

# Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower

Toshiyuki Ohtsuka\*, Tsuyoshi Akiyama, Yasushi Hashimoto, Motoko Inatomi, Toru Sakai, Shugang Jia, Wenhong Mo, Satoshi Tsuda, Hiroshi Koizumi

*Institute for Basin Ecosystem Studies, Gifu University, Gifu 501-1193, Japan*

Received 26 April 2004; accepted 4 August 2005

## Abstract

We measured the forest biomass and biometrically derived net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. NPP was calculated as the sum of the living biomass of new-season tissue in all organs ( $B$ ) and biomass of new-season tissue lost due to death ( $L$ ). Annual leaf-litter production was adopted as  $L$ . We regarded the total tree growth in the stand as  $B$ , and examined three methods for estimating  $B$  to discuss the practicality of continuous measurement of NPP to compare with corresponding estimates of eddy-covariance based net ecosystem exchange (NEE). The three methods were diameter at breast height (DBH)–growth allometry by stem analysis of sample trees (SA method), DBH–growth allometry by core sample analysis of sample trees (CS method) and direct measurement of stem growth by tree census (TC method). The total annual tree growth in the forest stand estimated by the SA, CS and TC methods was 2.26, 1.60 and 2.38  $\text{Mg ha}^{-1}$ , respectively, and NPP was 5.64, 4.98 and 5.74  $\text{Mg ha}^{-1}$ . The slope of the regression of DBH against annual tree growth was slightly smaller for the CS method than for the SA method; the CS method underestimated the growth of several sample trees that had no clear main stem and, as a result, greatly underestimated  $B$ . To estimate  $B$ , the SA and CS methods depend on the use of DBH–growth allometry. Thus, it is difficult to determine species-dependent growth in natural mixed forests by these methods if only a few sample trees are used. In contrast, the TC method can directly and continuously measure the growth of all tree stems. Therefore, the TC method is the most suitable method for measuring NPP through annual measurements of tree diameter and leaf-litter production allowing for direct comparison with eddy-covariance based estimate of NEE.

© 2005 Elsevier B.V. All rights reserved.

**Keywords:** Biometric method; Carbon uptake; Cool-temperate forest; Forest biomass; Net primary production

## 1. Introduction

The mechanisms of carbon sequestration in forest ecosystems have yet to be fully clarified due to uncertainty in estimating carbon budgets in terrestrial ecosystems (IPCC, 1996). Recently, net ecosystem  $\text{CO}_2$  exchange (NEE) in forest ecosystems has been

measured using the eddy-covariance method in various types of forest (Wofsy et al., 1993; Black et al., 1996; Grace et al., 1996; Greco and Baldocchi, 1996; Valentini et al., 1996; Saigusa et al., 2002). These studies have shown the variations in annual net  $\text{CO}_2$  uptake among forest types and even among years at the same site. For example, the annual net uptakes of  $\text{CO}_2$  in 1994, 1995 and 1996 were 420, 240 and 500  $\text{g CO}_2 \text{ m}^{-2}$ , respectively, at the Takayama Forest Research Station (Yamamoto et al., 1999), the site of the cool-temperate forest stand used in the present study. In contrast, biometric estimation of net ecosystem production (NEP) is conceptually equivalent to eddy-

\* Corresponding author. Present address: Laboratory of Ecology, Faculty of Science, Ibaraki University, Bunkyo 2-1-1, Mito, Ibaraki 310-8512, Japan. Tel.: +81 555 72 6192; fax: +81 555 72 6192.

E-mail address: [toshi@mx.ibaraki.ac.jp](mailto:toshi@mx.ibaraki.ac.jp) (T. Ohtsuka).

covariance based NEE. Thus, comparison of NEP and NEE can work as a cross-check and help increase the accuracy of estimating forest carbon storage, potentially providing insight into the causes of variation in annual CO<sub>2</sub> uptake in forest ecosystems (Curtis et al., 2002).

Biometric estimation of NEP (annual carbon budgets) for plant communities is determined from the balance of net primary production (NPP), or C uptake, and decomposition of soil organic matter (C loss) by soil micro-organisms (Grogan and Chapin, 2000). Continuous measurements of soil respiration using a static chamber IRGA system were developed beneath a flux tower (Savage and Davidson, 2003; Mo et al., 2005). In contrast, there have been many studies of NPP in forest communities, especially in Japan, where the International Biological Program (IBP, Shidei and Kira, 1977) has been underway since 1960. However, these studies have just examined typical climax forest communities in small quadrats, and few studies have measured long-term variations in NPP in forest communities.

Biometric NPP is commonly calculated from repeated measurements of the forest biomass (total tree growth), litter production and herbivory loss in forest stands (the harvest method, Shidei and Kira, 1977). Litter traps are useful for measuring litter

production. However, there are several ways to estimate the amount of annual tree growth in forest stands. For continuous estimation of NPP, and for comparison of NEE and NEP in forest stands beneath a flux tower, we first need an accurate biometric estimate of total annual tree growth every year. Our objectives were: (1) to estimate forest biomass and biometric NPP in the cool-temperate deciduous forest beneath a flux tower, and (2) to discuss the practicality of continuous biometric estimation of NPP in forest ecosystems simultaneously with eddy-covariance based measurement of NEE.

## 2. Methods

### 2.1. Study site

The study site is located in the Takayama Forest Research Station, Institute for Basin Ecosystem Studies, Gifu University, on the middle slopes of Mt. Norikura in central Japan (Fig. 1, 36°08'N, 137°25'E, 1420 m a.s.l.). The original vegetation around the research station is a cool-temperate deciduous broad-leaved forest, dominated by Japanese beech (*Fagus crenata*). However, the primary beech forests around the station have been utilized for producing charcoal, and the study site now consists of secondary deciduous broad-leaved forest.

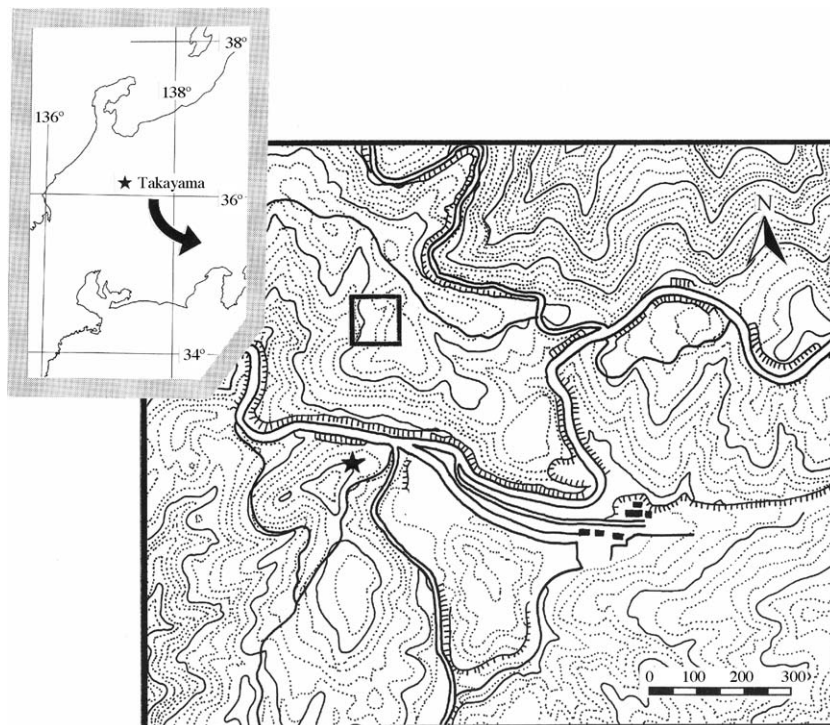


Fig. 1. Location of the study site at Takayama Forest Research Station (★), Gifu University, central Japan. Square indicates the permanent quadrat of 100 m × 100 m.

