



Title	Decomposition Process and Dynamics of Nutrient Elements in Deciduous Broad-leaved Forests and Evergreen Coniferous Forests of Northern Hokkaido, Japan
Author(s)	HARDIWINOTO, Suryo
Citation	北海道大學農學部 演習林研究報告, 48(2), 325-353
Issue Date	1991-09
Doc URL	http://hdl.handle.net/2115/21344
Type	bulletin (article)
File Information	48(2)_P325-353.pdf



[Instructions for use](#)

Decomposition Process and Dynamics of Nutrient Elements in Deciduous Broad-leaved Forests and Evergreen Coniferous Forests of Northern Hokkaido, Japan *

By

Suryo HARDIWINOTO **

北海道北部の落葉広葉樹林と常緑針葉樹林における
葉と枝の分解*及びその養分動態

スルヨ ハルディウイノト**

Abstract

The decomposition process of leaves and branches, and the dynamics of such nutrient elements as nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) during the decomposition were studied in the deciduous broad-leaved forests (P1 and P2) and the evergreen coniferous forests (P3 and P4).

Leaves of broad-leaved tree species (*Quercus mongolica* var. *grosseserrata* and *Betula platyphylla* var. *japonica*) in P1 decomposed significantly faster than those in P2, P3 and P4. Leaves of the undergrowth of *Sasa senanensis* (Ss L) also tended to decompose faster in P1 than those in P4. On the other hand, needles of coniferous tree species (*Abies sachalinensis* and *Picea glehnii*) in P3 and P4 decomposed significantly faster than those in P1 and P2. In all study sites, leaves of *Q. mongolica* var. *grosseserrata* (Qm L) showed the fastest-decomposition, followed by those of *B. platyphylla* var. *japonica* (Bp L), *P. glehnii* (Pg L), with needles of *A. sachalinensis* (As L) showing the slowest. The leaves decomposed seasonally, with high mass decreases during the snow cover season. Decomposition rates of branches were very slow, and generally showed no obvious differences among the study sites.

Concentrations of N, P and Ca in the Qm L, Bp L, As L and Pg L showed similar trends, with a tendency to increase after 7, 12 and 19 months of decomposition. In the Ss L, the concentrations of N and P decreased after 7 months elapsed, while those of Ca showed no definite changes during decomposition. Concentrations of K decreased sharply from the first sampling date (after 7 months of decomposition); while those of Mg

Received March 30, 1991.

- * This paper is a part of the Doctoral thesis in Agriculture of Hokkaido University, Japan.
- ** Laboratory of Silviculture, Faculty of Agriculture, Hokkaido University, Sapporo 060, JAPAN.
北海道大学農学部林学科造林学講座
Present address: Faculty of Forestry, Gadjah Mada University, Yogyakarta, INDONESIA.

showed no obvious changes during decomposition. Although there were some increases in the absolute amounts of N and Ca, as a result of the leaf mass decreases, they generally decreased during decomposition.

Key words : Decomposition process, Leaves, Branches, Nutrient elements.

1. Introduction

The decomposition of plant litter is one of the most important stages in the biogeochemical cycle of forest ecosystems. The decomposition rate determines the rate at which nutrients become available for renewed uptake by plants (DECATANZARO and KIMMINS, 1985). The rates of breakdown of organic matter by microbes depend on the quality of the material, the microbial activities and the environmental conditions (WITKAMP, 1969; BINKLEY, 1986), and they vary greatly from place to place (OLSON, 1963). Studies on the decomposition process of plant litter, have already been carried out in various types of forest in relation to both litter quality (chemical and physical properties) and environmental factors such as temperature, humidity and precipitation.

EDMONDS (1979) who investigated the decomposition rates of needle litter in an age sequence of Douglas-fir stands found that the maximum decomposition rate occurred in the 24-year old stand, after 2 years. But DECATANZARO and KIMMINS (1985) found no significant difference in decomposition rate of conifer foliage which decomposed in sites located along a topographic sequence of forest ecosystems in the University of British Columbia Research Forest. Decomposition of Douglas-fir needle litter on the Andrews Experimental Forest, west Oregon, was highly correlated with temperature and humidity (FOGEL and CROMACK, 1977). In Alaskan taiga forest ecosystems, FLANAGAN and VAN CLEVE (1983) found that the decomposition rate was highest in sites with the highest concentration of fungal tissue per gram of organic matter.

FLANAGAN and VAN CLEVE (1983) recognized that the major factor determining the rate of decay of a particular substrate is the quality of the substrate itself. TAKEDA et al. (1987) reported that leaf hardness and such chemical properties as initial contents of lignin, cellulose, soluble carbohydrates and soluble wax were significantly related to the decomposition rates of leaf litter. FOGEL and CROMACK (1977) found that the rate of annual weight loss of Douglas-fir litter in western Oregon was more influenced by lignin content than by C : N ratio. Needles of coniferous trees generally decompose more slowly than leaves of deciduous trees (WILLIAMS and GRAY, 1974).

In Japan, ANDO (1970) determined the decomposition rates of leaf litter using fine and coarse mesh litterbags in some evergreen coniferous forests. KAWAHARA and SATO (1974), and KAWAHARA (1975) studied the decomposition rates of *Magnolia obovata*, *Cyclobalanopsis glauca* and mixed leaf litter. The decay rates of wood litter were studied by YONEDA (1975a, 1975b), and YONEDA and KIRITA (1978). TAKEDA et al. (1987) investigated the decomposition of leaf litter in relation to litter quality and site conditions. However, few studies on the dynamics of nutrient elements during the decomposition of plant litter have been carried out.

In Hokkaido, the northernmost main island of Japan, a few studies have been made on the decomposition of plant litter such as SIMARANGKIR and IGARASHI (1986, 1987), and they

reported the decomposition process of plant litter in an evergreen coniferous forest which lies in a sub-arctic zone; while data on the decomposition process in deciduous broad-leaved forests and the dynamics of nutrient elements during the decomposition of the litter have not yet been obtained. Thus the data sets about the decomposition of plant litter are not sufficient enough in Hokkaido. The purposes of this study are to clarify:

1) the decomposition rates of leaves and branches of broad-leaved and coniferous tree species and the undergrowth of *Sasa senanensis*, 2) the release of such nutrient elements as N, P, K, Ca and Mg during decomposition of the leaves in the deciduous broad-leaved forests and the evergreen coniferous forests which are located in the northern part of the island.

2. Study area, materials and methods

This study was carried out in the Moshiri district, at the Uryu Experiment Forest of Hokkaido University. It is situated approximately at E 142°1' - 20', N 44°3' - 29', and has an elevation range of about 175-900 m above sea level. Four study plots, P1, P2, P3 and P4 were established in May, 1987. General climatic conditions and stand structure of the study sites have previously been reported (HARDIWINOTO, 1991). P1 was classified as a *Quercus mongolica* var. *grosseserrata* forest, P2 as a *Betula platyphylla* var. *japonica* forest, P3 as an *Abies sachalinensis* forest, and P4 as a *Picea glehnii* forest.

Leaves of *Q. mongolica* var. *grosseserrata* (Qm L) and *B. platyphylla* var. *japonica* (Bp L), and needles of *A. sachalinensis* (As L) and *P. glehnii* (Pg L), as well as branches of *Q. mongolica* var. *grosseserrata* (Qm Br), *B. platyphylla* var. *japonica* (Bp Br), *A. sachalinensis* (As Br) and *P. glehnii* (Pg Br) were obtained from their parent trees prior to abscission, during the last week of July, 1988. In addition to this, leaves (Ss L) and culms (Ss Cl) of the undergrowth *Sasa senanensis* were also taken at the same time. The materials were brought to the laboratory, and air dried. Branches which have diameter of less than 1 cm were cut into lengths of 2-7cm.

In this study, 1-mm mesh litter bags, sized 20 cm × 20 cm, were used. The air dried materials were weighed to the equivalent of 10 g oven-dried weight, and put into the litter bags. In the field, L-layer of forest floor of the study plots was removed before placement of the litter bags. The bags were placed on the forest floor of the DBF (P1 and P2) and the ECF (P3 and P4), with the following treatments.

A: The litter bags containing leaves and branches of each species were placed on October 30-31, 1988 on the forest floor of P1, P2, P3 and P4. The leaf litter bags were collected at the end of May, 1989, the end of October, 1989, the end of May, 1990 and the end of October, 1990, or after 7, 12, 19, and 24 months of decomposition respectively. On the other hand, the branch litter bags were collected only at the end of October, 1989 and 1990 (after 12 and 24 months of decomposition).

B: In order to quantify rates of monthly decomposition during the snowless season, five leaf litter bags from each species were placed at the end of May, 1989, and collected at the end of June, 1989 (one month later). At the same time, new litter bags were placed which would be collected at the end of the following month. The placement and collection were carried out until end of September, and October, 1989, respectively.

C: Ten leaf litter bags from each species were placed at the end of May, 1989. The litter bags were then collected at the end of October, 1989 and the end of May, 1990. The results of this treatment were compared with results from treatment A over the same period (one year) of decomposition.

