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Nutrient dynamics in decaying leaves of *Fagus sylvatica* L. and needles of *Abies alba* Mill.

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Abstract The dynamics of nutrients (N, P, K, Ca, Mg) in decomposing beech and fir litters was studied. N, P, Mg and Ca content increased in all litters, whereas K content decreased. Nutrient content correlated to mass loss with a few exceptions for K and P. Final N, K, Mg and Ca content was higher the lower the initial content and the higher the initial C/nutrient ratio was. Final P content correlated neither with initial P content nor with initial C/P ratio. All litters lost K very quickly, mainly by leaching. P was lost initially by leaching, although at a lower rate than K, and later by mineralization. Mg, Ca and N showed alternate phases of accumulation and release. Mg losses by leaching occurred only in litters with high initial Mg content; in litters with low initial Mg content, Mg losses occurred by mineralization. Ca and N were lost only by mineralization. A mobility series K>P>Mg>Ca=N is suggested.

Key words Beech · Fir · Litter decomposition · Nutrient dynamics

Introduction

The nutrient release from decomposing litter is an important stage of nutrient recycling in terrestrial ecosystems that influences primary productivity. Plant nutrients are released from litter both by physical leaching and the breakdown of structural organic components by soil organisms. Different elements are retained by differing strengths in decomposing litters, and one mechanism behind this is microbial immobilization. Thus, the dynamics of a single element depends on its status as a limiting or non-limiting nutrient for microbial growth (Gosz et al. 1973; Parnas 1975; Swift et al. 1979). Elements in limiting concentrations are retained in litter up to a certain critical concentration and then released at the same rate as organic matter mass decreases (Staaf and Berg 1981).

Nutrient dynamics of decomposing litter has been studied in several species (Berg et al. 1987; Cameron and Spencer 1989; Laskowski et al. 1995; Schlesinger 1985; Shankar 1994; Vitousek et al. 1994); however, no general model has been suggested up to now. More studies are required, since critical nutrient levels appear to vary with the system, as has been shown for N by Berg and Staaf (1981), and nutrient composition of litter in the very same species may vary among years. Litter decomposition in the mediterranean area has been poorly investigated, and the studies on nutrient dynamics are scanty (Fioretto et al. 1995). This research aims at describing nutrient accumulation and/or release of beech and silver-fir litter incubated in their own stands in litter bags excluding the activity of the meso- and macrofauna. Meso- and macrofauna seem to have a limited impact on the rate of disappearance of beech leaves (Wise and Schaefer 1994). Some data on beech and fir-litter decomposition are reported in the literature (Anderson 1973; Gourbière 1986; Wise and Schaefer 1994), but generally examine only N dynamics. In this paper, which is part of a research project dealing with factors regulating decomposition of beech and fir litter, we analyse the dynamics of the nutrients N, P, K, Ca and Mg.

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Materials and methods

Site description

Two stands in Mount Taburno state forest 50 km east of Naples (41°05′N, 12°07′E) were studied: a pure beech (*Fagus sylvatica* L.) stand at 1100 m a.s.l. and a mixed beech-fir (*Abies alba* Mill.) stand at 1000 m a.s.l.; the latter derived from a pure beech stand, fir being an introduced species. In the beech stand, the trees were about 100 years old. The tree cover of the beech-fir stand was composed of 50% 90-year-old beeches and 50% 70-year-old silver firs. The soil of both stands was a slightly acidic brown earth. Details of climate, soil characteristics and vegetation are reported in Virzo De Santo et al. (1976).

Litter analyses

The study was carried out on beech (*F. sylvatica* L.) leaf litter and fir (*A. alba* Mill.) needle litter. Brown leaves and needles were collected just before the natural fall from branches cut from several trees selected at random. Beech leaves were collected in December 1981 and in November 1982; fir needles were collected in December 1981 and in March 1983. Annual mean temperature was 8 °C for 1981 and 8.8 °C for 1982. Annual precipitation was 1678 mm in 1981 and 1478 mm in 1982. Temperature and precipitation did not differ significantly between the years that preceded the collection of beech leaves or fir needles.