The forest floor is covered by a dense bamboo grass community (Nishimura et al., 2004). A permanent plot of 1 ha (100 m × 100 m) was set on a west-facing slope (Fig. 1, ca. 1395–1425 m a.s.l.). A flux tower for measuring CO<sub>2</sub> flux by the eddy-covariance method (Saigusa et al., 2002) is included in the permanent plot.

The study area has a seasonal cool-temperate climate. Annual mean air temperature of the site is 7.3 °C, annual rainfall is about 2400 mm, distributed throughout the year; snow depth is usually 1–2 m in winter (December–April).

## 2.2. Community structure and biomass

All trees in the permanent plot taller than 1.3 m in height were numbered and identified in autumn 1998. We painted the measuring position of the diameter at breast height (DBH, cm) for each tree stem, and we used a steel tape measure to accurately record the DBH in March and May 1999, before the growing season. Nomenclature followed by Satake et al. (1989).

In December 1998, 24 sample trees (12 species) near the permanent plot, ranging from 1.7 to 29.0 cm in DBH, were cut off at ground level. In addition, the coarse roots of seven of these trees were also dug out for

analysis (Table 1). For assessment of total biomass, the fresh-weight biomass of stem, branches and coarse roots of each individual was obtained. There was no foliage because it was winter. The dry weight of all collected biomass was calculated from the water content of subsamples dried at 80 °C. DBH–biomass relationships were developed from these sample trees using the allometric method (Kira and Shidei, 1967). The biomass of the stand (excluding foliage) was then calculated (DBH–weight allometry) for all tree stems in 1999 by the following relationships:

$$\log W = 2.334 \log D - 0.946 \quad (r^2 = 0.98, n = 24) \quad (1)$$

$$\log W_s = 2.367 \log D - 1.061 \quad (r^2 = 0.97, n = 24) \quad (2)$$

$$\log W_b = 2.221 \log D - 1.663 \quad (r^2 = 0.88, n = 24) \quad (3)$$

$$\log W_r = 1.977 \log D - 1.074 \quad (r^2 = 0.92, n = 7) \quad (4)$$

where  $W$  is the total above-ground weight (kg) and  $W_s$ ,  $W_b$  and  $W_r$  are the dry weights (kg) of stem, branches and coarse roots, respectively, and  $D$  is the DBH (cm).

Fourteen litter traps (each 1 m<sup>2</sup> in area) made of nylon net were set up on the forest floor to estimate leaf

Table 1  
Tree size and dry weights of sample trees used for analysis of DBH–weight allometry

No.	Species	DBH (cm)	Height (m)	Stem dry weight (kg)	Branch dry weight (kg)	Above-ground total (kg)	Coarse roots dry weight (kg)
1	<i>Acer rufinerve</i>	29.0 <sup>a</sup>	18.4	321.55	64.94	386.49	–
2	<i>Betula platyphylla</i> var. <i>japonica</i>	25.5 <sup>a</sup>	19.7	159.42	32.58	192.00	–
3	<i>Quercus crispula</i>	18.3	13.4	61.83	19.05	80.88	30.95
4	<i>Acer distylum</i>	17.0 <sup>a</sup>	15.6	99.59	15.94	115.53	–
5	<i>Magnolia obovata</i>	16.0 <sup>a</sup>	17.1	63.46	3.44	66.91	–
6	<i>Betula platyphylla</i> var. <i>japonica</i>	12.2	7.5	17.83	9.67	27.50	9.60
7	<i>Prunus sargentii</i>	12.2 <sup>a</sup>	12.9	36.98	7.60	44.58	–
8	<i>Carpinus japonica</i>	10.9 <sup>a</sup>	9.8	25.73	2.54	28.28	–
9	<i>Betula ermanii</i>	10.8 <sup>a</sup>	16.0	39.55	3.50	43.06	–
10	<i>Quercus crispula</i>	10.5	6.7	17.30	5.37	22.67	10.86
11	<i>Betula platyphylla</i> var. <i>japonica</i>	9.8	9.0	16.16	3.90	20.06	6.43
12	<i>Quercus crispula</i>	8.2	6.1	9.57	1.12	10.69	4.26
13	<i>Quercus crispula</i>	6.5 <sup>a</sup>	8.9	11.82	2.37	14.19	–
14	<i>Acanthopanax sciadophylloides</i>	6.4 <sup>a</sup>	10.2	7.47	0.49	7.96	–
15	<i>Quercus crispula</i>	6.4 <sup>a</sup>	9.4	12.75	0.95	13.70	–
16	<i>Betula platyphylla</i> var. <i>japonica</i>	6.2	4.3	4.84	1.94	6.78	4.51
17	<i>Betula platyphylla</i> var. <i>japonica</i>	6.2	6.5	5.69	1.42	7.11	–
18	<i>Acanthopanax sciadophylloides</i>	5.9 <sup>a</sup>	9.4	6.74	0.65	7.39	–
19	<i>Acer sieboldianum</i>	5.6	4.7	5.18	0.90	6.08	2.28
20	<i>Acer japonicum</i>	5.3 <sup>a</sup>	6.5	4.14	1.04	5.18	–
21	<i>Betula ermanii</i>	4.8 <sup>a</sup>	7.3	3.41	0.46	3.88	–
22	<i>Betula ermanii</i>	4.4	4.2	2.60	0.49	3.09	–
23	<i>Betula platyphylla</i> var. <i>japonica</i>	3.7	3.7	1.72	1.26	2.98	–
24	<i>Symplocos coreana</i>	1.7 <sup>a</sup>	2.0	0.31	0.09	0.40	–

<sup>a</sup> Indicates 14 sample trees used for DBH–growth allometry analysis by the SA and the CS methods.

biomass and loss of dead plant parts. Fine litter in the traps was collected every 2 months and sorted into leaves and other materials (mainly dead branches and twigs). The materials were oven dried at 80 °C and weighed. The amount of annual leaf fall was regarded as the total leaf biomass of the stand, because almost all trees (97.2% of total basal area) were deciduous species.

### 2.3. Net primary production of forest stands

Net primary production ( $P$ ) of  $\Delta t$  between the two time points  $t_1$  and  $t_2$  as estimated by the harvest method is expressed by the following equation (Shidei and Kira, 1977):

$$P = B + L + G \quad (5)$$

where  $B$  is the biomass of new tissue in all organs produced between  $t_1$  and  $t_2$ ;  $L$  is the loss due to the death of tissue produced between  $t_1$  and  $t_2$ ;  $G$  is the loss due to animal grazing of tissue produced between  $t_1$  and  $t_2$ .

