DOI: 10.1007/s11676-007-0051-7

Landscape patterns of overstory litterfall and related nutrient fluxes in a cool-temperate forest watershed in northern Hokkaido, Japan

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Abstract: Within a forested watershed at the Uryu Experimental Forest of Hokkaido University in northern Hokkaido, overstory litterfall and related nutrient fluxes were measured at different landscape zones over two years. The wetland zone covered with *Picea glehnii* pure stand. The riparian zone was deciduous broad-leaved stand dominated by *Alnus hirsuta* and *Salix* spp., while the mixture of deciduous broadleaf and evergreen conifer dominated by *Betula platyphylla*, *Quercus crispula* and *Abies sachalinensis* distributed on the upland zone. Annual litterfall averaged 1444, 5122, and 4123 kg·hm^{-2}·a^{-1} in the wetland, riparian and upland zones, respectively. Litterfall production peaked in September-October, and foliage litter contributed the greatest amount (73.4%–87.6 %) of the annual total litterfall. Concentrations of nutrients analyzed in foliage litter of the dominant species showed a similar seasonal variation over the year except for N in *P. glehnii* and *A. hirsuta*. The nutrient fluxes for all elements analyzed were greatest on riparian zone and lowest in wetland zone. Nutrient fluxes via litterfall followed the decreasing sequence: N (11-129 kg·hm^{-2}·a^{-1}) > Ca (9-69) > K (5-20) > Mg (3-15) > P (0.4-4.7) for all stands. Significant differences were found in litterfall production and nutrient fluxes among the different landscape components. There existed significant differences in soil chemistry between the different landscape zones. The consistently low soil C:N ratios at the riparian zone might be due to the higher-quality litter inputs (largely N-fixing alder).

Keywords: Landscape; Litterfall; Nutrient cycling; Soil chemistry; Temperate forest

Introduction

Litterfall studies in forest stands have been conducted for over a century. The earlier studies mainly emphasized fluctuations and composition of litterfall. Recent studies on litterfall have concentrated on nutrient cycling particularly in forest ecosystems (Waring and Schlesinger 1998). Litterfall, together with root turnover, represents one of the major pathways for the return of organic matter and nutrients from vegetation to soil (Vogt *et al*. 1986; Gallardo *et al*. 1998; Hodge 2004), and therefore contributes significantly to soil formation and fertility (Fisher and Binkley 2000). This is of key importance in maintenance of forest productivity.

Plant foliage constitutes one of the most important pools of essential nutrients, but there is pronounced seasonal change in foliage nutrient content that again influences the nutrient concentrations in litterfall. Litterfall is in fact an integrated response between biological heredity of the trees and the influence of environmental fluctuations, and can present the possibility that landscape-level differences in plant community composition could influence soil chemical and biological properties. In this way it can be perceived as an indicator of forest condition. Therefore, to evaluate the contributions of landscape components is important for evaluating the factors regulating dynamics and availability of nutrient within watersheds (Grigal and Homann 1994; Ohrui and Mitchell 1998; Ohrui *et al.* 1999). Within the Dorogawa watershed in northern Hokkaido (Fig. 1), there is a broad diversity of landscape components including lakes, streams, forested wetlands, and upland forests, and each of which may have distinctive nutrient cycling characteristics (Shibata *et al*. 2005; Ogawa *et al*. 2006). The interrelationships among these landscape components are expected to contribute to the spatial patterns of nutrient dynamics within this watershed.

The present study is part of a multi-disciplinary program working on forest ecosystem function in watershed-level (Shibata *et al*. 2005; Kanao *et al*. 2007). The purposes of this study are to quantify (a) total annual overstory litterfall and inputs by components; (b) patterns of nutrient fluxes by overstory litterfall within different landscape components in cool-temperate forests, with a view to gaining further insights into the recycling of aboveground organic matter and associated bioelements.

Study area and methods

Study site

This study was conducted in Dorogawa watershed at Uryu Experimental Forest, Hokkaido University, located in the northern part of Hokkaido (44°12'N and 142°11'E), Japan (Fig. 1). The climate at the study area is characterized by abundant rainfall throughout year and very low air temperature with a deep snow pack in winter. The annual mean precipitation is 1 375 mm,

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Foundation project: The project was supported by Japanese Society for Promotion of Sciences (15P03118).

