J For Res (2004) 9:23–31
DOI 10.1007/s10310-003-0047-x

ORIGINAL ARTICLE

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Potassium, calcium, and magnesium dynamics during litter decomposition in a cool temperate forest

Received: April 21, 2003 / Accepted: June 16, 2003

Abstract The dynamics of K, Ca, and Mg were investigated during the decomposition of 14 litter types over a 3-year period on the upper and lower parts of a forest slope in a cool temperate forest in Japan. Potassium dynamics were divided into initial leaching phase and late phase. Initial K concentrations for the initial phase were correlated with the rate of decrease in K concentration during the initial phase. The late phase was characterized by seasonal fluctuations in concentration: K concentration increased from April to November and decreased during the winter period. The pattern of change in Ca concentration was divided into initial increase phase and late decrease phase in some litter types, or consisted of the late phase only in other litters. Calcium concentration of the initial litter was not predictable for the pattern of change in Ca concentration nor the rate of change in Ca concentration during the initial phase. Initial Ca concentration for the late phase was correlated with the rate of change in Ca concentration during the late phase. The pattern of change in Mg concentration was divided into initial leaching phase and late immobilization phase. Initial Mg concentration for the initial phase was correlated with the rate of change in Mg concentration during the initial phase. At the lower site, initial Mg concentration for the late phase was correlated with the rate of change in Mg concentration during the late phase, while such a relationship was not observed at the upper site. Concentrations of K, Ca, and Mg showed a convergent trend at the end of the study period. The final concentration differed between the upper and lower sites.

Key words Calcium · Decomposition · Magnesium · Nutrient · Potassium

Introduction

In forest ecosystems, decomposition of plant litter is an important process controlling nutrient cycling. Potassium (K), calcium (Ca), and magnesium (Mg) are essential macronutrients for energy metabolism, photosynthesis, and membrane transport of plants (Slovic 1997). Litter is a major source of these nutrients available to forest trees (Chapin 1991; Likens and Bormann 1995). Many authors have described the dynamics of K, Ca, and Mg during litter decomposition: K leached out quickly from decomposing litters, Ca decreased as carbon loss during litter decomposition, and Mg often showed an intermediate release pattern (e.g., MacLean and Wein 1978; Blair 1988; O'Connell 1988; Berg and Cortina 1995; Adams and Angradi 1996; Hasegawa and Takeda 1997). Few studies described general patterns for the dynamics of these elements, but Laskowski et al. (1995a) developed a method to analyze K dynamics in decomposing litters and described a general pattern for K dynamics that holds in northern and central Europe and in the northern USA. This method may be useful for examining general patterns for the dynamics of K, Ca, and Mg in other regions.

In a series of papers, we have reported on the dynamics of lignin, holocellulose, nitrogen and phosphorus (Osono and Takeda, unpublished) during a 3-year decomposition of 14 litter types in a cool temperate deciduous forest in Japan. In the present study we describe the pattern of changes in K, Ca, and Mg in the same experiment. The method of Laskowski et al. (1995a) was applied to the data to examine general patterns for the dynamics of these nutrients in the study site.

Materials and methods

Study area

The study was carried out in a cool temperate deciduous forest dominated by *Fagus crenata* and *Quercus crispula* in

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Ashiu Experimental Forest of Kyoto University (35°18′N, 135°43′E) about 40 km north of Kyoto, Japan. Mean annual temperature is about 10°C and mean monthly temperature ranged from 0.4° in January to 25.5°C in August. The mean annual precipitation over a 56-year period is 2495 mm. The study area was covered with snow during the winter period from December to April.

Two study sites were chosen that were located on a northwest-facing slope about 200 m long. One site was located on the upper part of the slope and the other on the lower part. Soil organic layer shows a moder and a mull humus form in the upper and lower site, respectively (Takeda and Kaneko 1988). The vegetation of the upper and lower site is described in Tateno and Takeda (2003). A study plot 20 × 10 m in area was laid out at the most representative location of each site and there was no replication by site type. The study plots were divided into ten subplots of 4 × 5 m for survey of litter mass and chemical changes.

Litter bag method

Decomposition processes of leaf litter of 14 tree species were studied using a litter bag method (Crossley and Hoglund 1962). The plant species used in this study are listed in Table 1. Nomenclature follows Satake et al. (1989). Freshly fallen leaves were collected from forest floors in the study area during November 1996, the peak period of litter fall (Takeda and Kaneko 1988). The leaves were taken to the laboratory and oven-dried at 40°C for 1 week. Then, 3 g of the litter was enclosed in each litter bag (15 × 15 cm), made of polypropylene shade cloth with a mesh size of approximately 2 mm. A total of 2800 bags were prepared. About 10 g of the initial sample material was preserved for chemical analyses.

The decomposition study covered over a 35-month period from December 1996 to November 1999. Litter bags were placed in the litter layer on December 1996. The litter bags were attached to the forest floor by metal pins to prevent movement and to ensure a good contact between the bags and the litter layer. Sampling of the bags took place ten times, at 5 (May 1997), 7 (July 1997), 9 (September 1997), 11 (November 1997), 16 (April 1998), 19 (June 1998), 21 (September 1998), 23 (November 1998), 29 (May 1999), and 35 months (November 1999) after the placement. On each sampling occasion, 200 bags were collected from 20 subplots, placed in paper bags and taken to the laboratory. Foreign plant remains attached to the outside of the bags were carefully removed with forceps. The losses of dry mass were determined after drying the samples to a constant mass at 40°C and mean values of mass loss were calculated for each sampling.

Chemical analyses

The samples were combined and ground in a laboratory mill to pass through a 0.5-mm screen. After an acid wet oxidation in HNO_3 + $HClO_4$, flame photometry was performed for potassium and atomic absorption for calcium and magnesium (atomic absorption spectrophotometer 170-30S; Hitachi, Tokyo, Japan). The results for *Fagus crenata* have already been presented by Osono and Takeda (2001).