In the treatments B and C, leaf litter bags of *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica*, *A. sachalinensis* and *P. glehnii* were placed on the forest floor of P1, P2, P3, and P4, respectively. Each of the collection in the three treatments, five litter bags from each species were taken and brought to the laboratory. The remaining mass in the litter bags was transferred into paper bags, and was oven-dried at 85°C for about three days before weighing. Mass losses during the decomposition were calculated by subtracting the remaining mass from the initial weight.

In order to clarify the release of nutrient elements during the decomposition, the remaining mass of the leaves was analyzed for the concentrations of N, P, K, Ca and Mg. The concentration of nitrogen was determined by an automatic micro-Kjeldal method, while that of phosphorus by molybdenum yellow colorimetric method. Contents of potassium were analysed by a flame photometric method, and those of calcium and magnesium by atomic absorption spectrophotometry. Changes in amounts which are sometimes referred to as "absolute" amounts (MacLean and Wein, 1978) of nutrient elements during the decomposition are expressed as absolute amounts per litter bag.

3. Results

3.1 Decomposition of leaves and branches

Fig. 1a illustrates weight loss of *Q. mongolica* var. *grosseserrata* leaves in different study plots (P1, P2, P3, and P4). After 12, 19 and 24 months of decomposition, leaves of *Q. mongolica* var. *grosseserrata* in P1 decomposed significantly (t-test, $P < 0.01$) faster than those in P2, P3 and P4 (Fig. 1). After 12 months, the remaining mass was 36.5% in P1, 47.4% in P2, 44.6% in P3, and 48.3% in P4; while that after 24 months was 18.3% in P1, 32.5% in P2, 29.6% in P3 and 28.6% in P4.

In Figs. 1b and 1c, the weight losses of Bp L and Ss L in the four sites are shown. After 24 months had elapsed, it can be seen that the weight loss of Bp L in P1 was significantly higher than that in P2 ($P < 0.01$), P3 ($P < 0.05$) and P4 ($P < 0.01$), with the remaining mass of 30.7% in P1, 39.4% in P2, 35.1% in P3 and 38.5% in P4. After 12 and 19 months of decomposition, weight loss of Ss L in P1 was also higher (significant at $P < 0.01$) than that in P4, with rates of 47.1 and 53.5% in P1, and 41.8 and 45.0% in P4, respectively; though there was no significant difference after 24 months.

The weight loss of *A. sachalinensis* needles during decomposition in the four study sites is shown in Fig. 1d. After 24 months, As L in the ECF (P3 and P4) obviously decomposed faster ($P < 0.01$) than that in the DBF (P1 and P2), with mass decreases of 42.3, 42.9, 53.7 and 50.7% in P1, P2, P3 and P4, respectively. After 19 and 24 months of decomposition, Pg L also showed similar rates in their decomposition. The weight loss was significantly higher ($P < 0.01$) in P3 and P4 than that in P1 and P2 (Fig. 1e), with the remaining mass after 19 months of 56.2% in P1, 58.1% in P2, 46.1% in P3, and 50.4% in P4; that after 24 months was 51.6% in P1, 53.2% in P2, 35.0% in P3 and 38.3% in P4.

Branches and culms were very slow in their decomposition. The remaining mass of

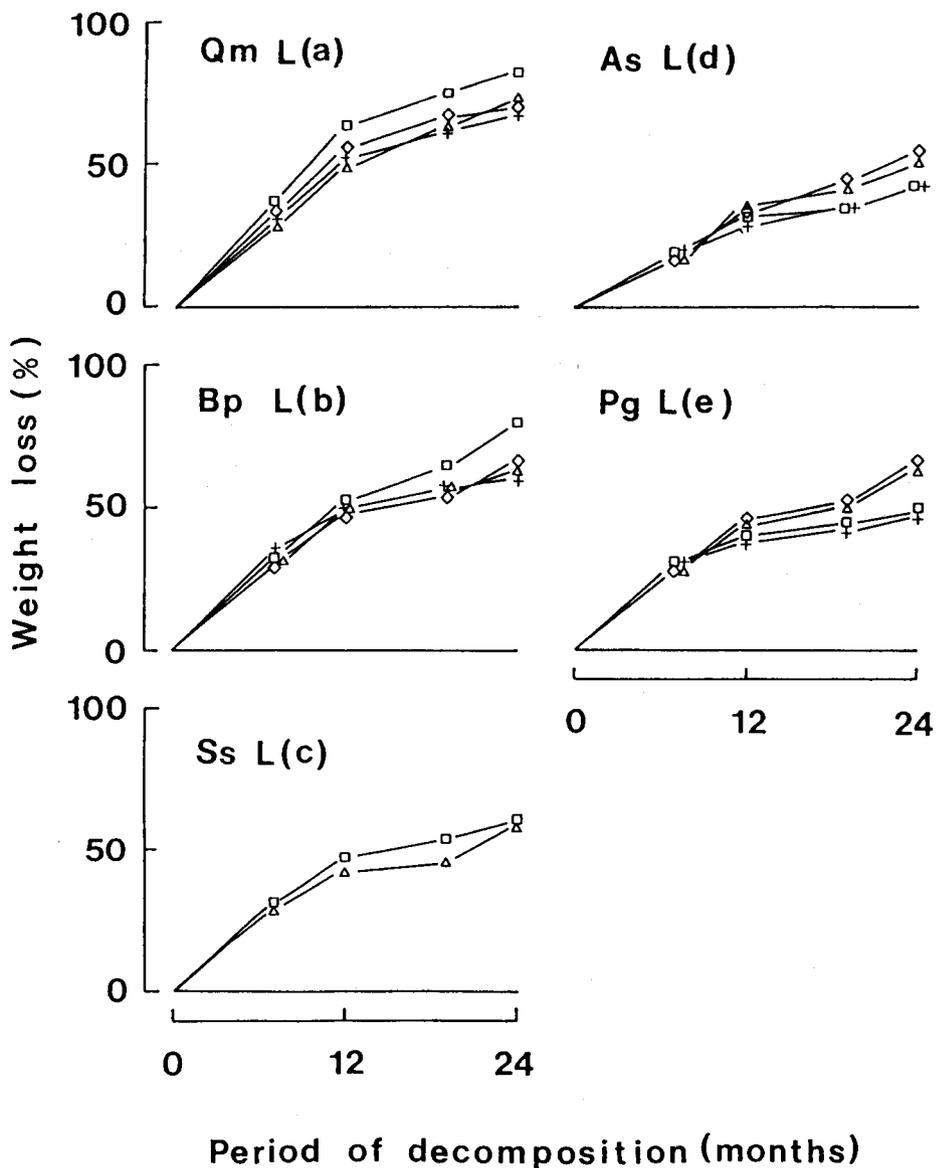


Fig. 1. Weight losses (%) of leaves of four tree species and a sasa during decomposition.

Note:

Qm L, Bp L and Ss L are leaves of *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica* and *Sasa senanensis*. As L and Pg L are needles of *Abies sachalinensis* and *Picea glehnii*, respectively.

Symbols:

□ P1, + P2, ◇ P3, △ P4

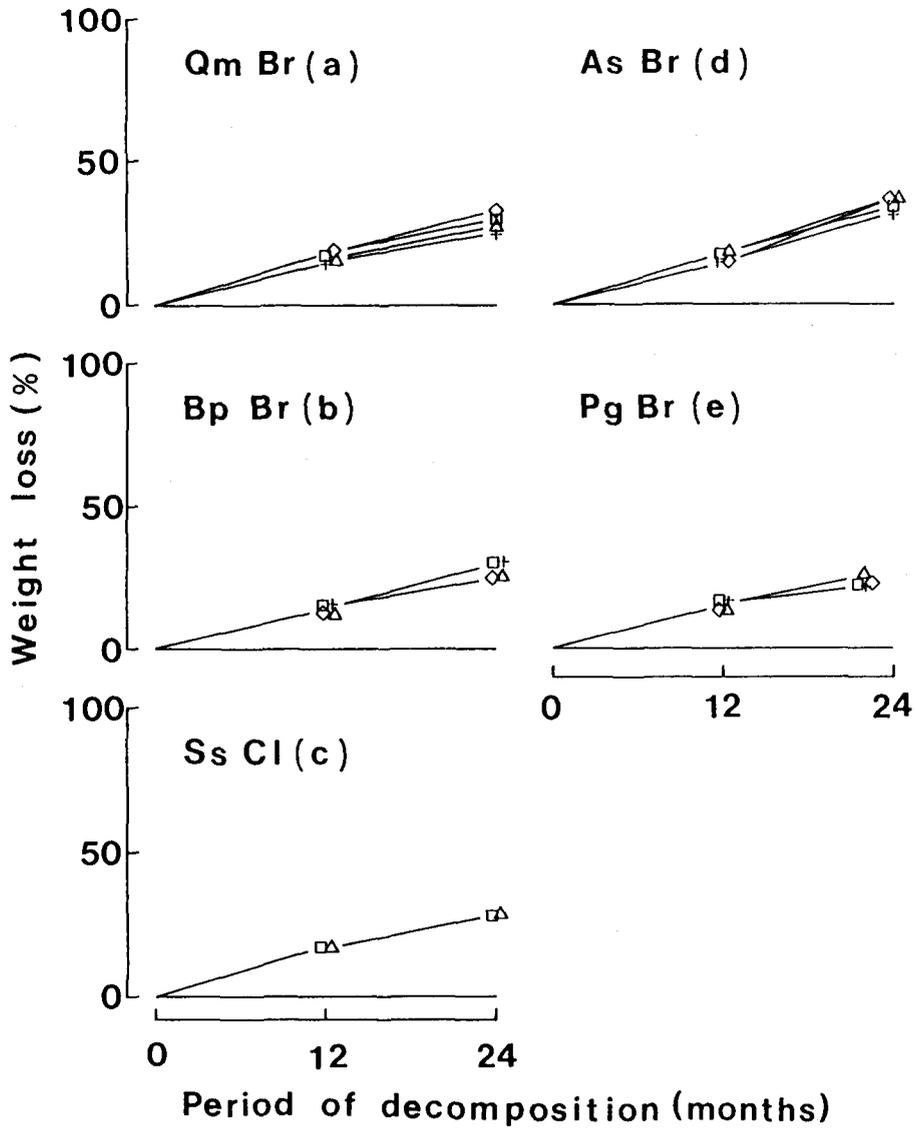


Fig. 2. Weight losses (%) of branches of four tree species and culms of sasa during decomposition.

