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## Stand Biomass, Net Production and Canopy Structure in a Secondary Deciduous Broad-leaved Forest, Northern Japan

by

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### 北方落葉広葉樹二次林における現存量、純生産量と林冠構造

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#### Abstract

Stand biomass, net production and canopy structure were determined in a secondary deciduous broad-leaved forest (ca. 56 year-old) in the Tomakomai Experimental Forest of Hokkaido University, northern Japan, by felling all trees within a 10-m × 10-m plot. This forest was dominated by *Quercus crispula* and *Phellodendron amurense* at canopy layer, while *Carpinus cordata* and *Sorbus alnifolia* dominated in subcanopy layer. The maximum tree height and diameter were 16.7 m and 25.8 cm, respectively. Total above- and below-ground biomass of trees > 3.0 cm in trunk diameter was 130.4 t ha<sup>-1</sup>, and the ratio of above- to below-ground biomass was 5.16. Total above-ground net production was 6.13 t ha<sup>-1</sup> (2.47 t ha<sup>-1</sup> by leaves and 4.15 t ha<sup>-1</sup> by woody parts). Total leaf area of this stand was 5.1 ha ha<sup>-1</sup> with two peaks at herbs/saplings and canopy trees. Herbs occupied 84.1% of leaf area at 0-2 m in height class. About 64% of total leaf area was concentrated in between the top of canopy (16.7 m) and 10 m from ground. Relative photosynthetic photon flux density was decreased in proportion to the cumulative leaf area from the top of canopy, while specific leaf area (leaf area per dry mass) was increased. The net production of leaves for each tree was linearly increased with tree height, while that of woody parts was exponentially increased. This suggests that the net production rate per leaf mass for the intermediate-sized trees was lower than that for saplings and canopy trees. Thus, the vertical profile of leaf distribution regulated the production and growth of trees through the distribution of available resources.

**Key words** : allometry, biomass, clear cut, net production, deciduous forest

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## Introduction

Canopy structure has a significant effect on the productivity of a plant community by regulating light penetration into canopies (Monsi and Saeki 1953). The presence of leaves in the upper canopy has a great effect on the growth and productivity of plants in lower layers by reducing light resources available to plants, which in turn reflects the stand structure. Plant growth is regulated not only by the position of the vertical canopy layer but also by the allocation to leaves and the production rate per unit leaf area. Thus, to evaluate production and/or growth of a plant community quantitatively, studies of the productivity should take into account the allocation to each organ (e.g., trunk, branches and leaves) and production rate per unit leaf area.

In general, forests consist of various life forms, i.e., tree species, shrubs and herbaceous species. In deciduous broad-leaved forests, herbaceous species often dominate on forest floor (Ogino 1977, Kojima 1994). King (1990) found that understory species had a larger assimilative area as compared with saplings of canopy and subcanopy tree species of the same size. In a herbaceous plant community, Hirose and Werger (1995) observed that taller species obtained a large fraction of light resource by the investment in leaf support organs, while smaller species had an advantage in efficiency using their biomass to capture light resources. Such a difference in allocation pattern in crown architecture between different life forms bring about the differentiation in the regeneration capacity among life forms. Thus, biomass and its partitioning to each organ along the vertical gradient within the canopy is important in understanding the stand productivity. The purpose of this study was to examine the biomass and production rate of woody and herbaceous species in a secondary deciduous broad-leaved forest in Hokkaido, northern Japan, in relation to its canopy structure.

## Study site

This study was carried out at the Tomakomai Experiment Forest (TOEF) of Hokkaido University in northern Japan (42° 40' N, 141° 36' E, 90 m above the sea level). The mean annual temperature and the Warmth Index at TOEF during from 1961 to 1990 were 7.1°C and 57.3°C month, respectively. Mean annual precipitation was 1236.7 mm, most of which fall in summer. The land of TOEF is on a deep deposit of the last eruption of Mt. Tarumae in 1739. The vast area of the TOEF was the second-growth forest developing after a typhoon in 1954, and the forest of the TOEF consisted of about 30 tree species and was dominated by deciduous broad-leaved species such as *Quercus crispula* Blume, *Acer mono* Maxim., *Acer palmatum* subsp. *matsumurae* Koidz., *Magnolia obovata* Thunberg (Hiura et al. 1998). The forest floor was covered by ferns, predominantly *Dryopteris crassirhizoma* Nakai. Understory dwarf bamboo *Sasa nipponica* Makino et Shibata and *Sasamorpha borealis* Makino were distributed in part of this experimental forest stand.

## Materials and methods

A 20-m × 20-m plot was established in a secondary deciduous broad-leaved forest by the southern terrace of Horonai River in TOEF in 1997, and was further divided into 16 cells of 5-m × 5-m. The forest is the regrowth from coppice sprouts and seedlings after the artificial clear felling for fuel production some 50 years ago. Species, diameter at breast height (DBH) and crown diameter were measured for trees larger than 3.0 cm in DBH. In this study, saplings were defined as individuals

smaller than 3.0 cm in DBH. We set a 10-m  $\times$  10-m plot for cutting at the center of the 20-m  $\times$  20-m plot. We measured the photosynthetic photon flux density beneath the canopy at the 10-m  $\times$  10-m plot, using LI-190 SA quantum sensors (LI-COR), in mid August 1997. The measurement was conducted at 87 randomly-located points between 1-m and 10-m above the ground. Incoming radiation was measured in a large open site near the study plot at the same time. Canopy transmittance could then be calculated as the ratio of photosynthetic photon flux density beneath the canopy to that in the open site. Saplings, trees and herbaceous plants were measured as follows.