Data analysis

Data were analyzed according to the method described in Laskowski et al. (1995a). This analysis method consisted of three steps.

In the first step, concentrations of K, Ca, and Mg were compared with accumulated mass loss of litter. Two separate phases were observed in K, Ca, and Mg dynamics (Fig.

Table 1. Initial concentration for the initial phase (C_0), initial phase slope (IPS), initial concentration for late phase (C_{min}), and late phase slope (LPS) of K concentration dynamics

Litter type	Initial phase			Late phase			
	C_0	Upper IPS	Lower IPS	Upper		Lower	
				C_{min}	LPS	C_{min}	LPS
Mallotus japonicus	12.7	−0.193	−0.213	1.7	−0.012	2.2	0.012
Swida controversa	8.5	−0.144	−0.204	1.6	−0.013	1.6	−0.008
Pterostyrax hispida	8.1	−0.155	−0.161	1.6	−0.013	1.7	0.005
Carpinus laxiflora	5.9	−0.098	−0.099	1.4	−0.005	1.7	0.015
Castanea crenata	3.0	−0.062	−0.069	1.4	−0.005	1.5	0.011
Magnolia obovata	2.8	−0.061	−0.053	1.6	−0.015	1.7	−0.008
Quercus crispula	2.2	−0.069	−0.081	1.2	−0.001	1.3	0.012
Acer mono var. *marmoratum* f. dissectum	4.9	−0.155	−0.154	1.3	−0.012	1.5	0.003
Betula grossa	1.5	0.000	0.006	1.5	−0.016	1.6	0.000
Acer rufinerve	4.2	−0.144	−0.162	1.3	−0.003	1.4	0.005
Cryptomeria japonica	0.9	−0.013	−0.018	0.7	−0.005	0.7	0.005
Pterocarya rhoifolia	3.8	−0.145	−0.162	1.7	−0.027	1.7	−0.029
Fagus crenata	1.6	−0.066	−0.109	1.2	−0.007	1.2	0.009
Aesculus turbinata	2.0	−0.126	−0.141	1.2	−0.019	1.4	−0.011
Mean	4.4	−0.102	−0.116	1.4	−0.011	1.5	0.002
Standard deviation	3.4	0.058	0.067	0.3	0.007	0.3	0.012

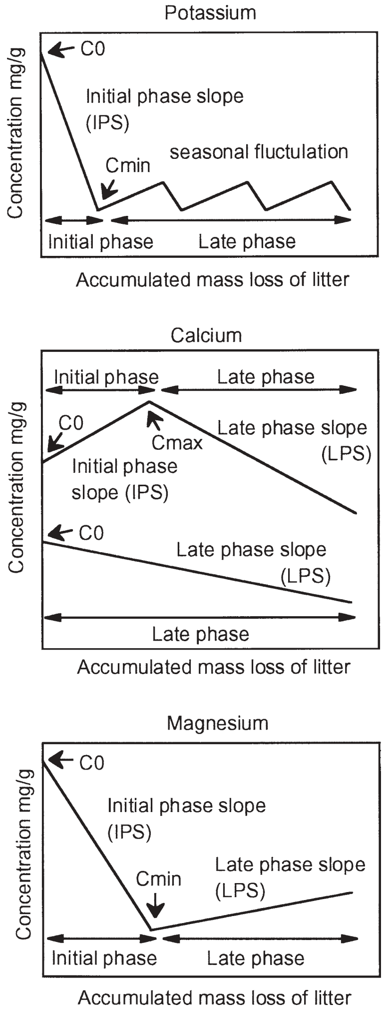

Fig. 1. Overview graphs for changes in K, Ca, and Mg concentrations with accumulated mass loss of litter. Initial concentrations of K, Ca, and Mg (C_0), minimum concentrations of K and Mg (C_{min}), and maximum concentration of Ca (C_{max}) are indicated. Slopes of concentration changes in the initial phase (*IPS*) and in the late phase (*LPS*) are indicated. Some litter types showed the late phase of Ca only, with concentrations decreasing over the decomposition period. Note that the patterns of change in Ca concentration were not related to initial Ca concentrations

1). The K dynamics were divided into an initial phase of fast leaching from decomposing litter during the first 5 months and a late phase of fluctuations in concentration. The Ca dynamics were divided into an initial phase of increase in concentration and a late phase of decrease. Some litter types had a one-phase dynamic, with concentrations decreasing over the decomposition period. The Mg dynamics were divided into an initial leaching phase and a late phase of slow increase in concentrations. Some litter types showed initial phase or late phase of Mg only.

In the second step, the slope was calculated with simple linear regression of concentrations of K, Ca, and Mg on accumulated mass loss of litter for the phases separately (Fig. 1). The outputs of this part of the analysis were sets of regression line slopes: initial phase slope (IPS) and late phase slope (LPS) of each of K, Ca, and Mg dynamics. In some cases, only two measurement points could be used for the slope determination. This could not be treated in terms of its statistical significance in the regression analysis. The slopes were then calculated by dividing the change in concentration by accumulated mass loss of litter during the phase. The IPS values for K dynamics were calculated based on two measurement points in all litter types. Correlation coefficients of the LPS calculation for K dynamics ranged from 0.01 to 0.71 ($n = 10$) and the LPS was significant at the 10% level in 3 out of 28 data sets. The IPS values for Ca dynamics were calculated based on two measurement points in 9 out of 18 data sets. Correlation coefficients of the IPS calculation for Ca dynamics in the other nine data sets ranged from 0.06 to 1.00 ($n = 3$ to 9) and the IPS was significant at the 10% level in 3 out of the 9 data sets. Correlation coefficients of the LPS calculations for Ca dynamics ranged from 0.46 to 0.97 ($n = 3$ to 11) and the LPS was significant at the 10% level in 26 out of 28 data sets. The IPS values for Mg dynamics were calculated based on two measurement points in 11 out of 26 data sets. Correlation coefficients of the IPS calculations for Mg dynamics in the other 15 data sets ranged from 0.63 to 1.00 ($n = 3$ to 11) and the IPS was significant at the 10% level in 9 out of the 15 data sets. Correlation coefficients of the LPS calculations for Mg dynamics ranged from 0.18 to 0.96 ($n = 4$ to 11) and the LPS was significant at the 10% level in 16 out of 25 data sets.

