Biometric and eddy-covariance-based estimates of carbon balance for a warm-temperate mixed forest in Japan

Yuji Kominami [a,*], Mayuko Jomura [b], Masako Dannoura [c], Yoshiaki Goto [d], Koji Tamai [d], Takafumi Miyama [a], Yoichi Kanazawa [c], Shinji Kaneko [e], Motonori Okumura [f], Noriko Misawa [c], Shogo Hamada [c], Taizo Sasaki [c], Hitoshi Kimura [c], Yoshikazu Ohtani [d]

[a] Kansai Research Center, Forestry and Forest Products Research Institute, Momoyama-cho, Fushimi-ku, Kyoto 612-0855, Japan
[b] Agro-Meteorology Division, National Institute for Agro-Environmental Sciences, Tsukuba, Ibaragi 305-8604, Japan
[c] Graduate School of Science and Technology, Kobe University, Kobe 657-8501, Japan
[d] Department of Meteorological Environment, Forestry and Forest Products Research Institute, Tsukuba, Ibaragi 305-8687, Japan
[e] Department of Forest Site Environment, Forestry and Forest Products Research Institute, Tsukuba, Ibaragi 305-8687, Japan
[f] Graduate School of Energy Science, Kyoto University, Uji 611-0011, Japan

ARTICLE INFO

ABSTRACT

To estimate net ecosystem exchange (NEE) and net ecosystem production (NEP) in a forest situated on complex terrain, we evaluated the sensitivity of the estimates of NEE to the choice of a friction velocity (u^*) correction for the estimation of flux on calm night. And compared these estimates with estimates based on biometric data using a warm-temperate deciduous and evergreen mixed forest in Japan. Biometric approaches were based on analyses of autotrophic carbon pools and heterotrophic carbon fluxes (NEP) versus changes in two major carbon pools (ΔC). To estimate ΔC, we calculated contributions to the soil carbon pool by litter and coarse woody debris (CWD) independently. The 3-year mean annual NEE from 2000 to 2002 was -1.23 MgC ha^{-1} year^{-1} (a negative flux indicates carbon gain). Estimated ΔC and NEP were 1.73 and 0.91 MgC m^{-2} year^{-1}, respectively (a positive flux indicates carbon gain). The increment of live biomass contributed 76% of total ΔC. Estimated NEP varied widely due to large spatial variation in soil respiration. A realistic u^* threshold was 0.4 m s^{-1}. The estimated NEE value was larger than NEP. The change in NEE as a function of the u^* threshold was marked, and most of the measured data (about 80%) could be eliminated by using the 0.4 m s^{-1} u^* threshold. These results seem to be caused by the loss of most nocturnal respiration as a result of horizontal advection or drainage flow (because the study site was located on complex terrain). This tendency was consistent for towers located on a ridge and in a valley.

1. Introduction

A better understanding of the global carbon balance is required for estimation of the potential global warming that may occur in the coming years (Baldocchi et al., 2001). Understanding the role of forests and their response to changing environmental factors will be particularly important in evaluating the terrestrial carbon cycle. Measurements of the

net ecosystem exchange (NEE) of various forests around the world have mainly been conducted using micrometeorological methods. Combinations of eddy-covariance methods and changes in CO_2 storage have also been commonly adopted. However, because the eddy-covariance method requires adequate mixing of the air and measuring changes in CO_2 storage requires conditions under which horizontal advection can be ignored, the use of eddy fluxes may underreport nocturnal respiration during periods with low wind speed (Wofsy et al., 1993; Ruimy et al., 1995; Black et al., 1996; Goulden et al., 1996; Baldocchi et al., 1997). Moreover, this underreporting may not be compensated for by changes in storage measurement when measurement sites are located on sloping terrain. Kominami et al. (2003) concluded that most nocturnal respiration could not be measured on calm nights in forests situated in complex terrain based on a comparison of eddy-covariance estimates with the respiration measured by automated chambers. Therefore, it is necessary to compensate for the estimation of nocturnal respiration and identify a suitable method to detect periods when the eddy-covariance technique cannot be applied. Studies of CO_2 exchange in complex terrain should thus employ a combination of approaches (e.g., mesoscale modeling, remote sensing, ecophysiological measurements) to constrain fluxes (Baldocchi, 2003).

To compare NEE values estimated using the eddy-covariance method with net ecosystem production (NEP) estimated by means of biometric measurements, Curtis et al. (2002) defined biometric measurements as follows. For several decades, ecologists have evaluated net primary production (NPP) as the difference between gross primary production (GPP) and autotrophic respiration (R_a), which can also be expressed in terms of the change in biomass due to growth, decay, and herbivory:

$$NPP = GPP - R_a = L + D + H \tag{1}$$

where L is the increment in live plant biomass, D the increment in dead plant biomass (detritus), and H is the increment lost to herbivory (Waring and Schlesinger, 1985). In principle, each parameter in this model includes both above- and belowground processes. However, additional NPP components (e.g., nectar and pollen production, volatile organic compounds, carbon transport by vertebrates) are commonly not accounted for and are assumed to be small. The net gain or loss of carbon from an ecosystem is defined as NEP, and results from the gain of carbon by autotrophic organisms (GPP) minus its loss by autotrophic (R_a) and heterotrophic (R_h) respiration:

$$NEP = GPP - R_a - R_h \tag{2}$$

Combining Eqs. (1) and (2), NEP can be expressed as the difference between NPP and R_h:

$$NEP = (L + D + H) - R_h \tag{3}$$

If mass losses from H, volatile organic compounds, or other processes are small, annual forest carbon storage (ΔC) can also be expressed as the annual increment in the plant biomass (ΔW) plus soil (ΔS) carbon pools:

$$\Delta C = \Delta W + \Delta S \tag{4}$$

where S is the difference between D and R_h. Although NEP and ΔC are not independent, ΔC does not require the evaluation of spatial variation of soil respiration and the separation of root respiration from soil respiration, which facilitates measurements because these parameters are difficult to measure at a forest situated on complex terrain.

In the present study, we also separated ΔS into ΔS provided by inputs of litter and coarse woody debris (CWD), and estimated annual carbon storage using biometric methods. We then compared the results with estimates of NEE for the same site based on the eddy-covariance method. In this paper, we also discuss variation in the estimates as a result of their sensitivity to the u^* threshold and develop an interpolation function using the biometric data for a forest situated in complex terrain in Japan.