Received:2007-08-17; Accepted:2007-09-27

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The online version is available at http://www. Springlink.com

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Responsible editor: Chai Ruihai

ranging from 1 120 to 2 200 mm during the past 30 years, with approximately 50% falling as rain between May and November and the remainder as snow (water equivalent). Annual mean temperature is 2.5ºC, with a maximum of 33.7℃ on August 16, 1984, and a minimum of –42.9 ºC on February 5, 1982 (Uryu Experimental Forest, Hokkaido University). The area is one of the snowiest and coldest regions in Japan, in which snow-covering period is about 7 months (from November to the following May) with a maximum snow pack of about 3.0 m.

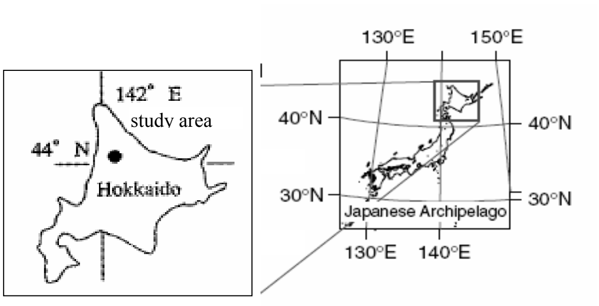

Fig. 1 Location of the study area

The watershed has a diversity of landscape components including lakes, streams, forested wetlands, and upland forests, with an elevation ranging from 284 m to 680 m asl. The bedrock is composed of Tertiary andesite covering the upland area and Quaternary sedimentary rock in the bottom valley (Ozawa *et al.* 2001). The soils are Sphagnofibrist on the wetland, and Dystrochrept on the uplands (Soil Survey Staff, USA 1994). The forest belongs to the pan mixed forest zone, and is mainly composed of *Abies sachalinensis* Masters, *Picea glehnii* Masters, *Quercus crispula* Blume, and *Betula* spp. including *B. platyphylla* var. *japanica* Hara and *B. ermannii* Cham. on the uplands (Hardiwinoto *et al.* 1991; Ogawa *et al.* 2006). However, *Alnus hirsuta* Turcz., *Salix* spp. including *S. sachalinensis* Fr. Schm. and *S. pet-susu* Kimura, and *Fraxinus mandshurica* var. *japanica* Maxim. dominate on the riparian zone, and *Picea glehnii* Masters on the wetland area. The undergrowths for both the uplands and wetland and riparian zones are dominated by the dense dwarf bamboo, *Sasa kurilensis* Makino et Shibata (Ogawa *et al.* 2006). The nomenclature of tree species in the present paper follows “Trees and Shrubs in Hokkaido” edited by Sato (2002).

Litterfall measurement

Six litter traps were placed randomly in each of six 20 m×20 m plots within the watershed. One plot was located on the wetland, two on the riparian zone and three on the upland. Each site represented a different plant community type (Table 1). Traps had a circular opening of about 65 cm in diameter, consisting of a sheet of nylon muslin attached to a plastic hoop by means of a drawstring. The hoop was positioned 1.5–1.8 m above the soil surface with plastic stakes to avoid the effect of dwarf bamboo. The mesh of the muslin is about 1 mm square. Litterfall was collected at monthly or two-week intervals for a two-year period from 2003 to 2004. It was very difficult to collect the litterfall during the snow-covering season (from November to the following May), therefore, the litter collection was made only during the snow uncovered season (from June to October). The litterfall collected was brought to the laboratory and separated into individual litter components; foliage (leaves and needles), fine woody litter (including twigs, small branches with diameter less than 2.0 cm and barks), reproductive material (flowers, seeds, scale, cone, and fruits) and miscellaneous material. In addition, foliage litter was separated again by dominant species. The sorted material was oven-dried to a constant weight at 70℃, weighed and then milled for chemical analysis.

