



Title	Allometric Relationships and Carbon and Nitrogen Contents for Three Major Tree Species ( <i>Quercus crispula</i> , <i>Betula ermanii</i> , and <i>Abies sachalinensis</i> ) in Northern Hokkaido, Japan
Author(s)	Takagi, Kentaro; Kotsuka, Chikara; Fukuzawa, Karibu; Kayama, Masazumi; Makoto, Kobayashi; Watanabe, Tsunehiro; Nomura, Mutsumi; Fukazawa, Tatsuya; Takahashi, Hiroyuki; Hojyo, Hajime; Ashiya, Daitaro; Naniwa, Akihiko; Sugata, Sadao; Kamiura, Tatsuya; Sugishita, Yoshiyuki; Sakai, Rei; Ito, Kinya; Kobayashi, Makoto; Maebayashi, Mamoru; Mizuno, Masato; Murayama, Takeshi; Kinoshita, Koji; Fujiwara, Daisaku; Hashida, Shukichi; Shibata, Hideaki; Yoshida, Toshiya; Sasa, Kaichiro; Saigusa, Nobuko; Fujinuma, Yasumi; Akibayashi, Yukio
Citation	Eurasian Journal of Forest Research, 13(1), 1-7
Issue Date	2010-08
Doc URL	<a href="http://hdl.handle.net/2115/43850">http://hdl.handle.net/2115/43850</a>
Type	bulletin (article)
File Information	EJFR13-1_001.pdf



[Instructions for use](#)

## Allometric Relationships and Carbon and Nitrogen Contents for Three Major Tree Species (*Quercus crispula*, *Betula ermanii*, and *Abies sachalinensis*) in Northern Hokkaido, Japan

TAKAGI Kentaro<sup>1\*</sup>, KOTSUKA Chikara<sup>1</sup>, FUKUZAWA Karibu<sup>2</sup>, KAYAMA Masazumi<sup>1</sup>, MAKOTO Kobayashi<sup>2</sup>, WATANABE Tsunehiro<sup>3</sup>, NOMURA Mutsumi<sup>1</sup>, FUKAZAWA Tatsuya<sup>4</sup>, TAKAHASHI Hiroyuki<sup>1</sup>, HOJYO Hajime<sup>1</sup>, ASHIYA Daitaro<sup>1</sup>, NANIWA Akihiko<sup>1</sup>, SUGATA Sadao<sup>1</sup>, KAMIURA Tatsuya<sup>1</sup>, SUGISHITA Yoshiyuki<sup>1</sup>, SAKAI Rei<sup>1</sup>, ITO Kinya<sup>1</sup>, KOBAYASHI Makoto<sup>1</sup>, MAEBAYASHI Mamoru<sup>5</sup>, MIZUNO Masato<sup>5</sup>, MURAYAMA Takeshi<sup>5</sup>, KINOSHITA Koji<sup>5</sup>, FUJIWARA Daisaku<sup>5</sup>, HASHIDA Shukichi<sup>5</sup>, SHIBATA Hideaki<sup>1</sup>, YOSHIDA Toshiya<sup>1</sup>, SASA Kaichiro<sup>1</sup>, SAIGUSA Nobuko<sup>6</sup>, FUJINUMA Yasumi<sup>7</sup>, and AKIBAYASHI Yukio<sup>1</sup>

<sup>1</sup>Field Science Center for Northern Biosphere, Hokkaido University, Sapporo 060-0809, Japan

<sup>2</sup>Graduate School of Agriculture, Hokkaido University, Nayoro 096-0071, Japan

<sup>3</sup>Graduate School of Environmental Science, Hokkaido University, Nayoro 096-0071, Japan

<sup>4</sup>Graduate School of Engineering, Hokkaido University, Sapporo 060-8628, Japan

<sup>5</sup>Research and Development Department, Hokkaido Electric Power Co., Inc., Ebetsu 067-0033, Japan

<sup>6</sup>Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba 305-8506, Japan

<sup>7</sup>Department of Environmental Management, Tottori University of Environmental Studies, Tottori 689-1111, Japan

### Abstract

To evaluate the biomass of conifer-broadleaf mixed forests in northern Hokkaido, Japan, the relationships between tree dry masses (including belowground roots) and diameter at breast height (DBH) and tree height ( $H$ ) for major three tree species (*Quercus crispula* Blume, *Betula ermanii* Cham., and *Abies sachalinensis* (F. Schmidt) Mast.) were calculated. In addition, carbon and nitrogen contents of each tree organ were measured for an accurate estimation of the carbon and nitrogen stocks in the trees. For all three species, one allometric equation explained the relationship between  $DBH$  (or  $DBH^2 \times H$ ) and the dry masses of whole tree, aboveground total, trunk, branch, and coarse root. Leaf dry mass of *Abies*, a coniferous species, was higher than that of the two deciduous species at the same DBH. The allometric equations, except that for coniferous leaf, were comparable to previous studies in Hokkaido. The difference in the stand density is a likely reason for the large difference in the coniferous leaf dry mass between studies. Carbon and nitrogen contents for *Abies* were higher and lower, respectively, than the other two species for all organs (leaf, branch, trunk, and coarse root). Nearly all the measured carbon contents were less than but close to 0.5, and use of the constant value 0.5 caused 1–7% error in the carbon stock estimate of a tree.