2. Study site

Observations were conducted in the Yamashiro Experimental Forest, located in a mountainous region of western Japan (lat. 34°47′N, long. 135°51′E; Fig. 1). The study site was a 1.7-ha watershed. As the topographical map shows, the terrain was complex, and the zero-order stream that ran through the study site formed a V-shaped valley. The angle of the slope between the ridge and the valley was steep (about 30°), but the slope of the main course of the river was gentle (about 5°). Two meteorological towers were established at an elevation of about 220 m asl. The fetch was about 3 km to the south and east and more than 5 km to the north and west. Wind direction usually changed during the course of the day, ranging from northeast in the morning to southwest in the afternoon.

The forest at the study site was originally dominated by *Pinus densiflora* Sieb. et Zucc. About 30 years ago, pine wilt disease caused by the pinewood nematode (*Bursaphelenchus xylophilus*) spread through the area, killing most of the *P. densiflora*, and broadleaved species took their place. In 1999, the living tree biomass (DBH $\geq$ 3 cm) was estimated to be 51.01 MgC ha^{-1}, and deciduous broadleaved tree species such as *Quercus serrata* Thunb. ex Murray, evergreen broadleaved tree species such as *Ilex pedunculosa* Miq., and coniferous tree species such as *P. densiflora* accounted for 66, 28, and 6% of that biomass, respectively (Goto et al., 2003). A number of standing and downed dead *P. densiflora* were observed in the forest (6.79 MgC ha^{-1}). The annual mean temperature was 15.5 °C, and the hourly maximum and minimum temperatures in 2002 were observed in August (34.8 °C) and January (−3.9 °C). Annual mean precipitation from 1994 to 2002 was 1449 mm; the rainy season occurred in late June and early July, and typhoons occurred during the summer and fall. There was no significant change in vegetation within the fetch, with the exception of small bamboo communities (*Phyllostachys heterocycla* Carr. Mitf.) growing in patches. Canopy height averaged 12.0 m, and the mean DBH of the living trees (i.e., DBH $\geq$ 3 cm) was 7.4 cm. The mean stand density was 3209 trees ha^{-1}, and
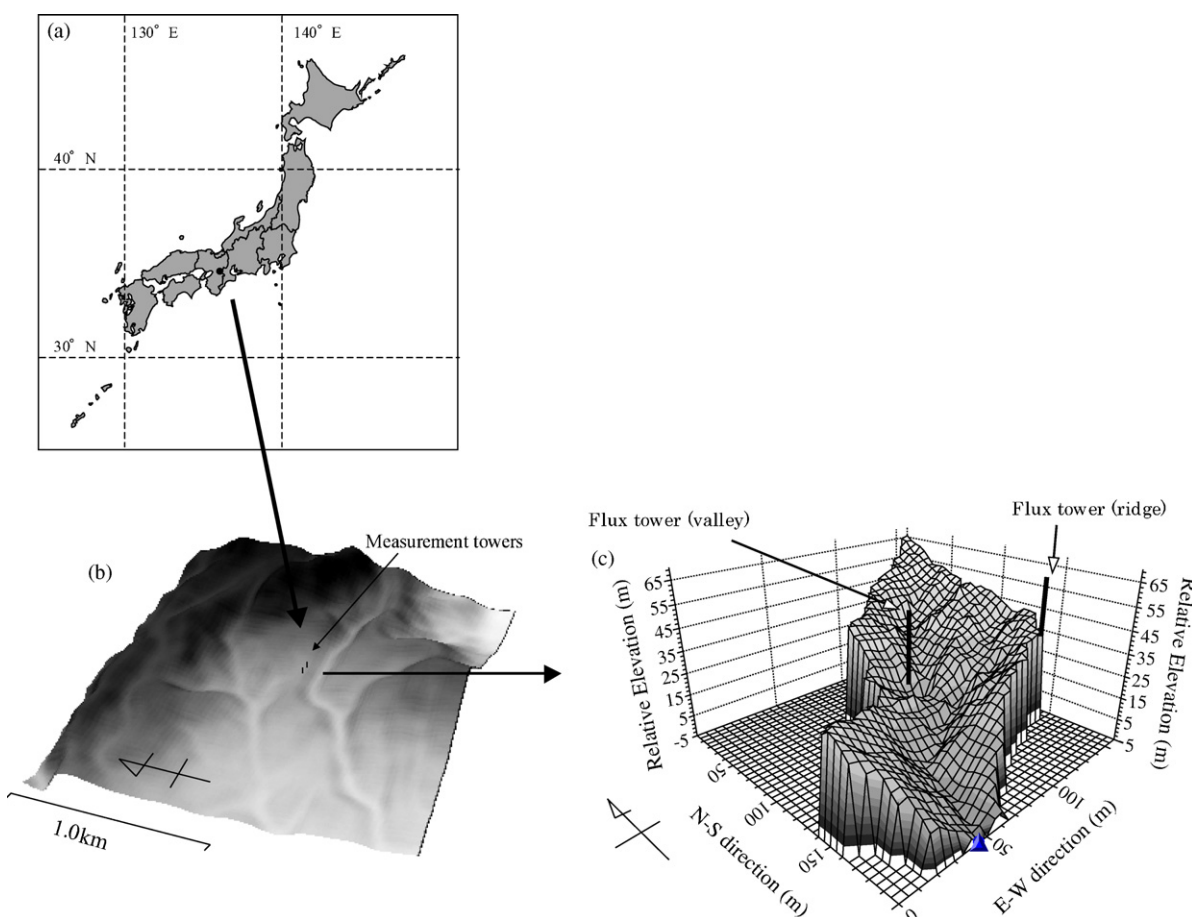
Fig. 1 – (a) Location of Yamashiro Experimental Forest, Japan. (b) Geographical feature around the study site. (c) Topographic map of the study site (1.7 ha) and locations of meteorological towers.

the mean total basal area was 20.7 $m^2\,ha^{-1}$ (Goto et al., 2003). Soils are Regosols (IUSS Working Group WRB, 2006) with a sandy loam or loamy sand texture and contain many fine granitic gravels (53% on a weight basis).

Two meteorological towers were constructed in this forest to permit measurements of CO_2 flux between the forest ecosystem and the atmosphere (Kominami et al., 2003). Measurements of foliage CO_2 exchange on dominant species (*Q. serrata* and *I. pedunculosa*) (Miyama et al., 2003, 2006), soil respiration (Nobuhiro et al., 2003; Tamai et al., 2005), root respiration (Dannoura et al., 2006) and CWD respiration (Jomura et al., 2007) have been conducted at this site using chamber methods. Databases of forest inventory, biomass, and production data have been compiled (Goto et al., 2003) to evaluate NEE measured at the towers.

