 cm for pine and eucalyptus and 8 cm for oak. This fresh litter was placed in polypropylene litterbags, each containing 6 g of leaves or 10 g of twigs.

At the beginning of the study (December 1997), eight subsamples were collected at a depth of 0–20 cm from each plot to make a composite sample. Some general soil chemical parameters for different tree species and parent materials are presented in Table 1. All soils are considerably developed, acid, rich in organic matter, and have low effective cation exchange capacity and high aluminium saturation.

The previously prepared litterbags, 21×13 cm^2 with 2-mm mesh, were placed in the organic layer of soils sustaining the same tree species in December 1997. Thereafter, three litterbags containing leaves were removed monthly from each experimental plot from January to June 1998, making a total of 324 litterbags. Similarly three litterbags containing twigs were removed in March and in June 1998, making a total of 162 litterbags. The material from the litterbags was stripped of adhering mineral particles, oven-dried at 105°C to a constant weight, weighed and finely ground for analysis. C, N and S were determined by dry combustion in a LECO-2000 autoanalyser. Sample aliquots were acid-digested according to the Kjeldahl method and the digests analysed for Ca and Mg by atomic absorption spectrometry (AAS), K by flame atomic emission spectrometry (AES) and P by visible spectrophotometry with ammonium molybdate. The final amounts of each element in litterbags were calculated by multiplying the final weight by the final concentration.

Analysis of variance (ANOVA) was performed using the statistical programme SPSS 9.0 for Windows and consisted of a two-way ANOVA to test if tree species and parent material exerted main effects on litter decomposition. The Tukey test was used to compare groups.

Results and discussion

Neither the mass loss nor the nutrient release were significantly affected by the parent material, whichever tree species was considered. However, some reports indicate differences in litter decomposition between soils differing in pH or chemical fertility (Howard and Howard 1980; Hobbie and Vitousek 2000). In this study, the lack of influence may result from the fact that all the studied soils had very similar chemical properties (Table 1), being comparably acid and depleted of nutrients, in spite of being developed from different parent materials. Moreover the composition of litter from each species was similar for all soils. Accordingly, the data will be discussed as a function of the species, regardless of the soil parent material.

Mass loss

The mass remaining after six months in bags containing oak, pine and eucalyptus leaves or twigs is shown in Fig. 1. The average mass loss undergone by leaves after this period was 40% (eucalyptus), 35% (oak) and 31% (pine), but the analysis of variance indicated that the differences among species were not significant ($p < 0.05$). This lack of significance could be attributable to the large variability of the experimental data or to the shortness of the study period.

Louzada et al. (1997) in Brazil reported the same mass loss (40%) for eucalyptus leaves in a similar period, while Jones et al. (1999) measured mass losses of between 44% and 52% in NW Spain and between 16% and 40% in central Portugal. Tavakol and Proctor (1994) in Scotland and Kim et al. (1996)

Table 1 General soil (0–20 cm depth) properties averaged for each tree species and for each parent material. C, N and S as percentage; effective cation exchange capacity (ECEC), in cmole (+) kg^{-1}

Vegetation	Pine		Eucalyptus		Oak	
	Average	SD	Average	SD	Average	SD
pH H_2O	4.8^{a}	0.15	5.0^{b}	0.17	4.8^{ab}	0.23
pH KCl	4.1^{a}	0.15	4.0^{b}	0.17	3.9^{b}	0.10
C	4.2^{a}	1.63	4.0^{a}	1.09	3.6^{a}	1.53
N	0.24^{a}	0.11	0.23^{a}	0.08	0.26^{a}	0.12
S	0.05^{a}	0.01	0.04^{a}	0.01	0.03^{a}	0.01
C/N	17^{a}	2.70	17^{a}	1.45	16^{a}	2.60
ECEC	9.4^{a}	1.42	7.6^{a}	3.81	5.8^{a}	2.55
%Al	77^{a}	14.3	55^{b}	12.5	70^{a}	21.7
Material	**Limestone**		**Slate**		**Granodiorite**	
	Average	SD	Average	SD	Average	SD
pH H_2O	4.8^{a}	0.16	4.9^{a}	0.15	4.9^{a}	0.24
pH KCl	3.9^{ab}	0.17	3.9^{a}	0.15	4.1^{b}	0.10
C	3.1^{a}	1.08	4.6^{a}	1.64	3.5^{a}	1.53
N	0.15^{a}	0.07	0.31^{a}	0.12	0.22^{a}	0.12
S	0.04^{a}	0.01	0.05^{a}	0.01	0.03^{a}	0.01
C/N	17^{a}	1.45	16^{a}	2.70	18^{a}	2.58
ECEC	9.1^{a}	1.05	8.7^{a}	0.43	7.1^{a}	0.73
%Al	70^{a}	3.47	77^{a}	4.31	59^{a}	6.26