*Key words:* allometric equation, biomass, birch, fir, oak

### Introduction

Trees are recognized as a possible carbon reservoir, and as carbon dioxide concentrations increase in the atmosphere, precise and convenient methods for forest biomass estimation are needed. Allometric relationships of tree biomass to trunk diameter are basic for the estimation of forest biomass. In Japan, research on the biomass of naturally regenerated forests is increasing, with comparisons between the annual carbon stock change and net ecosystem carbon dioxide exchange of forests evaluated by the eddy covariance technique (Ohtsuka *et al.* 2005, Hirata *et al.* 2008, Kominami *et al.* 2008), but comprehensive data sets for naturally regenerated forests including large trees (in diameter or height) or data for belowground biomass are still

limited (Li *et al.* 2003, Kominami *et al.* 2008). In addition, because the carbon allocation among tree organs can change according to its environmental condition (Lacointe 2000), it is helpful to show the present status of the allocation pattern of trees in northern Hokkaido, Japan for comparisons of the allocation patterns among different biomes, or for evaluations of the effect of future climate change on the allocation patterns. Moreover, the availability of nitrogen represents a key constraint on carbon cycling in terrestrial ecosystems, and ecosystem  $CO_2$  uptake capacity in temperate and boreal forests scales directly with whole-canopy N concentrations (Magnani *et al.* 2007, Ollinger *et al.* 2008). Thus, it is important to show the information on the nitrogen content of tree

organs in northern Hokkaido. In this study, we calculated the allometric relationships between tree dry mass of each organ, including belowground roots, and diameter at breast height (DBH) and tree height ( $H$ ) for three major species (*Quercus crispula* Blume, *Betula ermanii* Cham., and *Abies sachalinensis* (F. Schmidt) Mast.) in northern Hokkaido, Japan. In addition, carbon and nitrogen contents of each organ were measured to provide an accurate estimation of the carbon and nitrogen stock in mixed forests of northern Hokkaido.

### Materials and Methods

The study site was located in the Teshio Experimental Forest, Hokkaido University (45°03'N, 142°07'E) in northernmost Hokkaido, Japan. The soil is Gleyic Cambisol and has a surface organic horizon of ca. 10 cm thick. The dominant tree species were *Q. crispula*, *B. ermanii*, *A. sachalinensis*, *Betula platyphylla* Sukaczew var. *japonica* (Miq.) H. Hara, *Picea jezoensis* (Sieb. et Zucc.) Carr., and *Acer mono Maxim.* The evergreen dwarf bamboos *Sasa senanensis* (Franch. et Sav.) Rehder and *Sasa kurilensis* (Rupr.) Makino et Shibata formed dense undergrowth on the forest floor. Maximum and mean heights of the tree canopy were about 24 and 20 m, respectively. Stand density and the basal area of canopy trees (DBH > 6 cm) were ca. 600 trees ha<sup>-1</sup> and 22 m<sup>2</sup> ha<sup>-1</sup>, respectively (Koike et al. 2001).

Field surveys for the three tree species (*Q. crispula*, *B. ermanii*, and *A. sachalinensis*) were conducted in late August from 2001 through 2007 (Table 1). The numbers of surveyed trees (all trees were naturally regenerated) were 7 for *Betula*, 7 for *Quercus*, and 8 for *Abies*, and samples were distributed over a wide range of DBH. The DBH and the branch spread length for the four cardinal directions (north, south, east, and west) were measured before cutting each tree, and the trunk top height and trunk diameters at 2-m height intervals were measured after cutting. The fresh mass of each organ (trunk, branches, and leaves) was weighed at 2-m height intervals along the trunk. The trunk was defined as the part that directly connects with roots and reaches the top of the tree, and the remaining woody aboveground parts were categorized as branches. The heights of branches and leaves were categorized based on the actual position in the stand, not by the height connecting with the trunk. Branches were divided into three categories based on diameter (<2 cm, 2–5 cm, and >5 cm), and the fresh mass was measured for each category at 2-m height intervals. For *Betula* and *Quercus*, all leaves were separated from the trunks and branches and the fresh mass was measured. For *Abies*, all leaves were separated from the trunk and branches when these woody parts were more than 2 cm in diameter; for those branches less than 2 cm in diameter, the part of the branches with leaves (>1.5 kg fresh mass) was separated into leaves and branches at 2-m height intervals, and the leaf/branch dry mass ratio was applied to all the branches with leaves to estimate each leaf and branch dry mass for each height. For an *Abies* tree with a 50.16-cm DBH, the leaf/branch dry mass ratio ranged 0.430–0.468, and the average and standard