#### Herbaceous plants

The 10-m  $\times$  10-m plot was divided into 100 1-m  $\times$  1-m grids. Coverage (%) and plant height were measured for each herbaceous species at each grid on 19-20 August 1997, i.e. before the cutting of trees. Soon after the measurements, five 2-m  $\times$  2-m subquadrats were established at the 10-m  $\times$  10-m plot. Above-ground parts of plants within the subquadrats were cut and divided into leaf blades and non-photosynthetic organs. The dry mass of each part was determined after oven-drying for at least 48 hours at 80°C. Although we did not measure specific leaf area (leaf area per dry mass, SLA) for all herbaceous species, the mean SLA (467.7 cm<sup>2</sup> g<sup>-1</sup>) of dominant five herbaceous species (*Trillium tschonoskii*, *Polygonatum odoratum* var. *maximowiczii*, *Smilacina japonica*, *Maianthemum dilatatum*, *Cacalia delphinifolia*) was used to estimate the total leaf area in the 10-m  $\times$  10-m plot.

#### Saplings (DBH smaller than 3.0 cm)

An additional 10-m  $\times$  10-m plot, about 15 m distant from the 20-m  $\times$  20-m plot, was established on 5 July 1998. For all saplings within the plot, species, trunk height and diameter at 1/10 height were recorded. About 30 individuals smaller than 50 cm in trunk height were randomly selected for measurements of dry mass. Their trunk heights and diameters at 1/10 trunk height were measured after cutting and were divided into trunk, branch and leaves. The dry mass of each part were measured in the same manner that the herbaceous plants were measured. Leaf area of some leaf blades for each sapling was determined with a digital image processor, and then SLA was obtained. Total leaf area of each sapling was estimated by multiplying the dry mass of leaf blades per sapling by its SLA. In addition to the saplings (0-0.5 m tall) sampled in this study, we used data of saplings (0.5-2.0 m tall) sampled under closed-canopy conditions for the estimation of leaf area and dry masses of leaves, branches and trunk.

#### Trees (larger than 3.0 cm in DBH)

All trees (19 individuals) within the 10-m  $\times$  10-m plot, located at the center of the 20-m  $\times$  20-m plot, were cut at the base of the trunk on 8-11 September 1997. Although the diameter of *Prunus ssiiori* (No. 487) was smaller than 3.0 cm (Appendix 1), this individual was included into the analysis. Four individuals next to the 10-m  $\times$  10-m plot were also cut for analysis. After the cutting, several architectural dimensions (i.e., trunk top height, trunk diameter at 1/10 trunk height, trunk diameter and height at the base of the lowest branch, and trunk diameters at 1-m intervals) were measured. The height of the base of the branch and the height of the lowest leaf layer were also measured for each branch of each tree. Several architectural dimensions of sampled trees are listed in Appendix 1.

The measurement of dry mass of each part (trunk, branches, leaves and coarse roots) was as follows. The trunk stem was cut at 1-m intervals, and then the fresh mass of each 1-m trunk sample was measured. A disk of ca. 10 cm thick was taken from each 1-m trunk sample, and then the fresh

mass was measured. Each disk was oven-dried for a week at 100°C and the dry mass was measured. The total trunk dry mass was then obtained by multiplying its total fresh mass by the mean dry/fresh ratio of the disk samples.

As for the branches, the fresh mass was measured for each branch, and several disks with ca. 15-20 cm thick were taken from each branch at arbitrarily selected points. For each disk, the dry mass was obtained as described above for the disks of the trunk. The dry mass of each branch was estimated by multiplying the fresh mass of the branches by the mean dry/fresh ratio of the disks.

As for the leaves, the fresh mass of all leaves was measured for each branch of each individual tree. Several leaves were taken from each branch of each individual tree, and were separated into leaf blades and petioles. Leaf area was measured with a digital image processor. The dry masses of the leaf blades and petioles were weighed after oven-drying at 80°C for at least 2 days. The total leaf dry mass of each branch was then calculated by multiplying the total fresh mass by the ratio of dry/fresh mass. The total leaf area was obtained by multiplying the estimated dry mass of leaves by its SLA and the ratio of leaf blades to leaves.

After bringing all samples from the 10-m × 10-m plot, stumps with roots were pulled out using a backhoe. The soil was completely washed out by spraying river water with a compressor, and the fresh mass of the stumps and roots was measured. The total dry mass of roots of each individual tree was recorded in the same manner as described for the branches.

#### Radial and height growth rate in trunk stem

The widths of tree-rings in the disks taken from the trunk stem were read to the nearest 0.1 mm. We used the disk taken at 1 m above ground for the analysis of trunk diameter growth rate. It was difficult to measure the annual growth rate of suppressed trees. Therefore, annual diameter growth rate was determined using the growth rate for the recent 5 years. Recent relative growth rate in trunk diameter (RDGR, year<sup>-1</sup>) was then obtained with the following equation:

$$\text{RDGR} = (\ln D_{97} - \ln D_{92})/5,$$

Where  $D_{97}$  and  $D_{92}$  are the trunk diameters at 1 m above ground in 1997 and 1992, respectively. Recent height growth rate of each individual tree was calculated using the disk taken at the highest position among the sample disks. Let  $t$  be the number of annual rings of the disk at the highest position among the sampled disks within a tree. Then the relative height growth rate (RHGR, year<sup>-1</sup>) can be calculated as follows:

$$\text{RHGR} = (\ln H_{97} - \ln H_{97-t})/t,$$

Where  $H_{97}$  and  $H_{97-t}$  are trunk heights in the year 1997 and the year (1997- $t$ ), respectively. We could not estimate these values for two suppressed trees because its tree ring width was too narrow to be counted. The dry mass of each organ and the relative growth rates in trunk diameter and height for the sampled trees are listed in Appendix 2.