Different letters (a,b) indicate significant differences ($p < 0.05$). ECEC: effective cation-exchange capacity; %Al: Al saturation. SD: standard deviation

in Michigan reported mass losses between 30% and 35% for leaves of the genus Quercus in a similar period. Ouro et al. (2001) reported a mass loss of 31% for leaves of *Pinus radiata* in Galicia over a six-month period. According to Briones and Ineson (1996), eucalyptus debris decomposes rapidly. On the contrary, Adams and Atiwill (1986), from studies of eucalyptus forests in Australia over a range of climates, assert that litter decomposition is strongly influenced by climatic conditions and litter quality, being very slow in subalpine forests. Guo and Sims (2002) reported different decomposition rates for various eucalyptus species (*E. globulus*, *E. botryoides* and *E. ovata*) in a climate similar to that of Galicia; according to these authors, the mass losses from eucalyptus leaves in a period similar to that in the present study were: *E. globulus* (52.7%) > *E. botryoides* (32.8%) > *E. ovata* (24.3%).

In the case of twigs, the mass loss was 22% for oak and eucalyptus and 27% for pine (Fig. 1), though the difference among species was not significant ($p < 0.05$).

Some authors (Blair 1988a) suggest that during the first six months of decomposition the mass loss is related to the content of soluble compounds, whereas the lignin concentration is more important in the last stages. Other authors (Boerner 1984; Taylor et al. 1989; Kim et al. 1996; Heal et al. 1997; Limpens and Berendse 2003) state that the nitrogen concentration and the C/N ratio are the best parameters to predict the decomposition rate of plant residues. In the present study, no significant differences between species were found for mass loss, although initial N concentration and C/N ratio were significantly ($p < 0.05$) different (Tables 2 and 3). This agrees with the results of Ribeiro et al. (2002), who did not

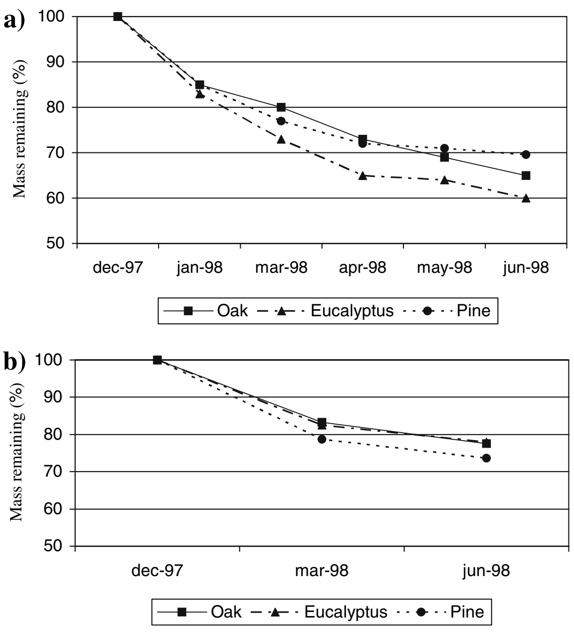

Fig. 1 Percentage mass remaining during six months of decomposition of oak (O), eucalyptus (E) and pine (P) leaves (**a**) and twigs (**b**)

find a correlation between the rate of decomposition and the concentration of N in eucalyptus leaves in Portugal.

No significant differences attributable to species were found for the decomposition rates of twigs, despite the significant differences in the initial N concentration and C/N ratio (Tables 2 and 4). According to Taylor et al. (1989) these parameters are not good predictors of decomposition rates in the case of woody material (twigs, stems, roots). Nevertheless, significantly lower decomposition rates were measured for twigs as compared to leaves, according to the higher C/N ratios of twigs.

Decomposition of both leaves and twigs of the three species studied showed an initial rapid phase, followed by a slower phase (Fig. 1). The slow decomposition phase corresponds to a period of nitrogen immobilisation, which is evident in leaves (Fig. 2).

Carbon mineralisation

The initial carbon concentration in the decomposing leaves was very similar in pine and eucalyptus

Table 2 Average initial concentrations of various elements (i) and concentration decrease as percent of initial value at the end (f) of the six-month period, in leaves and twigs from oak, eucalyptus and pine (negative values of Δ parameters indicate concentration increase)