Litter was stored at 2 °C for 2 days to equilibrate water content and then placed in nylon net bags (20 × 20 cm) with a mesh size of 0.8 mm (4 g for each bag). Litter bags were randomly placed on the A_{00} soil layer in 24 plots (1981 litter) or in 20 plots (1982–1983 litters). Field exposure of the litter was mainly carried out for each litter in its respective stand, but transplants were made. Fir-needle litter collected in 1983 was also exposed in the beech stand. Furthermore, bags of beech litter collected in 1982 and of fir litter collected in 1983 were suspended 1.5 m above the forest floor of the beech-fir stand. The incubation of 1981 leaf and needle litter began in December 1981 and lasted 3 years; the incubation of 1982 beech-leaf litter began in December 1982 and lasted 2.5 years; the incubation of 1983 fir-needle litter began in March 1983 and lasted 2 years. Every 2 months during the study period, three replicates of each bag type were collected from the field plots and the mass loss of litter was determined after drying at 75 °C until constant mass (Rutigliano et al. 1996). Litter replicates were mixed and ground by a common grinding mill to obtain homogeneous samples with a grain size of about 1 mm.

Subsamples were used to determine N content by a semimicro-Kjeldahl procedure (Nihlgård 1972) and C content by potassium dichromate digestion according to Springer-Klee (Steubing 1965). To measure P, K, Mg and Ca concentrations, the remaining subsamples were ashed at 550 °C for 12 h and extracted in HCl (Bruno et al. 1973). K concentration was measured by flame photometry, while Ca, P and Mg were determined by colorimetric procedures. Calcium was determined according to Ray Sarkar and Chauhan (1967), P was evaluated by the method of Zilversmith and Davis (1950), and Mg was measured by the Gemini procedure (Gindler and Heth 1971).

Statistical analysis

Differences between different types of litter for each of the studied nutrients were investigated by one-way ANOVA. Correlations between the analysed parameters were determined with Pearson's coefficient.

Results and discussion

Initial chemical composition of the litters

Initial chemical composition and C/nutrient ratio of beech litter and fir litter are shown in Table 1. The initial N content (Table 1) was significantly higher in the 1981 beech litter than in the 1982 beech litter ($P < 0.005$), which showed a significantly higher C/N ratio ($P < 0.05$). Initial N content for the 1981 material was higher in beech than in fir, while the opposite was true for 1982–1983 (Table 1).

The initial P content (Table 1) was comparable between species and years of collection. The C/P ratio (Table 1) was significantly higher in fir than in beech ($P < 0.01$). The initial K content (Table 1) in the beech litter was significantly ($P < 0.005$) lower in 1981 than in 1982; it must be pointed out that the litter was collected in 1981 just after a very intense rainy period, which likely caused K leaching. Thus, the 1982 beech litter showed a significantly ($P < 0.01$) lower C/K ratio (Table 1). Differences in K content between beech and fir were relevant only for the 1981 collection. The highest Ca content and the lowest C/Ca ratio were observed in the 1981 beech litter of the beech stand (Table 1). For both the 1981 and 1982–1983 collections, the Mg content was lower in the fir litter than in the beech litter (Table 1), but differences were not significant. C/Mg ratios were higher in fir litter than in beech litter (Table 1). Ash content (Table 1) was higher in the beech litter than in the fir litter for both the 1981 and 1982–1983 collections. However, differences were not significant because of the high variance.

Table 1 Initial content of nutrients and ash (g kg^{-1} dry weight) and initial C/nutrient ratio of beech leaf litter and fir needle litter. The site where litter was incubated is indicated in parentheses. *bfs* Beech-fir stand, *bs* beech stand, *bfsab* beech-fir stand aerial bags

	N (g kg^{-1})	C/N	P (g kg^{-1})	C/P	K (g kg^{-1})	C/K	Ca (g kg^{-1})	C/Ca	Mg (g kg^{-1})	C/Mg	Ash (g kg^{-1})
Leaf and needle litter sampled in December 1981											
Beech (bfs)	17.2	24	1.0	419	1.4	286	10.0	42	2.0	207	62
Beech (bs)	17.2	25	1.2	359	1.3	319	15.9	27	2.4	175	76
Fir (bfs)	13.4	37	1.0	482	4.7	105	10.0	49	1.0	491	40
Leaf litter sampled in November 1982											
Beech (bfs, bfsab)	10.5	41	1.0	412	6.1	70	9.5	46	2.9	151	88
Beech (bs)	9.8	46	1.1	398	6.4	71	9.7	47	2.9	157	82
Needle litter sampled in March 1983											
Fir (bfs, bs, bfsab)	12.3	42	1.0	494	5.0	105	10.2	51	1.0	519	48

Nutrient dynamics in decomposing litters

Changes of nutrient content and nutrient absolute quantity, as a percent of initial quantity, in decomposing litters were measured throughout the study period.