3. Methodology

3.1. CO_2 flux above the forest

Both meteorological towers were equipped with a system for measuring eddy covariance that used a closed-path CO_2 analyzer to measure the CO_2 flux above the forest and to examine the effects of the complex topography on the

measurements. The first tower (35 m tall) was erected in a valley; the other (26.5 m tall) was situated on a ridge. The eddy-covariance sensors were mounted at the top of each tower, and other meteorological variables were measured at various heights. The eddy-covariance measurements were obtained using a three-dimensional ultrasonic anemometer (model DAT-600-3TV, Kaijo, Tokyo, Japan) and a closed-path CO_2 infrared gas analyzer (IRGA; model LI-6262, LI-COR, Lincoln, NE, USA). The sampling frequency was 10 Hz.

The air sampled to determine CO_2 concentrations was drawn into a gas analyzer installed at the bottom of the tower. The distance from the air inlet to the gas analyzer was about 29 m for the ridge tower and 38 m for the valley tower. The delay time between sample collection and measurement ranged from 9.6 to 10.2 s under a suction of about 9.6 L min^{-1}; the flow rate to the sample cell of the analyzer was maintained at 2.0 L min^{-1} using a mass-flow controller (SEC-400, STEC, Kyoto, Japan). Water vapor in the sample air was removed by an air dryer (MD gas dryer, ZBJ02502-72P, Perma-Pure, Thomas River, NJ, USA). This dryer has a high-polymer membrane tube that is only permeable to water vapor. The sample air is passed through the membrane tube, and dry air is passed along the outside of the tube; as a result, the water vapor moves in the direction of the reduced water vapor pressure, from the inside to the outside of the

membrane tube. The water vapor in the sample air can thus be removed at high speed. Although the chance to measure water vapor flux is lost, dehumidification avoids the risk of dew formation in the sample cell. Moreover, cancellation of air temperature fluctuations by tube sampling and that of humidity fluctuations have the advantage of allowing CO_2 flux to be calculated without requiring the WPL correction (Webb et al., 1980), and also standard gases were used to calibrate the IRGA once per day to air base 0 ppm and approximately 400 ppm CO_2.

The eddy-covariance measurement system used at this site was originally designed and tested at another site by Yasuda et al. (1998), and was modified for extended long-term flux monitoring. CO_2 flux above the canopy was measured using the eddy-covariance method every 30 min. The approach used three-dimensional axis rotation (McMillen, 1988) and included corrections for the effects of lateral wind and water vapor on sonic velocity (Kaimal et al., 1968).

Two data quality tests were implemented to identify inappropriate data: (1) charts showing fluctuations in the raw data for the entire period were drawn for the wind velocity components, air temperature, CO_2 concentration, and vapor pressure, and obviously erroneous data were eliminated, and (2) the quality control procedures for raw data described by Foken and Wichura (1996) and Vickers and Mahrt (1996) were performed. Vertical profiles of CO_2 concentration were also obtained from air samples taken at eight heights (1.1, 3.1, 5.3, 6.9, 8.9, 14.2, 20.0, 25.7 m (Ridge), 1.1, 3.1, 5.3, 6.9, 8.9, 17.2, 25.0, 34.6 m (Valley)) and pumped through Teflon-lined tubing to the IRGA (model LI-6262, LI-COR, Lincoln, NE, USA). To measure CO_2 concentrations at eight heights with an IRGA, we switched eight sampling lines. Sampling period of each channel was 2 min (16 min for eight heights measurements) and we obtained three sets of eight heights CO_2 concentration data in each 1-h. The system for dehumidification and calibration was same with eddy-covariance measurement system. Vertical profiles from successive 20-min measurement periods were subtracted from each other to measure the changes in CO_2 storage within the canopy over these periods. Other meteorological parameters, such as air temperature, radiation, wind velocity, and soil temperature, were also measured every 30 s on and near the tower, and mean values were recorded every 5 min using a datalogger (CADAC2, Eto, Tokyo, Japan).

The CO_2 flux measurements (F_{eddy}) obtained by means of the eddy-covariance method at heights of 26.5 m (the ridge tower) and 35.0 m (the valley tower) were combined with the vertical CO_2 concentration profiles to provide a direct measurement of NEE:

$$NEE = F_{eddy} + \frac{dC}{dt} \tag{5}$$

where $c(z)$ is the CO_2 concentration at height z and

$$\frac{dC}{dt} = \frac{d}{dt}\int c(z)\,dz \tag{6}$$

is the rate of change of the CO_2 concentration between ground level (0 m) and the top of the tower. The available data from

the ridge tower covered 87% of the measurement time from 2000 to 2002. Small gaps (up to 2 h) that resulted from equipment error and maintenance and from data transfer were filled by means of interpolation. Larger gaps in the data that occurred during quality checks or as a result of equipment failure were filled in as follows. First, if ambient photosynthetically active radiation (APAR) was less than 10 μmol m^{-2} s^{-1}, we assumed these periods were during the night and estimated respiration using an annual-course exponential function that related nocturnal respiration to soil temperature at a 5-cm depth:

$$F_{night} = a\exp(b\,T_{soil}) \tag{7}$$

where F_{night} is nocturnal respiration and T_{soil} is the soil temperature at a 5-cm depth.

Second, if APAR was greater than 10 μmol m^{-2} s^{-1}, we assumed these periods were during the day, and filled gaps in the data using the Michaelis–Menten equation:

$$F_{day} = -\frac{a'\,APAR\,AG_{max}}{AG_{max} + a'\,APAR} \tag{8}$$

where F_{day} represents the measured NEE, a' represents the ecosystem quantum yield, and AG_{max} represents the GPP at the light saturation point. Parameters for Eq. (8) were derived monthly. The underestimation of nocturnal CO_2 flux measured by the eddy-covariance method under low-turbulence conditions, especially in complex terrain, appears to be mainly caused by horizontal advection and drainage flow (which is common in steep terrain such as that of the study site). To correct for this underestimation, methods capable of removing this bias are required (e.g., Baldocchi, 2003). Kominami et al. (2003) reported that nocturnal CO_2 flux measured by means of the eddy-covariance method was 60% lower than that measured by means of the chamber method at this study site even after accounting for changes in CO_2 storage. Furthermore, Kominami et al. (2005) compared seasonal changes in nocturnal respiration at the study site based on the eddy-covariance method with estimates based on chamber measurements. In the present study, we assessed the sensitivity of estimated respiration to changes in the u^* threshold using Eq. (7) to assess the nocturnal CO_2 flux. This correction is necessary because when wind velocity (u) is too low, eddy-covariance methods cannot be used to produce accurate results. To eliminate the effects of this problem, friction velocity (u^*) effects must be accounted for, and a threshold value of u^* (sometimes called a "filter") must be selected so that inaccurate measurements can be excluded from the data set. This threshold value is defined by increasing the filter value until the flux estimates stabilize.