deviation of the 10 height categories (21.35 m in the tree height) were 0.446 and 0.011, respectively. Even if we assume that the deviation in the ratio among the height categories was caused only by the sampling error, this leaf dry mass estimation procedure causes < ±2% error (or ±1.9 of 117 kg dry leaf mass) for this tree. Stumps with roots were pulled out using a backhoe, and the remaining roots were dug up manually using shovels (the digging up process took ca. 5 days × persons for trees with >50-cm DBH). The soil on roots was completely washed away by spraying river water on site with a compressor and using brushes. Roots were split into four categories based on diameter (< 2 cm, 2–5 cm, 5–10 cm, and >10 cm), and the fresh mass was measured for each category. Fine roots (< ca.0.5 cm in diameter) were not collected.

Dry mass of each organ (trunk, branches, leaves, and coarse roots) was measured as follows. A disk of ca. 3 cm thick was taken from each 2-m interval of trunk, and the fresh mass was measured. Each disk was oven-dried at 70–80°C until there was no change in the mass (typically it took 1 month), and the dry mass was measured. The trunk dry mass was then estimated at each 2-m interval by multiplying its fresh mass by the dry/fresh mass ratio of the disk sample. For branches, coarse roots, and leaves, typically 1–3 kg of the fresh sample was weighed for each 2-m height interval and each branch and coarse-root diameter class and oven-dried at 70–80°C until there was no change in the mass. The dry mass was estimated by multiplying the fresh mass by the dry/fresh mass ratio of the sample for each diameter (branches and coarse roots) and height classes.

The allometric relationships between DBH (or  $DBH^2 \times H$ ) and dry mass of each organ were determined using the following equation:

$$\ln Y = a \ln X + b, \quad (1)$$

where  $Y$  represents dry mass,  $X$  represents  $DBH$  or  $DBH^2 \times H$ , and  $a$  and  $b$  are coefficients.

Carbon and nitrogen contents were measured using a PE2400 II analyzer (Perkin Elmer Inc., Waltham, MA, USA) for *Quercus* and *Abies* and a Flash EA1112 analyzer (Thermo Electron Corp., Waltham, MA, USA) for *Betula*. The accuracy of the measurement was within 0.3% for both carbon and nitrogen contents for both analyzers. The numbers of samples for each tree and organ are listed in Table 3. One-way ANOVA was used to determine differences in carbon and nitrogen contents among species with Tukey's HSD multiple comparison test. Levene's test was applied to check the homogeneity of variance.

### Results and Discussion

There was no significant difference among the three species for the relationships between DBH (or  $DBH^2 \times H$ ) and dry masses of the whole tree, aboveground total, trunk, branch, and coarse root, and one allometric equation for each organ explained the relationships for all three species (Fig. 1). The coefficients  $a$  and  $b$  are listed in Table 2. Previous studies also reported that one

Table 1. Surveyed trees.

ID	DBH (cm)	Height (m)	Canopy width (m)		Dry mass (kg)							Surveyed year *
			North-south direction	East-west direction	Trunk	Branch	Leaf	Coarse root	Cone & Spike	Total		
<i>Betula ermanii</i>												
a	51.50	20.80	11.20	11.50	984.83	267.24	27.05	458.79	7.13	1745.05	2003	
b	31.85	17.37	8.12	10.35	360.95	162.83	17.80	154.83	1.20	697.61	2003	
c	29.08	19.40	9.64	7.53	230.40	80.07	6.70	104.79	0.69	422.65	2003	
d	16.30	11.87	4.97	5.20	70.58	31.34	2.00	52.11	n.o.	156.03	2005	
e	11.11	9.35	3.11	2.89	25.20	5.89	1.66	15.59	0.00	48.35	2003	
f	6.83	7.53	3.38	2.63	9.70	2.43	0.25	3.98	n.o.	16.36	2005	
g	6.50	6.76	2.25	2.45	7.08	1.80	0.73	3.10	n.o.	12.71	2005	
<i>Quercus crispula</i>												
h	55.00	17.50	n.d.	n.d.	936.97	710.75	36.88	286.86	n.o.	1971.46	2001	
i	38.80	15.45	n.d.	n.d.	407.06	166.47	17.87	113.44	n.o.	704.85	2001	
j	21.40	10.67	6.38	8.14	103.47	72.98	7.16	54.87	0.01	238.49	2005	
k	19.90	10.60	6.15	6.40	97.91	48.42	5.17	48.39	n.o.	199.90	2005	
l	10.23	6.90	5.22	4.68	15.77	10.02	1.68	13.03	n.o.	40.50	2005	
m	8.80	7.00	n.d.	n.d.	12.35	5.52	1.14	4.91	n.o.	23.92	2001	
n	3.76	4.08	2.10	2.10	1.85	0.36	0.19	1.40	n.o.	3.80	2005	
<i>Abies sachalinensis</i>												
o	50.16	21.35	8.24	9.17	695.41	465.35	117.04	315.31	0.81	1593.91	2002	
p	37.48	18.50	8.75	9.90	324.01	312.44	88.25	189.86	8.07	922.63	2002	
q	31.80	16.40	8.40	8.50	259.10	187.85	49.78	119.06	0.19	615.98	2007	
r	18.40	12.60	4.35	4.05	61.82	30.38	25.80	35.56	0.22	153.78	2007	
s	13.15	9.72	3.30	3.00	26.39	7.91	7.95	16.41	n.o.	58.66	2005	
t	11.75	9.88	3.48	3.77	20.45	8.54	6.19	6.68	n.o.	41.86	2002	
u	10.50	7.48	2.97	3.20	18.76	5.34	4.41	5.99	n.o.	34.50	2005	
v	6.10	4.75	1.87	1.72	3.92	1.33	1.27	2.59	n.o.	9.10	2007	