In the third step, we investigated the relationship between the initial concentrations of K, Ca, and Mg for the initial phase (C_0) and the IPS of dynamics of each element and between the initial concentrations for the late phase and the LPS (Fig. 1). The initial K concentration for the late phase corresponded to the concentration at the 5th month (denoted as C_{min}). The initial Ca concentration for the late phase corresponded to the maximum value of Ca concentration during decomposition (C_{max}). For litter types that showed late phase only, C_{max} was equal to C_0 of Ca. The initial Mg concentration for the late phase corresponded to the minimum value of Mg concentration during decomposition (C_{min}). For litter types that showed late phase only, C_{min} was equal to C_0 of Mg.

The late phase of K dynamics was characterized by seasonal fluctuations in K concentrations (Fig. 1). Therefore, one-way ANOVA was used to determine the differences in K concentrations among seasons (April–May, June–July, September, November) in the first and second years, and a *t*-test was used in the third year.

Results

Potassium dynamics

Initial K concentration (C_0) ranged from 0.9 mg/g in *Cryptomeria japonica* to 12.7 mg/g in *Mallotus japonicus*, with a mean ± standard deviation of 4.4 ± 3.4 mg/g (Table 1). Two clearly separate phases were observed for K dynamics of all litter types (Fig. 2). The initial phase during the first 5

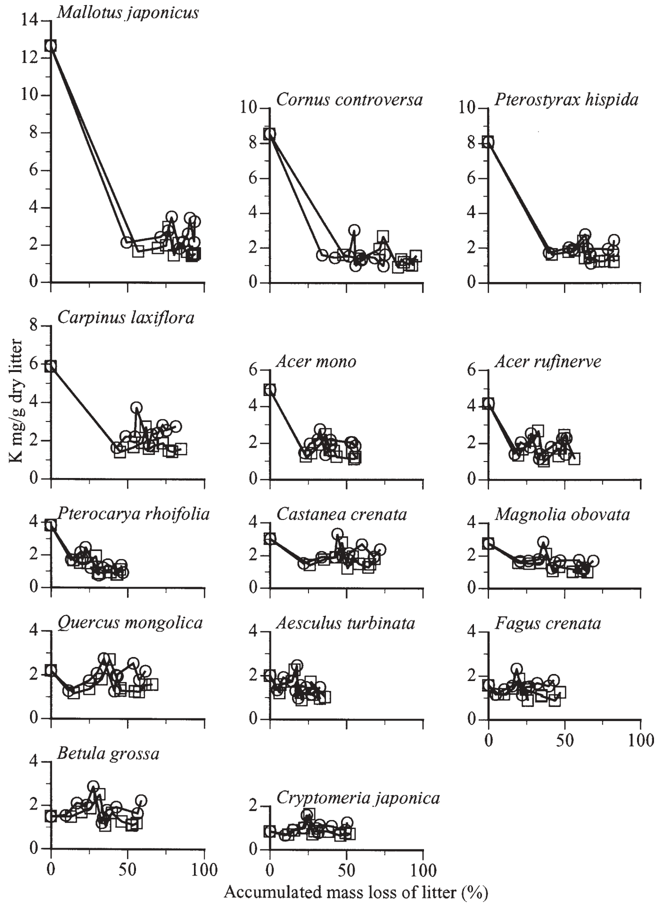

Fig. 2. Changes in K concentration as related to accumulated mass loss of litter. □ upper, ○ lower site

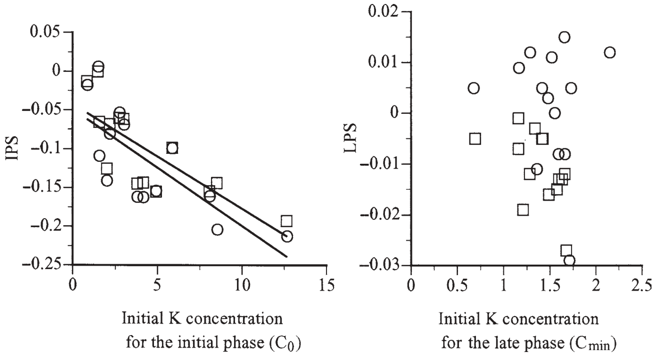

Fig. 3. Slopes of K concentration dynamics during the initial (*IPS*) and late phase (*LPS*) as related to the initial K concentration for each phase. Concentration of K is in mg/g. IPS, upper: $R = -0.78$, $n = 14$, $P < 0.001$; lower: $R = -0.76$, $n = 14$, $P < 0.01$. LPS, upper: $R = -0.51$, $n = 14$, nonsignificant; lower: $R = -0.09$, $n = 14$, nonsignificant. □ upper, ○ lower site

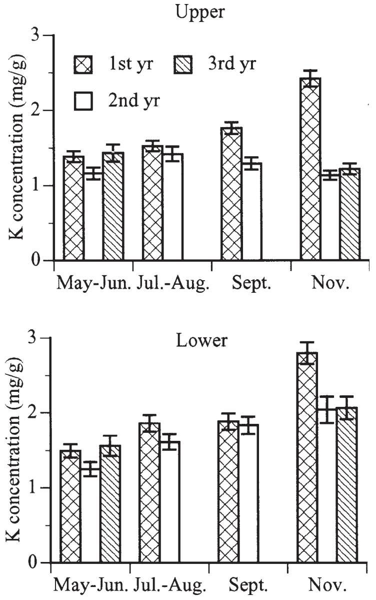

Fig. 4. Seasonal changes in K concentration in the late phase. *Bars* indicate standard errors for 14 litter types

months was characterized by a rapid drop in mass and concentration due to leaching. The late phase was characterized by a gradual mass loss and seasonal fluctuations in concentration.