Nitrogen

N content increased in all litters studied (Table 2), as was also observed by other authors (Berg et al. 1987; Lousier and Parkinson 1978; Rustad 1994; Singh and Shekar 1989), due to microbial immobilization and simultaneous degradation of easily decomposable substances, such as carbohydrates. The influence of microbial activity on N dynamics is confirmed by the significant linear relationship between N content and mass loss (Table 3). According to Lutz and Chandler (1946), the critical C/N ratio for forest soil organic matter ranges from 20 to 30; at ratios higher than the critical ratio, N is immobilized, whereas at lower ratios N is released or mineralized. N immobilization observed in the litters studied is consistent with the initial C/N ratio of more than 20 (Table 1).

The increase of N content assessed at the end of the study period in beech litter was significantly higher ($P<0.05$) in the 1982 collections than in the 1981 collections (Table 2), which showed a higher initial N content ($P<0.005$; Table 1) and a lower C/N ratio ($P<0.05$) than the 1982 beech litter. Final N content was negatively correlated with initial N content and positively correlated with initial C/N ratio (Fig. 1).

The N content in the decomposing litters was significantly higher ($P<0.0001$) in beech litter than in fir litter regarding the 1981 collection, but not for the 1982–1983 collections. Comparing the beech litter incubated in different years, N content was significantly higher in the 1981 than in the 1982 collection ($P<0.005$).

In all litters, N absolute quantities showed alternate phases of accumulation and release during decomposition (Fig. 2). At the end of study period, all litters appeared to have lost N although in different amounts (1–44% of initial N quantities), with the exception of some 1982 beech litters (bs and bfsab), which showed

Table 2 Nutrient content at the end of the study period expressed as the percentage of the initial content. *bfs* Beech-fir stand, *bs* beech stand, *bfsab* beech-fir stand aerial bags

	N_f (% N_i)	P_f (% P_i)	K_f (% K_i)	Ca_f (% Ca_i)	Mg_f (% Mg_i)
Leaf and needle litter sampled in December 1981					
Beech (bfs)	146	172	137	232	278
Beech (bs)	138	120	188	136	229
Fir (bfs)	134	143	24	216	364
Leaf litter sampled in November 1982					
Beech (bfs)	199	124	31	197	181
Beech (bs)	225	116	27	177	162
Beech (bfsab)	178	103	24	203	127
Needle litter sampled in March 1983					
Fir (bfs)	189	124	18	138	292
Fir (bs)	170	118	17	144	227
Fir (bfsab)	161	118	17	138	182

Table 3 Linear regression of nutrient content against mass loss for species and year of incubation. *bfs* Beech-fir stand, *bs* beech stand, *bfsab* beech-fir stand aerial bags

	Beech 1981		Beech 1982			Fir 1981	Fir 1983		
	bfs	bs	bfs	bs	bfsab	bfs	bfs	bs	bfsab
Nitrogen									
r	0.82	0.80	0.90	0.91	0.89	0.89	0.91	0.92	0.92
n	16	16	12	12	11	16	11	11	11
P<	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Phosphorus									
r	0.80	0.78	0.49	0.35	0.28	0.83	0.37	0.33	0.36
n	9	10	8	8	8	10	8	8	8
P<	0.01	0.01	n.s.	n.s.	n.s.	0.01	n.s.	n.s.	n.s.
Potassium									
r	0.74	0.54	−0.55	−0.73	−0.60	−0.68	−0.80	−0.78	−0.76
n	9	10	8	8	8	10	8	8	8
P<	0.05	n.s.	n.s.	0.05	n.s.	0.05	0.05	0.05	0.05
Calcium									
r	0.85	0.72	0.71	0.91	0.95	0.87	0.94	0.91	0.84
n	7	10	8	8	8	10	8	8	8
P<	0.05	0.05	0.05	0.01	0.001	0.01	0.001	0.01	0.01
Magnesium									
r	0.95	0.82	0.83	0.78	0.62	0.79	0.80	0.78	0.71
n	9	10	8	8	8	10	8	8	8
P<	0.001	0.01	0.05	0.05	n.s.	0.01	0.05	0.05	0.05