Litter type	C_i, mg g^{-1}	ΔC, %	N_i, mg g^{-1}	ΔN, %	P_i, mg g^{-1}	ΔP, %	S_i, mg g^{-1}	ΔS, %	K_i, mg g^{-1}	ΔK, %	Ca_i, mg g^{-1}	ΔCa, %	Mg_i, mg g^{-1}	ΔMg, %
Leaves														
O	443^a	4.3^a	21.7^c	3.8^b	3.5^c	28.6^c	1.7^c	58.8^b	10.0^c	76.0^c	4.5^c	−80^b	1.0^a	−60.0^a
E	500^b	17^c	18.3^b	10.3^c	2.6^b	7.7^b	1.3^b	53.8^a	6.2^a	38.7^a	2.3^b	−152^a	1.8^b	−27.7^b
P	502^c	8.7^b	15.2^a	−17.1^a	2.0^a	−30.0^a	1.1^a	54.5^a	8.2^b	62.2^b	1.6^a	−12.5^c	1.2^a	−16.6^c
Twigs														
O	450^b	1.5^b	12.0^c	3.3^c	2.6^c	−19.2^b	0.5^c	20^a	5.5^b	47.0^b	3.2^b	−68.7^b	0.9^a	−11.0^c
E	421^a	−4.5^a	4.2^a	−9.5^b	1.5^a	40.0^c	0.2^a	50^c	4.7^a	32.0^a	3.2^b	−109^a	1.4^b	−28.5^a
P	480^c	3.7^c	6.2^b	−24.1^a	1.7^b	−152^a	0.4^b	25^b	4.5^a	37.7^a	1.5^a	6.6^c	1.0^a	−20.0^b

Different letters (a,b,c) indicate significant differences ($p < 0.05$) among species (O = oak; E = eucalyptus; P = pine)

Table 3 Variation of C/N, C/P and C/S ratio in leaves and twigs during the study period

Elemental ratio	Dec 97	Jan 98	Mar 98	Apr 98	May 98	Jun 98
Leaves						
C/N						
Oak	22^{a}	22^{a}	20^{a}	24^{a}	21^{a}	20^{a}
Eucalyptus	27^{b}	26^{b}	25^{b}	27^{b}	26^{b}	24^{b}
Pine	32^{c}	29^{c}	28^{c}	32^{c}	27^{b}	25^{b}
C/P						
Oak	127^{a}	152^{a}	190^{a}	150^{a}	156^{a}	170^{a}
Eucalyptus	192^{b}	220^{c}	240^{c}	180^{b}	193^{b}	173^{a}
Pine	251^{c}	200^{b}	220^{b}	170^{b}	193^{b}	176^{a}
C/S						
Oak	261^{a}	320^{a}	346^{a}	420^{a}	406^{a}	606^{a}
Eucalyptus	385^{b}	368^{b}	430^{b}	426^{a}	500^{b}	692^{b}
Pine	456^{c}	380^{c}	420^{b}	430^{a}	496^{b}	916^{c}
Twigs						
C/N						
Oak	39^{a}		35^{a}			39^{a}
Eucalyptus	99^{c}		91^{c}			91^{c}
Pine	78^{b}		57^{b}			60^{b}
C/P						
Oak	173^{a}		243^{a}			143^{a}
Eucalyptus	281^{b}		366^{b}			489^{b}
Pine	282^{b}		240^{a}			107^{a}
C/S						
Oak	900^{a}		833^{a}			$1{,}108^{a}$
Eucalyptus	$2{,}105^{c}$		$1{,}766^{b}$			$3{,}228^{c}$
Pine	$1{,}200^{b}$		846^{a}			$1{,}540^{b}$

Different letters (a,b,c) indicate significant differences ($p < 0.05$) among species

(Table 2) and somewhat lower in oak. As for the twigs, the highest carbon concentration was found in pine (Table 2).

The carbon loss from decomposing material followed a pattern very similar to that of mass loss. The carbon loss after six months correlated significantly ($p < 0.01$) to the mass loss ($r = 0.96$ for leaves and $r = 0.90$ for twigs). The fact that C is a major component of plant material results in parallel losses of carbon and mass during decomposition (Berg and Staaf 1981). After six months, the carbon mineralisation from eucalyptus leaves (49%) was significantly ($p < 0.01$) higher than from oak (39%) or pine (37%) leaves (Table 4). The pine twigs underwent significantly ($p < 0.01$) higher carbon mineralisation (32%) than the oak (23%) or eucalyptus (18%) twigs. Albers et al. (2004) reported higher carbon mineralisation in spruce than in beech leaves, contradicting the general view of a greater resistance of coniferous litter to decomposition (Millar 1974; Kavvadias et al. 2001).

Nutrient dynamics

Nitrogen, phosphorus and sulphur

The initial N, P and S concentrations were highest in oak leaves and twigs (Table 2). Significant differences ($p < 0.01$) were found for these elements among tree species in both leaves and twigs, the sequences being $O^{a} > E^{b} > P^{c}$ for leaves and $O^{a} > P^{b} > E^{c}$ for twigs (O = oak, E = eucalyptus, P = pine; different superscripts indicate significant differences, $p < 0.01$). After six months, N, P and S

Table 4 Mass loss and losses of various elements in leaves and twigs at the end of the six-month study period, as a percentage of initial contents (negative values for Ca or P indicate mass increases for these element)