Note:

Qm Br, Bp Br, As Br and Pg Br are branches of *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica*, *Abies sachalinensis* and *Picea glehnii*, respectively, and Ss Cl is culm of *Sasa senanensis*.

Symbols: see Fig. 1

Qm Br in the four study sites ranged from 83.0 to 85.3% after 1 year and 68.9-74.6% after 2 years, Bp Br from 85.2 to 86.1% after 1 year and 74.2-79.1% after 2 years, Ss Cl from 82.2 to 82.3% after 1 year and 71.6-72.3% after 2 years, As Br from 82.3 to 84.7% after 1 year and 74.0-77.8% after 2 years, Pg Br from 84.1 to 85.2% after 1 year and 76.3-78.4% after 2 years. The branches and culms which had decomposed in different sites (P1, P2, P3 and P4), generally showed no obvious differences in their decomposition rates (Fig. 2).

Comparing the decomposition rates of leaves and needles of the five species, Qm L, Bp L, Ss L, As L and Pg L in the same site (P1), Qm L has extremely the highest rate of weight loss during decomposition, followed by Bp L, Ss L, Pg L and the lowest rate was obtained in As L (Fig. 3a). The remaining masses of Qm L after 12 and 24 months of decomposition were 36.5 and 18.3%, respectively; while those of As L was 68.6 and 57.7%. Among Qm L, Bp L, As L and Pg L, the remaining masses were significantly different from each other ($P < 0.01$) after 19 and 24 months of decomposition.

Similarly, in P2 and P3 Qm L also showed the fastest decomposition, followed by Bp L, Pg L, with As L as the slowest (Figs. 3b and 3c). The sequence from the highest to the lowest decomposition rate in P4 was Qm L, Bp L, Pg L, Ss L and As L. After 19 months elapsed, the remaining mass of Qm L in P4 was 34.5%, while those of Bp L, Pg L, Ss L and

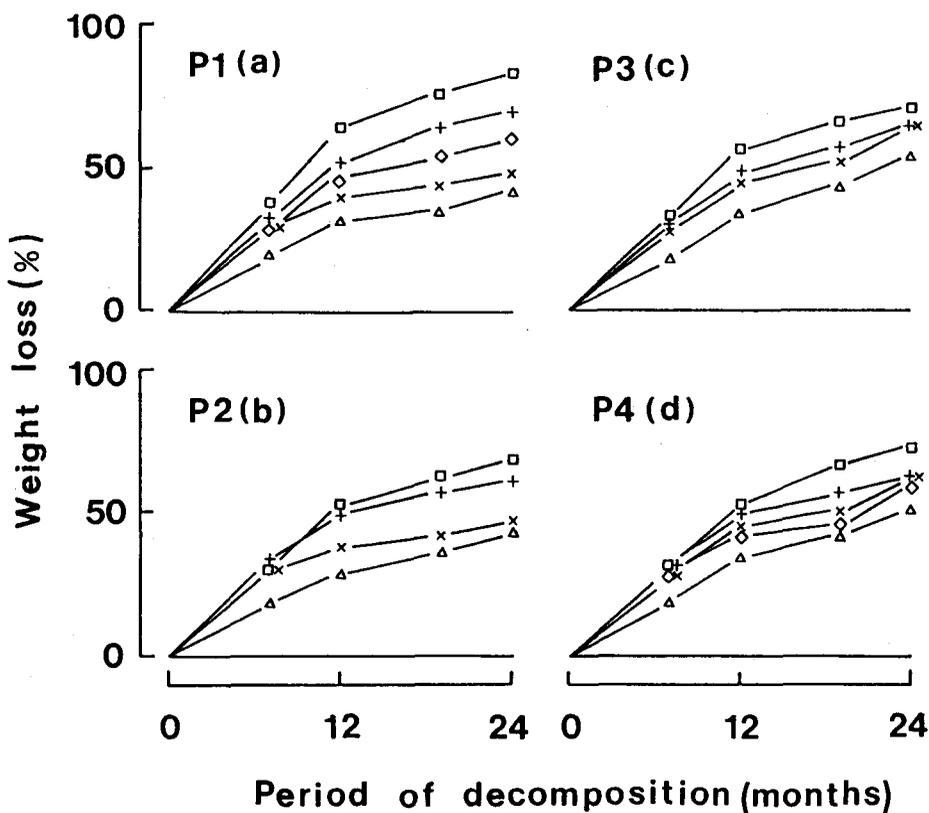


Fig. 3. Weight losses (%) of leaves in each study plot.

Symbols:

□ Qm L, + Bp L, ◇ Ss L, △ As L, × Pg L

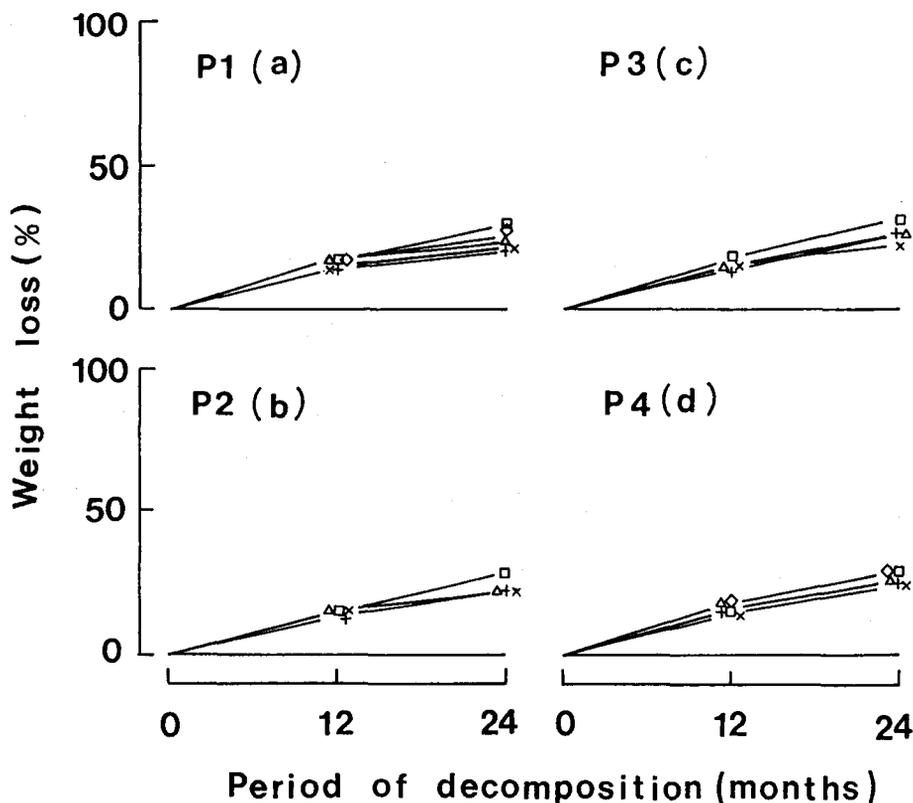


Fig. 4. Weight losses (%) of branches and culms in each study plot.
Symbols: see Fig. 3.

As L were 43.6, 50.4, 55.0 and 58.4%, respectively (Fig. 3d).

Against these, the branches of each species showed no obvious sequence in their decomposition rates after one year of decomposition, and the rates between the species were similar each other. After 2 years of decomposition Qm Br showed the fastest decomposition in all study sites, while the slowest rate of decomposition in the DBF was Bp Br, and that in the ECF was Pg Br. Among branches of the four tree species in P1 and P4, the remaining masses generally showed significant differences ($P < 0.05$) between each other, but not in P2 and P3 (Fig. 4).

Table 1 shows the remaining mass of leaves (needles) and branches of the four tree species after they had decomposed during the snow cover season and the snowless season. During the snow cover season (7 months), the remaining masses of Qm L, Bp L, As L and Pg L were 62.8, 66.1, 82.1 and 72.2%, while those of Qm Br, Bp Br, As Br and Pg Br were 90.8, 92.7, 89.3 and 89.1%, respectively. On the other hand, during the snowless season (5 months), the remaining masses of Qm L, Bp L, As L and Pg L were 51.5, 53.4, 75.2 and 69.6%, while those of Qm Br, Bp Br, As Br and Pg Br were 85.1, 89.9, 86.9 and 86.7%, respectively. During the snowless season, the average monthly rates of mass decrease in Qm L, Bp L, As L and Pg L were 9.7, 9.3, 5.0 and 6.1%, while those during the snow cover season were 5.3, 4.8, 2.5 and 4.0%, respectively.