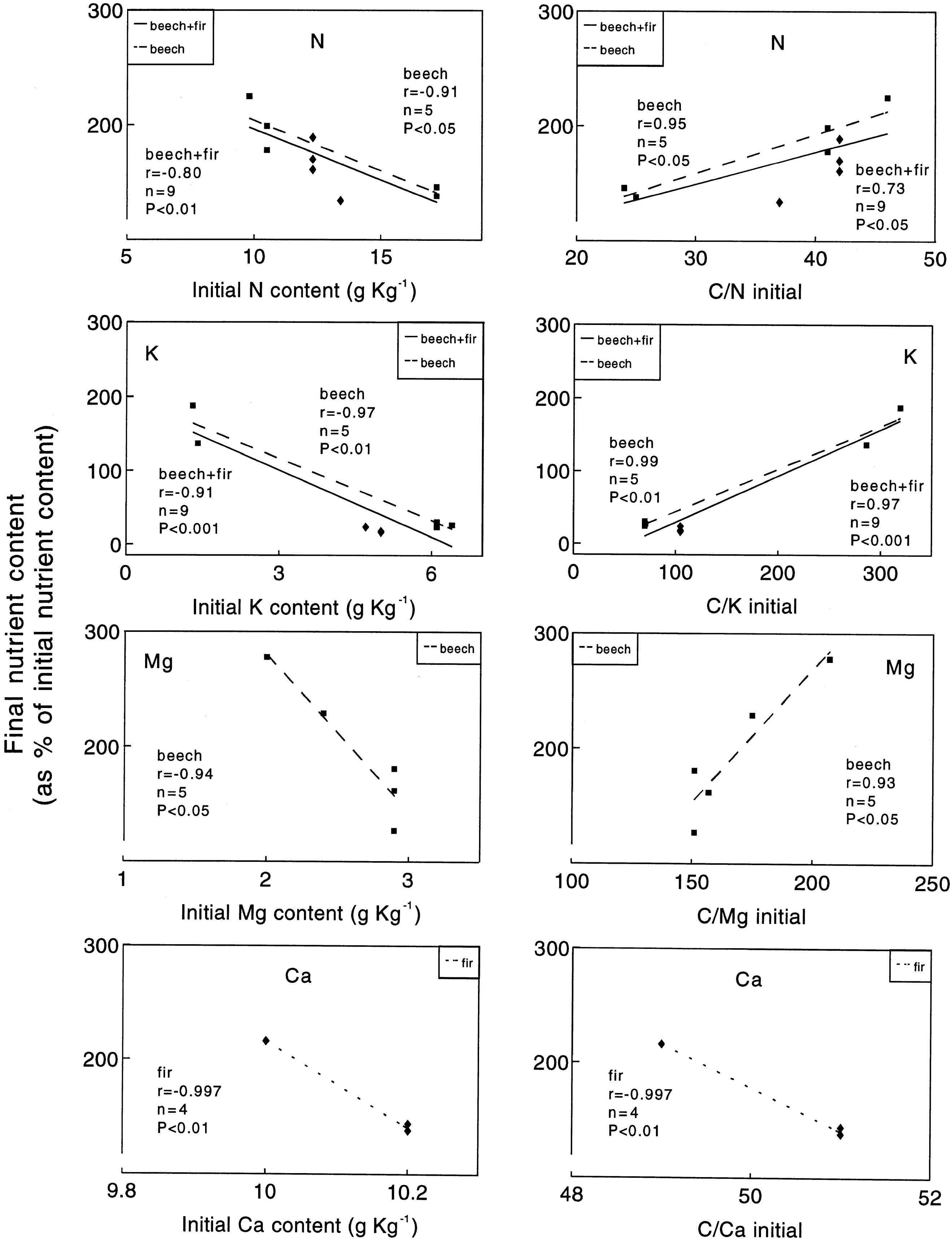

Fig. 1 Relationship between final nutrient content (as % of initial nutrient content) and both initial nutrient content (g kg^{-1} dry weight) and initial C/nutrient ratio in beech (■) and fir (◆) litters