The initial phase slope (IPS) of K varied from −0.193 to 0.000 at the upper site and from −0.213 to 0.006 at the lower site (Table 1). The IPS was significantly ($P < 0.05$) higher at the upper site than at the lower site. Initial K concentrations for the initial phase (C_0) were significantly and negatively correlated to the IPS at both sites (Fig. 3).

The K concentration at the end of the initial phase (at the 5th month, C_{min}) was 1.4 ± 0.3 mg/g (mean ± standard deviation) at the upper site and 1.5 ± 0.3 mg/g at the lower site (Table 1). C_{min} was significantly ($P < 0.01$) lower at the upper site than at the lower site. The standard deviation of C_{min} was significantly (*F* test, $P < 0.001$ at both sites) lower than that of the initial concentration (C_0) at both sites. Accumulated mass loss of litter at the end of the initial phase (at the 5th month) varied from 3.8% (*Fagus crenata* at the lower site) to 57.0% (*Mallotus japonicus* at the upper site).

The late phase slope (LPS) of K varied from −0.027 to −0.001 at the upper site and from −0.029 to 0.015 at the lower site (Table 1). The LPS was significantly ($P < 0.001$) higher at the lower site than at the upper site. The initial K concentration for the late phase (C_{min}) was not significantly correlated with the LPS at both sites (Fig. 3).

The potassium concentration fluctuated seasonally during the late phase (Fig. 4). At the upper and lower site, the K concentration increased significantly ($P < 0.001$ at both sites) from May to November during the first year and then decreased during winter period. At the upper site, the concentration did not show significant seasonal fluctuations during the second and the third years. At the lower site, on the other hand, the K concentration increased significantly from May to November during the second ($P < 0.001$) and the third years ($P < 0.001$) but the concentration in November was leveled off from the first to the third years.

The K concentration at the end of the late phase (i.e., the end of the experiment, the 35th month) was 1.2 ± 0.3 mg/g (mean ± standard deviation) at the upper site and 2.1 ±

0.6 mg/g at the lower site. The final concentration was significantly ($P < 0.01$) lower at the upper site than at the lower site.

Calcium dynamics

Initial Ca concentration (C_0) ranged from 5.0 mg/g in *Castanea crenata* to 26.1 mg/g in *Swida controversa*, with a mean ± standard deviation of 12.3 ± 5.6 mg/g (Table 2). Two phases were observed in Ca dynamics of seven litter types (*Mallotus japonicus*, *Castanea crenata*, *Quercus crispula*, *Betula grossa*, *Acer rufinerve*, *Cryptomeria japonica*, *Fagus crenata*) (Fig. 5). The initial phase was characterized by the increase in Ca concentration over 5 to 21 months. The late phase was characterized by the decrease in the concentration. In *Pterostyrax hidpida*, *Magnolia obovata*, and *Acer mono* var. *marmoratum* f. *dissectum*, the Ca dynamics were characterized by the decrease in Ca concentration (the late phase) only. Four litter types (*Swida controversa*, *Carpinus laxiflora*, *Pterocarya rhoifolia*, *Aesculus turbinata*) showed different patterns of Ca dynamics between the sites: a two-phase pattern at the upper site and a one-phase pattern at the lower site. Calcium mass of all litter types decreased during decomposition.

The initial phase slope (IPS) of Ca varied from 0.024 to 0.131 at the upper site and from 0.017 to 0.218 at the lower site (Table 2). The IPS was not significantly different between the upper and the lower site. The initial Ca concentration for the initial phase (C_0) was not significantly correlated with IPS at both sites (Fig. 6).

The late phase slope (LPS) of Ca varied from −0.532 to −0.072 at the upper site and from −0.571 to −0.049 at the lower site (Table 2). The LPS was not significantly different between the upper and the lower site. The initial Ca concentration for the late phase (C_{max}) was significantly and negatively correlated with LPS at both sites (Fig. 6).

The Ca concentration at the end of the experiment (at the 35th month) was 5.7 ± 1.3 mg/g (mean ± standard deviation) at the upper site and 3.9 ± 1.8 mg/g at the lower site.

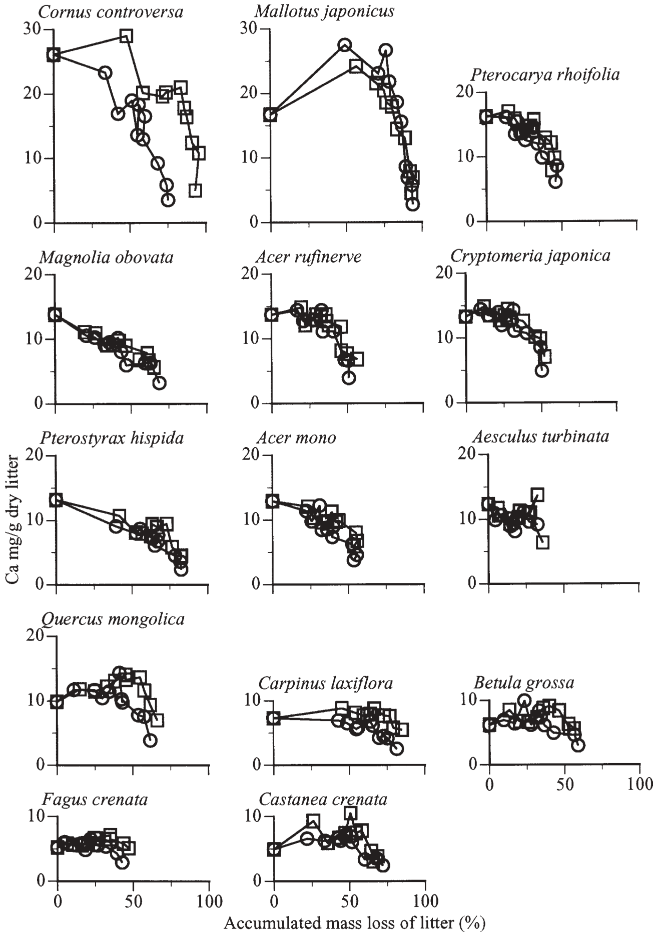

Fig. 5. Changes in Ca concentration as related to accumulated mass loss of litter. □ upper, ○ lower site