#### Above-ground net production

The above-ground net production rate in 1997 was determined from the sum of mass of the leaves and the mass increase in the trunk stem and branches from the previous year. Leaf production

( $\Delta W_L$ ) during 1997 was equal to the current leaf mass ( $W_L$ ) because the trees are deciduous. Mass increment ( $\Delta W_C$ ) of the above-ground woody parts (trunk and branches) was estimated by the following equation:

$$\Delta W_L = W_L - W_L \cdot W_{C96} / W_{C97}$$

where  $W_L$  is the observed dry mass of the above-ground woody parts in 1997,  $W_{C96}$  and  $W_{C97}$  are the dry masses of woody parts in 1996 and 1997, respectively, estimated from the allometric equation as a function of the product of the square of DBH and trunk height (Table 3). Trunk height ( $H_{96}$ ) and diameter ( $DBH_{96}$ ) in 1996 were estimated by the following equations as functions of current-year trunk height ( $H_{97}$ ) and diameter at breast height ( $DBH_{97}$ ) in 1997:

$$H_{96} = \exp(\ln H_{97} - RHGR) \text{ and}$$

$$DBH_{96} = \exp(\ln DBH_{97} - RDGR),$$

respectively. To estimate stand biomass and annual net production, various dimensions were estimated from DBH and from the product of the square of DBH and trunk height ( $D^2H$ ). We examined the leaf area and dry masses of leaves, trunk, branches and roots for trees larger than 3.0 cm in DBH.

## Results

### Species composition and size structure

A total of 19 species larger than 3.0 cm in DBH were present in the 20-m  $\times$  20-m plot. Of the 19 species, *Quercus crispula* and *Phellodendron amurense* had the large relative basal areas, but their relative densities were not so high (Table 1), i.e., they were dominant in the canopy layer (because of

**Table 1.** Trees (DBH > 3.0 cm) at 20-m  $\times$  20-m plot in Hokkaido, northern Japan.

Relative density (%) and relative basal area (%) are shown in parentheses. Only species with relative value > 5.0% in at least one of the relative values are listed.

Species	Density (/0.04 ha)	Basal area (cm <sup>2</sup> /0.04 ha)
<i>Quercus crispula</i>	10 (11.2)	2590.6 (25.3)
<i>Phellodendron amurense</i>	7 (7.9)	1755.4 (17.2)
<i>Carpinus cordata</i>	17 (19.1)	991.8 (9.7)
<i>Magnolia obovata</i>	8 (9.0)	942.4 (9.2)
<i>Sorbus alnifolia</i>	19 (21.4)	907.2 (8.9)
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	4 (4.5)	754.6 (7.4)
<i>Betula platyphylla</i> var. <i>japonica</i>	1 (1.1)	669.5 (6.6)
<i>Magnolia kobus</i>	5 (5.6)	320.7 (3.1)
Others	28 (31.5)	1291.5 (12.6)

their large individual sizes and small densities). By contrast, *Carpinus cordata* and *Sorbus alnifolia* had small basal areas (Table 1) and were dominant under the canopy (because of their small individual sizes and high densities). Frequency distribution of diameter at breast height (DBH) including all species showed an L-shaped pattern (Fig. 1). Ninety-five percent of the woody plants had a DBH smaller than 3.0 cm. In the height class of 0-2 m, a total of 68 herbaceous species were present in the 10-m  $\times$  10-m plot. Herbaceous species accounted for 82.3% of the forest floor and saplings of woody species accounted for 12.7% in number. Of the herb species that were present, *Dryopteris crassirhizoma* was the most dominant species with 35% in coverage (Table 2).

Most of canopy species regenerated during a short period between 1940 and 1947 in this stand, while subcanopy species as *Carpinus cordata* and *Sorbus alnifolia* did later between 1943 and 1958 (Fig. 2). Only two individuals of *Prunus ssiori* regenerated after 1958 (Appendix 1). Canopy species grew in height at constant rate after the germination (Fig. 2). On the contrary, Subcanopy species grew as fast as canopy species until ca. 1967, but their growth rate decreased later probably because of the suppression by taller trees. Therefore, the tree-height distribution for trees  $>$  3.0 cm in DBH showed a bimodal pattern with two peaks at canopy and subcanopy layers.

#### Stand biomass

Each dimension was closely correlated with DBH and  $D^2H$  (Fig. 3, Table 3). Although  $R^2$ s of the obtained regressions based on DBH were persistently higher than those based on  $D^2H$ , the maximum difference in  $R^2$ s between the DBH- and  $D^2H$ -based regressions was only ca. 0.04 for the regression of branch mass (Table 3). As for saplings, leaf area and dry masses of trunk, leaves and

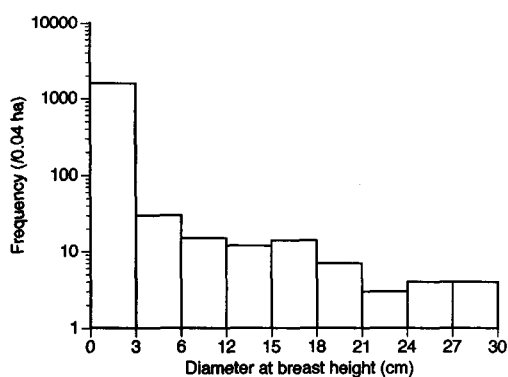


Fig. 1. Frequency distribution of trunk diameter at breast height (DBH) at 20-m  $\times$  20-m plot, in a deciduous broad-leaved forest in Hokkaido, northern Japan. Number of trees smaller than 3.0 cm in DBH was estimated from the density per 100 m<sup>2</sup>.

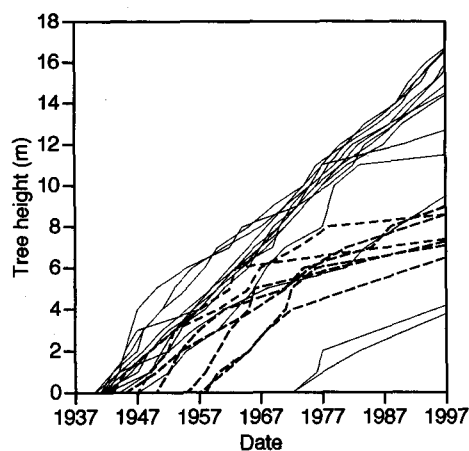


Fig. 2. Growth in height of all sampled trees ( $n=23$ ) in a deciduous broad-leaved forest in Hokkaido, northern Japan. Solid and broken lines indicate canopy and subcanopy species, respectively. Subcanopy species in this stand consisted of two species as *Carpinus cordata* and *Sorbus alnifolia*.