Table 1. Characteristics of forest types studied in Dorogawa watershed in Hokkaido, Japan

Forest type		Topography and soil	Forest structure	Major tree species
Spruce pure forest (U-1)		Wetland, peat soil; peat deposit about 2.5 m; water table near but not above the surface in growing season and waterlogged during snow-melt.	Canopy height 15-20 m, Mean DBH 24.7 cm (range 10-57 cm), density 400 # hm^{-2}, Basal Area (BA) 25 $m^2 \cdot hm^{-2}$; few small trees (DBH < 10 cm);	*Picea glehnii*;
Alder-willow young forest (U-2, U-3)		Flat riparian wetland never waterlogged; alluvial sediments, loamy sand, over 100 cm deep.	Canopy height 12-15 m; Mean DBH 15.8 cm (range 10-28 cm), density 1000 # hm^{-2}, BA 20 $m^2 \cdot hm^{-2}$; few small trees	*Alnus hirsute* *Salix sachalinensis* *Salix pet-susu*
Broad leaf-conifer mixed forest	U-4	Lower slope, sandy loam, 70-100 cm; well drainage;	Canopy height 15-25 m, Mean DBH 30.6 cm (range 10-64 cm), density 300-400 # hm^{-2}, BA 43 $m^2 \cdot hm^{-2}$; few small trees (DBH < 10 cm).	*Quercus crispula* *Abies sachalinensis* *Betula platyphylla*
	U-5	Middle slope, fine sandy loam, over 100 cm; well drainage;		
	U-6	Flat ridge, silt loam, over 100 cm; well drainage;	Canopy height 15-25 m, DBH 10-80 cm, density 300 # hm^{-2}, BA 30 $m^2 \cdot hm^{-2}$; old-growth with few small trees.	*Quercus crispula* *Betula platyphylla* *Abies sachalinensis*

Soil sampling

In each plot, the soils were sampled from 0–10 cm and 10–30 cm mineral layers at the position where litter traps fixed in August 2003. At each point, 3 samples were taken with an auger (about 7 cm diameter) and bulked into one composite sample for each layer. Thus, a total of 5 samples were collected for each soil layer in each plot. In the laboratory, these soil samples were air-dried, then passed through 2-mm sieve.

Chemical analysis

The contents of total organic carbon and nitrogen for both plant and soil samples were determined by Perkin Elmer series Ⅱ

CHNS/O Analyzer 2400. The subsamples of 0.5 g of the ground litter samples were wet digested by H_2SO_4-H_2O_2 reagent with Microwave Digestion System (O.I. Analytical Co. Ltd., Tokyo, Japan), and analyzed for the contents of P, K, Ca, and Mg by ICP-AES (Nippon Jarrell Ash Co. Ltd., Kyoto, Japan). Exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) were extracted using 1M NH_4Cl and determined by ICP-AES. Available P was determined by the Bray Ⅱ method and colorimetric analysis using FIA auto-analyzer (AACS-Ⅳ, BL-TEC Inc., Japan).

As there were not enough replicate plots within each landscape component, the significance of the differences in mean values for litterfall and related nutrient fluxes could not be statistically tested. Mean comparisons for soil chemistry and litter nutrient concentrations were made using Student-Newman-Keuls test (Statsoft Japan Inc. 1999). In all analyses, $P<0.05$ was the criterion for significant differences.

Results

Landscape pattern of soil chemical properties

The soil chemical properties among landscape components were summarized in Table 2. The lowest pH of soils at 0–30 cm depth was found on the flat drainage riparian zone. On the wetland conifer zone, soil pH was higher at 10–30 cm depth than at 0–10 cm depth. The upland broadleaf-conifer mixture zone had relatively high pH values in soils. Total C and N concentrations of soils were greatest on the wetland conifer zone and lowest for the old-growth forest on upland zone. The C:N ratios were 25.5 and 29.6 at 0–10 cm and 10–30 cm on the wetland zone, respectively, which were significant higher than those on both riparian (11.5–12.6) and upland (14.8–17.4) zones. Available P and exchangeable Ca^{2+} and Mg^{2+} were higher on the riparian zone while exchangeable K^+ and Na^{2+} were higher on the upland zone.