Annual leaf-litter production was adopted as  $L$  because almost all trees were deciduous. The amount of dead branches and twigs for the current year could be assumed to be small. Loss due to animal grazing ( $G$ ) was disregarded in this study.

The total tree growth in the forest stand was regarded as the biomass of new tissue in all organs ( $B$ ), and was calculated by the following three methods:

**Stem analysis method (SA method):** The stem volume increment was estimated by stem analysis of 14 (ranging from 1.7 to 29.0 cm in DBH) of the 24 sample trees that had been used for biomass estimation (Table 1). The growth in diameter of each sample tree over the last 10 years (1989–1998) was measured from differences in the diameters of successive annual rings on the surfaces of disks cut from the tree. These disks were cut at different tree heights (0, 0.3, 1.3 and 3.3 m, then at regular intervals of 2 m to the top of each tree; example, Fig. 2). The stem volume increment in each sample tree over the last 10 years was calculated by the change in volume of each cylinder, as delineated by the annual rings of each disk; the cross-sectional area of each cylinder was taken as the mean area of the rings at each end of the cylinder. The stem volume increment was converted into dry weight growth by the volume to weight ratios determined for each disk. The total stem growth (without bark) in the stand was calculated from all tree stems in 1999 using the logarithmic relation between annual increase in stem weight and DBH developed from the sample trees (DBH–growth allometry). Annual ring analysis of branches and

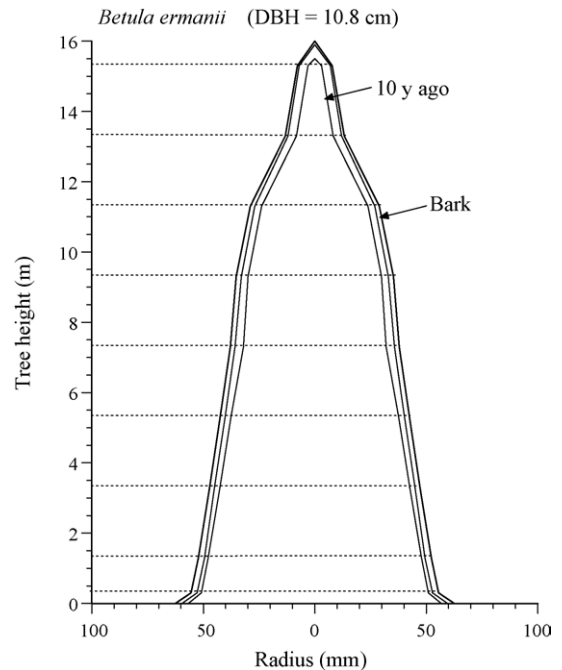


Fig. 2. Example of stem analysis of *Betula ermanii*. The stem volume increment of the sample tree was measured from diameter growth of annual rings of 10 disks at different tree heights, as shown by broken lines and the disk at 0 m.

coarse roots is often very difficult. Therefore, the CS method was used to estimate the annual growth of branches and coarse roots in the stand as described below. The growth of stem, branches and coarse roots was added to calculate the total annual tree growth in the stand ( $B$ ).

**Core sample method (CS method):** Total above-ground dry weight (in this study, without foliage) and dry weight of coarse roots of the sample trees were logarithmically related to their DBHs (Eqs. (1) and (4)). By assuming that the present allometric DBH–weight relationships existed in the forest community of 10 years ago, we estimated the past dry weight of the trees by measuring the annual rings of core samples or disks at breast height. The changes in diameter of the annual rings on the disks (rather than core samples) at breast height over the last 10 years (1989–1998) were measured for the same 14 sample trees that had been used for the SA method. The dry weights of above-ground parts and coarse roots of each sample tree for 10 years ago were calculated using DBH–weight allometry (Eqs. (1) and (4)). Annual growth of above-ground parts and coarse roots was estimated for each sample tree by the difference between present and past dry weights. The total annual tree growth in the stand ( $B$ ) was calculated from all

tree stems in 1999 using the logarithmic relation between annual growth and DBH (DBH–growth allometry) developed from the sample trees. The annual growth of branches was estimated by the same procedure, using Eq. (3).

*Tree census method (TC method):* By assuming that the present allometric relation between DBH and weight of trees in 1998 (Eqs. (1) and (4); above-ground parts and coarse roots, respectively) would continue to be a reasonable approximation for this forest community in 1999 and beyond, we estimated the annual growth of each tree by annual direct measurement of DBH for every stem. To investigate the annual diameter growth of all stems, the DBH was re-recorded in March and May 2000. The dry weight of all living stems after the 1999 growing season was calculated using DBH–weight allometry (Eqs. (1) and (4)). Annual growth of the above-ground parts and coarse roots was estimated from the differences between the dry weight before and after the 1999 growing season. The total annual tree growth in the stand (*B*) in 1999 was estimated from the sum of the growth of all living stems. All results referring to biomass or weight increment are on a dry weight basis.

### 3. Results

#### 3.1. Community structure and biomass

A total of 44 tree species were present in the permanent plot, including deciduous broad-leaved trees (34 species), evergreen conifer trees (3 species) and deciduous shrubs (7 species). The dominant three species in summed basal area were *Quercus crispula*, *Betula ermanii* and *B. platyphylla* var. *japonica* (Table 2). The combined basal area of the dominant three species was more than 65% of the total. Almost all species were deciduous broad-leaved trees, and only three evergreen conifers, *Abies homolepis*, *Pinus parviflora* and *Chamaecyparis pisifera* (2.8% of total basal area), were present. The total number of tree stems higher than 1.3 m was 1907 in 1999. More than a quarter of the total stems were shrub species (509), but these accounted for less than 2% of basal area. Maximum DBH was 67.9 cm (in *B. platyphylla* var. *japonica*), and the mean DBH of all stems was 11.4 cm. The total summed basal area of all tree stems was 32.34 m<sup>2</sup> ha<sup>-1</sup>.