**Table 2.** Mean coverage and height of herbaceous plants at five 2-m × 2-m quadrats in Hokkaido, northern Japan. Species with more than 1.0% in coverage are listed.

Species	Coverage (%)	Height (cm)
<i>Dryopteris crassirhizoma</i>	34.85	46.4
<i>Pachysandra terminalis</i>	10.29	20.7
<i>Rhus ambigua</i>	6.53	20.2
<i>Calamagrostis arundinacea</i>	1.78	24.3
<i>Trillium Smallii</i>	1.55	24.0
<i>Cardiocrinum cordatum</i> var. <i>Glehni</i>	1.29	25.2
<i>Phryma Leptostachya</i> subsp. <i>asiatica</i>	1.27	17.4
<i>Schizophragma hydrangeoides</i>	1.20	8.6
<i>Similacina japonica</i>	1.14	20.4
<i>Cacalia hastata</i> subsp. <i>orientalis</i>	1.05	134.2
Others	21.31	

branches were examined with  $D_{0.1}$  (diameter at 1/10 height) and  $D^2_{0.1}H$  as independent variables. All examined dimensions were well regressed by  $D_{0.1}$  and  $D^2_{0.1}H$  except for branch mass ( $R^2 \approx 0.40$ ). Although the obtained  $R^2$ s for the examined dimensions were higher in the  $D^2_{0.1}H$ -based regressions than in the  $D_{0.1}$ -based regressions (Table 3), the maximum difference was also small between the  $D_{0.1}$ - and  $D^2_{0.1}H$ -based regressions with only ca. 0.02.

Leaf area and dry mass of each organ of individual trees in the 20-m × 20-m plot were estimated from DBH for trees larger than 3.0 cm in DBH and from for saplings. The results are given in Table 4. Total above- and below-ground biomass was 130.t ha<sup>-1</sup>, and the ratio of above- to below-ground biomass was 5.16. Total leaf area index of this stand was 5.1 ha ha<sup>-1</sup> with two peaks in herbs/saplings- and canopy- layers (Fig. 4). Small plants, especially for herbaceous species, tended to allocate more to leaves (WL) than to non-photosynthetic organs such as branches and trunk stems (WC). Vertical distribution of leaf area showed that about 64% of the leaf area of this stand was concentrated between the top canopy (16.7 m) and 10 m in above-ground height. Herbaceous species accounted for 80% of leaf dry mass and 84% of the leaf area at 0-2 m height class.

Relative photosynthetic photon flux density (PPFD, %) was increased with height, but it showed only a little change between 2-6 m in above-ground height (Fig. 5). This corresponded to small leaf area at this height class (Fig. 4), because of the negative relationship between the relative PPFD (%) and the cumulative leaf area from the top of the canopy (Fig. 5). SLA was decreased with canopy height (Fig. 6). Since SLA was linearly correlated with the cumulative leaf area index except for SLA at the top of canopy (Fig. 6), SLA showed a little change between 2-8 m height class where leaves were not concentrated. Herbaceous species showed a higher SLA as compared with leaves of woody species within 0-2 m height class (Fig. 6).

**Table 3.** Allometric equations ( $\ln Y = a \ln X + b$ ) for trees (DBH > 3 cm) and for saplings (DBH < 3 cm) of deciduous broad-leaved tree species in Hokkaido, northern Japan. Trunk diameter (DBH or D0.1) and the product of trunk height and square of trunk diameter ( $D^2H$  or  $D^2_{0.1}H$ ) were used as independent variables ( $X$ ).

For trees	DBH (cm) as $X$			$D^2H$ (cm <sup>2</sup> m) as $X$			$n$
	$a$	$b$	$R^2$	$a$	$b$	$R^2$	
WT(kg)	2.424	-2.505	0.991	0.884	-3.089	0.992	23
WB(kg)	2.572	-4.453	0.871	0.917	-4.939	0.834	23
WR(kg)	2.247	-3.424	0.944	0.818	-3.978	0.925	18
WL(kg)	2.500	-6.288	0.891	0.904	-6.846	0.879	23
WC(kg)	2.461	-2.370	0.992	0.893	-2.937	0.984	23
AL(m <sup>2</sup> )	2.087	-2.414	0.839	0.755	-2.882	0.828	23

For saplings (mm)	D0.1 (mm) as $X$			$D^2_{0.1}H$ (cm <sup>3</sup> ) as $X$			$n$
	$a$	$b$	$R^2$	$a$	$b$	$R^2$	
WT(g)	3.049	-3.692	0.950	0.977	-1.294	0.977	185
WB(g)	2.810	-5.511	0.404	0.891	-3.269	0.390	156
WL(g)	2.101	-3.062	0.854	0.671	-1.409	0.878	185
WC(g)	3.091	-3.636	0.951	0.988	-1.197	0.974	185
AL(cm <sup>2</sup> )	1.909	3.066	0.847	0.611	4.571	0.869	185

WT, trunk dry mass; WB, branch dry mass; WR, root dry mass; WL, leaf dry mass; WC, dry mass of trunk and branches (WT+WB); AL, leaf area; D0.1, trunk diameter at 1/10 height.