%	Oak Average (SD)	Eucalyptus Average (SD)	Pine Average (SD)
Leaves			
Mass	36^{a} (3.5)	40^{a} (1.1)	33^{a} (3.1)
C	39^{a} (3.6)	49^{b} (1.2)	37^{a} (3.0)
N	37^{a} (2.0)	44^{a} (6.7)	19^{b} (1.6)
P	53^{a} (4.1)	42^{b} (5.4)	13^{c} (3.6)
S	66^{a} (0.5)	74^{b} (3.2)	69^{ab} (7.5)
K	79^{a} (0.5)	57^{b} (16.0)	74^{a} (5.7)
Ca	-24^{b} (10.8)	-52^{a} (15.0)	23^{c} (3.0)
Mg	20^{a} (0.5)	17^{a} (4.9)	21^{a} (4.8)
Twigs			
Mass	22^{a} (3.5)	22^{a} (2.8)	26^{a} (4.7)
C	23^{b} (4.0)	18^{a} (3.0)	32^{c} (5.0)
N	26^{a} (6.0)	16^{a} (4.6)	12^{a} (2.6)
P	8^{a} (7.0)	51^{a} (11.0)	-77^{b} (12.6)
S	39^{a} (6.6)	49^{a} (4.5)	46^{a} (0.5)
K	48^{a} (11.0)	46^{a} (7.7)	56^{a} (5.8)
Ca	-30^{b} (10.0)	-92^{a} (7.0)	34^{c} (4.0)
Mg	8^{ab} (4.0)	4^{a} (2.0)	16^{b} (4.0)

SD: standard deviation. Different letters (a,b,c) indicate significant differences ($p < 0.05$) among species

concentrations had decreased in eucalyptus and oak leaves, while N and P concentrations had increased in pine leaves and twigs (Table 2).

The patterns of N, P and S flux during the decomposition depend on the tree species and the type of debris (leaves or twigs) (Fig. 2). As a general trend, the highest N, P and S losses were observed in oak and eucalyptus leaves, which show very similar patterns of release. At the end of the study period, the S content in oak and eucalyptus leaves had decreased by 70% and N and P by 35–50% (Table 4). By this time the pine needles had lost 70% of S and nearly 15% of N and P (Table 4). Twigs from the three species showed a similar behaviour for N and S release, losing 12–26% N and 39–46% S. Eucalyptus twigs underwent a net P release, close to 50% of the initial content, whereas a net immobilisation of P was observed in pine twigs and almost no variation in oak (Table 4).

Two different phases can be distinguished in the N release from leaves: an initial phase characterised by nitrogen loss, lasting four months in oak and pine and five months in eucalyptus, and a subsequent phase of nitrogen immobilisation, which was more pronounced in pine needles. For a similar period of study, Berg and Staaf (1981, 1987) and Albers et al. (2004) also reported a phase of decomposition and one of N accumulation in leaves of coniferous and deciduous trees. According to Blair (1988a) the nitrogen lost during the initial phase originates from the most labile nitrogen compounds. Several authors reported increases of nitrogen concentration during litter decomposition (Melillo et al. 1982; Berg 1988; Kim et al. 1996; Wedderburn and Carter 1999; Herráez and Fernández Marcos 2000). These increases were attributed to microbial or nonmicrobial N immobilisation, deposition of atmospheric N or the activity of fungi, which translocate N from the environment to the decomposing litter (Berg and Soderston 1979). Berg and Soderstrom (1979) and Berg and Staaf (1987) attribute the nitrogen accumulation in pine needles either to the presence of fungal hyphae, which may have translocated N from surrounding environment, or to lignin products, which serve as a N sink. Although lignin was not analysed in litter in the present study, it can be expect