Table 2. Chemical properties of s oil for the sampling stands in Dorogawa watershed in Hokkaido, Japan

	Soil depth (cm)	U-1	U-2	U-3	U-4	U-5	U-6
pH (H_2O)	0-10 cm	5.0 (0.2)a	4.7 (0.2)b	4.7 (0.3)b	5.4 (0.1)c	5.3 (0.2)c	5.6 (0.1)d
	10-30 cm	5.3 (0.2)a	4.6 (0.2)b	4.6 (0.2)b	5.1 (0.2)c	5.1 (0.2)c	5.2 (0.2)c
Org-C ($mg\cdot g^{-1}$)	0-10 cm	261.14 (17.41)a	94.60 (6.85)b	96.07 (9.54)b	105.07 (17.44)c	76.88 (7.38)d	65.41 (1.27)e
	10-30 cm	269.55 (13.33)a	38.62 (5.02)b	46.23 (6.49)b	59.17 (10.67)c	28.81 (0.41)d	25.14 (2.19)d
Total N ($mg\cdot g^{-1}$)	0-10 cm	10.22 (1.13)a	8.13 (0.55)b	7.60 (0.87)b	6.51 (0.85)c	4.41 (0.88)d	3.85 (0.64)d
	10-30 cm	9.12 (0.78)a	3.37 (0.23)b	4.01 (0.45)c	3.87 (0.23)bc	1.91 (0.12)d	1.55 (0.25)d
Available P	0-10 cm	12.53 (1.26)a	19.46 (0.96)b	22.77 (1.33)c	32.71 (2.29)d	12.74 (0.68)a	12.32 (0.59)a
($mg\cdot kg^{-1}$)	10-30 cm	7.27 (0.92)ae	10.92 (1.05)b	16.53 (1.07)c	20.39 (2.71)d	7.58 (0.47)a	6.67 (0.53)e
Exchangeable cations (cmol (+)$\cdot kg^{-1}$)							
K	0-10 cm	0.35 (0.08)a	0.28 (0.03)b	0.45 (0.03)c	0.49 (0.03)c	0.57 (0.04)d	0.39 (0.02)a
	10-30 cm	0.14 (0.02)a	0.13 (0.01)a	0.51 (0.03)b	0.27 (0.02)c	0.32 (0.02)d	0.19 (0.01)a
Ca	0-10 cm	2.44 (0.37)a	2.39 (0.31)ab	4.29 (0.52)c	4.56 (0.51)c	2.58 (0.15)a	2.79 (0.19)ad
	10-30 cm	2.08 (0.41)a	0.48 (0.05)b	3.58 (0.65)c	2.14 (0.10)a	1.07 (0.06)d	1.01 (0.05)d
Mg	0-10 cm	1.28 (0.11)a	1.58 (0.03)b	1.99 (0.11)c	1.80 (0.09)cd	1.47 (0.08)bd	1.17 (0.06)a
	10-30 cm	1.11 (0.08)a	0.99 (0.08)a	1.07 (0.07)a	0.81 (0.06)b	0.95 (0.04)ac	0.66 (0.03)d
Na	0-10 cm	0.32 (0.03)a	0.24 (0.02)b	0.26 (0.02)b	0.38 (0.02)c	0.57 (0.03)d	0.31 (0.02)a
	10-30 cm	0.26 (0.02)a	0.19 (0.02)a	0.32 (0.02)b	0.24 (0.01)a	0.34 (0.02)b	0.26 (0.01)a

Note: Values with parentheses are the standard deviation of the mean (N = 5);
Values in the same row followed by the same letter in the same row indicate insignificant differences ($P < 0.05$).

Pattern of Litterfall

The mean annual rates of litterfall were 1 444 kg (D.W.)$\cdot hm^{-2}\cdot a^{-1}$ in the wetland spruce stand, 5 122 $kg\cdot hm^{-2}\cdot a^{-1}$ in the riparian alder-willow stand, and 4 123 $kg\cdot hm^{-2}\cdot a^{-1}$ in the upland mixed stands during the study period (Table 3). Leaf litter contributed the greatest amount with a range of 74.7%(wetland)–83.8% (riparian) of the annual mean total within watershed components. Fine woody litter was 11.4%(riparian)–8.7% (wetland) in different forests; reproductive materials and miscellaneous fractions accounted for 2.4%(riparian)–3.9%(upland) and 2.4% (riparian)–4.2%(upland), respectively.

The annual patterns of total litterfall and leaf litter varied markedly in the two years for all forest stands (Fig. 2), of which the peak occurred in September in the second year was caused by typhoon. The monthly mean leaf fall varied from 21 to 555 $kg\cdot hm^{-2}$ on wetland, 80 to 3 123 $kg\cdot hm^{-2}$ on the riparian and 11 to 3 958 $kg\cdot hm^{-2}$ on the upland zone. Leaf fall concentrated in September and October for all sites within the watershed during the study period.