The biomass of the permanent plot in 1999 by component was 113.6 Mg ha<sup>-1</sup> total stem biomass,

Table 2  
Species composition in the 1-ha permanent plot

Species	Basal area		Biomass (Mg ha <sup>-1</sup> )			Mean DBH (cm)	Maximum DBH (cm)	No. of stems	
	m <sup>2</sup> ha <sup>-1</sup>	%	Stem	Branches	Roots			(ha <sup>-1</sup> )	(%)
<b>Deciduous trees</b>									
<i>Quercus crispula</i>	8.71	26.9	31.0	4.9	8.7	17.0	61.9	312	16.4
<i>Betula ermanii</i>	7.95	24.6	29.2	4.5	7.9	21.3	59.4	198	10.4
<i>Betula platyphylla</i> var. <i>japonica</i>	4.71	14.6	17.2	2.7	4.7	20.2	67.9	128	6.7
<i>Magnolia obovata</i>	1.88	5.8	6.5	1.0	1.9	15.6	36.5	77	4.0
<i>Acer rufinerve</i>	1.47	4.6	5.0	0.8	1.5	15.1	37.7	65	3.4
<i>Tilia japonica</i>	1.35	4.2	4.7	0.7	1.3	17.4	37.0	48	2.5
Other trees (28 species)	4.74	14.7	14.2	2.3	4.6	8.3	37.0	551	28.9
Subtotal	30.81	95.3	107.7	16.9	30.6			1379	72.3
<b>Evergreen conifer trees</b>									
<i>Abies homolepis</i>	0.48	1.5	2.0	0.3	0.5	12.5	49.2	17	0.9
<i>Pinus parviflora</i>	0.28	0.9	1.4	0.2	0.3	59.7	59.7	1	0.1
<i>Chamaecyparis pisifera</i>	0.14	0.4	0.6	0.1	0.1	42.0	42.0	1	0.1
Subtotal	0.90	2.8	4.0	0.6	0.9			19	1.0
<b>Deciduous shrubs</b>									
<i>Hydrangea paniculata</i>	0.36	1.1	0.8	0.2	0.4	4.7	13.8	153	8.0
<i>Viburnum furcatum</i>	0.14	0.4	0.3	0.1	0.1	2.6	8.8	222	11.6
<i>Symplocos coreana</i>	0.08	0.2	0.1	0.0	0.1	3.2	8.5	78	4.1
Other shrubs (4 species)	0.05	0.1	0.6	0.1	0.2	3.0	6.3	56	2.9
Subtotal	0.63	1.9	1.9	0.4	0.9			509	26.7
Total	32.34	100.0	113.6	17.9	32.3	11.4	67.9	1907	100.0

17.9 Mg ha<sup>-1</sup> total branch biomass and 32.3 Mg ha<sup>-1</sup> total coarse root biomass. The total leaf biomass was 3.4 Mg ha<sup>-1</sup>, as estimated from the annual leaf fall in 1999. The total above-ground biomass in the stand in 1999 was 134.9 Mg ha<sup>-1</sup> and total tree biomass (including coarse roots) was 167.2 Mg ha<sup>-1</sup>.

The DBH class distribution of the dominant three species showed a peak in the 10–20 cm class (Fig. 3). *Quercus crispula* had more root suckers than *B. ermanii* and *B. platyphylla* var. *japonica*. Almost all stems less than 5 cm in DBH were shrub species, such as *Hydrangea paniculata* and *Viburnum furcatum*, which had many root suckers.

### 3.2. Total tree growth in the stand as measured by the three methods

The stem volume and dry weight increments of 14 sample trees were measured by the SA method (Table 3). Annual growth of above-ground, branches and coarse roots of the same 14 sample trees was measured by the CS method (Table 4). The annual dry-weight increment of each component was logarithmically related to the tree's DBH (Fig. 4). The total annual stem growth (without bark) in the stand was estimated to be 1.79 Mg ha<sup>-1</sup> by the SA method (Table 5) using DBH–stem growth allometry (Fig. 4A). The total

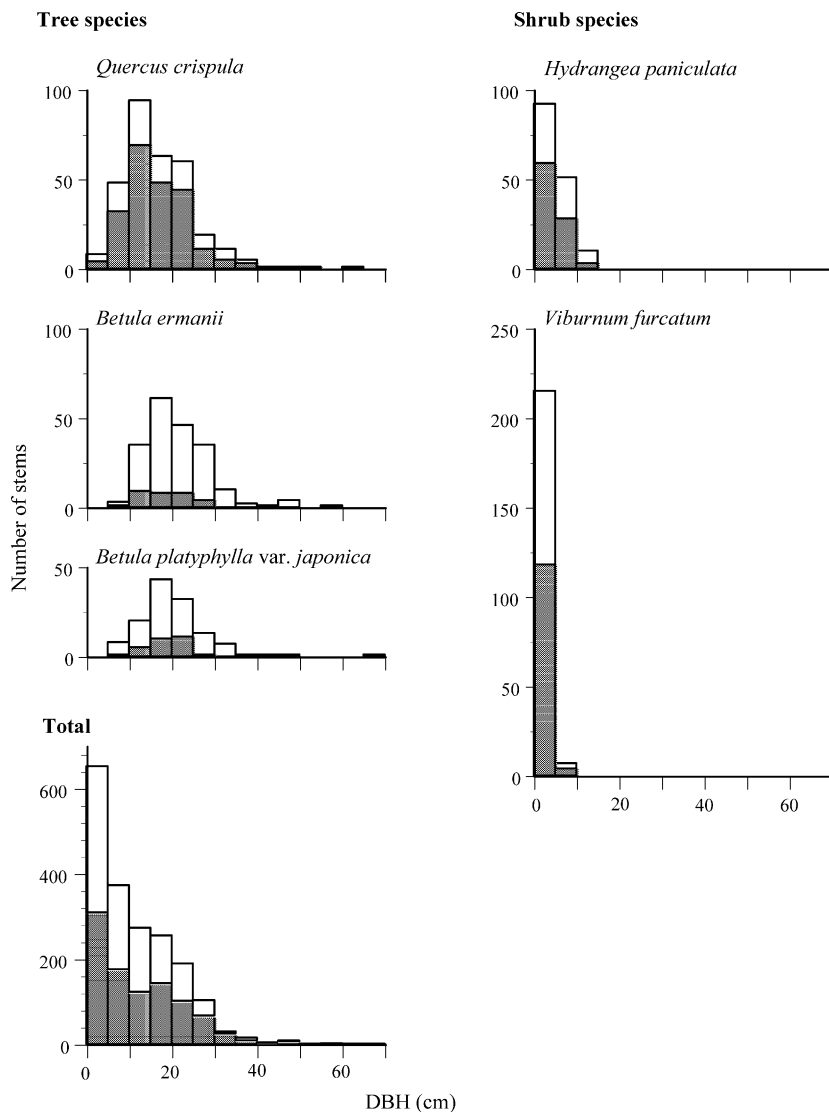


Fig. 3. DBH class distributions of the three main trees species and the two main shrub species in the permanent plot, (■): stems of root suckers.