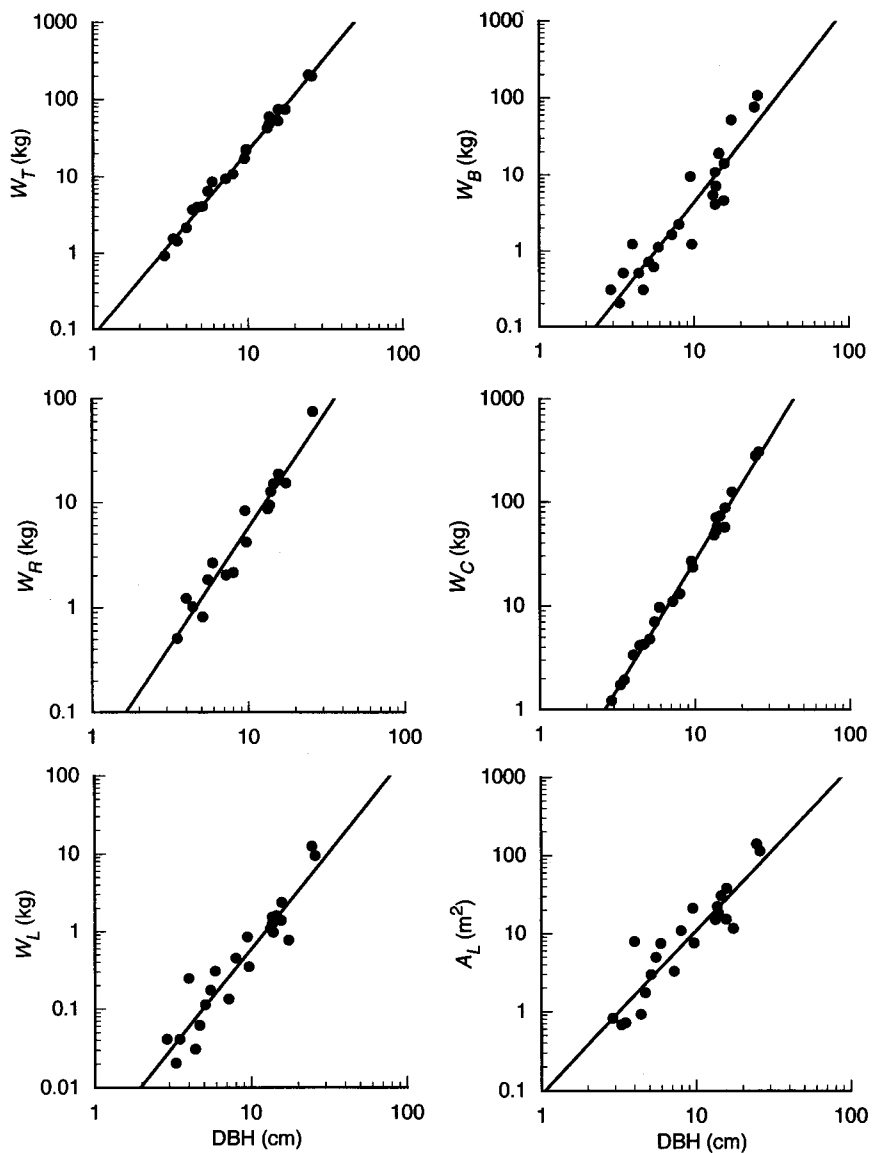


Fig. 3. Allometric relationships between various dimensions and DBH for deciduous broad-leaved tree species in Hokkaido, northern Japan. See Table 3 for allometric equations.

**Table 4.** Estimates of plant biomass and net production at 20-m × 20-m plot in a secondary broad-leaved forest in Hokkaido, northern Japan. Dimensions in empty cells were not measured in this study.

Size class	Dry mass and leaf area					Net production		
	$W_T$ (t ha <sup>-1</sup> )	$W_B$ (t ha <sup>-1</sup> )	$W_R$ (t ha <sup>-1</sup> )	$W_L$ (t ha <sup>-1</sup> )	$W_C$ (t ha <sup>-1</sup> )	$A_L$ (ha ha <sup>-1</sup> )	$\Delta W_C$ (t ha <sup>-1</sup> y <sup>-1</sup> )	$\Delta W_C \& W_L$ (t ha <sup>-1</sup> y <sup>-1</sup> )
Herbs				0.250	0.150	1.148		
Saplings ( $D < 3$ )	0.347	0.031		0.071	0.378	0.217		
Understory trees ( $D > 3 \& H < 10$ )	4.525	0.812	1.314	0.116	5.337	0.275	0.165	0.277
Canopy trees ( $H > 10$ )	83.066	18.386	19.860	2.352	101.452	3.423	3.984	5.857

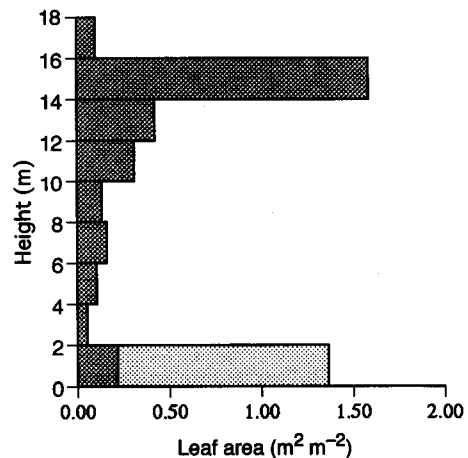
$D$ , DBH (cm);  $H$ , tree height (m);  $W_T$ , trunk dry mass;  $W_B$ , branch dry mass;  $W_R$ , root dry mass;  $W_L$ , leaf dry mass;  $W_C$ , dry mass of trunk and branches;  $A_L$ , leaf area.

#### Net production, allocation and growth rate

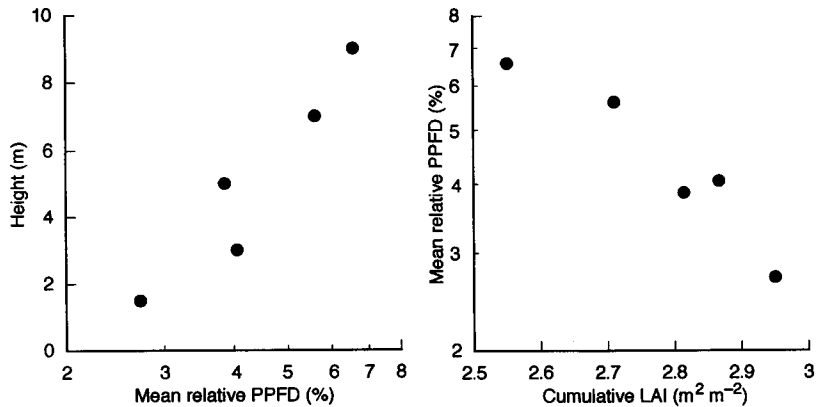
Above-ground net production for trees larger than 3.0 cm in DBH was 6.13 t ha<sup>-1</sup> (2.47 t ha<sup>-1</sup> by leaves and 4.15 t ha<sup>-1</sup> by woody parts as trunk and branch). In double-logarithmic plot, net production by leaves (i.e., current-year leaf mass) linearly increased with trunk height (Fig. 7). On the other hand, net production by woody parts exponentially increased with trunk height. These linear and non-linear relationships were supported by stepwise regression analysis, i.e. binomial expression was rejected in the  $\Delta W_L$ - $H$  relation, while was adapted in the  $\Delta W_C$ - $H$  relation. Relative growth rates in trunk diameter and height were lower for intermediate-sized trees than those for small saplings and large canopy trees (Fig. 8).