Table 3. Annual litterfall ($kg\cdot hm^{-2}$ D.W.) by litter component in different habitat types in Dorogawa watershed in Hokkaido during 2003-2004

Plot (site)	Period	Foliage	Woody	Reproductive	Miscellaneous	Total
U-1	Year 1	992.1	36.1	30.3	68.9	1127.4
(Wetland)	Year 2	1164.4	502.8	41.4	52.0	1760.6
	Mean	1078.2	269.5	35.8	60.5	1444.0
U-2	Year 1	4406.6	375.1	75.2	75.3	4932.2
(Riverine)	Year 2	3480.4	1001.3	215.7	228.4	4925.8
	Mean	3943.5	688.2	145.5	151.9	4929.0
U-3	Year 1	4835.4	118.1	39.3	72.4	5065.2
(Riverine)	Year 2	4480.3	814.2	154.8	115.0	5564.3
	Mean	4657.9	466.2	97.1	93.7	5314.8
U-4	Year 1	3708.2	248.7	44.2	152.7	4153.8
(Lower slope)	Year 2	2302.0	1326.0	49.0	352.6	4029.6
	Mean	3005.1	787.4	46.6	252.7	4091.7
U-5	Year 1	3673.4	327.1	444.0	93.4	4537.9
(Middle slope)	Year 2	2324.0	876.4	83.5	177.0	3460.9
	Mean	2998.7	601.8	263.8	135.2	3999.4
U-6	Year 1	4491.7	245.0	77.5	73.0	4887.2
(Upper slope)	Year 2	2211.4	1001.3	267.9	188.0	3668.6
	Mean	3351.6	623.2	172.7	130.5	4277.9

Nutrient concentrations in litter components

Differences among the dominant tree species in nutrient concentrations of leaf litter were most distinct within the watershed (Table 4). In general, the mean concentrations of C were higher while N were lower in coniferous trees than in the broad-leaved trees in this study. Within the conifers, *A. sachalinensis* had higher element concentrations (C, N, Ca and K) than *P. glehnii* did except for P and Mg. Among the broad-leaved trees, the mean N concentrations in leaf litter followed the decreasing sequence: *A. hirsuta* > *Salix* spp. > *Betula* spp. > *Q. crispula* > *A. mono*. *Salix* spp. had higher concentrations of Ca, K and P than the other species did. Within the upland zone, the concentrations of N, P, K and Mg in leaf litter were lower while Ca was higher in the old-growth stand than in the other stands (Table 4). Woody litter had low nutrient concentrations with no significant differences between the landscape components. However, Miscellaneous and reproductive materials had relatively high concentrations of N and P with low concentrations of C and Ca (data were not shown).

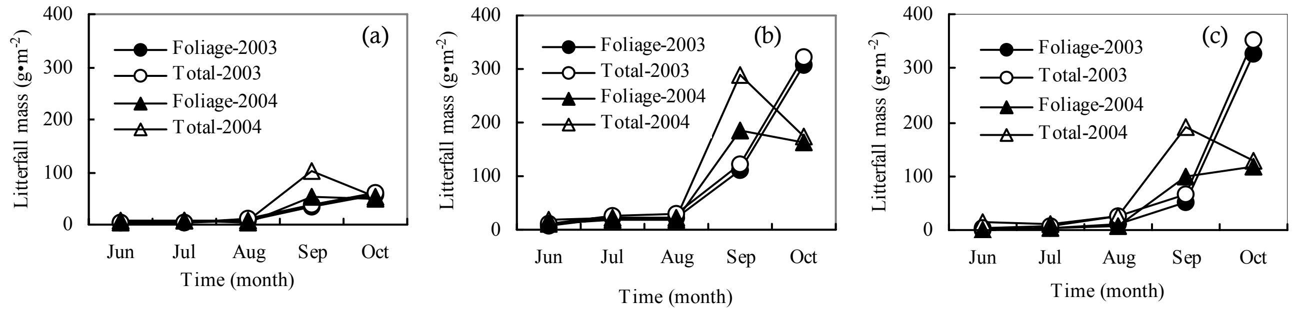

Fig. 2 Seasonal patterns of foliage and total fine litterfall in different habitat types in Dorogawa watershed during 2003-2004.
(a) Wetland zone (U-1); (b) Riparian zone (means of U-2 and U-3); (c) Upland zone (means of U-4, U-5 and U-6).