Table 2. Initial concentration for the initial phase (C_0), initial phase slope (IPS), initial concentration for late phase (C_{max}), and late phase slope (LPS) of Ca concentration dynamics

Litter type	Initial phase			Late phase			
	C_0	Upper IPS	Lower IPS	Upper		Lower	
				C_{max}	LPS	C_{max}	LPS
Mallotus japonicus	16.7	0.131	0.218	24.1	−0.532	27.5	−0.571
Swida controversa	26.1	0.059		29.0	−0.353	26.1	−0.286
Pterostyrax hispida	13.2			13.2	−0.096	13.2	−0.118
Carpinus laxiflora	7.3	0.033		8.8	−0.072	7.3	−0.049
Castanea crenata	5.0	0.065	0.036	10.6	−0.387	7.2	−0.197
Magnolia obovata	13.8			13.8	−0.112	13.8	−0.136
Quercus crispula	9.9	0.082	0.067	14.0	−0.295	14.3	−0.357
Acer mono var. *marmoratum* f. dissectum	12.9			12.9	−0.112	12.9	−0.164
Betula grossa	6.2	0.053	0.131	9.1	−0.240	9.9	−0.150
Acer rufinerve	13.7	0.057	0.041	14.9	−0.203	14.4	−0.266
Cryptomeria japonica	13.3	0.128	0.116	14.9	−0.154	14.5	−0.188
Pterocarya rhoifolia	16.2	0.052		17.0	−0.228	16.2	−0.206
Fagus crenata	5.2	0.052	0.249	7.2	−0.133	6.6	−0.144
Aesculus turbinata	12.4	0.024		13.7	−0.378	12.4	−0.056
Mean	12.3	0.067	0.123	14.5	−0.235	14.3	−0.206
Standard deviation	5.6	0.035	0.084	5.9	0.137	6.1	0.135

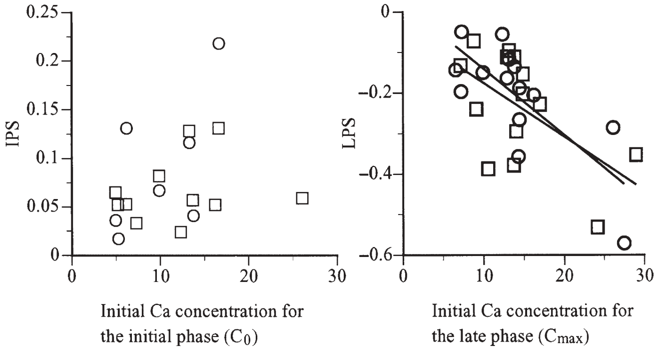

Fig. 6. Slopes of Ca concentration dynamics during the initial (*IPS*) and late phase (*LPS*) as related to the initial Ca concentration for each phase. Concentration of Ca is in mg/g. IPS, upper: $R = 0.23$, $n = 11$, nonsignificant; lower: $R = 0.62$, $n = 7$, nonsignificant. LPS, upper: $R = -0.57$, $n = 14$, $P < 0.05$; lower: $R = -0.75$, $n = 14$, $P < 0.01$. □ upper, ○ lower site

The final concentration was significantly ($P < 0.01$) higher at the upper site than at the lower site. The standard deviation of the final concentration at both sites was significantly (*F* test, $P < 0.01$ at both sites) lower than that of the initial concentration (C_0).

Magnesium dynamics

Initial Mg concentration (C_0) ranged from 1.2 mg/g in *C. japonica* to 4.7 mg/g in *Pterostyrax hispida*, with a mean ± standard deviation of 2.6 ± 1.1 mg/g (Table 3). Two phases were observed in Mg dynamics of most litter types (Fig. 7). The initial phase was characterized by a decrease in mass and concentration. The late phase was characterized by a slow mass loss and increase in concentration. *Quercus crispula* at both sites showed no initial phase of Mg, with concentration increasing over the decomposition period. *Acer rufinerve* at the upper site and *Pterocarya rhoifolia* at both sites showed no late phase of Mg, with concentrations decreasing over the decomposition period.

The initial phase slope (IPS) of Mg varied from −0.146 to −0.011 at the upper site and from −0.270 to −0.019 at the lower site (Table 3). The IPS was significantly ($P < 0.05$) higher at the upper site than at the lower site. No significant relationships were detected between the initial Mg concentration for the initial phase (C_0) and the IPS (Fig. 8), as *Aesculus turbinata* at both sites and *Fagus crenata* at the lower site had high IPS (i.e., rapid leaching). When these results were omitted in the analysis, however, *r* values were improved and the negative relationship was significant at the lower site and was significant, but only marginally, at the upper site. Accumulated mass loss of litter at the end of the initial phase varied from 3.8% (*F. crenata* at the lower site) to 70.1% (*Mallotus japonicus* at the upper site).

The late phase slope (LPS) of Mg varied from 0.009 to 0.027 at the upper site and from 0.002 to 0.026 at the lower site (Table 3). The LPS was significantly ($P < 0.01$) higher at the upper site than at the lower site. No significant relationships were detected between C_{min} and LPS at the upper site, while the negative relationship was significant at the lower site (Fig. 8).