### Discussion

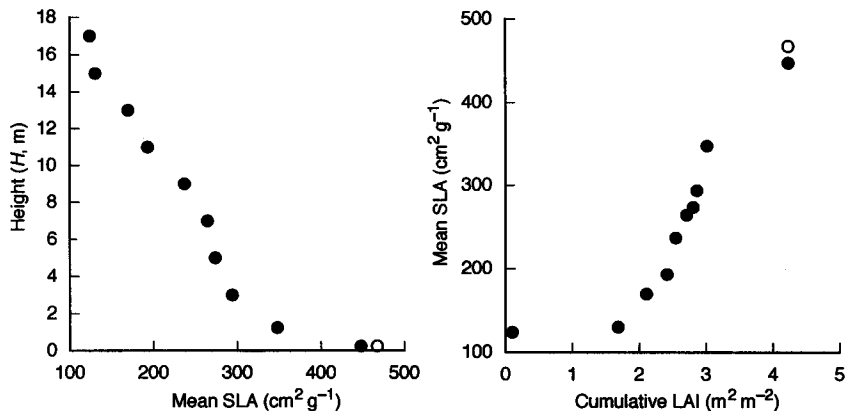
The vertical profile of leaf area of this stand showed a bimodal distribution with peaks at the canopy- and the understory saplings/herbaceous-layers. SLA rapidly decreased with canopy height from 10 m in height to the top canopy (16.7 m) and showed a small change between 0-10 m in height, because SLA was regulated by the light intensity which was determined by the cumulative leaf area from the top canopy. Intermediate-sized trees just under the dense leaf layer showed a lower net production rate of woody parts (trunk and branches) per leaf mass and a lower growth rate of trunk stem than other trees positioned at the understory and canopy layers. These results suggest that the vertical canopy structure affected the



**Fig. 4.** Leaf area distribution at the 10-m × 10-m plot in a deciduous broad-leaved forest in Hokkaido, northern Japan. Shaded and open areas indicate woody and herbaceous species, respectively.



**Fig. 5.** Relationships between mean relative photosynthetic photon flux density (PPFD, %) and canopy height (left) and between the cumulative leaf area index (LAI) from the top of canopy and mean PPFD (right).

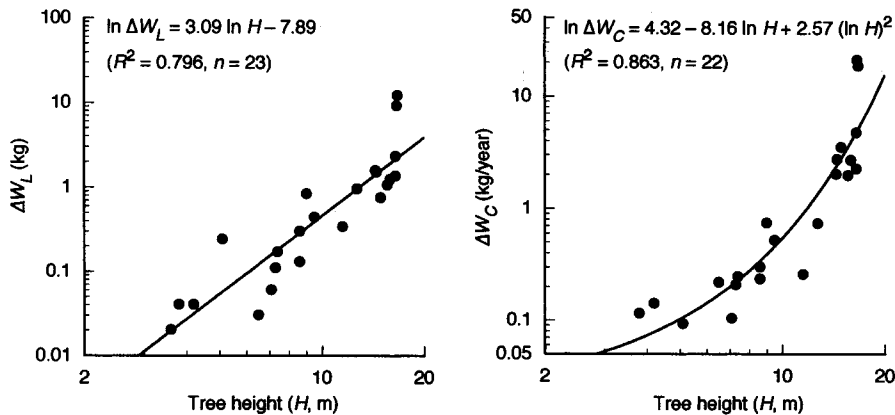


**Fig. 6.** Relationships between mean specific leaf area (SLA) and canopy height (left) and between mean SLA and cumulative leaf area index (LAI) from the top of canopy (right). Solid and open circles indicate woody and herbaceous species, respectively.

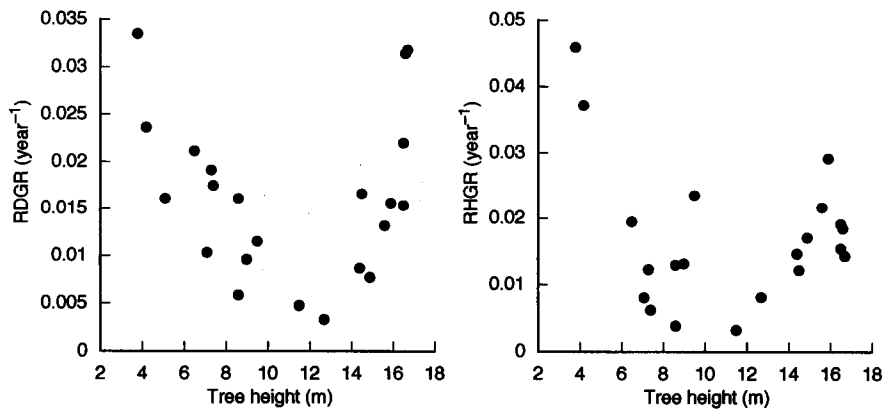
production and growth rates of trees.

Log-transformed relative light intensity linearly decreases with cumulative leaf area (Monsi and Saeki 1953, Werger and Hirose 1988). In this study, we observed that the SLA for woody species linearly increased with the cumulative leaf area from the top of the canopy except for SLA at the top of canopy. Although we did not record the vertical profile of light intensity from the top of the canopy to 10 m in height, the linear relationship between the cumulative leaf area and SLA suggests that SLA changed in proportion to the light intensity within the canopies.