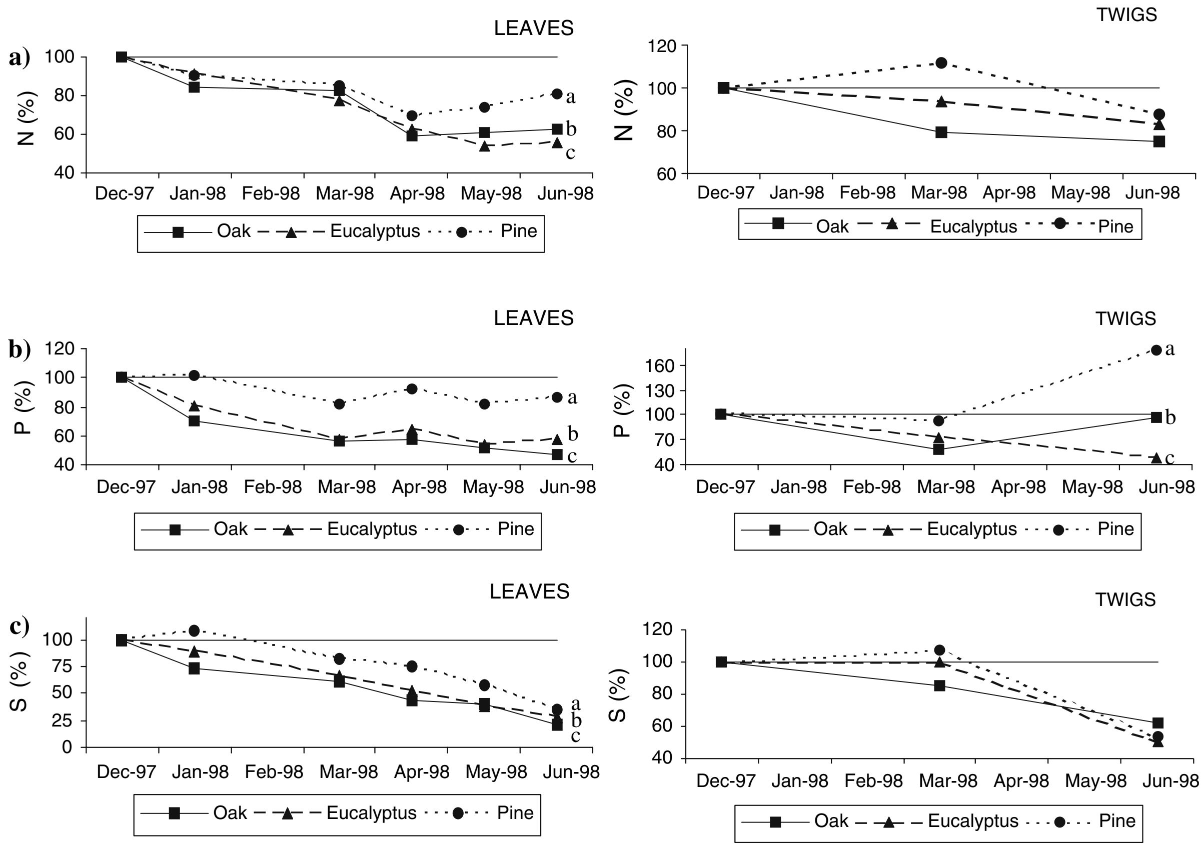

Fig. 2 Percentage of initial nitrogen (**a**), phosphorus (**b**) and sulphur (**c**) remaining during six months of decomposition of leaves and twigs from various tree species. Different letters indicate significant differences between species ($p < 0.05$) at the end of the study period

that the pine needles would have higher lignin concentrations than oak and eucalyptus leaves and therefore act as sink for N.

In the case of twigs, a net nitrogen mineralisation was observed during the study period in oak and eucalyptus stands. On the contrary, the pine twigs showed a net nitrogen immobilisation during the first phase (December 97–March 98) and a net N mineralisation at the end (March 98–June 98) (Fig. 2).

The C/N ratio (Table 3) varied slightly with time in most litter types, showing a decreasing trend only in pine twigs. Net nitrogen release or immobilisation can be predicted from the organic material's C/N ratio or N concentration. If the ratio C/N is lower than 20 or the N concentration is higher than 2.5%, N will be released and the material will decompose rapidly (Wedderburn and Carter 1999). In contrast, if the C/N ratio is much greater than 20 or the N concentration is below 0.7%, N is likely to be immobilised until decomposition and respiration lower the C/N ratio (Berg and Staaf 1981; Wedderburn and Carter 1999). In the present study, N concentrations were always lower than 2.5% (Table 2) and the C/N ratios were higher than 20 (Table 3), but not far from these values in the case of leaves. Other studies indicate that the transition between N immobilisation and mineralisation takes place at C/N ratios between 24 and 30 (Bargali et al. 1993), which are close to those in leaves in the present study. The N and C/N values, close to thresholds, are in good agreement with the inconsistent trend of variation of leaf C/N ratios with time (Table 3). The N concentrations were below 0.7% and the C/N ratios were much greater than 20 in eucalyptus and pine twigs. In spite of these values, net N mineralisation was observed in eucalyptus twigs (Fig. 2).

As regards P mineralisation, after an initial phase of P release until March, a subsequent phase of P immobilisation (for twigs) or minor variations (for leaves) took place from March to June. The eucalyptus twigs behaved differently from this general pattern, showing a net release during the whole period studied. The maximum phosphorus content in the decomposing material exceeded the initial amount in the case of pine twigs, attaining 180% of the initial value at the end of the experiment (Fig. 2).

Various authors (Blair 1998a; Bakker et al. 2001) point to the initial C/P ratio as a parameter determining P release or immobilisation, although different threshold values are reported for this parameter. Brinson (1977) specified a value of 200, above which P is immobilised, and Baker et al. (2001) place the limit at 358 for mixed-species litter. In the present study, the relatively low values of leaf C/P ratios (Table 3) compared to the above threshold values led to a net P mineralisation (Fig. 2). As for twigs, the P release or immobilisation does not seem to be related to the C/P value: pine and eucalyptus twigs, having similar initial C/P ratios (Table 3), showed opposite behaviours with respect to P mineralisation (Fig. 2). The N/P ratio is also lower than 15 in leaves as in twigs of all species (Table 5); this value is considered by some authors as a threshold for P mineralisation (Lockaby and Walbridge 1998).