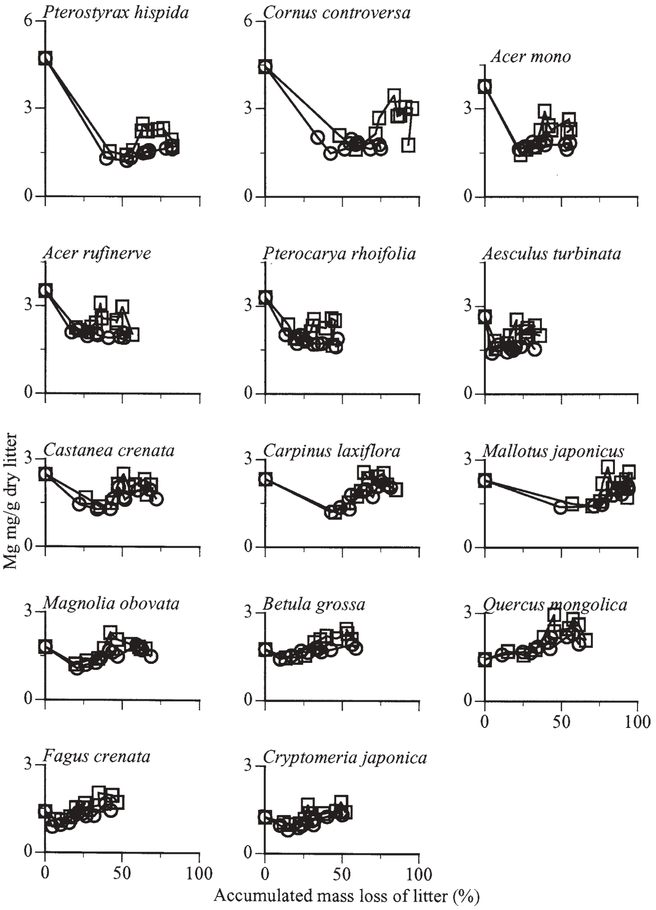

Fig. 7. Changes in Mg concentration as related to accumulated mass loss of litter. □ upper, ○ lower site

The Mg concentration at the end of the late phase (at the 35th month) was 1.8 ± 0.2 mg/g at the upper site and 1.7 ± 0.2 mg/g (mean ± standard deviation) at the lower site. The final concentration was significantly ($P < 0.05$) higher at the upper site than at the lower site. The standard deviation of the final concentration at both sites was significantly (*F* test, $P < 0.001$ at both sites) lower than that of the initial concentration (C_0).

Discussion

In the present study we describe general patterns for the dynamics of K, Ca, and Mg in a cool temperate forest in Japan and demonstrate that the initial concentrations (C_0) of K and Mg and the critical concentrations (C_{min} or C_{max}) of Ca and Mg were predictable for the pattern of change in concentrations during decomposition. The final concentrations were not dependent on the initial concentrations but on site conditions. We also confirmed the applicability of the method of Laskowski et al. (1995a) to the initial phase of K dynamics and the initial and late phase of Ca and Mg

Table 3. Initial concentration for the initial phase (C_0), initial phase slope (IPS), initial concentration for late phase (C_{min}), and late phase slope (LPS) of Mg concentration dynamics

Litter type	Initial phase			Late phase			
				Upper		Lower	
	C_0	Upper IPS	Lower IPS	C_{min}	LPS	C_{min}	LPS
Mallotus japonicus	2.3	−0.013	−0.019	1.4	0.024	1.4	0.017
Swida controversa	4.4	−0.048	−0.070	1.6	0.026	1.5	0.002
Pterostyrax hispida	4.7	−0.067	−0.071	1.4	0.009	1.2	0.014
Carpinus laxiflora	2.3	−0.025	−0.026	1.2	0.025	1.2	0.026
Castanea crenata	2.5	−0.031	−0.037	1.4	0.018	1.3	0.012
Magnolia obovata	1.8	−0.030	−0.035	1.2	0.012	1.1	0.012
Quercus crispula	1.4			1.4	0.019	1.4	0.013
Acer mono var. *marmoratum* f. dissectum	3.8	−0.099	−0.097	1.4	0.027	1.6	0.002
Betula grossa	1.7	−0.021	−0.034	1.5	0.021	1.4	0.008
Acer rufinerve	3.5	−0.011	−0.036	2.0		1.9	0.008
Cryptomeria japonica	1.2	−0.015	−0.030	1.0	0.014	0.8	0.017
Pterocarya rhoifolia	3.3	−0.013	−0.025	1.7		1.6	
Fagus crenata	1.4	−0.030	−0.137	1.1	0.020	0.9	0.017
Aesculus turbinata	2.6	−0.146	−0.270	1.6	0.020	1.4	0.008
Mean	2.6	−0.042	−0.068	1.4	0.020	1.3	0.012
Standard deviation	1.1	0.040	0.070	0.3	0.006	0.3	0.007

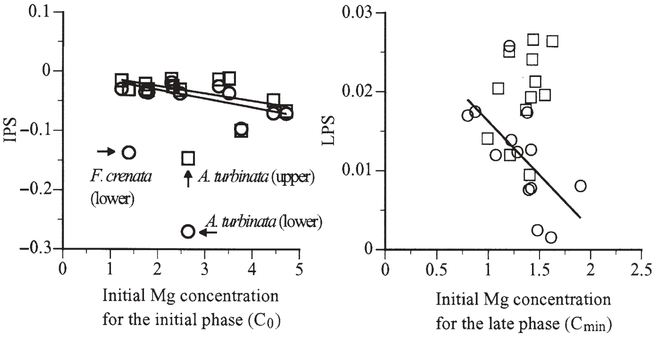

Fig. 8. Slopes of Mg concentration dynamics during the initial (*IPS*) and late phase (*LPS*) as related to the initial Mg concentration for each phase. Concentration of Mg is in mg/g. *Arrows* indicate data for *Fagus crenata* at the lower site and *Aesculus turbinata* at both sites. The *lines* are the regression equations with these data excluded. IPS, upper: $R = -0.57$, $n = 12$, $P = 0.06$; lower: $R = -0.70$, $n = 11$, $P < 0.05$. LPS, upper: $R = -0.39$, $n = 12$, nonsignificant; lower: $R = -0.60$, $n = 13$, $P < 0.05$. □ upper, ○ lower site

dynamics. However, the model did not hold in the late phase of K dynamics because the pattern of changes in K concentration was characterized by seasonal fluctuations rather than gradual increase with respect to accumulated mass loss of litter.