Table 1. The remaining mass (%) of leaves and branches per period of decomposition

Study plots	The remaining mass (%) after decomposition					
	IW % (SD)	Leaves Nov.-May (SD)	Jun.-Oct. (SD)	IW % (SD)	Branches Nov.-May (SD)	Jun.-Oct. (SD)
Qm P1	100.0 (1.0)	62.8 (1.8)	51.5 (2.0)	100.0 (0.1)	90.8 (0.5)	85.1 (0.6)
Bp P2	100.0 (0.1)	66.1 (0.8)	53.4 (4.6)	100.0 (0.2)	92.7 (0.8)	89.9 (3.5)
As P3	100.0 (0.2)	82.1 (1.8)	75.2 (1.6)	100.0 (0.2)	89.3 (0.5)	86.9 (1.2)
Pg P4	100.0 (0.1)	72.2 (2.5)	69.6 (1.0)	100.0 (0.3)	89.1 (0.6)	86.7 (0.8)

Note:

Qm, Bp, As and Pg are *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica*, *A. sachalinensis* and *P. glehnii*, respectively.

Further information no monthly rates of weight loss of the four species leaves are illustrated in Table 2. Monthly values during the snow cover season were obtained by making an average rate during the non-visiting season. The result generally shows that the high rates of weight loss occurred in August and September. The remaining masses in August were 64.9% for Qm L, 71.3% for Bp L, 85.3% for As L and 78.8% for Pg L; while those in September were 63.3% for Qm L, 61.7% for Bp L, 85.4% for As L and 76.3% for Pg L.

The starting time of placement on the forest floor has also influenced the

Table 2. The monthly remaining mass (%) of Qm L, Bp L, As L and Pg L during the decomposition

Study plots	The remaining mass (%) after decomposition in						
	IW (SD)	Nov.-May (SD)	Jun. (SD)	Jul. (SD)	Aug. (SD)	Sep. (SD)	Oct. (SD)
Qm L P1	100.0 (1.0)	62.8 (1.8)	87.2 (1.4)	82.1 (1.1)	64.9 (1.6)	63.3 (2.3)	73.9 (3.3)
Bp L P2	100.0 (0.1)	66.1 (0.8)	85.7 (0.9)	82.7 (1.5)	71.3 (2.3)	61.7 (2.0)	76.2 (2.6)
As L P3	100.0 (0.2)	82.1 (1.8)	94.6 (0.8)	91.2 (0.6)	85.3 (0.6)	85.4 (0.1)	88.4 (0.8)
Pg L P4	100.0 (0.1)	72.2 (2.5)	91.2 (2.6)	87.4 (3.8)	78.8 (0.9)	76.3 (1.5)	77.5 (1.1)

Note: see Fig. 1; Since in snow cover season (Nov.-May), investigations could not be carried out, the remaining mass of this season is indicated as that after seven-month-decomposition.

decomposition rates of the leaves and needles. After one year of decomposition, the weight losses of the four tree species leaves (needles) which were placed at the beginning of the snow cover season (end of October, 1988) were higher (significant at $P < 0.01$ for Qm L, Bp L, Pg L, and at $P < 0.05$ for As L) than those placed at the beginning of the snowless season (end of May, 1989). The remaining masses of Qm L, Bp L, As L and Pg L which were placed at the end of October were 36.5, 50.5, 66.4, 55.3%, while those placed at the end of May was 45.8, 54.6, 69.8 and 64.9%, respectively (Table 3).

3.2 Release of nutrient elements during decomposition of the leaves

Table 4 shows the concentrations of nitrogen during decomposition. The N concentrations in leaves of broad-leaved species (Qm L and Bp L) as well as in needles of coniferous species (As L and Pg L) obviously increased, while on the other hand, those in leaves of the undergrowth of *Sasa* showed decreases after seven months, though thereafter they tended to increase. After 12 and 19 months, N concentrations of Qm L and Bp L which decomposed in the ECF (P4) were slightly higher than those of Qm L in P1 and Bp L in P2. As L in P3 and Pg L in P4 had somewhat higher N concentrations than As L and Pg L in the DBF (P1).

Concentrations of phosphorus changed similarly to those of N during the decomposition (Table 5). They tended to increase in Qm L, Bp L, As L and Pg L, and had a tendency to decrease in Ss L. After 12 months, P concentrations of Qm L in P1 and Bp L in P2 were somewhat lower than those of Qm L and Bp L in the ECF (P4). P concentrations of As L in P3 were rather lower than those of As L in P1 (DBF).

In leaves of broad-leaved species and needles of coniferous species as well as the undergrowth of *Sasa*, the concentrations of potassium decreased markedly after the first sampling date. After 7 months, the K concentrations of Qm L in P1 and P4 decreased by as much as 0.11% from the initial concentration of 0.78%, those of Bp L by as much as 0.11

Table 3. The remaining mass (%) during the decomposition of leaves and needles which were placed at the end of October, 1988, compared with those placed at the end of May, 1989

Study plots	Period of decomposition (months)					
	0 (SD)	End of October		End of May		
		7 (SD)	12 (SD)	5 (SD)	12 (SD)	
Qm L	P1	100.0 (1.0)	62.8 (1.8)	36.5 (3.7)	51.5 (2.0)	45.8 (2.3)
Bp L	P2	100.0 (0.1)	66.1 (0.8)	50.5 (2.3)	56.2 (1.5)	54.6 (0.5)
As L	P3	100.0 (0.2)	82.1 (1.8)	66.4 (2.2)	75.2 (1.6)	69.8 (1.5)
Pg L	P4	100.0 (0.1)	72.2 (2.5)	55.3 (1.4)	69.6 (1.0)	64.9 (1.4)

Note: see Fig. 1.

-0.12% in P2 and 0.12% from 0.79%, As L by as much as 0.07-0.08% from 0.40%, Pg L by as much as 0.03-0.07% from 0.40%, and Ss L by as much as 0.14-0.15% from 0.91% (Table 6). The concentrations of K in the second collected samples (after 12 months) were higher than the first ones, and decreased again after 19 months.

Calcium concentrations in leaves of deciduous broad-leaved species increased after 7 months, rose to maximum after 12 months and decreased after 19 months. In needles of coniferous species, they also increased after 7 months, and they generally decreased after 12 and 19 months. The Ca concentrations of *Sasa* leaves in P4 showed a slight gradual

Table 4. Concentrations of N (%) during the decomposition of leaves and needles

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	1.29	2.95	3.01	2.52
	P4		2.90	3.20	2.65
Bp L	P2	1.72	2.59	2.70	2.53
	P4		2.83	2.79	2.80
Ss L	P4	2.30	1.50	1.61	2.10
	P1		1.46	1.70	2.07
As L	P3	1.25	1.47	1.92	1.99
	P1		1.47	1.83	1.94
Pg L	P4	0.82	1.05	1.66	1.50
	P1		1.00	1.37	1.39

Note: see Fig. 1.

Table 5. Concentrations of P (%) during the decomposition of leaves and needles

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	0.094	0.106	0.128	0.136
	P4		0.104	0.133	0.121
Bp L	P2	0.107	0.122	0.131	0.124
	P4		0.118	0.143	0.134
Ss L	P4	0.136	0.088	0.089	0.101
	P1		0.101	0.095	0.098
As L	P3	0.093	0.099	0.110	0.125
	P1		0.104	0.118	0.110
Pg L	P4	0.061	0.067	0.073	0.074
	P1		0.064	0.069	0.062

Note: See Fig. 1.

Table 6. Concentrations of K (%) during the decomposition of leaves and needles

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	0.78	0.11	0.29	0.15
	P4		0.11	0.30	0.16
Bp L	P2	0.79	0.11	0.21	0.11
	P4		0.12	0.27	0.12
Ss L	P4	0.91	0.14	0.16	0.12
	P1		0.15	0.17	0.12
As L	P3	0.44	0.08	0.13	0.11
	P1		0.07	0.14	0.09
Pg L	P4	0.40	0.07	0.14	0.09
	P1		0.03	0.11	0.07

Note: see Fig. 1.

Table 7. Concentrations of Ca (%) during the decomposition of leaves and needles

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	0.64	1.02	1.81	1.73
	P4		0.79	1.29	1.20
Bp L	P2	0.70	0.88	1.12	1.09
	P4		0.93	1.00	0.79
Ss L	P4	0.19	0.16	0.14	0.11
	P1		0.21	0.21	0.15
As L	P3	1.11	1.31	1.18	0.96
	P1		1.36	1.42	1.31
Pg L	P4	0.56	0.84	0.77	0.55
	P1		0.80	0.74	0.82

Note: see Fig. 1.

decrease during decomposition (Table 7). Those of Qm L and Bp L which decomposed in the DBF (P1 and P2, respectively) were higher than those in the ECF (P4). Those of As L in P3 (ECF) were lower than those in P1 (DBF). Mg concentrations showed slight increases and decreases during the decomposition of broad-leaved species leaves (Qm L and Bp L), and showed decreases in Ss L; while in the needles of coniferous species they showed no obvious changes (Table 8).