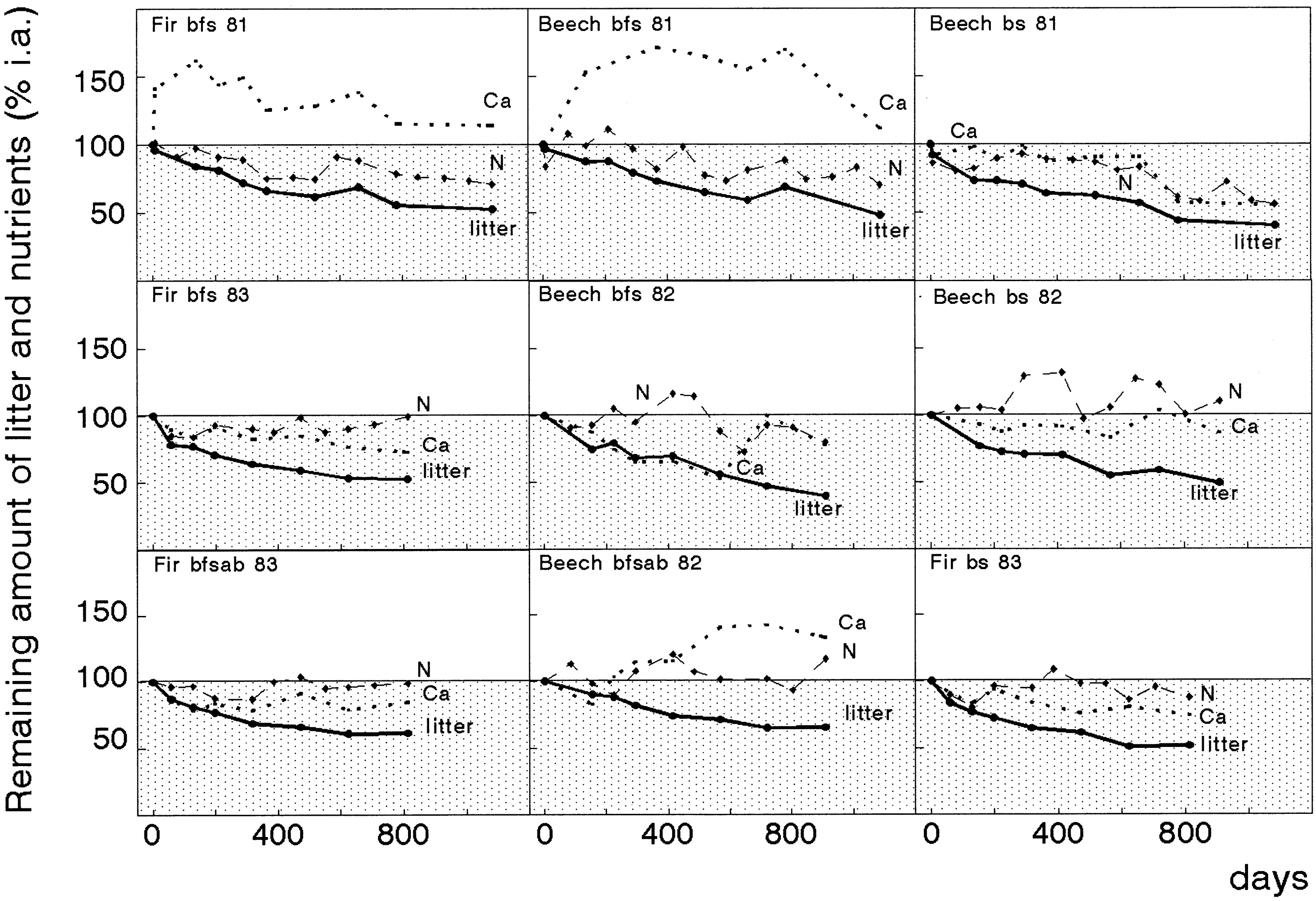

Fig. 2 Remaining quantities of litter, N and Ca (as % of initial amount) for species, beginning year of experiment, type of incubation. *bfs* Beech-fir stand, *bs* beech stand, *bfsab* beech-fir stand aerial bags

increased N quantities of up to 120%. Other authors (Berg and Staaf 1980; Day 1982; Gosz et al. 1973; Lousier and Parkinson 1978; Schlesinger 1985) have observed increases in N absolute quantity. Anderson (1973) found N accumulation up to 170% of initial quantities in a beech litter with a lower initial N (5.6 g kg^{-1}) than that which we used in this study (9.8–17.2 g kg^{-1}).

Litters with a higher C/N ratio and/or lower initial N content showed higher increases in N quantities. For the 1983 collection, fir litter incubated in the beech-fir stand showed lower N absolute quantities ($P<0.05$) in the A_{00} layer than at 1.5 m above the soil.