Table 4. Mean nutrient concentrations (mg·g^{-1}) in foliage litter for dominant tree species in different habitat types in Dorogawa watershed in Hokkaido during 2003-2004

Species	Site	C	N	P	K	Ca	Mg
Picea glehnii	U-1	527 (6.15)	7.56 (1.30)	0.85 (0.41)	2.76 (1.81)	7.24 (1.16)	1.63 (0.81)
Alnus hirsuta	U-2	539 (8.36)a	28.73 (3.74)a	1.03 (0.24)a	3.54 (1.73)a	13.86 (1.29)a	2.55 (0.19)a
	U-3	528 (8.63)a	28.02 (4.46)a	1.19 (0.49)a	3.91 (1.28)a	14.12 (1.38)a	2.94 (0.38)b
Salix spp.	U-2	515 (9.12)a	22.60 (4.99)a	1.34 (0.32)a	5.55 (1.01)a	13.99 (2.15)a	2.77 (0.19)a
	U-3	508 (4.99)a	22.41 (6.52)a	1.12 (0.44)a	4.13 (0.43)b	15.49 (2.16)b	2.29 (0.20)b
Abies sachalinensis	U-4	542 (7.87)a	8.65 (2.47)a	0.66 (0.21)a	4.68 (1.11)a	12.06 (2.08)a	2.02 (0.36)a
	U-5	536 (8.67)a	8.45 (2.83)a	0.68 (0.09)a	3.61 (0.84)b	13.16 (1.88)b	1.04 (0.09)b
	U-6	537 (9.89)a	7.88 (1.89)a	0.61 (0.26)a	2.28 (0.49)c	14.99 (2.25)c	1.03 (0.09)b
Acer mono	U-4	499 (6.61)a	11.61 (1.84)a	0.89(0.18)a	3.69 (1.35)a	11.91 (2.86)a	2.39 (0.58)a
	U-5	491 (5.33)a	9.90 (2.08)b	0.61 (0.13)b	3.71 (0.25)a	15.31 (1.95)b	2.55 (0.42)a
Betula spp.	U-4	508 98.23)a	17.96 (3.24)a	1.19 (0.15)a	5.96 (1.43)a	9.85 (2.08)a	3.46 (0.89)a
	U-5	506 (6.03)a	16.03 (2.63)b	0.70 (0.09)b	4.14 (0.63)b	13.95 (1.13)b	3.17 (0.15)a
	U-6	521 (8.67)b	13.38 (2.55)c	0.53 (0.13)c	2.53 (0.39)c	13.03 (1.22)b	3.06 (0.13)a
Quercus crispula	U-4	493 (6.56)a	12.43 (2.08)a	0.75 (0.10)a	4.01 (0.53)a	9.38 (1.47)a	2.57 (0.31)a
	U-5	5.04 (7.87)ab	13.24 (2.84)a	0.51 (0.12)b	4.09 (1.13)a	12.03 (2.28)b	2.09 (0.32)b
	U-6	513 (5.50)b	9.80 (2.82)b	0.42 (0.09)b	2.59 (0.54)b	12.72 (2.21)b	1.99 (0.22)b

Note: Means for the same species followed by the same letter in the same column indicate insignificant differences ($P < 0.05$).
Salix spp. indicate *S. sachalinensis* Fr. Schm. and *S. pet-susu* Kimura; *Betula* spp. indicate *B. plyphylla* var. *japanica* Hara and *B. ermanii* Cham.;

Annual nutrient inputs by litterfall

The amounts of nutrient input to forest floor through annual litterfall were given in Table 5. There existed significant differences of annual nutrient inputs by litterfall among landscape components for the nutrient elements analyzed. The nutrient inputs for all elements analyzed were greatest on the riparian zone and lowest in wetland zone. Nutrient accession to forest floor by litterfall followed the decreasing sequence: N > Ca > K > Mg > P for all stands.