\* Date: 20-23 Aug. 2001, 26-30 Aug. 2002, 18-21 Aug. 2003, 29 Aug.-2 Sep. 2005, and 27-30 Aug. 2007

DBH: diameter at breast height

n.d.: no data

n.o.: not observed

allometric equation could explain the DBH-dry mass relationship of several tree species in a forest stand and suggested the similarity of the relationships among trees growing in the same environment (Kitazawa *et al.* 1959, Research Group on Forest Productivity of the Four Universities (hereafter RGFPFU) 1960, Takahashi *et al.* 1999). For leaf, the dry mass of *Abies*, a coniferous species, was higher than that of the two

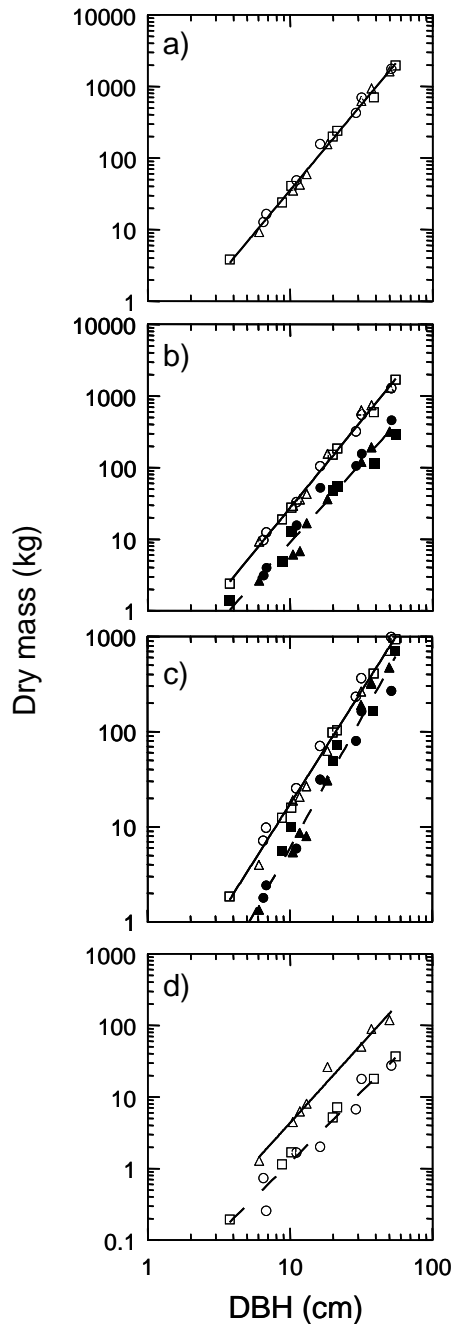


Fig. 1. Allometric relationships between DBH and dry mass for *Betula* (circles), *Quercus* (squares), and *Abies* (triangles): (a) whole tree biomass including coarse roots, (b) above- (open) and belowground (closed) total, (c) trunk (open) and branch (closed), and (d) leaf. See Table 2 for the coefficients of the allometric equations.

deciduous species at the same DBH. The  $R^2$  values of the regressions based on  $DBH$  were the same or higher than those based on  $DBH^2 \times H$ , except for coarse roots and *Abies* leaf, but in each case the difference in  $R^2$  values was within 0.02. Takahashi *et al.* (1999) also reported the better fit for equations with  $DBH$  as the independent variable than with  $DBH^2 \times H$ .