Laskowski et al. (1995a) estimated the equilibrium level of K concentration at which no change in concentration should be observed. The equilibrium level was estimated by solving the regression equation for initial K concentrations for the late phase with LPS set to zero. In the present study, however, we did not estimate this equilibrium concentration for K, Ca, and Mg because of extrapolation of the estimation.

Potassium was leached out from litter during the first 5 months and the decrease was correlated to the initial concentration for the initial phase. This result is consistent with previous studies (Gosz et al. 1973; Lousier and Parkinson 1978; Laskowski et al. 1995a; Adams and Angradi 1996; Liu et al. 2000). Potassium is not a structural material and exists mainly in solution in plant cells. Mobile K thus leached out quickly from decomposing litters. The late phase of K dynamics was, on the other hand, characterized by seasonal changes. A similar seasonal pattern has been reported in decomposing litter of *Betula pubescens* in Sweden (Berg and Staaf 1987). The seasonal fluctuation of K concentration in litter may be ascribed to leaching of K from the forest canopy and accumulation in the forest floor during the growing season and leaching from the forest floor at snow melt. Potassium concentration of canopy throughfall fluctuated seasonally with the peak during autumn (Iwatsubo and Tsutsumi 1968; Katagiri and Tsutsumi 1976). The decreasing trend of K concentration in November from the first to third year may be due to the downward movement of the decomposing litter. The K concentration was lower at the upper site than at the lower site, indicating the hygrological movement of K along the forest slope.

Calcium dynamics in decomposing litter showed either increase and decrease phases or the decrease phase only. Previous studies have also observed the two-phase pattern (Attiwill 1968; Lousier and Parkinson 1978; Berg and Staaf 1987; Berg et al. 1987; Laskowski and Berg 1993; Berg and Cortina 1995; Edmonds and Thomas 1995; Hasegawa and Takeda 1997; Bhatta et al. 2000) or the one-phase pattern (MacLean and Wein 1978; Edmonds 1984; Arianoutsou 1993; Adams and Angradi 1996). Calcium concentration of initial litter was not predictable for the pattern of change of Ca concentration nor IPS of Ca dynamics. This may be because Ca is covalently bonded to pectin within the middle lamella in litter. Leaching or decomposition of more readily available organic components may cause the relative increase in Ca concentration without a net increase in Ca mass, independent of initial Ca content. In the late phase of Ca dynamics, on the other hand, the release of Ca was dependent on the decomposition of structural components and the initial Ca concentration for the late phase (C_{max}) could predict LPS of Ca dynamics.

Magnesium dynamics in decomposing litter showed two phases; the initial leaching phase and the late immobilization phase. This pattern of change of Mg concentration has been reported in previous studies (Attiwill 1968; Edmonds 1984; Berg et al. 1987; Blair 1988; Laskowski and Berg 1993; Hasegawa and Takeda 1997; Salamanca et al. 1998). Magnesium is not a structural material and exists mainly in solution in plant cells and thus leached out from litter in the initial phase of decomposition. Litters of *Fagus crenata* and *Aesculus turbinata* showed high leaching of Mg in spite of their low initial concentration. Excluding these data yielded the result that the rate of concentration change was dependent on the initial Mg concentration for the initial phase. In the late phase of Mg dynamics, a slight increase in concentration was observed. The initial Mg concentration for the late phase (C_{min}) was correlated with LPS at the lower site, while the relationship was not significant at the upper site. This suggests that C_{min} of Mg was not necessarily predictable for the rate of concentration change.

Litter was transformed to humus components during decomposition and provided a large quantity of negatively charged exchange sites (Staaf and Berg 1982). These cation exchange sites are capable of holding cations released from litter. In the study site, litters showed a convergent trend of K, Ca, and Mg concentrations at the end of study period compared with the concentrations in initial litter. The convergent concentrations of these elements were significantly different between upper and lower site, suggesting that cation exchange capacity of humus substances formed during litter decomposition depends on site conditions rather than initial litter quality. The concentrations of K, Ca, and Mg in decomposing litters may reach to the value of the underlying layer. Laskowski et al. (1995a) estimated the equilibrium value of K concentration for Scots pine litter to be 0.78 mg/g dry litter, which was close to the measured value of the humus layer in a Scots pine stand (0.93 mg/g).

The mobility of nutrient was in the order K > Mg > Ca. The same order has also been reported previously (Lousier and Parkinson 1978; Edmonds 1984; Maheswaran and Attiwill 1987; Blair 1988; O'Connell 1988; Laskowski et al. 1995b; Rutigliano et al. 1998; Salamanca et al. 1998; Bhatta et al. 2000). This difference in mobility can be ascribed to the distribution of nutrients within plant tissues and the electric charge of ions as discussed above. In summary, the pattern of change in K concentration was determined by water movement rather than microbial decomposition, that of Mg by water movement first and then microbial decomposition, and that of Ca mostly by microbial decomposition. The dynamics of these cationic nutrients are in contrast to nitrogen and phosphorus, which are immobilized as a major constituent of soil organic matter or microbial biomass during decomposition (Osono and Takeda, unpublished). Further studies are required to assess whether the results of the present study can be applied to litter decomposition in other temperate forests.

Acknowledgments We thank Dr. S. Kojima for his valuable suggestions on Ca dynamics; members of the Laboratory of Forest Ecology for help with the fieldwork and useful discussions. This study received partial financial support from International Geosphere Biosphere Program-MESSC (IGBP-MESSC) and from the Japanese Ministry of Education, Culture, Sports, Science and Technology (No. 08308030).