Table 3  
Annual stem growth (without bark) of the sample trees by the SA method

Species	DBH (cm)	Stem volume without bark (m <sup>3</sup> )		Stem biomass without bark (kg)		Annual stem growth (kg year <sup>-1</sup> )
		Present	10 years ago	Present	10 years ago	
<i>Betula platyphylla</i> var. <i>japonica</i>	25.5	0.3593	0.3241	141.31	126.84	1.45
<i>Acer distylum</i>	17.0	0.1545	0.1316	87.31	74.10	1.32
<i>Magnolia obovata</i>	16.0	0.1208	0.1011	55.47	46.05	0.94
<i>Prunus sargentii</i>	12.2	0.0516	0.0317	33.82	20.92	1.29
<i>Carpinus japonica</i>	10.9	0.0341	0.0275	22.65	18.26	0.44
<i>Betula ermanii</i>	10.8	0.0622	0.0539	35.25	30.31	0.49
<i>Quercus crispula</i>	6.5	0.0097	0.0080	10.64	8.75	0.19
<i>Acanthopanax sciadophylloides</i>	6.4	0.0153	0.0073	6.99	3.33	0.37
<i>Quercus crispula</i>	6.4	0.0154	0.0073	10.60	5.00	0.56
<i>Acanthopanax sciadophylloides</i>	5.9	0.0128	0.0080	6.20	3.90	0.23
<i>Acer japonicum</i>	5.3	0.0065	0.0031	3.68	1.75	0.19
<i>Betula ermanii</i>	4.8	0.0057	0.0023	3.14	1.31	0.18
<i>Symplocos coreana</i>	1.7	0.0004	0.0001 <sup>a</sup>	0.26	0.04 <sup>a</sup>	0.04

<sup>a</sup> Stem volume and stem biomass of 5 years ago.

annual growth was estimated for the stand by the CS method using DBH–growth allometry (Fig. 4B and C); the results were 1.30 Mg ha<sup>-1</sup> for all above-ground parts, 0.17 Mg ha<sup>-1</sup> for branches and 0.30 Mg ha<sup>-1</sup> for coarse roots (Table 5).

The annual diameter growth (mm) of all stems during 1999 in the stand was measured by the TC method. No growth was detected (0 or negative) for 354 of the total 1822 living stems (Fig. 5). More than half of the stems had an annual growth in DBH of less than

2 mm. Using the TC method, the total annual growth in the stand in 1999 was estimated to be 1.96 Mg ha<sup>-1</sup> for above-ground parts and 0.42 Mg ha<sup>-1</sup> for coarse roots (Table 5). There were species-specific relationships between tree size and annual growth (Fig. 6). *Quercus crispula* had a higher annual growth rate than the two *Betula* species at all DBH sizes except for the less than 10 cm size class in *B. ermanii*. *Betula platyphylla* var. *japonica* had an extremely low annual growth rate over the range of DBHs. Fig. 7 shows the annual above-

Table 4  
Annual growth of the sample trees by the CS method

Species	DBH (cm)	Biomass estimated from disk sample taken at a height of 1.3 m (kg)								
		Above-ground		Branches		Coarse roots		Annual growth (g year <sup>-1</sup> )		
		Present	10 years ago	Present	10 years ago	Present	10 years ago	Above-ground	Branches	Coarse roots
<i>Acer rufinerve</i>	29.0	312.14	255.35	40.81	33.71	69.20	58.38	5678.8	709.9	1082.4
<i>Betula platyphylla</i> var. <i>japonica</i>	25.5	194.54	182.09	26.02	24.44	46.37	43.84	1245.3	158.8	252.7
<i>Acer distylum</i>	17.0	74.54	67.58	10.45	9.51	20.57	18.93	696.0	93.0	163.9
<i>Magnolia obovata</i>	16.0	65.13	49.72 <sup>a</sup>	9.19	7.11 <sup>a</sup>	18.35	14.60 <sup>a</sup>	770.3	104.0	187.5
<i>Prunus sargentii</i>	12.2	33.82	22.00	4.92	3.27	10.53	7.32	1181.3	165.3	321.4
<i>Carpinus japonica</i>	10.9	21.99	18.02	3.27	2.71	7.31	6.18	396.4	56.3	113.3
<i>Betula ermanii</i>	10.8	27.05	24.55	3.98	3.63	8.72	8.03	250.6	35.2	68.9
<i>Quercus crispula</i>	6.5	9.19	7.75	1.42	1.21	3.49	3.02	143.6	21.3	46.8
<i>Acanthopanax sciadophylloides</i>	6.4	7.78	3.89	1.22	0.63	3.03	1.69	389.1	58.8	134.8
<i>Quercus crispula</i>	6.4	8.14	4.08	1.27	0.66	3.15	1.76	406.1	61.2	139.7
<i>Acanthopanax sciadophylloides</i>	5.9	6.39	3.93	1.01	0.63	2.57	1.70	246.7	37.5	86.9
<i>Acer japonicum</i>	5.3	4.44	2.09	0.71	0.35	1.89	1.00	235.2	36.5	89.1
<i>Betula ermanii</i>	4.8	3.33	1.69	0.54	0.28	1.48	0.83	164.2	25.8	64.7
<i>Symplocos coreana</i>	1.7	0.27	0.003 <sup>b</sup>	0.05	0.001 <sup>b</sup>	0.18	0.004 <sup>b</sup>	53.7	9.8	34.6

<sup>a</sup> Biomass of 20 years ago.

<sup>b</sup> Biomass of 5 years ago.

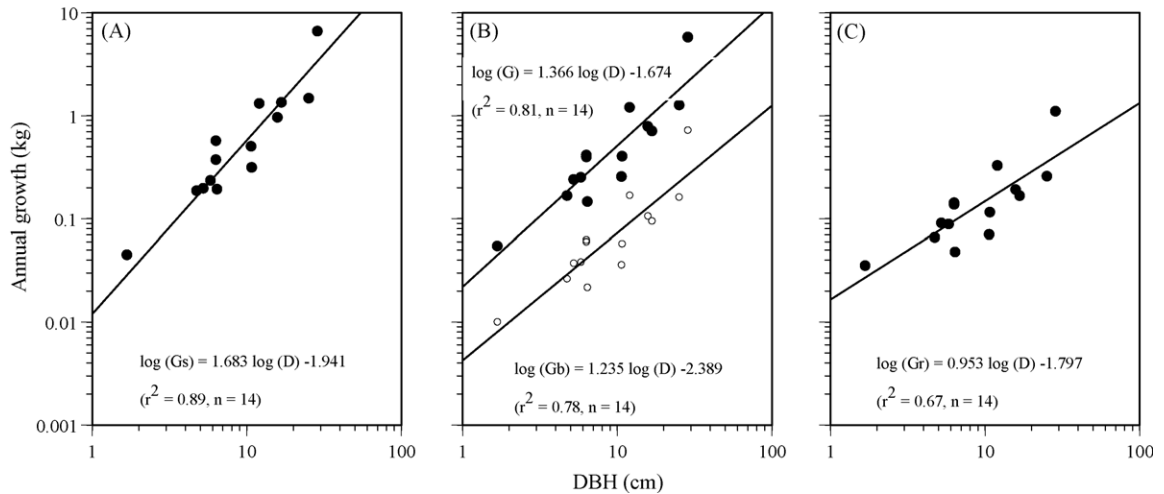


Fig. 4. Allometric relationships between annual growth of sample trees and their DBHs. Annual stem growth by the SA method (A), annual growth of above-ground parts (●) and branches (○) by the CS method (B), and annual growth of coarse roots by the CS method (C). Regression equations are shown with coefficient of determination;  $G_s$  is the annual stem growth without bark ( $\text{kg year}^{-1}$ );  $G$ ,  $G_b$  and  $G_r$  are the annual growths of above-ground parts (stem and branches), branches and roots ( $\text{kg year}^{-1}$ ), respectively.  $D$  is the DBH (cm) of each sample tree.

ground growth estimated by the three methods and the number of stems in each DBH size class. Annual above-ground growth (stem growth only for the SA method) for all trees below 5 cm DBH was less than 5% of the total increment for all methods, although this DBH class accounted for nearly one-third of the total stem number. The annual growth estimates for each of the three methods were similar in the DBH classes less than 15 cm. However, the SA method and the TC method gave larger growth rates than the CS method in the >20 cm DBH class. In particular, the TC method yielded the largest stem growth in DBH classes above 25 cm, in which there were few stems.