The allometric equations in this study were compared with those reported in previous studies (Fig. 2). Takahashi *et al.* (1999) reported equations for trees in a secondary deciduous broad-leaved forest in Tomakomai Experimental Forest, Hokkaido University, located in southern Hokkaido, where the dominant species were *Q. crispula*, *Carpinus cordata* Blume, and *Sorbus alnifolia* (Sieb. et Zucc.) K. Koch, and the RGFPFU (1960) reported equations for three coniferous trees (*A. sachalinensis*, *P. jezoensis*, and *Picea glehnii* (F. Schmidt) Mast.) in northeastern Hokkaido. Stand density and the basal area of canopy trees ( $DBH > 6$  cm) were ca. 1700 trees  $ha^{-1}$  and 26  $m^2$

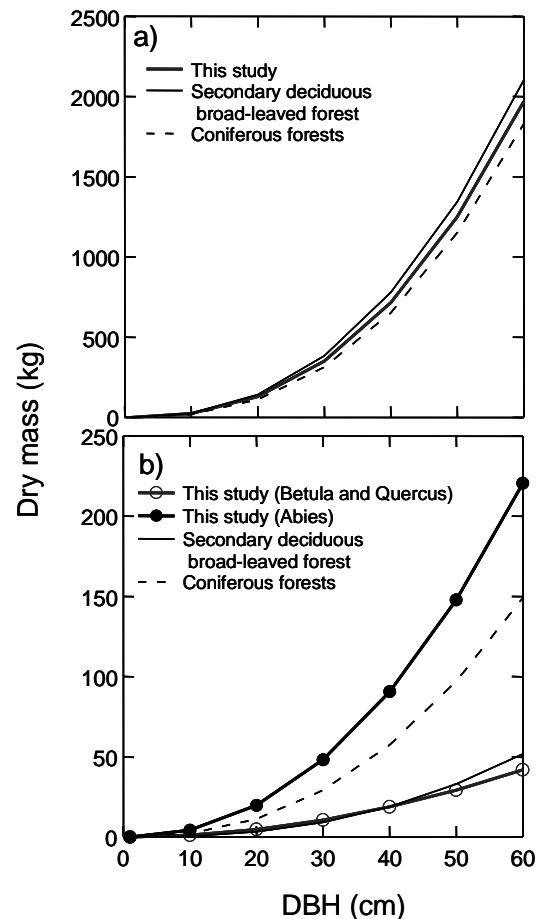


Fig. 2. Comparison of allometric relationships with previous studies: (a) stem + branch dry mass, (b) leaf dry mass. Equations for trees in the secondary deciduous broad-leaved forest are from Takahashi *et al.* (1999) and those for the coniferous trees are from Research Group on Forest Productivity of the Four Universities (1960).

Table 2. Allometric equations ( $\ln Y = a \ln X + b$ ) of dry masses for three tree species in northern Hokkaido. Trunk DBH and the product of trunk height and square of trunk DBH ( $DBH^2 H$ ) were used as independent variables ( $X$ ).

Y (kg)	DBH (cm) as X			$DBH^2 H$ (cm <sup>2</sup> m) as X		
	a	b	R <sup>2</sup>	a	b	R <sup>2</sup>
Whole tree	2.389	-1.928	0.994	0.917	-2.548	0.993
Above ground total	2.428	-2.282	0.994	0.932	-2.906	0.991
Trunk	2.365	-2.596	0.991	0.909	-3.217	0.991
Branch	2.713	-4.456	0.979	1.039	-5.138	0.972
Leaf ( <i>Betula</i> & <i>Quercus</i> )	1.974	-4.347	0.958	0.762	-4.884	0.939
Leaf ( <i>Abies</i> )	2.192	-3.579	0.983	0.818	-3.965	0.988
Coarse root	2.224	-2.918	0.967	0.855	-3.504	0.968

ha<sup>-1</sup>, respectively, for the deciduous forest and ca. 2300–4100 trees ha<sup>-1</sup> and 18–55 m<sup>2</sup> ha<sup>-1</sup>, respectively, for the coniferous forests. The DBH of surveyed trees ranged from 2.9 to 25.8 cm for the deciduous forest and from 0.6 to 31.7 cm for the coniferous forests.

The difference in the dry mass of trunks + branches was 34 kg or 9.7% (between this study and the deciduous forest) and 38 kg or 10.8% (between this study and the coniferous forests) at 30 cm in DBH, and was 96 and 99 kg (or 7.7 and 7.9%) at 50 cm in DBH, respectively (Fig. 2a). There was little difference in the leaf dry mass between deciduous trees in this study (*Quercus* and *Betula*) and trees in the deciduous forest over a wide range of DBH (0–50 cm), and the difference in the dry mass was 3.6 kg at 50 cm in DBH (Fig. 2b). By contrast, the difference in the coniferous leaf dry mass was very large between the studies (19 kg at 30 cm in DBH). Takahashi *et al.* (1999) and the RGPFU (1960) included the same tree species as were measured in this study; however the apparent difference in the allometric relationship for leaf dry mass was observed only between our study and RGPFU (1960). The difference in stand density is a likely reason for the large difference in the coniferous leaf dry mass. In the study by the RGPFU (1960), trees in the stand density of 4,100 trees ha<sup>-1</sup> (DBH > 6 cm) were included, and there were no leaves in the lower part of the canopy due to self-shading, whereas the stand density in this study site was ca. 600 trees ha<sup>-1</sup> (DBH > 6 cm; Koike *et al.* 2001) and trees have leafy branches even in the lower part of the canopy.