Table 9 shows the absolute amounts of N in leaves per litter bag during decomposition. The amounts of N in leaves of deciduous broad-leaved species increased after 7 months, but they decreased after 19 months because of the leaf mass losses. In the needles of

Table 8. Concentrations of Mg (%) during the decomposition of leaves and needles

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	0.10	0.08	0.12	0.10
	P4		0.10	0.16	0.13
Bp L	P2	0.15	0.12	0.15	0.14
	P4		0.09	0.12	0.09
Ss L	P4	0.07	0.03	0.04	0.04
	P1		0.03	0.04	0.04
As L	P3	0.06	0.06	0.05	0.06
	P1		0.06	0.06	0.05
Pg L	P4	0.04	0.03	0.04	0.05
	P1		0.03	0.03	0.04

Note: see Fig. 1.

Table 9. Changes in amounts of N (mg) in leaves per litter bag during the decomposition

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	12.9	18.5	11.0	6.0
	P4		20.0	15.5	9.1
Bp L	P2	17.2	17.1	13.6	11.0
	P4		19.5	14.0	12.2
Ss L	P4	23.0	10.5	9.4	11.5
	P1		10.2	9.0	9.6
As L	P3	12.5	12.1	12.8	11.3
	P1		11.9	12.6	12.6
Pg L	P4	8.2	7.6	9.2	7.6
	P1		7.0	8.2	7.8

Note: see Fig. 1.

coniferous species the amounts of N showed decreases after 7 and 19 months of decomposition, with slight increases occurring after 12 months. The N amounts in *Sasa* leaves showed marked decreases during decomposition.

Absolute amounts of P in Qm L, Bp L, As L and Pg L per litter bag showed gradual decreases during decomposition (Table 10), while those in Ss L showed great losses after the first sampling date (after 7 months of decomposition). The amounts of K per litter bag changed in similar trends among each species, which were marked by great K losses after the first sampling date (Table 11).

After 19 months, the absolute amounts of Ca in leaves per litter bag of all species had

Table 10. Changes in amounts of P (mg) in leaves per litter bag during the decomposition

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	0.94	0.66	0.47	0.32
	P4		0.72	0.64	0.42
Bp L	P2	1.07	0.81	0.66	0.54
	P4		0.81	0.72	0.58
Ss L	P4	1.36	0.62	0.52	0.55
	P1		0.70	0.50	0.46
As L	P3	0.93	0.81	0.73	0.71
	P1		0.84	0.81	0.72
Pg L	P4	0.61	0.48	0.40	0.37
	P1		0.45	0.41	0.35

Note: see Fig. 1.

Table 11. Changes in amounts of K (mg) in leaves per litter bag during the decomposition

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	7.8	0.69	1.01	0.36
	P4		0.76	1.45	0.55
Bp L	P2	7.9	0.73	1.06	0.47
	P4		0.83	1.36	0.52
Ss L	P4	9.1	0.98	0.93	0.66
	P1		1.05	0.90	0.56
As L	P3	4.4	0.66	0.86	0.63
	P1		0.57	0.96	0.59
Pg L	P4	4.0	0.50	0.78	0.45
	P1		0.21	0.66	0.39

Note: see Fig. 1.

decreased obviously, with the highest Ca losses in Ss L. Slight increases of Ca amounts were found only in Qm L (in P4) after 12 months of decomposition and in Pg L (in P4) after 7 months of decomposition (Table 12). Though with different rates, the amounts of Mg in all leaves and needles showed clearly decreases as a result of leaf mass loss during decomposition (Table 13).

Table 12. Changes in amounts of Ca (mg) in leaves per litter bag during the decomposition

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	6.4	6.40	6.60	4.12
	P4		5.46	6.23	4.14
Bp L	P2	7.0	5.82	5.66	4.73
	P4		6.40	5.01	3.44
Ss L	P4	1.9	1.12	0.82	0.60
	P1		1.46	1.11	0.70
As L	P3	11.1	10.76	7.84	5.47
	P1		11.00	9.75	8.51
Pg L	P4	5.6	6.06	4.26	2.77
	P1		5.62	4.44	4.61

Note : see Fig. 1.

Table 13. Changes in amounts of Mg (mg) in leaves per litter bag during the decomposition

	Study plots	Period of decomposition (months)			
		0	7	12	19
Qm L	P1	1.0	0.50	0.44	0.24
	P4		0.69	0.77	0.45
Bp L	P2	1.5	0.79	0.76	0.61
	P4		0.62	0.60	0.39
Ss L	P4	0.7	0.21	0.23	0.22
	P1		0.21	0.21	0.19
As L	P3	0.6	0.49	0.33	0.34
	P1		0.49	0.41	0.33
Pg L	P4	0.4	0.22	0.22	0.25
	P1		0.21	0.18	0.22

Note : see Fig. 1.

4. Discussion

4.1 Decomposition of leaves and branches

As fore-mentioned, decomposition rates of plant litter in forest stands are affected by various factors, both organic and inorganic factors such as stand age (EDMONDS, 1979), microbial populations in those sites (WITKAMP, 1966), temperature and moisture (FOGEL and CROMACK, 1977 ; GILL and LAVENDER, 1983) etc.. In this study, characteristic relation between decomposition rates of leaves of each species and forest types of study plots were

observed, namely leaves of *Q. mongolica* var. *grosseserrata*., *B. platyphylla* var. *japonica* and *Sasa senanensis* decomposed significantly faster in P1 and coniferous needles (As L and Pg L) had obviously decomposed faster in coniferous stands (P3 and P4) than in deciduous broad-leaved stands (P1 and P2). P2, P3 and P4 were located closed each other at an altitude of about 300 m, while P1 was about 5 km from the three plots, at an altitude of about 370 m. Thus the study sites were different in their locations and their forest types, these might generate the differences in such environmental factors as temperature and humidity, and soil macro- and micro-organism, and might affect the decomposition rate of plant litter in those sites.

After 19 and 24 months of decomposition, although the rates of weight loss in the leaves of the four tree species were different in each study site, in general they were similar in their sequence; the fastest is *Q. mongolica* var. *grosseserrata*, followed by those of *B. platyphylla* var. *japonica*, *P. glehnii*, with needles of *A. sachalinensis* as the slowest. MACLEAN and WEIN (1978) recognized same tendency that hardwood leaves of four species were also decomposed significantly faster than pine needles in New Brunswick forest stands. Furthermore WILLIAMS and GRAY (1974) and TAKEDA et al. (1987) indicated similar trends for the decomposition of tree leaves.

Within the broad-leaved tree species, after 19 months of decomposition, leaves of *Q. mongolica* var. *grosseserrata* clearly decomposed faster than those of *B. platyphylla* var. *japonica* in all plots, and within the coniferous tree species, weight losses of needles of *P. glehnii* were higher than those of *A. sachalinensis* in all plots. FLANAGAN and VAN CLEVE (1983) recognized that the major factor determining the rate of decay of a particular substrate is the quality of the substrate itself. TAKEDA et al. (1987) reported that leaf hardness and such chemical properties as initial contents of lignin, cellulose, soluble carbohydrates and soluble wax were significantly related to the decomposition rates of leaf litter. The decomposition rates of leaf litter were reported to be correlated with the initial contents of lignin and cellulose (O'CONNELL, 1987), the initial contents of nitrogen and phosphorus (TANNER, 1981; OHLSON, 1987), and the initial lignin : nitrogen ratio (MELILLO et al., 1982). FOGEL and CROMACK (1977) found that the rate of annual weight loss of Douglas-fir litter in Western Oregon was more influenced by lignin content than by C : N ratio. Therefore, the differences between the decomposition rates of leaves observed within each life form may be due to chemical and mechanical properties of their leaves.

Decomposition rates of branches and culms were very slow. After one year had elapsed, decomposition rates of branches of the four tree species which were placed on the same study sites generally were similar to each other. After two years of decomposition, Qm Br showed the fastest decomposition in all study sites, with Bp Br and Pg Br as the slowest in the DBF and the ECF, respectively. Among branches of the four tree species in P1 and P4, the remaining masses generally showed significant differences ($P < 0.05$) between one another, but not in P2 and P3. Branches of the four tree species which decomposed in different study sites (P1, P2, P3 and P4) generally showed no obvious difference between the study sites. Over a similar period of observation, MACLEAN and WEIN (1978) also found no significant differences in weight loss of pine branches among five forest sites in New Brunswick forest, Canada. A similar result was reported by FOGEL and CROMACK (1977) in seven stands of the Andrews Experimental Forest, Western Oregon. A longer period of investigation might be needed to demonstrate any definite differences

among the study sites.

Rates of leaf mass decrease changed seasonally, the mean monthly mass decrease of Qm L, Bp L, As L and Pg L during the snowless season was significantly higher ($P < 0.05$) than that during the snow cover season. As temperature is one of the major factors controlling litter decomposition (WILLIAMS and GRAY, 1974), the higher rates of decomposition during the snowless season might be attributable to the higher temperature during the season. However after one year of decomposition, weight losses of leaves and needles which were placed at the beginning of the snow cover season were higher than those placed at the beginning of the snowless season, the reason of this difference is unclear.