### 3.3. Net primary production of the stand

Annual leaf- and branch-litter fall varied from year to year in the stand (Table 6). Mean production (1993–1998) of leaf and branch litter was 3.38 and 1.21  $\text{Mg ha}^{-1} \text{ year}^{-1}$ , respectively. Annual production in 1999 was 3.36  $\text{Mg ha}^{-1} \text{ year}^{-1}$  for leaf-litter and 0.46  $\text{Mg ha}^{-1} \text{ year}^{-1}$  for branch litter. Mean leaf-litter production was used for  $L$  in the SA and CS methods, which were used to estimate mean annual forest growth for the last 10 year (1989–1998). Annual leaf-litter production in 1999 was used for  $L$  in the TC method, which was used to estimate the annual forest growth in

Table 5  
Annual net primary production of the forest stand estimated by the three methods

	SA method	CS method	TC method
The total annual growth ( $\text{Mg ha}^{-1}$ ); $B$			
Stem	1.79		
Branches	0.17 <sup>a</sup>		
Above-ground total	(1.96)	1.30	1.96
Coarse roots	0.30 <sup>a</sup>	0.30	0.42
Annual litter production of new-season's organs ( $\text{Mg ha}^{-1}$ ); $L$			
Foliage	3.38 <sup>b</sup>	3.38 <sup>b</sup>	3.36 <sup>c</sup>
Net primary production ( $\text{Mg ha}^{-1}$ ); $B + L$	5.64	4.98	5.74

<sup>a</sup> Amount of annual growth was calculated by the CS-method.

<sup>b</sup> Mean annual litter production (1993–1998).

<sup>c</sup> Annual litter production in 1999.



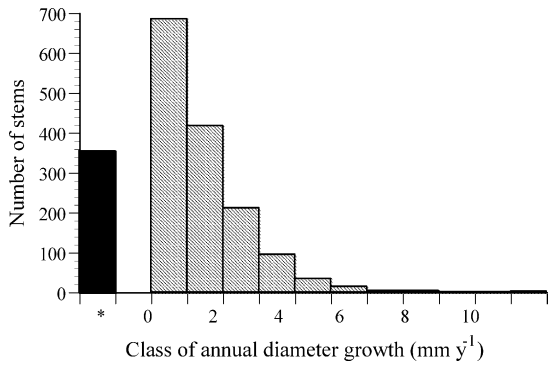


Fig. 5. Class distribution of annual diameter growth (1999–2000) for all stems in the permanent plot, as measured by the TC method. “\* (■)” indicates stems for which no annual growth was detected, i.e., diameter growth in 2000 was zero or negative.

1999. The net primary production of the stand was calculated by the SA, CS and TC methods at 5.64, 4.98 and 5.74 Mg ha<sup>-1</sup> year<sup>-1</sup>, respectively (Table 5).

#### 4. Discussion

##### 4.1. Net primary production of cool-temperate deciduous forest stands

The above-ground biomass (including foliage) of our stand (134.9 Mg ha<sup>-1</sup>) was less than half of that of natural Japanese beech (*Fagus crenata*) forests (250–400 Mg ha<sup>-1</sup>), which are the climax forests of the cool-temperate zone (Maruyama, 1971; Kawaguchi and Yoda, 1986; Tadaki et al., 1988). The stem density of the

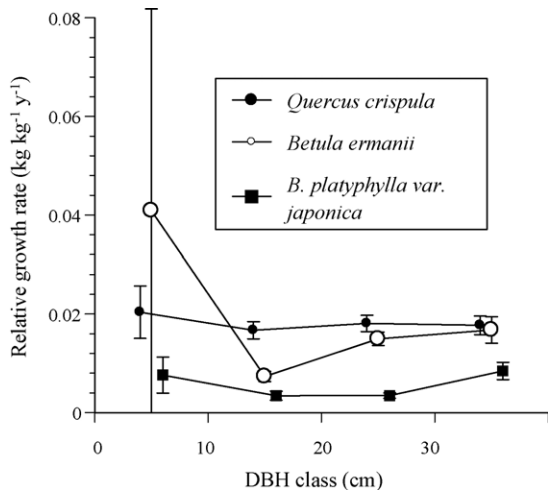


Fig. 6. Annual relative growth rates (RGRs) of DBH of the three dominant species, as measured by the TC method: (●) *Quercus crispula*, (○) *Betula ermanii* and (■) *Betula platyphylla* var. *japonica*. Bars indicate the S.E. of the mean.  $RGR = L_n - L_{n-1}$  (DBH in 1999).

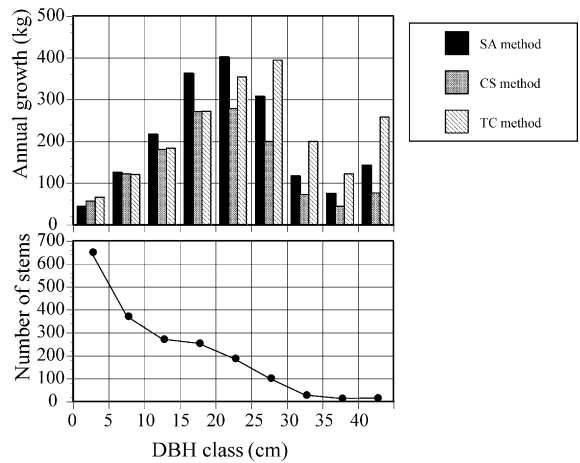


Fig. 7. Amount of annual above-ground growth (stem growth for the SA method) estimated by the three methods for each DBH size class, and number of stems in each DBH size class.

stand (1907 ha<sup>-1</sup> over 1.3 m tree height) was higher than that of typical climax beech forests. Kira (1977) reviewed previous studies and reported that the above-ground net primary production of cool-temperate deciduous broad-leaved forests in Japan was 8.74 ± 3.47 Mg ha<sup>-1</sup> year<sup>-1</sup> (n = 55). Annual above-ground net primary production (excluding coarse root growth) of our stand was estimated to range from 4.68 to 5.34 Mg ha<sup>-1</sup> year<sup>-1</sup> (Table 5), which was significantly smaller than the values reported by Kira. The present forest stand might have a below average NPP for a cool-temperate forest because of its status as a pioneer community in secondary succession. Moreover, the earlier studies of NPP in cool-temperate forests might have produced higher than average estimates if they focused on mature climax forests on high productivity site.