In the case of S, a continuous S release was observed in oak leaves and twigs as well as in eucalyptus leaves. The pine needles and twigs and the eucalyptus twigs showed an initial phase of sulphur immobilisation or minor variations, followed by a period of sulphur release (Fig. 2). The maximum amount of sulphur in the decomposing material, relative to the initial amount, was 110% in pine twigs and 105% in eucalyptus twigs. Blair (1988a) reported S immobilisation in litter from *Acer rubrum* and *Quercus prinus*, and net S mineralisation in *Cornus florida* litter, during a 732-day period. The different behaviour is attributed by the author to the different initial C/S ratios, specifying a threshold value of 300, below which S is mineralised from decomposing leaves. In the present study, net sulphur mineralisation was observed, throughout the whole period under study, from oak leaves, with a low C/S ratio (Table 3), but also from oak twigs, with a C/S ratio of 900 (Table 3). Eucalyptus leaves, with a C/S ratio of 385, also underwent net sulphur mineralisation until the end of the study. In contrast, an initial period of sulphur immobilisation was observed in pine leaves and both eucalyptus and pine twigs, with high C/S ratios. It appears that litter composition is not the only factor determining its decomposition behaviour, and the environment plays a major role. The environmental conditions in oak stands seem to favour N, P and S mineralisation. Similarly, Albers et al. (2004), comparing litter decay in beech, spruce and mixed forests, report faster decomposition in beech than in spruce stands.

In the whole period studied, the C/S ratios tended to increase in both leaves and twigs (Table 3), indicating that S mineralisation is higher than C mineralisation. The increase of the N/S ratio at the end of the study period (Table 5) indicates net S mineralisation in leaves and twigs from all species. In contrast, Ribeiro et al. (2002) report S immobilisation in eucalyptus leaves, in Portugal, over a four-month period.

Table 5 Average C/element ratios at the beginning (i) and at the end (f) of the six-month period studied in leaves and twigs from oak, eucalyptus and pine

Litter type	C/K_i	C/K_f	C/Ca_i	C/Ca_f	C/Mg_i	C/Mg_f	N/P_i	N/P_f	N/S_i	N/S_f
Leaves										
Oak	44^a	177^a	98^a	52^a	443^a	265^b	6.20^a	8.36^b	12.76^a	29.86^a
Eucalyptus	81^c	109^c	217^b	71^a	278^b	180^a	7.04^{ab}	6.83^a	14.08^c	27.33^a
Pine	61^b	148^b	314^c	254^b	418^a	327^c	7.60^b	6.85^a	13.82^b	35.60^b
Twigs										
Oak	82^a	153^a	141^a	82^a	500^a	443^a	4.62^c	3.74^b	24.00^c	29.00^b
Eucalyptus	90^b	137^a	131^a	66^a	301^b	244^b	2.80^a	5.11^c	21.00^b	46.00^c
Pine	107^c	165^b	320^b	330^b	480^a	385^{ab}	3.65^b	1.79^a	15.50^a	25.67^a

Different letters (a,b,c) indicate significant differences ($p < 0.05$) among species

Potassium, calcium and magnesium

Oak was the species that presented the highest initial Ca and K concentrations in both leaves and twigs, whereas eucalyptus presented the highest Mg concentrations (Table 2). At the end of the study, Ca and Mg concentrations had increased in most cases, while decreases were observed in all K concentrations. In various cases, pine litter released the most Ca, Mg and K (Fig. 3), showing a behaviour opposite to that of N, P and S. At the end of the study, a net release of K and Mg was observed from leaves and twigs of the three species, with K losses highest (45–80%). On the contrary, Ca was immobilised in both leaves and twigs of oak and eucalyptus. These nutrients exhibited quite different patterns of release through the studied period.

The evolution of K concentrations in decomposing leaves (Fig. 3) showed a quick release, which reached 40–50% during the first month, followed by a much slower release thereafter. K release from twigs reached 50% from December to March; afterwards the K concentrations tended to remain steady in oak and eucalyptus residues. Various authors reported potassium to be the most leachable cation during decomposition of plant debris, undergoing a rapid initial loss (Blair 1988b; Berg and Staaf 1987; Herráez and Fernández Marcos 2000; Guo and Sims 2002). Several authors (Staaf and Berg 1981; Schlesinger 1985; Herráez and Fernández Marcos 2000) also reported the existence of two phases in K loss: an initial phase of rapid leaching, related to rapidly decomposable components of the litter, followed by a slow release, governed by refractory components. Some papers report K immobilisation by heterotrophic organisms after the initial leaching phase (Cameron and Spencer 1989).