4.2 Release of nutrient elements during decomposition of the leaves

Concentrations of nitrogen in leaves of deciduous broad-leaved species (Qm L and Bp L) and needles of coniferous species (As L and Pg L) showed obvious increasing trends during decomposition (Table 3). Absolute amounts of N in Qm L and Bp L increased after 7 months, and in As L and Pg L amounts of N were rather constant than decreasing obviously. The increases of concentration or absolute amount of N during decomposition have been reported by many workers such as MACLEAN and WEIN (1978), EDMONDS (1979), BOERNER (1984), TWILLEY et al. (1986), WEBER (1987), O'CONNELL (1988) and BLAIR et al. (1990). It is supposed that the increases of N concentration and mass occurred because of microbiological retention of N (MACLEAN and WEIN, 1978), atmospheric precipitation, insect frass and plant material which fell from the tree canopy (BOCOCK, 1963, 1964), fungal translocation and /or immobilization (MELILLO et al., 1982).

Phosphorus concentrations showed similar trends to those of N, with a tendency to increase in Qm L, Bp L, As L and Pg L, and to decrease in Ss L. Since the increasing rates of P concentration were lower than the decreasing rates of leaf mass, the absolute amounts of P in leaves and needles of all species showed gradual decreases during the decomposition. The increase of P concentration during decomposition was also reported by O'CONNEL (1988) in most litter of *Eucalyptus diversicolor* forests. MACLEAN and WEIN (1978) noted the different patterns in the changes of P concentration among the site types in New Brunswick forest stands. EDMONDS (1980) also found the phosphorus release patterns varied among forest ecosystems in western Washington. It is suggested that the decrease of P concentration is a result of the susceptibility of P to the leaching process, while the possible sources of P input are plant reproductive materials and green litterfall (LOUSIER and PARKINSON, 1978).

Concentration and absolute mass of potassium in leaves and needles of all species decreased sharply from the first sampling date (after 7 months had elapsed). A number of researchers such as Hodkinson (1975), EWEL (1976), MACLEAN and WEIN (1978), EDMONDS (1980), SWIFT et al. (1981), DECATANZARO and KIMMINS (1985) have also reported rapid decreases of K concentration and absolute amount during decomposition. Since potassium is very easily removed by rainfall, its rapid decreases have been explained as a result of the leaching process (GOSZ et al., 1973).

Steady loss of calcium throughout a 24 month period was reported by EDMONDS (1980). MACLEAN and WEIN (1978) found a decrease of Ca concentration during the 1st year, but an increase during the period of 21-24 months. GOSZ et al. (1973) also reported that the change in Ca concentration with time showed patterns of increase and decrease. In the

case of this study Ca concentration in Qm L, Bp L, As L and Pg L increased during decomposition, while that in Ss L showed slight gradual decreases. Slight increases of absolute amount of Ca mass were found only in Qm L (in P4) after 12 months of decomposition, and in Pg L (in P4) after 7 months of decomposition. After 19 months had elapsed, absolute losses of Ca mass were obvious in leaves and needles of all species.

Magnesium concentrations in needles of coniferous species (As L and Pg L) showed no obvious changes during the decomposition. A similar result was obtained in litter of *Eucalyptus diversicolor* forests over a period of 82 weeks (O'CONNELL, 1988). In leaves of broad-leaved species (Qm L and Bp L), the Mg concentrations showed increases and decreases during decomposition. Over 18 months of observation, Mg concentration in needle litter decreased for the first 6 months, and then increased, but in big-leaf maple leaf litter it decreased over time (DECATANZARO and KIMMINS, 1985). BOERNER (1984) reported a decrease in Mg concentration during the 1st and 2nd year. MACLEAN and WEIN (1978) noted that Mg was an erratic element, occasionally showing sharp increases and decreases. WEBER (1987) suggested that variable dynamics of Mg seem to be specific to local conditions.

Acknowledgments

The author wishes to express his high appreciation to Prof. Dr. T. IGARASHI, Prof. Dr. S. TAKIKAWA, Prof. Dr. T. TADANO and Assoc. Prof. Dr. T. YAJIMA for their valuable comments and suggestions on this manuscript, and their kind guidance, assistance and encouragement during the course of this research. Thanks are extended to Dr. K. MATSUDA, Dr. M. KADOMATSU, Dr. M. HAYASHIDA, Mr. M. MATSUMOTO and all members of the Uryu Experiment Forest, Hokkaido University, for their kind assistance and useful advice especially during field work, and to Mr. S. FUJIMOTO, Mr. M. SHIBUYA, Mr. K. TADOKORO, Mr. T. KISHIMOTO and all members of the Laboratory of Silviculture, Hokkaido University, for their kind help and useful advice during the field and laboratory work.

References

- 1) ANDO M. (1970). Litterfall and decomposition in some evergreen coniferous forests. Jap. J. Ecol. 20 (5): 170-181.
- 2) BINKLEY, D. (1986). Forest nutrition management. John Wiley & Sons, New York. 290 pp.
- 3) BLAIR, J. M., Parmelee, R.W. and BEARE, M. H. (1990). Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. Ecol. 71 (5): 1976-1985.
- 4) BOCOCK, K. L. (1963). Changes in the amount of nitrogen in decomposing leaf litter of sessile oak (*Quercus petraea*). J. Ecol.: 555-566.
- 5) BOCOCK, K. L. (1964). Changes in the amounts of dry matter, nitrogen, carbon and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. J. Ecol. 52: 273-284.
- 6) BOERNER, R. E. J. (1984). Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio. Can. J. For. Res. 14: 794-802.
- 7) DECATANZARO, J. B. and KIMMINS, J. P. (1985). Changes in the weight and nutrient composition of

- litterfall in three forest ecosystem types on coastal British Columbia. *Can. J. Bot.* 63: 1046-1056.
- 8) EDMONDS, R. L. (1979). Decomposition and nutrient release in Douglas fir needle litter in relation to stand development. *Can. J. For. Res.* 9: 132-149.
 - 9) EDMONDS, R. L. (1980). Litter decomposition and nutrient release in Douglas fir, red alder, western hemlock and Pacific silver fir ecosystems in western Washington. *Can. J. For. Res.* 10: 327-337.
 - 10) EWEL, J. J. (1976). Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. *J. Ecol.* 64: 293-307.
 - 11) FLANAGAN, P. W. and VAN CLEVE, K. (1983). Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Can. J. For. Res.* 13: 795-817.
 - 12) FOGEL, R. and CROMACK, K. Jr. (1977). Effect of habitat and substrate quality in Douglas fir needles decomposition in western Oregon. *Can. J. Bot.* 55: 1632-1640.
 - 13) GILL, R. N. and LBVENDER, D. P. (1983). Litter decomposition in coastal hemlock stands: Impact of nitrogen fertilizers on decay rates. *Can. J. For. Res.* 13: 116-121.
 - 14) GOSZ, J. R., LIKENS, G. E. and BORMAN, F. H. (1973). Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecol. Monog.* 43: 173-191.
 - 15) HARDIWINOTO, S., YAJIMA, T. and IGERASHI, T. (1991). Stand structure and litter production of deciduous broad-leaved forests and evergreen coniferous forests in northern Hokkaido. *Res. Bull. Exp. For. Hokkaido Univ.* 48 (1): 115-155.
 - 16) KAWAHARA, T. (1975). Decomposition of litter on forest floor (II) Effect of the mixture of two kinds of leaf litter on their decomposition rate. *Jap. J. Ecol.* 25 (2): 71-75 (in Japanese with English synopsis).
 - 17) KAWAHARA, T. and SATO, A. (1974). Decomposition of litter in forest floor (I) Study on the decomposition rate by litter bag method. *J. Jap. For. Soc.* 56 (7): 258-261.
 - 18) LOUSIER, J. D. and PARKINSON, D. (1978). Chemical element dynamics in decomposing leaf litter. *Can. J. Bot.* 56: 2795-2812.
 - 19) MACLEAN, D. A. and WEIN, R. W. (1978). Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. *Can. J. Bot.* 56: 2730-2749.
 - 20) MILLO, J. M., ABER, J. D. and MURATORE, J. F. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecol.* 63 (3): 621-626.
 - 21) O'CONNELL, A. M. (1987). Litter dynamics in Karri (*Eucalyptus diversicolor*) forests of south-western Australia. *J. Ecol.* 75: 781-796.
 - 22) O'CONNELL, A. M. (1988). Nutrient dynamics in decomposing litter in Karri (*Eucalyptus diversicolor* F. Muell) forests of south-western Australia. *J. Ecol.* 76: 1186-1203.
 - 23) OHLSON, M. (1987). Spatial variation in decomposition rate of *Carex rostrata* leaves on a Swedish mire. *J. Ecol.* 75: 1191-1197.
 - 24) OLSON, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecol.* 44 (2): 322-331.
 - 25) SIMARANGKIR, B. D. A. S. and IGERASHI, T. (1986). Litterfall and decomposition process in a sub-arctic evergreen coniferous forest in northern Hokkaido, Japan (II) Monthly fluctuations of litterfall and the decomposition in a year. *Trans. Mtg. Jap. For. Soc.* 97: 215-216 (in Japanese).
 - 26) SIMARANGKIR, B. D. A. S. and IGERASHI, T. (1987). Litterfall and decomposition process in a sub-arctic evergreen coniferous forest in northern Hokkaido, Japan (III) Seasonal changes of litterfall and decomposition. *Trans. Mtg. Jap. For. Soc.* 98: 191-192 (in Japanese).
 - 27) SWIFT, M. J., RUSSELL-Smith, A. and PERFECT, T. J. (1981). Decomposition and mineral-nutrient