The maximum net photosynthesis at light saturation for deciduous broad-leaved tree species increases with a decrease of SLA (Koike 1988, Reich *et al.* 1991), because the maximum net photosynthesis at light saturation is positively correlated with nitrogen content per leaf area and because nitrogen content per leaf area for deciduous tree species is regulated by SLA (Ellsworth and Reich 1993). Therefore, it is suggested that the linear relationship between the cumulative leaf area and



**Fig. 7.** Net production by leaves (left;  $\ln \Delta W_L = 3.09 \ln H - 7.89$ ,  $R^2 = 0.796$ ,  $n = 23$ ) and by woody parts as trunk stem and branches (right;  $\ln \Delta W_C = 4.32 - 8.16 \ln H + 2.57 (\ln H)^2$ ,  $R^2 = 0.863$ ,  $n = 22$ ) in relation to trunk height ( $H$ ) for deciduous broad-leaved tree species.



**Fig. 8.** Relative growth rate in trunk diameter (left) and in trunk height (right) in relation to trunk height for deciduous broad-leaved tree species.

log-transformed SLA contributed to the maximization of net production at the stand level. Ellsworth and Reich (1993) also pointed out the importance of the change in the leaf dry mass per area (i.e., the inverse of SLA) along the vertical-canopy profile for the maximization of stand-level production. On the other hand, understory saplings can gather more light resources per leaf dry mass by leaves with large SLA, which increases the survival of saplings under closed-canopy conditions with the shortage of light resources. The dominance of herbaceous plants on the forest floor was probably due to the high efficiency for light interception by the high allocation to leaves and high SLA as compared with saplings with tree species.

As for woody species, 77% of leaf area was concentrated between the top of the canopy and 10 m in height, and therefore, a large proportion of the relative photon flux density (92%) was absorbed by the upper dense canopy layer from the top of the canopy to 10 m in above-ground height. Intermediate-sized trees (ca. 10 m in top height) just under the dense leaf layer showed a lower net

production per leaf mass than the smaller- and larger-sized trees, which resulted in the low relative growth rates in both trunk height and diameter. It is expected that intermediate-sized trees cannot capture enough light resources for the cost of maintenance (respiration and turnover of leaves). Thus, the intermediate-sized trees hardly grew in suppressed conditions as compared with small-sized trees or saplings. It is suggested that growth traits within the vertical canopy structure segregated into two types, i.e., a rapid growth with full sunlight for canopy trees versus a high investment in leaves to survive under a closed canopy for saplings.

Total leaf areas of woody and herbaceous species in this secondary stand were 3.92 and 1.15 ha ha<sup>-1</sup>, respectively. In a mature deciduous broad-leaved forest at TOEF, Fukushima *et al.* (in press) reported the total leaf area of woody species was 7.59 ha ha<sup>-1</sup> and herbaceous species distributed sparsely on the forest floor as compared with this study site in a secondary forest. Similarly, the total leaf areas were 5.4 and 1.4 ha ha<sup>-1</sup> for trees and herbaceous species, respectively, in a mature beech forest (Ogino 1977), 6.24 for trees and 0.40 ha ha<sup>-1</sup> for herbaceous species in a warm temperate secondary forest (Nagano & Kira 1978), respectively. On the other hand, Yamakura *et al.* (1986) reported that total leaf area of herbaceous species was only 0.177 ha ha<sup>-1</sup> in a mature tropical rain forest in Indonesia, while total leaf area of woody species was 7.79 ha ha<sup>-1</sup>. Alaback (1982) described the negative relationship between understory biomass and the stand basal area in sitka spruce-western hemlock forests in Alaska. Although we have only limited information on biomass of herbaceous species in forests, it is suggested that negative relationships between the dominance of herbaceous species and tree species were common not only to within-forest ecosystems but also to between-forest ecosystems.

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## 要 約

北海道大学苫小牧演習林の落葉広葉樹二次林において、現存量、純生産量、そして林冠構造が調べられた。この森林では、上層ではミズナラ・キハダが、そして下層ではサワシバ・アズキナシが優占していた。最大樹高と最大直径は、それぞれ16.7mと25.8cmだった。胸高直径3cm以上の木本個体の地上部・地下部の総現存量は130.4 t ha<sup>-1</sup>で、地下部に対する地上部の比率は5.16だった。一年間の地上部の純生産量は合計6.13 t ha<sup>-1</sup> (葉: 2.47 t ha<sup>-1</sup>, 幹枝: 4.15 t ha<sup>-1</sup>) であった。この森林の総葉面積は5.1ha ha<sup>-1</sup>で、林冠層と稚樹/草本層の2ヶ所にピークが認められた。葉面積は高さ0-2mの範囲内では、草本植物は全体の葉面積の84.1%を占めていた。約64%の葉面積は高さ10m以上の樹冠上部に集中していた。相対光量子密度は樹冠上部からの積算葉面積に比例して減少し、一方、葉の乾重当たりの葉面積は増加した。木本個体の葉の純生産量は樹高に比例して増加したが、地上部木部の純生産量は指数関数的に増加した。これは、樹高10m前後の個体の葉量当たりの純生産量が最も低いことを示唆している。これらの結果から、葉群の垂直分布が樹冠内での光の通過を規定することにより、木本個体の生産量と成長を規定していることが示唆された。

キーワード：相対成長、現存量、皆伐、純生産量、落葉樹林

Appendix 1. Tree age and size of sample trees larger than 3.0 cm in trunk diameter at breast height in the 10-m $\times$ 10-m plot. Individual number with asterisk indicates tree located outside the 10-m $\times$ 10-m plot. Tree ages of the No. 446 and No. 482 could not be measured in this study.