In this study, we used eddy-covariance flux data and storage change data at the ridge tower from 1 January 2000 to 31 December 2002. And eddy-covariance measurements were obtained from 4 April 2001 to 31 December 2001 and storage change measurements were obtained from 12 January 2002 to 2 December 2002 at the valley tower. IRGAs positioned at the two towers were calibrated using the same standard gas to permit a comparison of the absolute CO_2 concentrations at the two towers. Comparison of CO_2

flux at ridge and valley tower was conducted with no gap filled data.

3.2. Biometric measurements

3.2.1. NEP estimation

To estimate NEP at the study site, we had previously evaluated aboveground biomass (Goto et al., 2003), belowground biomass (Dannoura et al., 2005a), soil respiration (Tamai et al., 2005), root respiration (Dannoura et al., 2005b, 2006), and CWD respiration (Jomura et al., 2005, 2007). By integrating these results, we were able to estimate the increment in live plant biomass (L), the increment in dead plant biomass (D), and heterotrophic respiration (R_h). We also estimated NEP at the study site from biometric measurements. Loescher et al. (2006) noted that there are several potential sources of error in NEP estimation based on the mass-balance approach.

(1) Instrument and human errors.
(2) Sampling errors arising from the use of a limited number of sample points.
(3) Parameterization errors that result from the use of scaling parameters derived from data in other studies (e.g., non-site-specific allometric biomass equations or decomposition constants).

To decrease these errors, we estimated site- and species-specific allometric equations for aboveground biomass and a site-specific ratio of aboveground to belowground biomass (the TR-ratio). We also measured the DBH of all trees with a DBH $\geq$ 3 cm to increase the sample size. To estimate a site-specific decomposition constant, we evaluated the spatial variation in soil respiration using 264 soil collars (Fig. 1) and estimated a site-specific ratio of root respiration to soil respiration using a newly developed method (Dannoura et al., 2006). We estimated heterotrophic respiration (R_h) in total soil respiration (R_{soil}). Moreover, we estimated heterotrophic respiration from CWD (R_{cwd}) independently from our estimate of CWD carbon balance (Jomura et al., 2007).

3.2.2. ΔS estimation

Since the 6th century, the forests around the study site have been harvested heavily and then abandoned, leaving much of the ground bare until the early 20th century. Moreover, accelerated erosion rates and high storm runoffs on mobile soil at steep hill slope had prevented invasion of the site by most plants (Kimoto et al., 2002). As a result, there was probably little carbon accumulation in the soil during this period. During the early 1900s, an extensive reforestation effort using *P. densiflora* was carried out. This was the first broad-scale revegetation work in Japan in modern times. However, between about 1975 and 1984, most of these trees were killed by the pine wilt disease. Broadleaved species such as *Q. serrata* and evergreen species as *I. pedunculosa* that had invaded the site during the 1950s gradually became the dominant canopy species. Consequently, much of the biomass produced by *P. densiflora* was still present at the site in the form of CWD.

In evaluating the heterotrophic carbon balance, independent estimation of the litter and CWD carbon balance was required. In this study, we assumed that losses from H, volatile organic compounds, and other processes were small (i.e., that $\Delta C = \Delta W + \Delta S$), and divided S into the carbon input from litter and CWD:

$$\Delta S = \Delta S_{litter} + \Delta S_{CWD} \tag{9}$$

ΔS_{litter} was estimated using version 26.3 of the RothC model (see Section 3.2.5 for more details). ΔS_{CWD} was estimated by subtracting respiration of CWD from the CWD input for this forest (Jomura et al., 2007).

3.2.3. Aboveground net primary production

In this section, we will provide only a summary of our methods. Details of the determination of aboveground biomass were reported by Goto et al. (2003). In this analysis, aboveground carbon stored in wood was estimated using allometric equations that related DBH to stem, branch, stump, and leaf biomass (based on a total of 46 trees from 9 species of deciduous broadleaved tree, 8 species of evergreen broadleaved tree, and 3 species of evergreen needle-leaved tree). The wood increment was estimated by measuring the 5-year change in DBH of all trees (DBH $\geq$ 3 cm). Allometric relationships for canopy trees were developed by means of destructive sampling. The species-specific allometric equations developed in this manner were then employed to estimate biomass in the present study. Annual production of fine litter (e.g., leaves, flowers, fruits) was estimated using 20-l collection baskets (0.9 m × 0.9 m) placed on the forest floor and emptied every month so their contents could be dried and weighed. The measurement period extended from September 1999 to August 2003. The contributions of understory vegetation, including lianas and herbaceous vegetation, to aboveground NPP were estimated using allometric equations for woody vegetation and destructive sampling of herbaceous vegetation in a 0.17-ha subplot.

3.2.4. Belowground net primary production

The amount of carbon stored below the ground as wood (i.e., stumps and large lateral roots) was derived from allometric equations that related D_0 (tree diameter at ground height) to woody root biomass. For most tree species, only general relationships are available, in which belowground wood biomass is set at a fixed fraction of aboveground wood biomass (generally 20%; e.g., Perala and Alban, 1994; Jackson et al., 1996). However, in the present study, we improved on this approach by developing simple allometric relationships for woody roots as a function of DBH (for all species combined rather than species-specific relationships) based on destructive sampling of trees, including all woody roots larger than 2 mm in diameter (16 trees, 13 species). The annual increment in woody root carbon was estimated from the annual change in DBH using these equations. The fine-root carbon pool was measured using soil cores at 10 plots located randomly within the site. Measurements were conducted in November 2000 and September 2001 (Dannoura et al., 2005a).

3.2.5. Determining the carbon balance of litter using the RothC model

The RothC model simulates the turnover of soil organic carbon by accounting for the effects of soil type and environmental

factors on the turnover process (Jenkinson et al., 1987; Jenkinson and Coleman, 1994). In addition, if the input of plant residues (litter and CWD) and the decomposability of the incoming plant material (the ratio of decomposable to resistant plant material, DPM/RPM) can be obtained, this model allows the estimation of soil carbon storage.