- dynamics of plant litter in a regenerating bush-fallow in sub-humid tropical Nigeria. J. Ecol. 69: 981-995.
- 28) TAKEDA, H., ISHIDA, Y. and TSUTSUMI, T. (1987). Decomposition of leaf litter in relation to litter quality and site conditions. Mem. Coll. Agric. Kyoto Univ. 130: 17-38.
- 29) TANNER, E. V. J. (1981). The decomposition of leaf litter in Jamaican montane rain forests. J. Ecol. 69: 263-275.
- 30) TWILLYE, R. R., LUGO, A. E. and PATTERSON-ZUCCA, C. (1986). Litter production and turnover in basin mangrove forests in southwest Florida. Ecol. 67 (3): 670-683.
- 31) WEBER, M. G. (1987). Decomposition, litterfall, and forest floor nutrient dynamics in relation to fire in eastern Ontario jack pine ecosystems. Can J. For. Res. 17: 1496-1506.
- 32) WILLIAMS, S. T. and Gray, T. R. G. (1974). Decomposition of litter on the soil surface. In: Biology of plant litter decomposition 2: 611-632.
- 33) WITKAMP, M. (1966). Decomposition of leaf litter in relation to environment, microflora and microbial respiration. Ecol. 47 (2): 194-201, ed. Duvigneaud, P., Unesco, Paris.
- 34) WITKAMP, M. (1969). Forest soil microflora and mineral cycling. In: Productivity of forest ecosystems. Proc. Brussels Symy. : 413-434.
- 35) YONEDA, T. (1975a). Studies on the rate of decay of wood litter on the forest floor (I) Some physical properties of decaying wood. Jap. J. Ecol. 25 (1): 40-46.
- 36) YONEDA, T. (1975b). Studies on the rate of decay of wood litter on the forest floor (II) Dry weight loss and CO₂ evolution of decaying wood. Jap. J. Ecol. 25 (3): 132-140.
- 37) YONEDA, T. and Kirita, H. (1978). Fall rate, accumulation and decomposition of wood litter. In: Biological production in a warmtemperate evergreen oak forest of Japan, JIBP Synthesis 18: 258-272, eds. Kira, T., Ono, Y. and Hosokawa, T. Univ. of Tokyo Press, Japan.

摘 要

本研究は北海道大学農学部附属雨龍地方演習林で行った。1988年5月に4つの方形調査区, P1, P2, P3, P4を設定した。相対胸高断面積と上木の相対密度によって, P1をミズナラ (*Quercus mongolica* var. *grosseserrata*) 優占林分, P2をシラカンバ (*Betula platyphylla* var. *japonica*) 優占林分, P3をトドマツ (*Abies sachalinensis*) 優占林分, P4をアカエゾマツ (*Picea glehnii*) 優占林分とした (HARDIWINOTO et al., 1991)。

葉と枝の分解を調べるため, 各プロットの優占樹種であるミズナラ, シラカンバ, トドマツ, アカエゾマツと林床植物の優占種であるクマイザサを対象として葉と枝を一定量リターバックに詰め, 調査地の林床で分解させた。これらの試料は7, 12, 19, 24カ月後に回収し, 重量を求めた。分解に伴う養分動態を把握するため分解させた葉を試料として, 養分分析を行った。分析した養分は窒素, リン, カリウム, カルシウム, マグネシウムであった。

1. 葉と枝の分解

ミズナラとシラカンバの葉の分解はP1でP2, P3, P4より速かった。クマイザサの葉の分解もP1ではP4より速い傾向が認められた。トドマツとアカエゾマツの葉はP3とP4でP1とP2より速く分解された。P1とP2は落葉広葉樹林でP3とP4は常緑針葉樹林である。こ

のような林種の違いにより温度や水分、林床と土壤動物、菌類など、分解速度に影響を与える物理的、生物的環境条件が異なるためと考えられる。

それぞれの調査地ではミズナラの葉は最も速く分解された。次いでシラカンバの葉、アカエゾマツの葉、トドマツの葉の順であった。広葉樹類の葉は針葉樹類の葉より速く分解した。分解の速度を決定する主要要素はその基質、例えば化学的にはリグニン、セルロース、溶性炭水化物の初期容量、窒素とリンの初期容量、リグニンと窒素の割合、炭素と窒素の割合などであり、物理的には葉の硬さと報告されている。葉の分解には季節変化が見られ、無積雪期の月平均の葉の分解速度は積雪期のものより高い値が得られたが、積雪下でも無積雪期の50-65%の分解が認められた。

枝の分解は非常に遅く、ミズナラ、シラカンバ、トドマツ、アカエゾマツの4樹種とも、全調査地においてあまり相違点が認められなかった。

2. 葉の分解の進行と養分変動

ミズナラ、シラカンバ、トドマツ、アカエゾマツの葉の窒素濃度は分解の進行にともなって高くなった。クマイサザの葉の場合は7カ月後にいったん低下した後、高くなった。窒素総量は7カ月後のミズナラの葉、7カ月と12カ月後のシラカンバの葉で高くなった。窒素の濃度と総量の増加の要因としては微生物の窒素保持、降水、林冠から葉下する虫のふんや植物リター、菌の影響が考えられる。リンの濃度変動は窒素の濃度変動と類似していた。重量の減少に伴ってリン濃度は増加したが総量は減少した。リンの供給源として考えられるのは樹木の生殖器官と緑色リターであり、一方、減少は溶脱のためであると報告されている。カリウムの濃度は最初に標本を採取した7カ月後に非常に低い値を示して、総量も同様であった。カリウムは非常に溶脱しやすいためこの結果になったと考えられる。カルシウム濃度は4樹種とも分解の進行とともに高くなった。マグネシウム濃度には大きい変動が認められなかった。

Appendix

As a supplement, the raw data on decomposition processes of leaves, branches and culms of this study species are indicated in follows. Appendixes 1-4 are the data of Fig. 1, and Appendixes 5-8 the data of Fig. 2 in the text. Appendixes 9-12 correspond to Fig. 3, and Appendixes 13-16 to Fig. 4, respectively.

Appendix 1. The remaining mass (%) of Qm L during the decomposition in the four study plots

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Qm L	P1	100.0 (1.0)	62.8 (1.8)	36.5 (3.7)	23.8 (2.7)	18.3 (3.4)
	P2	100.0 (1.0)	69.2 (1.4)	47.4 (3.8)	37.8 (1.6)	32.5 (1.6)
	P3	100.0 (1.0)	66.9 (1.5)	44.6 (3.0)	34.4 (5.5)	29.6 (5.9)
	P4	100.0 (1.0)	69.1 (3.7)	48.3 (3.3)	34.5 (3.1)	28.6 (3.4)

Note :

Qm L=Leaves of *Q. mongolica* var. *grosseserrata*. Numbers in parentheses are standard deviations.

Appendix 2. The remaining mass (%) of Bp L and Ss L during the decomposition in the four study plots

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Bp L	P1	100.0 (0.1)	67.7 (2.8)	48.0 (2.4)	35.7 (5.1)	30.7 (2.1)
	P2	100.0 (0.1)	66.1 (0.8)	50.5 (2.3)	43.4 (2.6)	39.4 (2.4)
	P3	100.0 (0.1)	68.9 (2.5)	52.2 (3.4)	43.5 (3.3)	35.1 (3.2)
	P4	100.0 (0.1)	68.8 (1.7)	50.2 (3.0)	43.6 (5.5)	38.5 (3.5)
Ss L	P1	100.0 (0.2)	69.6 (1.8)	52.9 (1.0)	46.5 (0.8)	40.5 (3.7)
	P4	100.0 (0.2)	70.3 (1.5)	58.2 (1.9)	55.0 (3.6)	41.2 (5.8)

Note :

Bp L and Ss L are leaves of *B. platyphylla* var. *japonica* and *S. senanensis*, respectively. Numbers in parentheses are standard deviations.

Appendix 3. The remaining mass (%) of As L during the decomposition in the four study plots

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
As L	P1	100.0 (0.2)	80.9 (1.7)	68.6 (1.6)	65.0 (1.6)	57.7 (2.1)
	P2	100.0 (0.2)	81.4 (0.7)	71.5 (0.5)	64.6 (2.4)	57.1 (4.2)
	P3	100.0 (0.2)	82.1 (1.8)	66.4 (2.2)	57.0 (6.3)	46.3 (2.6)
	P4	100.0 (0.2)	81.5 (2.4)	65.4 (1.6)	58.4 (6.4)	49.3 (3.4)

Note :

As L=Needles of *A. sachalinensis*. Numbers in parentheses are standard deviations.**Appendix 4.** The remaining mass (%) of Pg L during the decomposition in the four study plots

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Pg L	P1	100.0 (0.1)	70.3 (0.5)	60.0 (0.8)	56.2 (1.6)	51.6 (1.8)
	P2	100.0 (0.1)	70.3 (1.6)	62.1 (1.4)	58.1 (1.4)	53.2 (1.8)
	P3	100.0 (0.1)	71.6 (2.4)	54.6 (0.4)	47.8 (2.7)	35.0 (2.6)
	P4	100.0 (0.1)	72.2 (2.5)	55.3 (1.4)	50.4 (2.0)	38.3 (2.2)

Note :

Pg L=Needles of *P. glehnii*. Numbers in parentheses are standard deviations.