No.	Species	Species abbreviation	Age (year)	H (m)	DBH (cm)	$D_{0.1}$ (cm)	$A_C$ (m <sup>2</sup> )	$H_B$ (m)	$D_B$ (cm)
1*	<i>Quercus crispula</i>	Qm	55	16.7	24.6	24.3	39.9	9.0	19.3
444*	<i>Carpinus cordata</i>	Cc	52	9.0	9.5	9.9	38.5	2.1	9.5
445	<i>Carpinus cordata</i>	Cc	50	7.4	5.5	6.1	7.3	4.7	3.6
446	<i>Sorbus alnifolia</i>	Sa		3.6	3.3	4.1	6.0	3.3	2.1
447	<i>Magnolia obovata</i>	Mo	53	15.6	13.3	12.8	6.8	9.7	8.2
448*	<i>Acer mono</i>	Am	56	14.4	14.5	14.1	13.2	5.0	12.1
450	<i>Sorbus alnifolia</i>	Sa	42	7.3	5.1	5.4	5.6	5.8	2.8
451	<i>Carpinus cordata</i>	Cc	47	8.6	7.2	7.1	5.4	4.0	5.9
453	<i>Quercus crispula</i>	Qm	56	16.6	25.8	25.1	45.9	5.9	22.1
454	<i>Phellodendron amurense</i>	Pa	56	16.5	15.6	15.1	11.7	10.9	7.7
474	<i>Quercus crispula</i>	Qm	57	12.7	13.9	14.2	17.3	5.1	10.9
475	<i>Magnolia obovata</i>	Mo	56	16.5	15.7	15.9	22.1	3.7	15.0
477	<i>Sorbus alnifolia</i>	Sa	39	6.5	4.4	4.6	2.7	3.0	3.6
478	<i>Sorbus alnifolia</i>	Sa	40	7.1	4.7	5.0	2.4	6.0	1.8
479	<i>Sorbus alnifolia</i>	Sa	54	8.6	5.9	6.2	5.0	7.4	2.9
482	<i>Carpinus cordata</i>	Cc		5.1	4.0	4.8	14.2	1.9	3.4
483	<i>Prunus maximowicziana</i>	Pm	55	14.9	17.4	16.9	24.5	2.6	16.6
485	<i>Prunus ssiiori</i>	Ps	25	4.2	3.5	4.2	8.7	1.2	3.8
486	<i>Quercus crispula</i>	Qm	50	11.5	9.7	9.7	5.1	3.9	8.6
487	<i>Prunus ssiiori</i>	Ps	25	3.8	2.9	3.5	6.1	1.3	2.9
489	<i>Magnolia obovata</i>	Mo	55	15.9	13.7	13.5	12.4	9.1	8.1
493	<i>Fraxinus mansurica</i> var. <i>japonica</i>	Fm	56	14.5	13.7	13.4	20.2	9.2	9.5
515*	<i>Magnolia kobus</i>	Mk	57	9.5	8.0	8.4	11.0	5.0	6.5

H, trunk height; DBH, diameter at breast height;  $D_{0.1}$ , trunk diameter at 1/10 height;  $A_C$ , crown projection area;  $H_B$ , height of the base of the lowest branch;  $D_B$ , trunk diameter at the base of the lowest branch.

**Appendix 2.** Plant mass and growth rate in various dimensions of sample trees larger than 3.0 cm in trunk diameter at breast height, in the 10-m  $\times$  10-m plot. Species abbreviations are listed in Appendix 1. Individual number with asterisk indicates tree located outside the 10-m  $\times$  10-m plot.

No.	Species	$W_T$ (kg)	$W_L$ (kg)	$W_B$ (kg)	$W_R$ (kg)	$A_L$ (m <sup>2</sup> )	$W_{LB}/W_L$ (%)	RDGR (y <sup>-1</sup> 10 <sup>3</sup> )	RHGR (y <sup>-1</sup> 10 <sup>3</sup> )
1*	Qc	202.9	12.17	74.6		137.3	100.0	31.75	14.27
444*	Cc	17.0	0.83	9.3	8.2	20.7	94.5	9.53	13.09
445	Cc	6.0	0.17	0.6	1.8	4.8	95.0	17.40	6.17
446	Sa	1.4	0.02	0.2		0.7	95.0		
447	Mk	41.7	1.06	5.3	8.5	14.7	95.2	13.12	21.64
448*	Am	53.2	1.56	18.8	14.9	30.0	87.1	8.63	14.61
450	Sa	4.0	0.11	0.7	0.8	2.9	95.3	19.06	12.21
451	Cc	9.2	0.13	1.6	2.0	3.2	95.9	5.80	12.87
453	Qc	196.1	9.24	105.8	73.8	111.6	100.0	31.37	18.41
454	Pa	51.7	1.35	4.5	18.6	14.9	84.2	15.27	15.39
474	Qc	49.7	0.95	7.0	12.5	18.0	100.0	3.25	8.10
475	Mo	72.6	2.32	14.0	16.2	37.3	94.1	21.94	19.06
477	Sa	3.6	0.03	0.5	1.0	0.9	96.0	21.07	19.42
478	Sa	3.5	0.06	0.3		1.7	95.0	10.26	8.02
479	Sa	8.0	0.30	1.1	2.6	7.3	95.0	16.01	3.81
482	Cc	1.9	0.24	1.2	1.2	7.7	95.0	16.01	
483	Pm	72.4	0.75	50.8	15.2	11.3	94.6	7.64	17.05
485	Ps	1.4	0.04	0.5	0.5	0.7	92.3	23.56	37.10
486	Qc	21.8	0.34	1.2	4.1	7.4	100.0	4.71	3.18
487	Ps	0.9	0.04	0.3		0.8	90.8	33.41	45.85
489	Mo	47.6	1.23	4.0	9.3	16.4	90.7	15.51	29.13
493	Fm	58.7	1.50	10.7		21.8	78.8	16.54	12.13
515*	Mk	10.6	0.44	2.2	2.1	10.6	95.1	11.43	23.49

$W_T$ , trunk dry mass;  $W_L$ , leaf dry mass;  $W_B$ , branch dry mass;  $W_R$ , root dry mass;  $A_L$ , leaf area;  $W_{LB}$ , leaf-blade dry mass; RDGR, relative growth rate in trunk diameter; RHGR, relative growth rate in trunk height.