Phosphorus

In all litters, the P content at the end of the study period was higher than the initial values (Table 2), as also observed by other authors (Berg et al. 1987; Singh and Shekhar 1989); however, in the 1982 beech litter and 1983 fir litter, the increase in P content occurred after an initial decrease. In the 1981 litters, P content was positively correlated with mass loss (Table 3). Final P content correlated neither with initial P content nor with initial C/P ratio. The P content of the decomposing litters was significantly higher ($P<0.05$) in the 1981 beech litter of the beech-fir stand than in the same litter from the 1982 collection.

Absolute quantities of P decreased in all leaf and needle litters (Fig. 3) to 17–51% of the initial mass. P losses were faster in the 1982 beech litter and 1983 fir litter than in the 1981 litters. After about 1 year of decomposition, P losses were 8–33% and 47–60%, respectively, in the 1981 and in the 1982–1983 collections. Absolute quantities of P were significantly higher ($P<0.0001$) in the 1981 beech litter incubated in the beech-fir stand than in that incubated in the beech stand. For both the beech and fir litters incubated in the beech-fir stand, absolute quantities of P were higher in the 1981 than in the 1982 and 1983 collection ($P<0.01$).

Potassium

K content generally decreased quickly during litter decomposition (Table 2), as also observed by other authors (Laskowski and Berg 1993; Singh and Shekhar 1989). However, it increased in the 1981 beech litter