Appendix 5. The remaining mass (%) of Qm Br during the decomposition in the four study plots

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Qm Br	P1	100.0 (0.1)	83.0 (1.5)	70.8 (1.9)
Qm Br	P2	100.0 (0.1)	85.3 (1.1)	74.6 (3.8)
Qm Br	P3	100.0 (0.1)	81.8 (1.1)	68.9 (2.0)
Qm Br	P4	100.0 (0.1)	83.6 (0.6)	72.7 (1.3)

Note :

Qm Br=Branches of *Q. mongolica* var. *grosseserrata*, SD=Standard deviations.

Appendix 6. The remaining mass (%) of Bp Br and Ss Cl during the decomposition in the four study plots

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Bp Br	P1	100.0 (0.2)	86.1 (1.4)	79.1 (0.9)
Bp Br	P2	100.0 (0.2)	85.9 (3.3)	78.0 (2.8)
Bp Br	P3	100.0 (0.2)	85.7 (0.9)	74.2 (2.7)
Bp Br	P4	100.0 (0.2)	85.2 (2.0)	75.0 (3.6)
Ss Cl	P1	100.0 (0.2)	82.3 (0.8)	72.3 (4.2)
Ss Cl	P4	100.0 (0.2)	82.2 (2.0)	71.6 (3.9)

Note :

Bp Br=Branches of *B. Platyphylla* var. *japponica*, Ss Cl=Culms of *S. senanensis*, SD=see Appendix 5.

Appendix 7. The remaining mass (%) of As Br during the decomposition in the four study plots

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
As Br	P1	100.0 (0.2)	83.2 (1.0)	76.1 (0.7)
As Br	P2	100.0 (0.2)	84.7 (1.4)	77.8 (2.0)
As Br	P3	100.0 (0.2)	84.6 (1.7)	74.3 (1.6)
As Br	P4	100.0 (0.2)	82.3 (0.4)	74.0 (2.1)

Note:

As Br=Branches of *A. sachalinensis*, SD=see Appendix 5.**Appendix 8.** The remaining mass (%) of Pg Br during the decomposition in the four study plots

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Pg Br	P1	100.0 (0.3)	84.1 (0.7)	78.4 (1.0)
Pg Br	P2	100.0 (0.3)	84.7 (0.4)	77.6 (1.6)
Pg Br	P3	100.0 (0.3)	85.2 (0.8)	78.2 (0.6)
Pg Br	P4	100.0 (0.3)	84.6 (1.1)	76.3 (1.0)

Note:

Pg Br=Branches of *P. glehnii*, SD=see Appendix 5.

Appendix 9. The remaining mass (%) of Qm L Bp L, Ss L, As L and Pg L during the decomposition in P1

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Qm L	P1	100.0 (1.0)	62.8 (1.8)	36.5 (3.7)	23.8 (2.7)	18.3 (3.4)
Bp L	P1	100.0 (0.1)	67.7 (2.8)	48.0 (2.4)	35.7 (5.1)	30.7 (2.1)
Ss L	P1	100.0 (0.2)	69.6 (1.8)	52.9 (1.0)	46.5 (0.8)	40.5 (3.7)
As L	P1	100.0 (0.2)	80.9 (1.7)	68.6 (1.6)	65.0 (1.6)	57.7 (2.1)
Pg L	P1	100.0 (0.1)	70.3 (0.5)	60.0 (0.8)	56.2 (1.6)	51.6 (1.8)

Note:

Qm L, Bp L and Ss L are leaves of *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica* and *S. senanensis*, respectively; As L and Pg L are needles of *A. sachalinensis* and *P. glehnii*, respectively: SD=Standard deviations.

Appendix 10. The remaining mass (%) of Qm L, Bp L, As L and Pg L during the decomposition in P2

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Qm L	P2	100.0 (1.0)	69.2 (1.4)	47.4 (3.8)	37.8 (1.6)	32.5 (1.6)
Bp L	P2	100.0 (0.1)	66.1 (0.8)	50.5 (2.3)	43.4 (2.6)	39.4 (2.4)
As L	P2	100.0 (0.2)	81.4 (0.7)	71.5 (0.5)	64.6 (2.4)	57.1 (4.2)
Pg L	P2	100.0 (0.1)	70.3 (1.6)	62.1 (1.4)	58.1 (1.4)	53.2 (1.8)

Note: see Appendix 9.

Appendix 11. The remaining mass (%) of Qm L, Bp L, As L and Pg L during the decomposition in P3

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Qm L	P3	100.0 (1.0)	66.9 (1.5)	44.6 (3.0)	34.4 (5.5)	29.6 (5.9)
Bp L	P3	100.0 (0.1)	68.9 (2.5)	52.2 (3.4)	43.5 (3.3)	35.1 (3.2)
As L	P3	100.0 (0.2)	82.1 (1.8)	66.4 (2.2)	57.0 (6.3)	46.3 (2.6)
Pg L	P3	100.0 (0.1)	71.6 (2.4)	54.6 (0.4)	47.8 (2.7)	35.0 (2.6)

Note : see Appendix 9.

Appendix 12. The remaining mass (%) of Qm L, Bp L, Ss L, As L and Pg L during the decomposition in P4

	Study plots	Period of decomposition (months)				
		0 (SD)	7 (SD)	12 (SD)	19 (SD)	24 (SD)
Qm L	P4	100.0 (1.0)	69.1 (3.7)	48.3 (3.3)	34.5 (3.1)	28.6 (3.4)
Bp L	P4	100.0 (0.1)	68.8 (1.7)	50.2 (3.0)	43.6 (5.5)	38.5 (3.5)
Ss L	P4	100.0 (0.2)	70.3 (1.5)	58.2 (1.9)	55.0 (3.6)	41.2 (5.8)
As L	P4	100.0 (0.2)	81.5 (2.4)	65.4 (1.6)	58.4 (6.4)	49.3 (3.4)
Pg L	P4	100.0 (0.1)	72.2 (2.5)	55.3 (1.4)	50.4 (2.0)	38.3 (2.2)

Note : see Appendix 9.

Appendix 13. The remaining mass (%) of Qm Br, Bp Br, Ss Cl, As Br and Pg Br during the decomposition in P1

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Qm Br	P1	100.0 (0.1)	83.0 (1.5)	70.8 (1.9)
Bp Br	P1	100.0 (0.2)	86.1 (1.4)	79.1 (0.9)
Ss Cl	P1	100.0 (0.2)	82.3 (0.8)	72.3 (4.2)
As Br	P1	100.0 (0.2)	83.2 (1.0)	76.1 (0.7)
Pg Br	P1	100.0 (0.3)	84.1 (0.7)	78.4 (1.0)

Note :

Qm Br, Bp Br, As Br and Pg Br are branches of *Q. mongolica* var. *grosseserrata*, *B. platyphylla* var. *japonica*, *A. sachalinensis* and *P. glehnii*, respectively ; Ss Cl = Culms of *S. senanensis* : SD = Standard deviations.

Appendix 14. The remaining mass (%) of Qm Br, Bp Br, As Br and Pg Br during the decomposition in P2

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Qm Br	P2	100.0 (0.1)	85.3 (1.1)	74.6 (3.8)
Bp Br	P2	100.0 (0.2)	85.9 (3.3)	78.0 (2.8)
As Br	P2	100.0 (0.2)	84.7 (1.4)	77.8 (2.0)
Pg Br	P2	100.0 (0.3)	84.7 (0.4)	77.6 (1.6)

Note : see Appendix 13.

Appendix 15. The remaining mass (%) of Qm Br, Bp Br, As Br and Pg Br during the decomposition in the four study plots

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Qm Br	P3	100.0 (0.1)	81.8 (1.1)	68.9 (2.0)
Bp Br	P3	100.0 (0.2)	85.7 (0.9)	74.2 (2.7)
As Br	P3	100.0 (0.2)	84.6 (1.7)	74.3 (1.6)
Pg Br	P3	100.0 (0.3)	85.2 (0.8)	78.2 (0.6)

Note: see Appendix 13.

Appendix 16. The remaining mass (%) of Qm Br, Bp Br, Ss Cl, As Br and Pg Br during the decomposition in P4

	Study plots	Period of decomposition (months)		
		0 (SD)	12 (SD)	24 (SD)
Qm Br	P4	100.0 (0.1)	83.6 (0.6)	72.7 (1.3)
Bp Br	P4	100.0 (0.2)	85.2 (2.0)	75.0 (3.6)
Ss Cl	P4	100.0 (0.2)	82.2 (2.0)	71.6 (3.9)
As Br	P4	100.0 (0.2)	82.3 (0.4)	74.0 (2.1)
Pg Br	P4	100.0 (0.3)	84.6 (1.1)	76.3 (1.0)

Note: see Appendix 13.