Discussion

Litterfall dynamics

Litterfall is usually strongly seasonal and is driven by air temperature and precipitation patterns (Bray and Gorham 1964). Climatic conditions affect the phenology of the dominant tree species, for instance, bud burst, flowering and fruiting of different trees, which are reflected bylitterfall (Ferrari and Sugita 1996). In the present study, the major peak of litterfall, particularly leaf fall, occurred consistently in the period of September–October for both deciduous broadleaved and evergreen coniferous species. The seasonality of litterfall in this study agrees with the previous reports for other forests in the same area (Hardiwinoto *et al*. 1991). In 2004, the peak of litterfall occurred in September, which was driven by typhoon. Over 70% of the leaf fall in this period consisted of green leaves. The annual litterfall rates decreased in 2004 in upland zone because of the strong typhoon disturbance that caused 10% to 20% of trees uprooted and trunk snapped. It demonstrates that typhoon disturbance is a determinant factor controlling annual litterfall rate and its seasonality (Xu *et al*. 2000 & 2004). However, at the study site, strong typhoons are seldom, which occurs in an interval about 50 years (database of Uryu Experimental Forest, Hokkaido University).

Table 5. Mean annual nutrient returns (kg·hm^{-2}·a^{-1}) by litterfall in different habitat types in Dorogawa watershed during 2003-2004.

Plot	Litter component	C	N	P	K	Ca	Mg
U-1	Foliage litter	572.60	8.77	0.29	3.72	6.15	2.33
	Others	189.02	2.43	0.14	0.92	2.96	0.60
	Total	761.62	11.20	0.43	4.64	9.11	2.93
U-2	Foliage litter	2131.87	104.90	4.24	15.20	51.20	10.20
	Others	504.29	17.01	0.49	2.09	6.64	1.58
	Total	2636.16	121.91	4.73	17.29	57.84	11.78
U-3	Foliage litter	2459.20	119.50	3.06	19.36	65.12	14.02
	Others	346.07	9.16	0.19	0.77	3.96	0.59
	Total	2805.27	128.66	3.25	20.13	69.08	14.61
U-4	Foliage litter	1537.41	44.49	1.68	12.20	34.90	7.29
	Others	552.32	12.62	0.27	1.41	7.23	1.14
	Total	2089.73	57.11	1.95	13.61	42.13	8.43
U-5	Foliage litter	1533.43	32.21	1.10	10.37	35.63	7.23
	Others	511.22	10.07	0.56	2.46	6.06	1.02
	Total	2044.65	42.28	1.66	12.83	41.69	8.25
U-6	Foliage litter	1748.26	36.30	1.31	9.86	39.10	7.46
	Others	490.67	9.68	0.28	1.44	4.33	0.85
	Total	2238.93	46.98	1.59	11.30	43.43	8.31

Litterfall rate differed significantly between landscape components. The highest rate was found in the riparian deciduous broad-leaved stand, and the lowest rate was found in the wetland evergreen coniferous stand. This landscape pattern for litterfall could be determined by the stand structure, species composition, and site conditions (Ferrari 1999; Ohrui *et al*. 1999).

Litterfall rate (1 444 kg·hm^{-2}·a^{-1}) of the evergreen conifer on wetland in this study was rather low in comparison with the mean values (3 144 kg·hm^{-2}·a^{-1}) for cold temperate evergreen conifers worldwide (Vogt *et al*. 1986). In the present study, no measurement was made during the winter because of heavy snow, which could cause the underestimate for the litterfall mass. Based on the result that the fine litterfall in winter contributed about 30%–38% of the annual total (over 60% was fine woody litter) in evergreen coniferous stands at the same study area (Hardiwinoto *et al*. 1991), the annual litterfall for the wetland coniferous stand should be 1 877–1 993 kg·hm^{-2}, which was comparable with that in a Scots pine stand on a bog (Finér 1996). The low litterfall of this wetland forest should be resulted by the lower density and the poor site condition.

Litterfall rates of the riparian and upland forests in the present study are within the range (4 070–4 570 kg·hm^{-2}·a^{-1}) of the temperate forests in Japan (Iwatsubo 1996). However, our results are much higher than those in cold temperate forests worldwide (3144–3590 kg·hm^{-2}·a^{-1}) by Vogt *et al*. (1986). The differences in litter production of similar forest type could be contributed to the differences in tree species composition (Bray and Gorham 1964), forest structural parameters (Hardiwinoto *et al*. 1991; Xu *et al*. 2000), precipitation (Bray and Gorham 1964; Schuur 2001), and disturbances (Xu *et al*. 2004).