The temporal trend for the input of leaf litter and fine roots from the establishment of the forest (ca. 1900) to the present was estimated based on the assumption that the rate of production of leaf biomass and fine roots as a function of the total aboveground tree biomass was constant; this value was estimated as 5.3% by Goto et al. (2003) and as 1.2% by Dannoura et al. (2006). Total aboveground tree biomass was estimated based on the balance between tree growth and mortality. Tree-ring analysis (data not shown) revealed that the biomass of individual trees increased linearly during the study period. The mortality rate was assumed to be 1.4% based on tree census data from 2003 (Jomura et al., 2007). *P. densiflora* was assumed to have become established in 1900, versus 1960 for broadleaved trees, based on tree-ring analysis (data not shown). Total aboveground biomass in 1999 was assumed to be 51.01 MgC ha^{-1} (Goto et al., 2003). Unfortunately, the aboveground biomass of *P. densiflora* at the beginning of the occurrence of pine wilt disease could not be directly quantified from our data. Soil core sampling was conducted at 18 points at the study site, and soil carbon storage was estimated to be 30.0 MgC ha^{-1}. Based on these biomass values and the proportion of *P. densiflora* trees in the current forest, we estimated the current aboveground and belowground biomass of *P. densiflora*, then calculated values at previous points in time on the assumption that peak mortality caused by the pine wilt disease occurred between 1975 and 1984, and that mortality rates during this period were 20 times the current mortality rate (in the absence of the disease). We calculated the carbon balance of litter from 1900 to 2004 using the RothC model based on the litter input estimated as described above and on soil data (the clay content of the soil and soil depth) and on environmental data for this period obtained from the Japan Meteorological Service (monthly mean air temperature, monthly total precipitation).

Then, we assumed that no soil carbon had accumulated in 1900. We used the default DPM/RPM ratio of 0.25 that is used in the RothC model for woodland.

3.2.6. Estimation of the CWD carbon budget and CWD respiration

The amount of carbon stored as CWD in 2003 was derived using three plots with different sizes for three diameter (D_{CWD}) classes: $7 > D_{CWD} \geq 3$ cm, 0.045 ha; $10 > D_{CWD} \geq 7$ cm, 0.188 ha; and $D_{CWD} \geq 10$ cm, 1.7 ha). In addition, we recorded the characteristics of the CWD (log, standing dead tree or snag, or fallen dead tree; species; decay class). We also inventoried the dead trees and classified the dead wood as either snags or logs in 2000, 2001, 2003, and 2004. Annual respiration of CWD (R_{CWD}) for the forest was estimated by summing all values of R_{CWD} calculated using the CWD accumulation data and the estimation function for R_{CWD} based on flux measurements for the CWD.

The relationship between respiration of R_{CWD} (mgCO$_2$ m^{-2} s^{-1}) and changes in CWD temperature (T_c(°C)),

CWD water content (θ_{CWD} (%)), the diameter of the CWD (D_{CWD} (cm)), and the density of the CWD (ρ_{CWD}(g cm^{-3})) was described using the following function (Jomura et al., 2007):

$$
\begin{aligned}
R_{CWD} = {}& 0.468 \exp(0.045T_c)(\theta_{CWD} \\
& + 0.073)(0.867 - \theta_{CWD})^{0.551}(-7.131 \log D_{CWD} \\
& + 28.096)(-20.177\,\rho_{CWD} + 15.670), \\
& r^2 = 0.54
\end{aligned}
\tag{10}
$$

Using the estimated input of CWD and the estimated CWD respiration rate, we calculated the annual contributions of R_{CWD} to the forest's annual R_h and of the CWD carbon budget to the forest carbon budget and forest NEP.

3.3. Soil respiration

Soil respiration measurements were conducted periodically (from one to four times per month, for a total of 74 times) at five locations (96 soil collars) from July 2002 to May 2003 using a static-chamber IRGA system (GMT-222, Vaisala Inc., Helsinki, Finland). Estimation functions were derived from the relationship between soil respiration (R_{soil} (mgCO$_2$ m^{-2} s^{-1})), soil temperature (T_{soi} (°C)), and soil water content (θ_{soil} (%)) following the modeling approach of Subke and Schlesinger (2003):

$$
R_{soil} = 0.566 \exp(0.0717T_{soil})\left(\frac{\theta_{soil}}{0.1089 + \theta_{soil}}\right)
\tag{11}
$$

To verify this function, we measured the soil respiration rate at another 264 soil collars from 26 to 27 June 2002, 25 to 27 July 2002, 7 to 8 August 2002, and 25 to 26 September 2002 (Tamai et al., 2005).

3.4. Root respiration and root production

Dannoura et al. (2006) conducted continuous measurements of fine-root respiration from April 2004 to September 2005 using an automated chamber system.
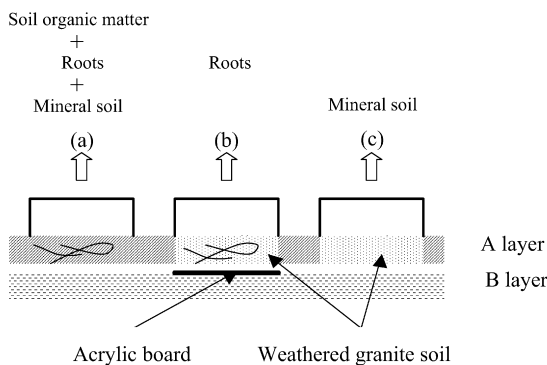
To separate root respiration (R_{root}) from soil respiration (R_{soil}), we carefully removed all soil in the A horizon (Fig. 2a) using a portable electric vacuum cleaner, leaving only the living roots (Fig. 2b). An acrylic board was then inserted between the A and B horizons to exclude CO$_2$ efflux from the B horizon (Fig. 2b). To protect the roots during subsequent measurements, we carefully replaced the removed soil with an equal depth of weathered granitic soil (obtained from a gardening supply store) that was similar in texture and other characteristics to the original A horizon at the study site. By comparing root respiration with soil respiration, we were able to estimate the ratio of R_{root} and R_{soil}. This ratio (R_{root}/R_{soil}) includes heterotrophic respiration resulting from turnover of fine roots. Moreover, respiration by both fine and large roots was measured using the sampling method of Dannoura et al. (2005b) and the relationship between R_{root} and root diameter was estimated. Combining these results allowed us to estimate root respiration with and without heterotrophic respiration.
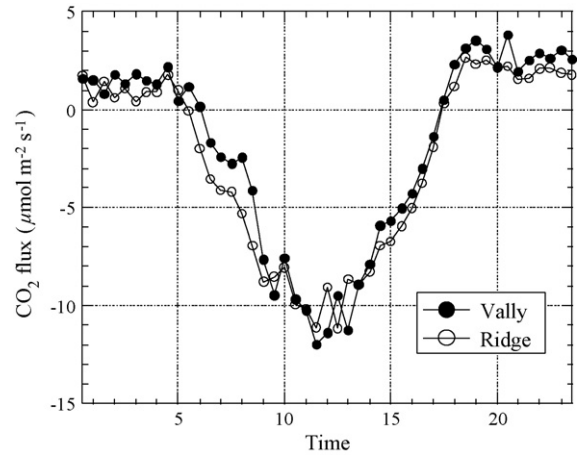
4. Results and discussion