Among the leaf litters, oak leaves, with the lowest C/K ratio (Table 5), showed the highest K release (Fig. 3), while the least K was released by eucalyptus

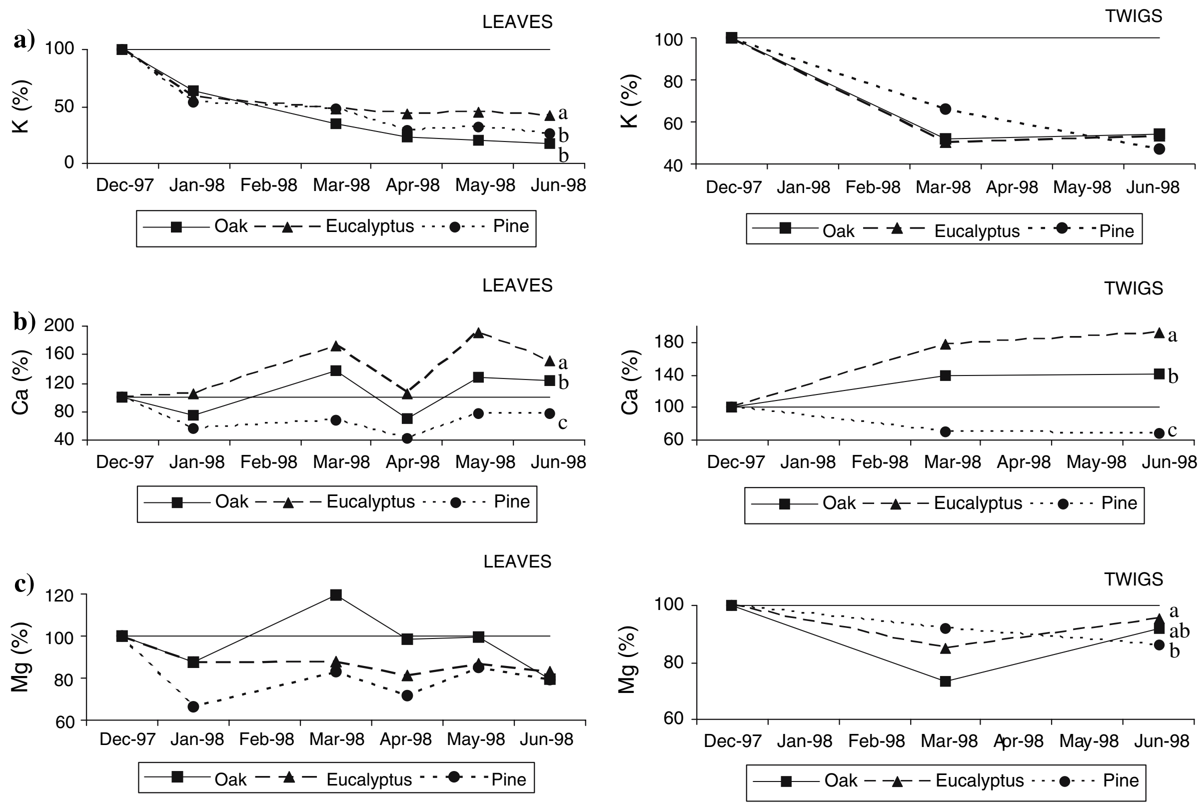

Fig. 3 Percentage of initial potassium (**a**), calcium (**b**) and magnesium (**c**) remaining during six months of decomposition of leaves and twigs from various tree species. Different letters indicate significant differences between species ($p < 0.05$) at the end of the study period

leaves, with the highest C/K ratio. As for twigs, both the C/K ratio and K release are similar for the three species. The C/K ratio always increased during the study period, as a result of the more intense K than C loss (Table 5).

The patterns of Ca flux during leaf decomposition (Fig. 3) showed alternate phases of Ca release and immobilisation. At the end of the six-month decomposing period, increases of 24% in oak and 52% in eucalyptus leaves were measured; on the contrary, the Ca contents in pine leaves had decreased by 23% (Table 4). The oak and eucalyptus twigs showed a Ca immobilisation trend during the whole period, more pronounced from January to March. The pine twigs showed a Ca release trend. Other studies also illustrate that Ca tends to immobilise in *Eucalyptus* (Guo and Sims 2002) and *Pinus* (Kavvadias et al. 2001) litter and is slowly released from litter of *Fagus* (Kavvadias et al. 2001) and *Quercus* (Tavatakol and Proctor 1994). The low Ca mobility indicates that it is released as a result of microbial activity rather than leaching (Ribeiro et al. 2002). Generally, the C/Ca ratios had decreased at the end of the period studied, showing immobilisation of Ca relative to C (Table 5).