Nearly all the measured carbon contents were less than but close to 50% (Table 3). Carbon and nitrogen contents for *Abies* were higher and lower, respectively, than those of the other two species for all organs, although some of the difference was not significant especially between nitrogen contents of *Quercus* and *Abies*. Nitrogen content for *Quercus* leaves was higher than that of the other two species, whereas nitrogen contents for branch, trunk, and root for *Betula* were higher than those of *Abies* and *Quercus*. The order of the nitrogen contents was leaf > branch > root > trunk

for all three species. Leaf nitrogen contents were within the range reported by previous studies (e.g. Aerts 1996, Reich *et al.* 1999, Ollinger *et al.* 2008). Although information for branch, stem and root nitrogen contents of trees are limited, the obtained values were comparable to previous reports (Ovington and Madgwick 1959, Tsutsumi 1987, Wang *et al.* 2000), excepting very high branch nitrogen contents for *Betula* (1.01 in average). One possible cause for the high concentration could be attributed to the sampling period for the trees (18–21 August, 2003), when *Betula* trees already started leaf yellowing. Nutrient resorption from senescing leaves is widely observed for perennial plants (Aerts 1996), and Chapin and Kedrowski (1983) reported *Betula* species also retranslocates the leaf nitrogen to the branches before the leaf senescing. They reported the increase in the branch nitrogen contents of birch trees during the leaf senescing period and their reported values of the nitrogen content are comparable to our results. Thus the retranslocation of *Betula* leaf nitrogen to the branch is considered to be the possible cause for the higher branch nitrogen content than other two species and lower leaf nitrogen content than *Quercus* trees in our study.

The value 0.5 is often used for the carbon content when converting dry mass to the amount of carbon in trees (e.g., Matsumoto 2001). To check the validity of this value, carbon stocks of each tree species were estimated using a constant carbon content of 0.5 (case 1) or the measured carbon content listed in Table 3 (case 2) with the equations listed in Table 2. For a tree with a 30-cm DBH, the differences between the two cases were 14, 11, and 2 kgC in the total carbon amount for a *Betula*, *Quercus*, and *Abies* tree, respectively. These errors account for 1–7% of the total carbon amount of a tree and are considered to be not serious in the estimation of carbon stock of a stand. When the annual carbon stock change was evaluated using annual DBH change and the constant carbon content (0.5), the error was also 1–7% of the annual carbon increment evaluated using measured carbon content.

Table 3. Carbon (C) and nitrogen (N) contents, and the ratio (C/N) for leaf, branch, trunk, and coarse root for three species.