4.1. Comparison of CO_2 flux between the two towers

Mean daytime CO_2 flux at the ridge tower was $-4.07\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$, versus $-4.14\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ for the valley tower, from 4 April 2001 to 31 December 2001. These values agreed well. The mean daily changes in the fluxes measured at the two towers were also closely related (Fig. 3). On the other hand, the relationship between the CO_2 flux at the two towers measured by means of the eddy-covariance method (Fig. 4) during the day shows relatively high dispersion. The root mean square error between the two towers in total CO_2 flux was 46%, and even compared with the daily mean flux, RMSE was still 25%. Deciduous species such as *Q. serrata* were mainly found in sunny positions along the ridge, whereas evergreen species were uniformly distributed across all topographic positions. Because the deciduous species occupied a relatively small proportion of the site (i.e., a small footprint), primarily near the ridge tower, this heterogeneity in the vegetation structure may be partially responsible for the differences in the CO_2 flux, particularly during the day. Detailed footprint analysis and estimation of the spatial variation in tree photosynthesis will be needed to confirm this hypothesis. Random errors in the eddy-covariance CO_2 flux (Richardson et al., 2006) may also be partially responsible for this variation. Separation of systematic errors and random errors in the flux data from the two towers will be required in future studies.

In the mean daily course of CO_2 storage at the two towers (Fig. 5), the two fluxes showed similar trends: both fluxes increase in the afternoon and decreased in the morning, but the change occurred about 1 h earlier at the valley tower than
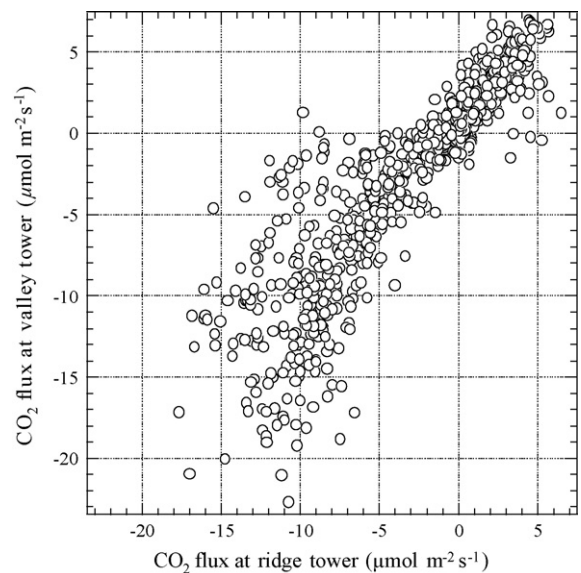

Fig. 3 – Mean daily changes in CO_2 flux measured by means of the eddy-covariance method at the ridge and valley towers. Mean daytime CO_2 flux at the ridge tower was $-4.07\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$, vs. $-4.14\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ for the valley tower, from 4 April 2001 to 31 December 2001.

at the ridge tower. The mean nocturnal CO_2 flux resulting from CO_2 storage equaled $0.123\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ at the ridge tower and $0.136\,\mu\text{mol m}^{-2}\,\text{s}^{-1}$ at the valley tower from 12 January 2002 to 2 December 2002, and the ratio of RMSE to mean storage change was 51.2%. The change in CO_2 concentration near the soil surface at the valley site was closely related to that at the ridge tower. Daily changes in CO_2 concentration at the two towers were small (usually <30 ppm), and these small changes resulted in a correspondingly small contribution of CO_2 storage change to the nocturnal flux. Mean nocturnal CO_2 flux at the ridge tower during the same period was

Fig. 2 – Illustration of the devices and system used in the root respiration (R_{root}) measurements. A chamber with automatic opening and closing was installed above the root system. Three plots were established to measure (b) R_{root}, and one plot each was established to measure (a) R_{soil} (total soil respiration) and (c) R_m (CO_2 efflux from mineral soil with no roots) near the R_{root} plots. In measuring R_{root}, (1) soil was removed from the A horizon using a portable vacuum cleaner that produced minimal disturbance of the remaining roots. (2) An acrylic board was inserted between the A and B horizons to exclude CO_2 efflux from the B horizon in chamber R_{root}. (3) Weathered soil (obtained from a gardening supply store) that produced a near-zero CO_2 efflux replaced the removed forest soil.

Fig. 4 – Relationship between CO_2 flux measured by means of the eddy-covariance method at the ridge and valley towers obtained from 4 April 2001 to 31 December 2001. Measurement heights were 34 m at valley tower and 26 m at ridge tower.
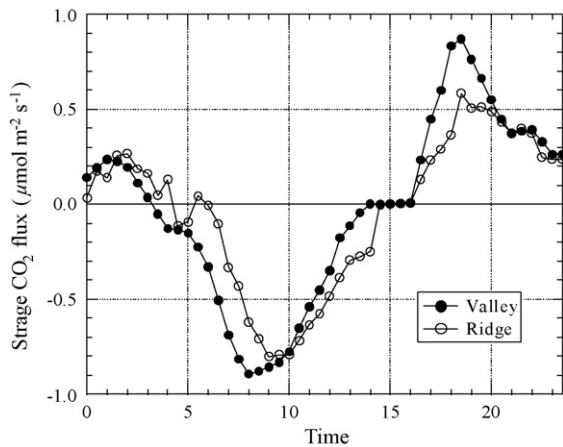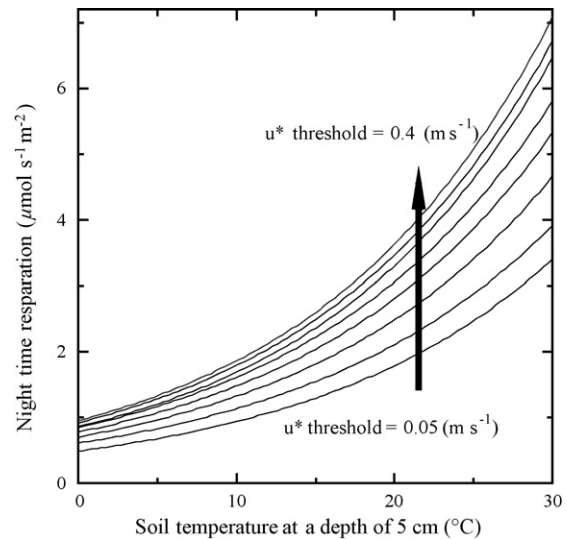
Fig. 5 – Mean daily changes in CO_2 storage flux at the ridge and valley towers from 12 January 2002 to 2 December 2002. The mean nocturnal CO_2 flux resulting from CO_2 storage equaled 0.123 μmol m^{-2} s^{-1} at the ridge tower and 0.136 μmol m^{-2} s^{-1} at the valley tower.