Similarly to calcium, the patterns of Mg flux during the decomposition of leaves (Fig. 3) showed alternate phases of Mg release and immobilisation. The oak and eucalyptus twigs exhibited an initial period of Mg release followed by a period of Mg immobilisation. The pine twigs showed a slow but continuous Mg release. Some authors reported a quick Mg release during the initial stage of litter decomposition followed by an immobilisation period (Mudrick et al. 1994). Others reported a continuous Mg loss, parallel to the mass loss, during decomposition of plant residues (De Catanzaro and Kimmins 1985; Tavakol and Proctor 1994). In the present study, Mg release, as for the Ca release, is not parallel to mass loss. The C/Mg ratios had decreased at the end of the study period, showing immobilisation of Mg relative to C (Table 5).

Litter decomposition and nutrient release

The mass loss and release of various nutrients from decomposing leaves of the three species studied, expressed as a percentage of the initial content, followed the order:

K > S > P > C ≈ N ≈ dry weight loss > Mg > Ca in *Q. robur*
S > K > C ≈ N ≈ P ≈ dry weight loss > Mg > Ca in *E. nitens*
K > S > C ≈ dry weight loss > Ca ≈ Mg ≈ N > P in *P. radiata*

Similarly, the weight loss and release of various nutrients from decomposing twigs of the three species studied, expressed as a percentage of the initial content, followed the order:

K > S > N ≈ C ≈ dry weight loss > P = Mg > Ca in *Q. robur*
P ≈ S ≈ K > dry weight loss > C ≈ N > Mg > > Ca in *E. nitens*
K > S > Ca ≈ C > dry weight loss > Mg > N > > P in *P. radiata*

Other studies report the following sequences for species similar to those in the present study:

K ≥ dry weight loss = Mg ≥ Ca ≥ N > P in *E. globulus* (Guo and Sims 2002)
K > Mg > Ca > N > P in *E. marginata*, *E. calophylla* and *E. diversicolor* (O'Connell and Grove 1996).
K > P > dry weight loss > Mg = Ca > N in *P. radiata* (Will et al. 1984)
K > P > Mg > N > Ca in *P. nigra* (Kavvadias et al. 2001)
K > Ca > Mg > P > N in *Fagus sylvatica* (Swift et al. 1979).

Although there were variations between the sequences of litter mass loss and nutrient release in the above studies, in general potassium was the most mobile nutrient, being consistently released most quickly. In the present study, as much as 40–50% was released after only one month (Fig. 3). O'Connell (1988) suggested that this rapid potassium loss was associated with its leaching in advance of microbial decay. The potassium is not a structural component of litter and its release is not dependent on biological activity. Also sulphur, in the conditions of the present study, was released at remarkable levels from decomposing litter, even more so than potassium in the eucalyptus leaves. This is in agreement with the rapid S release from eucalyptus litter reported by

Ribeiro et al. (2002) in a study conducted in Portugal. The K and S losses from all litter types correlated significantly with the initial concentration of these elements ($r = 0.90$ and 0.93 for K, and $r = 0.96$ and 0.82 for S, after four and six months, respectively), suggesting that litter composition is a major factor influencing K and S losses in the initial decomposition stages.

At the end of the studied period, K and S had undergone the greatest losses and Ca and Mg the smallest. The Ca immobilisation in oak and eucalyptus litter agrees with the results from Staaf and Berg (1982) and Blair (1988b). These authors reported that the initial leaching losses of Ca were much lower than for either K or Mg. This is due to the nature as Ca as a structural component of litter. Therefore the release of Ca is more dependent on biotic activity than on leaching. Some of the retention or accumulation of Ca in litter has been attributed to the formation of calcium oxalate by certain fungi (Cromarck et al. 1975).

Conclusions

Under the conditions of the present study, the parent material did not influence litter decomposition or nutrient dynamics in any of the studied forest species. The homogeneity of these soils, all acid and poor in nutrients, is the probable cause of this lack of influence.

Tree species significantly influenced nutrient release, while mass loss in these first stages of litter decomposition was not significantly different for the three species studied. The highest nitrogen and phosphorus losses with respect to their initial contents were showed by oak or eucalyptus litter, which also had the highest initial concentration of most nutrients.

During the decomposition of the plant debris, most elements showed alternate phases of mineralisation and immobilisation, with the exception of potassium, which was released throughout the period studied. At the end of the study, a net release was observed for most nutrients, except Ca, which was immobilised in eucalyptus and oak litters. As expected, mass loss and nutrient release were lower in twigs than in leaves.

Interestingly, greater differences were observed in nutrient release patterns between the two exotic species (*Pinus radiata* and *Eucalyptus nitens*) than between the two broadleaved species studied (*Quercus robur* and *Eucalyptus nitens*). From these results, it appears that the difference between broadleaved and coniferous species is more relevant to nutrient release than the difference between native and introduced species. Notably, the two broadleaved species contributed, in the same time period, more nutrients to soil, which is extremely important for acid and poor soils. These results are very relevant for the correct management of these poor soils. Leaving the organic debris, especially leaves, on the soil after harvesting is of major importance to maintaining soil fertility and the sustainability of these systems.

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