Herbivory loss of the forest stand was not considered for net production calculations in the present study. Bray (1961) estimated the herbivory loss of leaves in

Table 6  
Annual litter production (Mg ha<sup>-1</sup>) in the permanent plot using 14 litter traps

Year	Foliage	Branches and others	Total
1993	2.94	1.73	4.67
1994	No data		
1995	3.21	0.73	3.94
1996	3.30	1.27	4.57
1997	3.75	0.63	4.38
1998	3.70	1.67	5.37
Average	3.38	1.21	4.59
1999	3.36	0.46	3.82

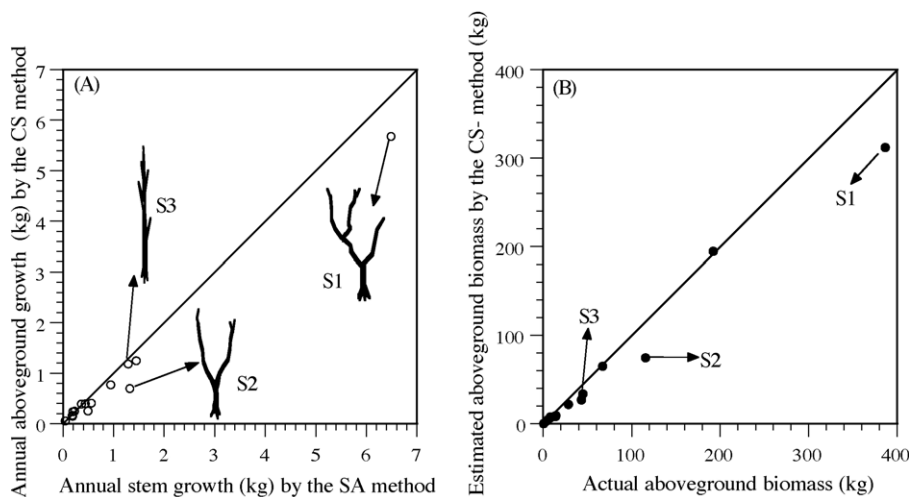


Fig. 8. Relationships between annual stem growth by the SA method and annual above-ground growth by the CS method for the same sample trees (A). Tree architecture of the typical sample trees is superimposed on the graph. S1 and S2 represent sample trees with several stems but no clear main stem, and S3 is a sample tree with an obvious main stem. The relationship between the actual dry weight and the dry weight as estimated by the CS method using DBH–weight allometry is also represented (B). The same sample trees are indicated by arrows.

several deciduous forests at 4.4–11.7%. Kimura et al. (1982) reported that animals consumed about 7.6% of annual leaf production or 10% of leaf mass found in the canopy at the end of the growing season in a warm-temperate oak coppice forest. They concluded that such loss is responsible for the reduction of the net production of canopy trees by about 3%. Thus, the total above-ground net production of our stand was slightly underestimated.

There have been relatively few studies of growth of below-ground components of trees. Scarascia-Mugnozza et al. (2000) studied the tree biomass and growth of European beech forests. They demonstrated that the biomass of coarse roots was 10 times greater than that of fine roots, but that fine roots had 2–5 times higher growth rates owing to their fast turnover. In our study, the coarse root biomass (Table 2) and the annual coarse root growth (Table 5) were nearly a quarter of their above-ground equivalents. However, the turnover (growth and loss) of fine roots could not be estimated by our methods. We need to undertake biometric study of fine root production using equipment such as mini-rhizotrons (Burton et al., 2000).

#### 4.2. Comparisons of the three methods of estimating total tree growth

Estimates of above-ground growth in the forest stand from the three methods ranged from 1.30 to 1.96 Mg ha<sup>-1</sup> year<sup>-1</sup> (Table 5). The SA estimate was about 1.5 times greater than the CS estimate for the

same period (1989–1998) and the same sample trees. Methods that use relationships of DBH–growth allometry of sample trees have been popular for estimating tree growth in temperate natural forests in the past (Kimura, 1960; Kan et al., 1965; Saito et al., 1965; Curtis et al., 2002; O’Connell et al., 2003). No studies, however, have compared the SA method with the CS method on trees from the same area.

Fig. 8A illustrates the annual above-ground growth of the 14 sample trees by the SA and CS methods. The two methods yielded almost the same estimates of annual growth for sample trees that had a clear main stem, such as S3 in Fig. 8A. However, for trees with several main stems (S1 and S2), the CS method underestimated annual growth. For example, annual growth of *Acer distylum*, which had two main stems over 4.1 m in height (S2), was estimated as only 0.70 kg using the CS method, but 1.32 kg using the SA method (Fig. 8A). The SA method was able to accurately measure stem growth through the analysis of the growth rings of multiple main stems. However, the CS method, using DBH–weight allometry, calculated the annual growth of sample trees as the difference between present and past biomass (Eq. (1)). The estimates of biomass of the sample trees with multiple main stems (S1 and S2) were smaller than the actual dry weights (Fig. 8B) using this approach. Thus, underestimation of dry weight resulted in underestimation of annual growth of the sample trees. Slight differences in the annual growth of some sample trees resulted in differences in the linear allometric regressions developed by the two

methods (Fig. 4A and B); a slight difference of the slopes in the regressions therefore resulted in a relatively large difference between the estimates of total tree growth in the stand produced by the two methods.

The total tree growth estimated by the TC method was nearly equal to that by the SA method, although the two estimates were for different periods. For large size class trees, which had few stems, the TC method produced much higher estimates of annual growth rate than the other two methods (Fig. 7). The maximum DBH of the sample trees was only 29.0 cm, in *A. rufinerve* (Table 1), whereas the maximum DBH of the stand was 67.9 cm, in *B. platyphylla* var. *japonica* (Table 2). Therefore, the annual growth of large-diameter trees that reached the canopy layer might have been greater than would be estimated by the allometric relationships we obtained for the SA and CS methods. On the other hand, one could speculate that the dry weight and annual growth of such large trees were overestimated by the TC method because it used DBH–weight relationships constructed from small diameter trees (Table 1). Either way, this shows that sample trees that are close to the maximum size of the stand should be used in constructing the allometric relationships to obtain more accurate stand-level estimations.

#### 4.3. Continuous estimation of net primary production beneath a flux tower

To estimate the total annual tree growth in a forest stand, the SA and CS methods depend on the use of DBH–growth allometry. Thus, it is hard to determine species-dependent growth in natural mixed forests by these methods from only a few sample trees. Our study forest was secondary mixed forest, and the growth rate differed among the species (Fig. 6). In contrast, the TC method provides much more accurate estimation of tree growth in natural mixed forests because it can directly measure the growth of all tree stems. Moreover, total tree growth (diameter growth) can be continuously measured by this method. Therefore, the TC method can be used to measure NPP through annual measurements of tree diameter and leaf-litter production, coinciding with the determination of CO<sub>2</sub> flux by the eddy-covariance method.

However, annual growth in DBH is small, especially in cool-temperate forests with their short growing season. To accurately measure the annual growth in tree diameter, it is important to paint the circumference of each tree clearly at the height where DBH will be measured. It is also important to understand the daily

and seasonal changes in tree diameter (Maruyama et al., 1985; Komiyama et al., 1987) of the main species under field conditions to determine the optimum time for measurement of DBH. The growth of large-diameter trees greatly affected our estimates of forest biomass and tree growth. Thus, the DBH range of sample trees used for biomass estimation is an important point to consider for accurate estimation of NPP in natural forest stands.