Fig. 6 – Changes in the relationship between nocturnal respiration (F_{night}) and soil temperature at a depth of 5 cm (T_{soil}) using u^* threshold values ranging from 0.05 to 0.4 m s^{-1} (at intervals of 0.05 m s^{-1}). A realistic u^* threshold for the study site would be 0.4 m s^{-1}. And function between Nocturnal respiration (μmol m^{-2} s^{-1}) and soil temperature at a depth of 5 cm ($^\circ$C) was $F_{night} = 9.543 \exp(0.0670 T_{soil})$.

0.523 μmol m^{-2} s^{-1}, and the contributions of CO_2 storage change to the mean nocturnal NEE were 18.9 and 20.1% at the ridge and valley towers, respectively. We estimated nocturnal CO_2 flux using chamber-based measurements of soil respiration and foliar respiration following the method of Kominami et al. (2003). The estimated mean nocturnal respiration was 1.204 μmol m^{-2} s^{-1}. This result suggests that 45% of the nocturnal CO_2 flux was lost by advection at both the ridge and the valley towers. We suspect that rapid drainage flow or horizontal advection over a larger distance than the distance between the ridge tower and the valley tower might be responsible for this loss of nocturnal flux.

4.2. Sensitivity of the NEE estimation to u^*

Fig. 6 shows the change in the function that relates nocturnal respiration and soil temperature at a depth of 5 cm as a function of changes in the u^* threshold at the ridge tower. Estimated respiration increases with increasing u^* threshold at all soil temperatures. However, the effects of choosing different u^* values can be seen by comparing the function for u^* values of 0.05 and 0.4 m s^{-1}: the estimated respiration at 25 $^\circ$C for $u^* = 0.4$ m s^{-1} was more than two times the value at $u^* = 0.05$ m s^{-1}. The relationship between changes in the 3-year-mean NEE and the u^* threshold (Fig. 7) shows that the mean net CO_2 flux for the study site is 3.12 MgC m^{-1} year^{-1} with no data being replaced (i.e., with a u^* threshold value of 0.0 m s^{-1}). With an increasing u^* threshold, the annual carbon uptake decreases rapidly, reaching 1.27 MgC ha^{-1} year^{-1} at a u^* threshold of 0.4 m s^{-1}. For thresholds above 0.4 m s^{-1}, total carbon uptake remains fairly constant. From this result, a realistic u^* threshold for the study site would be 0.4 m s^{-1}. And function between Nocturnal respiration (μmol m^{-2} s^{-1}) and soil temperature at the depth of 5 cm ($^\circ$C) was

$$F_{night} = 9.543 \exp(0.0670 T_{soil}) \qquad (12)$$

Similar analyses have been conducted in other studies of deciduous forests (e.g., Carrara et al., 2003; Knohl et al., 2003). Barford et al. (2001) made a similar comparison between the eddy-covariance method and biometric measurements in a 60- to 80-year-old oak forest and showed that the annual total NEE (with no gap filling) and NEP estimated using biometric measurements were −2.80 and 2.00 MgC ha^{-1} year^{-1}, respectively, and the u^* threshold was about 0.2 m s^{-1}. They concluded that annual NEE calculated using the eddy-covariance method was insensitive to u^* within the limits established for valid data. Knohl et al. (2003) also showed similar results in a u^* threshold, with NEE and NEP estimated using biometric measurements equal to −6.0 and 4.90 MgC ha^{-1} year^{-1}, respectively, and a u^* threshold ranging from 0.4 to 0.5 m s^{-1}. On the other hand, Miller et al. (2004) showed high sensitivity of NEP to the u^* threshold in a tropical forest. Estimated NEE changed from 4.0 to −1.0 MgC m^{-2} year^{-1} with a u^* threshold changing from 0.0 to 0.3 m s^{-1}. In their study, the annual total NEE calculated using the eddy-covariance method was highly sensitive to the u^* threshold, and they concluded that the annual nocturnal flux was large in the tropical forest, as high rates of respiration continued year-round.

The effect of the u^* filter was roughly proportional to the annual nocturnal flux in these studies, consequently the u^* filter caused a much greater change in the annual NEE at the tropical site than at the temperate sites. At our study site, this tendency also occurred during the summer. Fig. 8 shows monthly mean NEE with and without u^* screening using a u^* threshold of 0.4 m s^{-1}. In May and June, leafing of *Q. serrata* was complete and air and soil temperatures were relatively
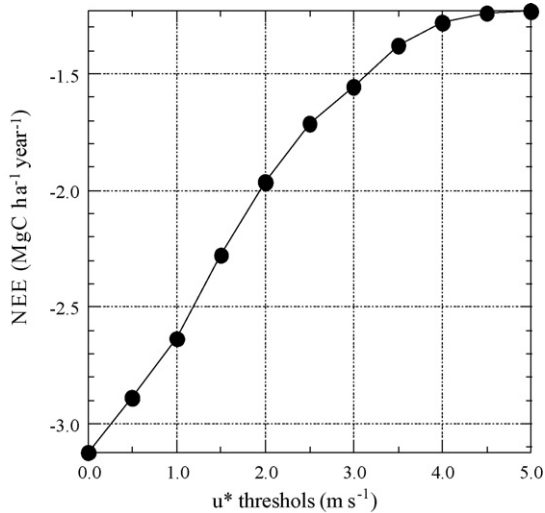
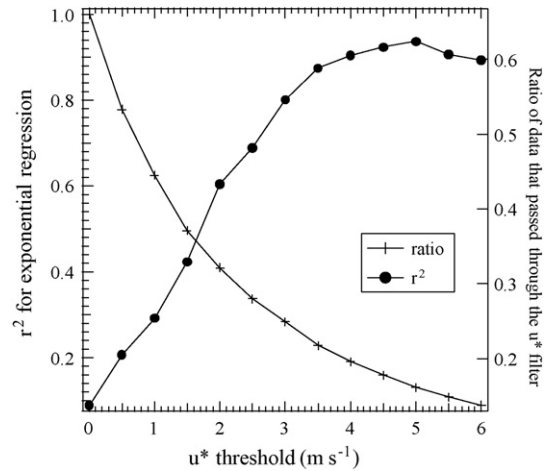Fig. 7 – Relationship between the 3-year-mean annual NEE estimated using the eddy-covariance data and u^* for the minimum friction velocity (u^*) threshold (with erroneous data removed, as described in the text). Flux values for periods with $u^* < u^*$ threshold were filled in by means of interpolation.