	<i>Betula ermanii</i>				<i>Quercus crispula</i>				<i>Abies sachalinensis</i>						
	ID	C (%)	N (%)	C/N	n	ID	C (%)	N (%)	C/N	n	ID	C (%)	N (%)	C/N	n
Leaf	a	46.1±0.3	1.64±0.11	28.1±2.0	3	h	47.7	2.47	19.4	2	o	53.3±0.4	1.35±0.08	39.6±2.2	9
	b	46.5±0.3	1.72±0.33	27.7±4.7	3	i	46.0±2.0	2.05±0.30	22.7±2.8	3	p	52.1±1.3	1.29±0.08	40.7±2.6	9
	c	45.4±0.6	1.85±0.05	24.6±1.0	3	m	45.5±1.8	2.34±0.31	19.6±1.8	3	t	52.5±0.8	1.44±0.17	37.1±4.7	9
	e	45.9±0.7	2.02±0.20	22.9±2.1	3	ave.	46.2±1.8 <sup>a</sup>	2.26±0.31 <sup>b</sup>	20.7±2.5	8	ave.	52.7±1.0 <sup>b</sup>	1.36±0.13 <sup>c</sup>	39.1±3.6	27
	ave.	46.0±0.6 <sup>a</sup>	1.81±0.23 <sup>a</sup>	25.8±3.3	12	ave.	46.2±1.8 <sup>a</sup>	2.26±0.31 <sup>b</sup>	20.7±2.5	8	ave.	52.7±1.0 <sup>b</sup>	1.36±0.13 <sup>c</sup>	39.1±3.6	27
Branch	a	46.9±0.6	0.64±0.03	73.2±4.6	3	h	48.1±1.1	0.56±0.19	95.7±32.8	10	o	49.5±1.2	0.47±0.09	110±19.4	9
	b	48.9±0.5	1.92±0.37	26.1±4.9	3	i	47.6±0.8	0.66±0.16	75.8±17.3	9	p	48.0±1.5	0.31±0.12	173±64.9	9
	c	46.9±0.5	0.79±0.41	79.2±57.0	3	m	48.0±2.0	0.52±0.15	99.8±30.0	7	t	51.7±1.3	0.85±0.35	69.6±26.6	9
	e	47.1±0.9	0.79±0.72	90.3±47.2	3	ave.	47.9±1.0 <sup>a</sup>	0.58±0.17 <sup>b</sup>	89.9±28.5	26	ave.	49.7±2.0 <sup>b</sup>	0.54±0.31 <sup>b</sup>	117±59.4	27
	ave.	47.4±1.0 <sup>a</sup>	1.01±0.67 <sup>a</sup>	69.0±41.8	12	ave.	47.9±1.0 <sup>a</sup>	0.58±0.17 <sup>b</sup>	89.9±28.5	26	ave.	49.7±2.0 <sup>b</sup>	0.54±0.31 <sup>b</sup>	117±59.4	27
Trunk	a	46.5±0.6	0.42±0.06	112±17.0	3	h	48.4±1.2	0.34±0.09	155±52.9	4	o	49.6±1.1	0.25±0.07	218±70.2	9
	b	46.4±1.0	0.36±0.03	129±11.8	3	i	47.7±0.4	0.46±0.17	112±35.4	3	p	47.8±1.3	0.13±0.09	570±423	9
	c	47.1±0.2	0.90±0.15	53.6±9.3	3	m	-	-	-	-	t	49.5±1.0	0.36±0.18	162±63.1	9
	e	46.4±0.2	0.34±0.03	136±12.6	4	ave.	48.1±1.0 <sup>ab</sup>	0.39±0.13 <sup>ab</sup>	137±48.4	7	ave.	48.9±1.4 <sup>b</sup>	0.24±0.15 <sup>b</sup>	317±303	27
	ave.	46.6±0.6 <sup>a</sup>	0.51±0.25 <sup>a</sup>	108±35.6	13	ave.	48.1±1.0 <sup>ab</sup>	0.39±0.13 <sup>ab</sup>	137±48.4	7	ave.	48.9±1.4 <sup>b</sup>	0.24±0.15 <sup>b</sup>	317±303	27
Coarse root	a	46.5±0.2	0.62±0.19	80.0±27.3	3	h	47.3±0.6	0.43±0.07	113±21.1	3	o	49.8±1.5	0.37±0.21	217±188	9
	b	46.9±0.4	1.11±0.33	45.6±16.5	3	i	46.5±0.9	0.46±0.27	144±116	3	p	49.1±0.8	0.35±0.25	261±235	9
	c	47.3±0.2	0.80±0.42	70.9±36.6	3	m	46.5±0.5	0.47±0.11	103±20.2	4	t	49.4±1.2	0.58±0.26	105±53.8	9
	e	48.1±3.0	0.56±0.11	87.9±13.3	3	ave.	46.7±0.7 <sup>a</sup>	0.45±0.15 <sup>ab</sup>	118±59.4	10	ave.	49.4±1.2 <sup>b</sup>	0.43±0.26 <sup>b</sup>	194±182	27
	ave.	47.2±1.4 <sup>a</sup>	0.77±0.33 <sup>a</sup>	71.1±27.2	12	ave.	46.7±0.7 <sup>a</sup>	0.45±0.15 <sup>ab</sup>	118±59.4	10	ave.	49.4±1.2 <sup>b</sup>	0.43±0.26 <sup>b</sup>	194±182	27

Values (mean±SD) followed by different letters indicate significant differences (Tukey's HSD multiple comparison test,  $P < 0.01$ ) among species for each content. See Table 1 for ID.

$n$  : sample number

## Acknowledgements

This research was a collaboration between Hokkaido University, National Institute for Environmental Studies, and Hokkaido Electric Power Co., Inc., through the project "CC-LaG Experiment" and it was partly supported by Grants-in-Aid for Scientific Research (nos. 13760109 and 18710002) from the Japanese Ministry of Education, Culture, Sports, Science and Technology. We thank Prof. M. Shibuya, Silviculture and Forest Ecology, Hokkaido University for his technical advice. This study was made possible by assistance from graduate students from the Departments of Agriculture, Engineering, and Environmental Science of Hokkaido University, undergraduate students of University of the Ryukyus and Nihon University, and staff of the Experimental Forests of Hokkaido University, National Institute for Environmental Studies, and Hokkaido Electric Power Co., Inc.