Literature cited

Adams MB, Angradi TR (1996) Decomposition and nutrient dynamics of hardwood leaf litter in the Fernow Whole-Watershed Acidification Experiment. For Ecol Manage 83:61–69

Arianoutsou M (1993) Leaf litter decomposition and nutrient release in a maquis (evergreen sclerophyllous) ecosystem of north-eastern Greece. Pedobiologia 37:65–71

Attiwill PM (1968) The loss of elements from decomposing litter. Ecology 49:142–145

Berg B, Cortina J (1995) Nutrient dynamics in some decomposing leaf and needle litter types in a *Pinus sylvestris* forest. Scand J For Res 10:1–11

Berg B, Staaf H (1987) Release of nutrients from decomposing white birch leaves and Scots pine needle litter. Pedobiologia 30:55–63

Berg B, Staaf H, Wessén B (1987) Decomposition and nutrient release in needle litter from nitrogen-fertilized Scots pine (*Pinus sylvestris*) stands. Scand J For Res 2:399–415

Bhatta BK, Takeda H, Tokuchi N (2000) Effect of soil nitrogen on decomposition and nutrient dynamics of Japanese black pine litter. Appl For Sci Kansai 9:75–81

Blair JM (1988) Nutrient release from decomposing litter of three tree species with special reference to calcium, magnesium and potassium dynamics. Plant Soil 110:49–55

Chapin FS III (1991) Effects of multiple environmental stresses on nutrient availability and use. In: Mooney HA, Winner WE, Pell EJ (eds) Response of plants to multiple stresses. Academic, San Diego, pp 67–88

Crossley DAJ, Hoglund MP (1962) A litter bag method for the study of microarthropods inhabiting leaf litter. Ecology 43:571–573

Edmonds RL (1984) Long-term decomposition and nutrient dynamics in Pacific silver fir needles in western Washington. Can J For Res 14: 395–400

Edmonds RL, Thomas TB (1995) Decomposition and nutrient release from green needles of western hemlock and Pacific silver fir in an old-growth temperate rain forest, Olympic National Park, Washington. Can J For Res 25:1049–1057

Gosz JR, Likens GE, Bormann FH (1973) Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest, New Hampshire. Ecol Monogr 43:173–191

Hasegawa M, Takeda H (1997) Carbon and nutrient dynamics in decomposing pine needle litter in relation to fungal and faunal abundances. Pedobiologia 40:171–184

Iwatsubo G, Tsutsumi T (1968) On the amount of plant nutrients supplied to the ground by rainwater in adjacent open plot and forests. II (in Japanese with English abstract). Bull Kyoto Univ For 40:110–124

Katagiri S, Tsutsumi T (1976) The relationship between site condition and circulation of nutrients in forest ecosystems. IV. The amount of mineral nutrient returned to forest floor (in Japanese with English abstract). J Jpn For Soc 58:79–85

Laskowski R, Berg B (1993) Dynamics of some mineral nutrients and heavy metals in decomposing forest litter. Scand J For Res 8:446–456

Laskowski R, Berg B, Johansson M, McClaugherty C (1995a) Release pattern for potassium from decomposing forest needle and leaf litter: long-term decomposition in a Scots pine forest. IX. Can J Bot 73: 2019–2027

Laskowski R, Niklinska M, Maryanski M (1995b) The dynamics of chemical elements in forest litter. Ecology 76:1393–1406

Likens GE, Bormann FH (1995) Biogeochemistry of a forested ecosystem. Springer, Heidelberg, Berlin, New York

Liu W, Fox JED, Xu Z (2000) Leaf litter decomposition of canopy trees, bamboo and moss in a montane moist evergreen broad-leaved forest on Ailao Mountain, Yunnan, south-west China. Ecol Res 15: 435–447

Lousier JD, Parkinson D (1978) Chemical element dynamics in decomposing leaf litter. Can J Bot 56:2795–2812

MacLean DA, Wein RW (1978) Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. Can J Bot 56:2730–2749

Maheswaran J, Attiwill PM (1987) Loss of organic matter, elements, and organic fractions in decomposing *Eucalyptus microcarpa* leaf litter. Can J Bot 65:2601–2606

O'Connell AM (1988) Nutrient dynamics in decomposing litter in karri (*Eucalyptus diversicolor* f. Muell.) forests of south-western Australia. J Ecol 76:1186–1203

Osono T, Takeda H (2001) Organic chemical and nutrient dynamics in decomposing beech leaf litter in relation to fungal ingrowth and succession during 3-year decomposition processes in a cool temperate deciduous forest in Japan. Ecol Res 16:649–670

Rutigliano FA, Alfani A, Bellini L, Virzo de Santo A (1998) Nutrient dynamics in decaying leaves of *Fagus sylvatica* L. and needles of *Abies alba* Mill. Biol Fertil Soils 27:119–126

Salamanca EF, Kaneko N, Katagiri S, Nagayama Y (1998) Nutrient dynamics and lignocellulose degradation in decomposing *Quercus serrata* leaf litter. Ecol Res 13:199–210

Satake Y, Hara H, Watari S, Tominari T (1989) Wild flowers of Japan: woody plants (in Japanese). Heibonsha, Tokyo

Slovic S (1997) Tree physiology. In: Huttl RF, Schaaf W (eds) Magnesium deficiency in forest ecosystems. Kluwer Academic, Dordrecht, pp 101–214

Staaf H, Berg B (1982) Accumulation and release of plant nutrients in decomposing Scots pine needle litter: long-term decomposition in a Scots pine forest II. Can J Bot 60:1561–1568

Takeda H, Kaneko N (1988) Patterns of humus accumulation in forests. I. Mull and moder type humus in a broad-leaved forest (in Japanese with English abstract). Bull Kyoto Univ For 60:33–45

Tateno R, Takeda H (2003) Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. Ecol Res, in press