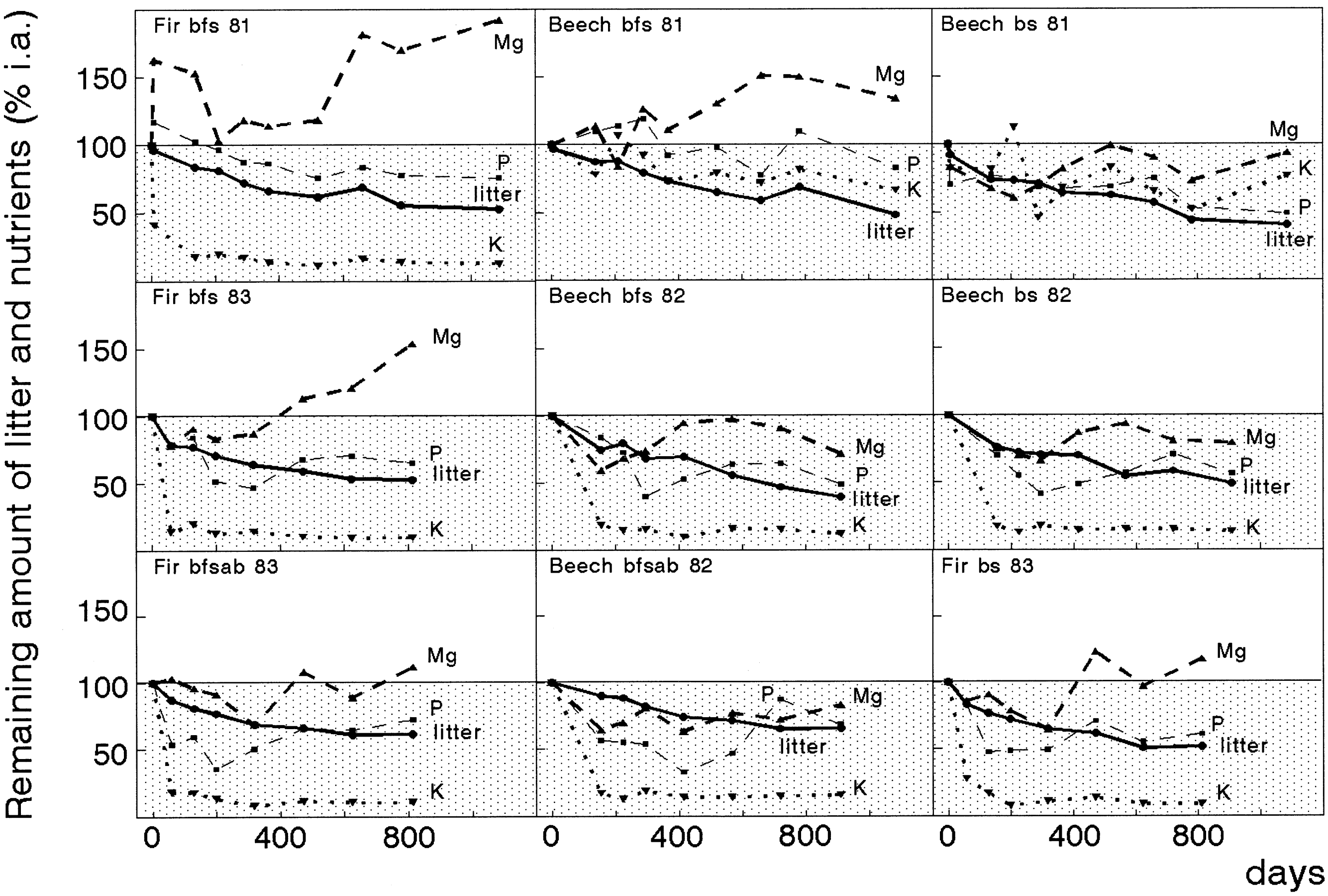

Fig. 3 Remaining quantities of litter, P, Mg and K (as % of initial amount) for species, beginning year of experiment, and type of incubation. *bfs* Beech-fir stand, *bs* beech stand, *bfsab* beech-fir stand aerial bags

(Table 2), which showed the significantly ($P<0.005$) lowest initial K content and the significantly ($P<0.0005$) highest initial C/K ratio (Table 1) as compared to the other litters studied. K variation at the end of study period correlated positively with C/K ratio and correlated negatively with initial content of K (Fig. 1). During the entire study period, K content in decomposing litters was not different between litter types, stands, or years of collection, except for initial content in the 1981 beech litter.

Absolute quantities of K decreased rapidly in all litters (Fig. 3) with the exception of the 1981 beech litter, which showed the lowest K concentration and a slow K release. Actually because K is not a structural element, it is susceptible to high initial loss by leaching, as also reported by Staaf (1980). After about 1 year of decomposition, the 1981 beech litter lost 26–32% of the initial K quantities, while the other litters lost 81–92%; thereafter, K quantities did not vary very much. Schlesinger (1985) observed K losses as high as 70–80% from *Ceanothus megacarpus* and *Salvia mellifera* litters after the first year of decomposition; Arianoutsou (1993) found K losses as high as 85–88% from *Arbutus unedo* and *Quercus coccifera* litters after 1 year of decomposition.

During the entire study period, absolute K quantities in the beech litter were significantly higher ($P<0.0001$) in the 1981 than in the 1982 collection (Fig. 3). In the 1981 collection, beech litter showed higher absolute K quantities than the fir litter ($P<0.001$).

Calcium

The content of Ca increased during decomposition (Table 2) and correlated significantly with mass loss (Table 3). Significant correlations between final Ca content and C/Ca ratio and initial Ca content were found only for fir (Fig. 1). During the entire study period, the content of Ca in decomposing leaf and needle litter was significantly higher in the 1981 than in the 1982 and 1983 collections ($P<0.005$).

Absolute quantities of Ca (Fig. 2) at the end of the study period were higher than the initial values in the 1981 beech and fir litters from the beech-fir stand, but lower in the 1981 beech litter from the beech stand (45% of initial absolutes quantities). Concerning the 1982 and 1983 litters, absolute Ca quantities were lower (13–27% of the initial amount), except in the beech litter incubated at 1.5 m above the soil in the beech-fir stand.

For beech litter, absolute quantities of Ca during the entire study period were significantly higher in the beech-fir stand than in the beech stand ($P<0.0001$) concernings the 1981 collection; the opposite was true for the 1982 collection ($P<0.05$). In the beech-fir stand, absolute Ca quantities were higher in the collection than in the 1982 and 1983 collections ($P<0.0001$).

Magnesium

The content of Mg increased in all leaf and needle litters (Table 2); however, in the 1982 beech litter from the beech-fir stand, incubated both in the A_{00} layer and at 1.5 m above the soil, Mg content increased after an initial decrease. Mg content generally correlated with mass loss (Table 3).

The increase of Mg content was higher in the fir litter than in the beech litter (Table 2), which showed a significantly lower initial C/Mg ratio ($P<0.01$; Table 1). The final Mg content of the beech litter correlated negatively with initial Mg content and correlated positively with C/Mg ratio (Fig. 1). In both the 1981 and 1982–1983 collections, the Mg content in decomposing litters was significantly higher ($P<0.01$) in the beech litter than in the fir litter.