#### Acknowledgments

We are grateful to staff of the Takayama Forest Research Station, and especially to Mr. K. Kurumado of the Institute for Basin Ecosystem Studies, Gifu University, for their cooperation. We also thank Ms. Y. Abe of the Yamanashi Institute of Environmental Sciences for her generous help in field survey and laboratory analysis.

#### References

- Black, T.A., Hartog, G.D., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Chen, S.G., Staebler, R., Novak, M.D., 1996. Annual cycles of water vapor and carbon dioxide fluxes in and above a boreal aspen forest. *Glob. Change Biol.* 2, 219–229.
- Bray, J., 1961. Measurement of leaf utilization as an index of minimum level of primary consumption. *Oikos* 12, 70–74.
- Burton, A.J., Pregitzer, K.S., Hendrick, R.L., 2000. Relationships between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. *Oecologia* 125, 389–399.
- Curtis, P.S., Hanson, P.J., Bolstad, P., Barford, C., Randolph, J.C., Schmid, H.P., Wilson, K.B., 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricult. For. Meteorol.* 113, 3–19.
- Grace, J., Malhi, Y., Lloyd, J., McIntyre, J., Miranda, A.C., Meir, P., Miranda, H.S., 1996. The use of eddy covariance to infer the net carbon dioxide uptake of Brazilian rain forest. *Glob. Change Biol.* 2, 209–217.
- Greco, S., Baldocchi, D., 1996. Seasonal variations of CO<sub>2</sub> and water vapor exchange rates over a temperate deciduous forest. *Glob. Change Biol.* 2, 183–197.
- Grogan, P., Chapin III, F.S., 2000. Initial effects of experimental warming on above- and belowground components of net ecosystem CO<sub>2</sub> exchange in arctic tundra. *Oecologia* 125, 512–520.
- International Panel on Climate Change (IPCC), 1996. Climate change 1995—the science of climate change. In: Houghton J.J. (Eds.), Contribution of Working Group I to the Second Assessment Report of the Inter-Governmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Kan, M., Saito, H., Shidei, T., 1965. Studies of the productivity of evergreen broad-leaved forests. *Bull. Kyoto Univ. For.* 37, 55–75 (in Japanese with English summary).
- Kawaguchi, H., Yoda, K., 1986. Carbon-cycling changes during regeneration of a deciduous broadleaf forest after clear-cutting. I. Changes in organic matter and carbon storage. *Jpn. J. Ecol.* 35, 551–563 (in Japanese with English summary).

- Kimura, M., 1960. Primary production of the warm-temperate laurel forest in the southern part of Osumi Peninsula, Kyushu, Japan. *Misc. Rep. Res. Inst. Nat. Resour.* 52/53, 36–47.
- Kimura, M., Funakoshi, M., Sudo, S., Masuzawa, T., Nakamura, T., Matsuda, K., 1982. Productivity and mineral cycling in an oak coppice forest. 2. Annual net production of the forest. *Bot. Mag. Tokyo* 95, 359–373.
- Kira, T., 1977. Production rates. In: Shidei, T., Kira, T. (Eds.), *Primary Productivity of Japanese Forests—Productivity of Terrestrial Communities*. Japanese Committee for the International Biological Program (JIBP) Synthesis, vol. 16. University of Tokyo Press, Tokyo, pp. 101–114.
- Kira, T., Shidei, T., 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. *Jpn. J. Ecol.* 17, 70–87.
- Komiyama, A., Inoue, S., Ishikawa, T., 1987. Characteristics of the seasonal diameter growth of twenty-five species of deciduous broad-leaved trees. *J. Jpn. For. Soc.* 69, 379–385 (in Japanese with English summary).
- Maruyama, K., 1971. Effect of altitude on dry matter production of primeval Japanese beech forest communities in Naeba Mountains. *Mem. Fac. Agr. Niigata Univ.* 9, 85–171.
- Maruyama, K., Fukumoto, Y., Kamitani, T., 1985. The daily radial fluctuation of trunks of some deciduous broad-leaved trees and its controlling factors. *J. Jpn. For. Soc.* 67, 148–152 (in Japanese with English summary).
- Mo, W., Lee, M.-S., Uchida, M., Inatomi, M., Saigusa, N., Mariko, S., Koizumi, H., 2005. Seasonal and annual variations in soil respiration in a cool-temperate deciduous broad-leaved forest, Japan. *Agricult. For. Meteorol.* (in this volume).
- Nishimura, N., Matsui, Y., Ueyama, T., Mo, W., Saijo, Y., Tsuda, S., Yamamoto, S., Koizumi, H., 2004. Evaluation of carbon budgets of a forest floor *Sasa senanensis* community in a cool-temperate forest ecosystem, central Japan. *Jpn. J. Ecol.* 54, 143–158 (in Japanese with English summary).
- O'Connell, K.E.B., Gower, S.T., Norman, J.M., 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. *Ecosystems* 6, 248–260.
- Saigusa, N., Yamamoto, S., Murayama, S., Kondo, H., Nishimura, N., 2002. Gross primary production and net ecosystem exchange of a cool-temperate deciduous forest estimated by the eddy covariance method. *Agricult. For. Meteorol.* 112, 203–215.
- Saito, H., Shidei, T., Kira, T., 1965. Dry-matter production by *Camellia japonica* stands. *Jpn. J. Ecol.* 15, 131–139.
- Satake, H., Hara, H., Watari, S., Tominari, T., 1989. *Wild Flowers of Japan—Woody Plants*. Heibonsha Ltd., Publishers, Tokyo.
- Savage, K.E., Davidson, E.A., 2003. A comparison of manual and automated systems for soil CO<sub>2</sub> flux measurements: trade-offs between spatial and temporal resolution. *J. Exp. Bot.* 54, 891–899.
- Scarascia-Mugnozza, G., Bauer, G.A., Persson, H., Matteucci, G., Masci, A., 2000. Tree biomass, growth and nutrient pools. In: Schulze, E.-D. (Ed.), *Carbon and Nitrogen Cycling in European Forest Ecosystems*. Springer-Verlag, Berlin, pp. 49–62.
- Shidei, T., Kira, T., 1977. *Primary Productivity of Japanese Forests—Productivity of Terrestrial Communities*. Japanese Committee for the International Biological Program (JIBP) Synthesis, vol. 16. University of Tokyo Press, Tokyo.
- Tadaki, Y., Yoda, S., Asai, S., 1988. Carbon cycling in middle-aged and old forests of Japanese beech (*Fagus crenata*). *J. Fac. Sci. Shinshu Univ.* 23, 7–20 (in Japanese with English summary).
- Valentini, R., De Angelis, P., Matteucci, G., Monaco, R., Dore, S., Mugnozza, G.E.S., 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Glob. Change Biol.* 2, 199–207.
- Wofsy, S.C., Goulden, B.C., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO<sub>2</sub> in a mid-latitude forest. *Science* 260, 1314–1317.
- Yamamoto, S., Murayama, S., Saigusa, N., Kondo, H., 1999. Seasonal and inter-annual variation of CO<sub>2</sub> flux between a temperate forest and atmosphere in Japan. *Tellus* 51B, 402–413.