## References

- Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.*, 84: 597-608.
- Chapin III, F.S. and Kedrowski, R.A. (1983) Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology*, 64: 376-391.
- Hirata, R., Saigusa, N., Yamamoto, S., Ohtani, Y., Ide, R., Asanuma, J., Gamo, M., Hirano, T., Kondo, H., Kosugi, Y., Li, S.-G., Nakai, Y., Takagi, K., Tani, M. and Wang, H. (2008) Spatial distribution of carbon balance in forest ecosystems across East Asia. *Agric. For. Meteorol.*, 148: 761-775.
- Kitazawa, Y., Kimura, M., Tezuka, Y., Kurasawa, H., Sakamoto, M. and Yoshino, M. (1959) A plant ecological study in southern Ohsumi peninsula. *Misc. Rep. Res. Inst. Natural Resourc.*, 49: 160-165. (in Japanese)
- Koike, T., Hojyo, H., Naniwa, A., Ashiya, D., Sugata, S., Sugishita, Y., Kobayashi, M., Nomura, M., Akibayashi, Y., Nakajima, J., Takagi, K., Shibata, H., Satoh, F., Wang, W., Takada, M., Fujinuma, Y., Shi, F., Matsuura, Y. and Sasa, K. (2001) Basic data for CO<sub>2</sub> flux monitoring of a young larch plantation: current status of a mature, mixed conifer-broadleaf forest stand. *Eurasian J. For. Res.*, 2: 65-79.
- Kominami, Y., Jomura, M., Dannoura, M., Goto, Y., Tamai, K., Miyama, T., Kanazawa, Y., Kaneko, S., Okumura, M., Misawa, N., Hamada, S., Sasaki, T., Kimura, H. and Ohtani, Y. (2008) Biometric and eddy-covariance-based estimates of carbon balance for a warm-temperate mixed forest in Japan. *Agric. For. Meteorol.*, 148: 723-737.
- Lacointe, A. (2000) Carbon allocation among tree organs: a review of basic processes and representation in functional-structural tree models. *Ann. For. Sci.*, 57: 521-533.
- Li, Z., Kurz, W.A., Apps, M.J. and Beukema, S.J. (2003) Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. *Can. J. For. Res.*, 33: 126-136.
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P., Kowalski, A.S., Lankreijer, H., Law, B.E., Lindroth, A., Loustau, D., Manca, G., Moncrieff, J.B., Rayment, M., Tedeschi, V., Valentini, R. and Grace J. (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, 447: 848-850.
- Matsumoto, M. (2001) Carbon stock and sequestration rate of Japanese forests. *Shinrin Kagaku*, 33: 30-36. (in Japanese)
- Ohtsuka, T., Akiyama, T., Hashimoto, Y., Inatomi, M., Sakai, T., Jia, S., Mo, W., Tsuda, S. and Koizumi, H. (2005) Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. *Agric. For. Meteorol.*, 134: 27-38.
- Ollinger, S.V., Richardson, A.D., Martin, M.E., Hollinger, D.Y., Frolking, S.E., Reich, P.B., Plourde, L.C., Katul, G.G., Munger, J.W., Oren, R., Smith, M.-L., Paw U, K.T., Bolstad, P.V., Cook, B.D., Day, M.C., Martin, T.A., Monson, R.K. and Schmid, H.P. (2008) Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. *PNAS*, 105: 19336-19341.
- Ovington, J.D. and Madgwick, H.A.I. (1959) The growth and composition of natural stands of birch. 2. The uptake of mineral nutrients. *Plant and Soil*, 10, 389-400.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. and Bowman, W.D. (1999) Generality of leaf trait relationships: A test across six biomes. *Ecology*, 80: 1955-1969.
- Research Group on Forest Productivity of the Four Universities (1960) Studies on the productivity of the forest. I. Essential needle-leaved forests of Hokkaido. *Kokusaku Pulp*, Tokyo, pp.99. (in Japanese)
- Takahashi, K., Yoshida, K., Suzuki, M., Seino, T., Tani, T., Tashiro, N., Ishii, T., Sugata, S., Fujito, E., Naniwa, A., Kudo, G., Hiura, T. and Kohyama, T. (1999) Stand biomass, net production and canopy structure in a secondary deciduous broad-leaved forest, northern Japan. *Res. Bull. Hokkaido Univ. For.*, 56: 70-85.
- Tsutsumi, T. (1987) Nutrient circulation in forest ecosystems. *UP biology 67*, University of Tokyo Press, Tokyo, pp. 124. (in Japanese)
- Wang, J.R., Letchford, T., Comeau, P. and Kimmins, J.P. (2000) Above- and below-ground biomass and nutrient distribution of a paper birch and subalpine fir mixed-species stand in the Sub-Boreal Spruce zone of British Columbia. *For. Ecol. Manage.*, 130: 17-26.