Compared to initial values, at the end of the study period the absolute quantities of Mg (Fig. 3) were higher in the 1981 leaf and needle litters incubated in the beech-fir stand and in the 1983 fir litter, but lower in the 1981 litter incubated in the beech stand (6% of the initial amount) and in the 1982 beech litter (17–28% of the initial amount). For both beech and fir litters incubated in the beech-fir stand, absolute Mg quantities were higher in the 1981 collection than in the 1982 and 1983 collections ($P<0.05$), respectively. Moreover, absolute Mg quantities showed higher values ($P<0.0005$) in the beech-fir stand than in the beech stand for the 1981 collection and, concerning litters incubated at 1.5 m above the soil in the beech-fir stand, higher values ($P<0.005$) for fir than for beech.

General remarks

The observed increases in the absolute quantities of Mg as well as the increases of Ca and N in decomposing litters are probably dependent on the input from exogenous sources with precipitation or slip water, translocation by fungal hyphae, or, as regards N, from biological fixation and animal excretions (Virzo De Santo et al. 1985).

The increase of N, P, Ca and Mg content (Table 2) observed in beech litter and fir litter suggests that these elements were limiting for microbial growth and consequently were immobilized by microorganisms, whereas K, which was released, appeared not to be limiting. Actually, N, P, Ca and Mg contents correlated positively with mass loss (Table 3). The initial nutrient content and the C/nutrient ratio significantly influenced the degree of immobilization (Fig. 1).

No significant difference was observed for the nutrient dynamics between types of incubation. Aerial bags provide a more hostile environment for microbial growth because of widely fluctuating temperature and the desiccation; it has been found that mass loss of litter incubated in aerial bags is reduced (Rutigliano et al. 1996); however, the trend of nutrient dynamics was not modified.

Relationship between change of nutrient quantity and mass loss

Losses of nutrients from litter in the early stage (first month) are generally caused by leaching (Bocock 1963). In the following stages, by comparing curves of litter decomposition and nutrient dynamics, it is possible to observe the release of nutrients due to leaching and to microbial decay, respectively (Figs. 2, 3). According to Gosz et al. (1973), if a nutrient is lost at a rate equal to or lower than mass loss, it is likely released by decomposition of organic matter; any nutrient loss at a rate higher than mass loss would result from leaching.

In the leaf and needle litters, K (Fig. 3) appeared to be mainly lost by leaching, except in the 1981 beech litter. P (Fig. 3) appeared to be lost by leaching in the early stage; it subsequently appeared to be lost by microbial decomposition. However, in the 1981 beech litter and fir litter of the beech-fir stand, P appeared to be lost only by microbial decomposition. Mg appeared to be lost by leaching in the early stage from beech litter, the only exception being the 1981 beech of the beech-fir stand. In the fir litter, Mg was already lost by microbial decomposition in the early stage of the process. Litters with higher initial Mg content (Table 1) were characterized by initial losses through leaching. N and Ca, as less mobile elements, generally did not show leaching (Fig. 2).

Among the nutrients analysed, K and P were lost from all decomposing litters (Fig. 3). When comparing the magnitude of the losses, it is evident that K was lost in the highest amounts (81–92%) after 1 year of decomposition, except for the 1981 beech litter, which showed losses of 26–32%. Moderate amounts of P (6–60%) were lost in the same period. Moreover, K, a very mobile element, was mainly lost from the litter by leaching, while P was lost by leaching in the early stage and by microbial decomposition in the late stage (Fig. 3). N, Ca (Fig. 2) and Mg (Fig. 3) showed alternate phases of accumulation and release. The observed losses of these three elements after 1 year of decomposition and at the end of the study period are comparable (1–45%). Mg appears to have been lost only by microbial decomposition in litters with low initial concentrations, while leaching in the early stage of decomposition occurred in the beech litter from the 1982 collection and in the 1981 beech litter in the beech stand, which showed relatively high initial Mg concentrations. Ca and N seem to have been lost by microbial decomposition.

On the basis of our data, we can suggest the mobility series K>P>Mg>Ca=N, which corresponds fairly well to that found by other authors for other types of litter in different systems. Indeed, Loissant (1973), for *Quercus ilex* litter of a Southern France maquis, and Schlesinger and Hasey (1981), for *Ceanothus megacarpus* and *Salvia mellifera* litters of the chaparral, observed nutrient losses following the mobility series K>P>Mg>N>Ca. Lousier and Parkinson (1878) found a mobility series K>P>Mg>Ca>N for *Populus tremuloides* and *P. balsamifera* litters of a Canada forest. Nevertheless Arianoutsou (1993) suggested a mobility series K>Ca=Mg>P=N for *Arbutus unedo* and *Quercus coccifera* litters of a Greece maquis.

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