Litterfall nutrient fluxes

Leaf litter contributed in the greatest proportion (73%–88%) to the total litterfall in this study, and had relatively high nutrient concentrations particularly for N, P and K. Therefore, foliage fraction is considered as the most important component of nutrient cycling in forest ecosystems (Miller 1984; Xu *et al*. 2004). The lowest concentrations of N and P in foliage litter of most species were observed in October (data were not shown), which were coincident with the peak in leaf fall. The finding is also supported by the reports from other studies (Chuyong *et al*. 2000; Liu *et al*. 2002). However, the lowest N concentration in foliage litter of *P. glehnii* occurred in July, which could be due to the long period waterlogged stress because of the superficial root system (Boggie 1972). The seasonal variation of N concentration in *A. hirsuta* was insignificant. These differences could be attributable to the physiological trait of species and nutrient and water regimes of the site (Vitousek *et al*. 1995; Burghouts *et al*. 1998; Pedersen 1999).

Nutrient fluxes by foliage litter are of interest with respect to understanding nutrient uptake in forests. Fluxes of elements via other litter components were insignificant probably because of the relatively small quantity. Litterfall N fluxes were 11−129 kg·hm^{-2}·a^{-1} in different landscape components. The next was Ca with 9–69 kg·hm^{-2}·a^{-1}. Fluxes of other elements in litterfall were much smaller than those for N and Ca. Within the watershed, lowest fluxes for all elements measured in the present study occurred at the wetland zone while the greatest fluxes occurred at riparian zone. The element fluxes at the upland zone were within the range of values for the Japanese temperate forests reported in previous studies (Iwatsubo 1996). Foliage element fluxes entirely dominated the total litterfall element fluxes even though some element concentrations in other components (such as reproductive and miscellaneous materials) usually exceeded the concentrations in foliage litter. In the present study, foliage litter N fluxes contributed 80%, 78% and 89% of total litterfall N fluxes at wetland, riparian and upland zones, respectively; and for P 69%, 78% and 92%; for Ca 70%, 85% and 91%.

The spatial variation observed in litterfall could give rise to heterogeneity of both chemical and physical features of forest soils (Auguto *et al*. 2002; Ferrari 1999; Lavery *et al* 2004). The measures of soil chemical properties indicated a clear influence of vegetation on the soils. There existed evident differences in soil chemistry between the different landscape zones in the present study. The consistently low soil C:N ratios at the riparian zone might be due to the higher-quality litter inputs (largely N-fixing alder). Regression analysis showed that surface soil C:N ratio is significantly negatively correlated to the annual N input by litterfall in this study (Fig. 3). Gill and Burke (1999) found supporting evidence in North America. The lower soil pH at the riparian zone could be resulted from the rapid rate of nitrification (Shibata *et al*. 2005; Xu and Shibata 2005). At the upland zone, the soil N and available P were greater on the lower slope than on the middle and upper slope, which might be attributable to the invasion of alder trees on the lower slope site after selected cutting. Results from other studies conducted in North America showed significant effects of alder on the adjacent forest site (Rhoades and Binkley 1992; Lavery *et al*. 2004). The results demonstrate that the biogeochemical processes in forested ecosystems can be influenced with altering litter composition.

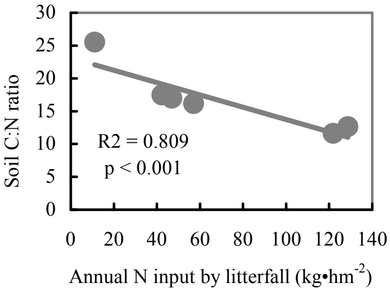

Fig. 3 Relationship between soil C:N ratio (0–10 cm) and annual N input by litterfall in the different forest stands within Dorogawa watershed in Hokkaido, Japan

Acknowledgements

This study was made possible by support from the Japanese Society for Promotion of Sciences (15P03118). The authors gratefully acknowledge Uryu Experimental Forest, the Field Science Center for Northern Biosphere, Hokkaido University, for permission to work. Prof. F. Satoh and K. Sasa are acknowledged for invaluable suggestions. Ms Y. Aoyagi and Mr. K. Hayakashi helped with fieldwork. Dr. K. Fukuzawa helped with laboratory analysis.

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