Fig. 9 – Variation in the correlation coefficient (r^2) of the exponential regression and in the proportion of the data that passed through the u^* filter according to the selection criterion (i.e., the value of the friction velocity below which the data are rejected, which is the u^* threshold).

low. Therefore, the monthly mean NEE was insensitive to u^*. On the other hand, during the summer (from July to October), air and soil temperatures were high (daily mean soil temperature exceeded 25 °C), and eddy-covariance values of NEE were highly sensitive to the u^* threshold, as was the case in tropical forest. Furthermore, most CO_2 efflux on calm nights was likely to be lost by horizontal advection and drainage flow through the valley because the study site was situated on steep slopes and in complex terrain. In addition, the contribution of the change in CO_2 storage to nocturnal NEE was only 28% on calm nights ($u^* \leq 0.4$ m s^{-1}). This may also increase sensitivity to the u^* threshold.

Fig. 8 – Monthly variation in NEE (3-year means from 2000 to 2002) with no data selected (no gap-filling) and with an exponential equation used for filling gaps in the data ($u^* < 0.4$ m s^{-1}).

As shown in Fig. 9, changes in the correlation coefficient for fitting of the exponential function as a function of changes in the u^* threshold showed a similar tendency to the changes in NEE in Fig. 7. The correlation was quite small ($r^2 = 0.15$) with no data being replaced. As the u^* threshold increased, the r^2 value increased rapidly, and above 0.4 m s^{-1}, r^2 remained fairly constant (at around 0.60), or decreased slightly at a u^* threshold higher than 0.5 m s^{-1}. This result seems to support our choice of a u^* threshold of 0.4 m s^{-1}. These results are similar to those of Aubinet et al. (2001) and Carrara et al. (2003). However, at a realistic u^* threshold, about 80% of the respiration data were eliminated and the value of nocturnal respiration could be predicted almost entirely by the estimation equation because most respiration values were estimated only as a function of soil temperature.

Miyama et al. (2006) estimated annual nocturnal respiration using chamber methods in the Yamashiro Experimental Forest and found that annual nocturnal respiration using chamber methods agreed with tower-based nocturnal respiration using a u^* threshold of 0.35 m s^{-1}. This u^* threshold approximately agrees with that estimated in the present study.

4.3. Seasonal variation in NEE of CO_2

Fig. 10a shows the course of daily mean NEE over a 3-year period. In this graph, net CO_2 uptake began from the last half of April to the first half of May and reached its peak in the last half of June, in parallel with the quick increase in leaf area index that occurs during this period. In every year, the minimum daily mean NEE reached nearly −90 mmol m^{-2} d^{-1}. This magnitude of the net CO_2 uptake is slightly less negative than that reported for other temperate mixed forests with deciduous and evergreen trees (e.g., McMillen, 1988; Knohl et al., 2003) and coniferous forest situated in same mountain area (about 24 km north east) with our study site (Ohkubo
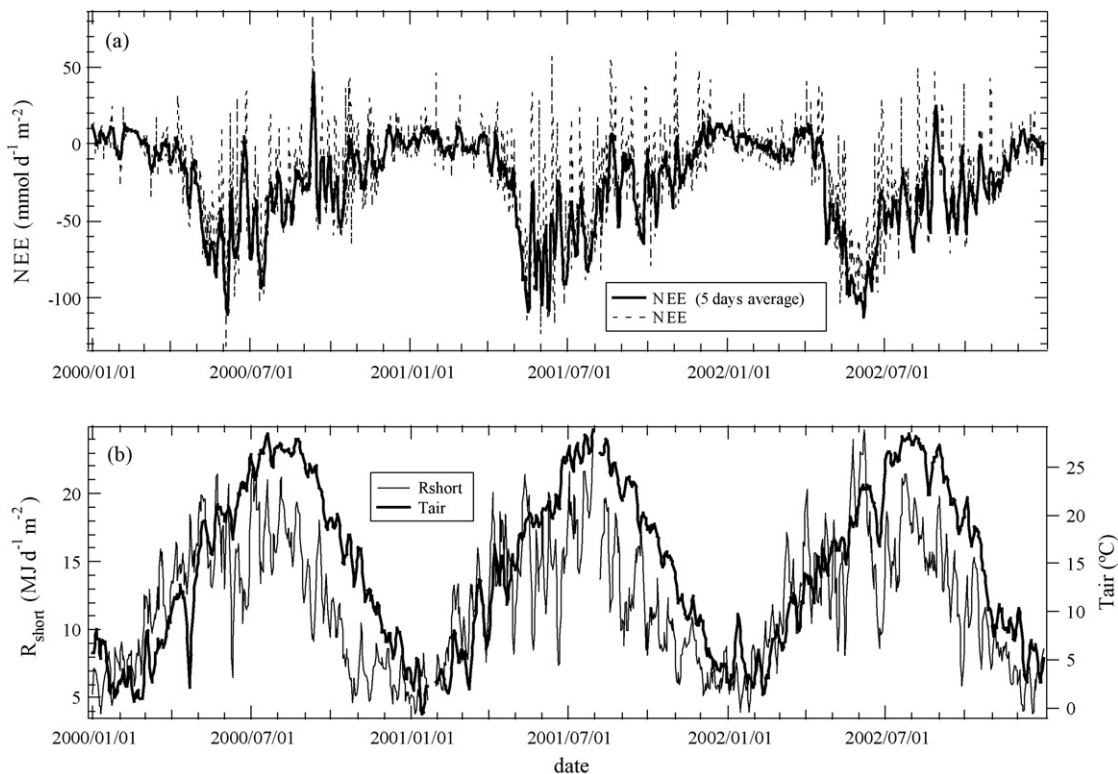
Fig. 10 – Evolution from 1 January 2000 to 31 December 2002 of (a) CO$_2$ exchange (NEE = eddy-covariance + storage term) and (b) daily mean air temperature (T_{air}) and daily mean incoming short-wave radiation (R_{short}). A solid line in (a) is daily mean NEE and a dash line is 5 days averaged NEE. NEE was calculated using data of ridge tower.

et al., 2007). Fig. 10b shows that NEE followed roughly the opposite of the pattern followed by air temperature. The pattern was less clear for short-wave radiation, which generally followed the trend for air temperature, but with considerably higher variation among days. The relatively small levels of biomass (about 50 MgC ha^{-1} for aboveground biomass) may be one cause of the small peak values of CO$_2$ uptake. Fig. 8 shows that even before the u^* correction, CO$_2$ uptake gradually decreases in midsummer (from the last half of July through August). On the other hand, air temperature and short-wave radiation reached their peak values in the same period (Fig. 10b). This change mainly results from the rapid increase in nocturnal respiration as air temperature increases. By interpolating nocturnal respiration using the previously described u^* threshold for each regression, the influence of interpolation on estimated NEE can be seen to be remarkable from late summer to early autumn (August, September, and October). In spring (May and June), just after leafing of the trees was complete, photosynthetic activity of deciduous trees increased rapidly. On the other hand, soil temperature and respiration had not yet reached their annual peak. Therefore, the difference between photosynthesis and respiration (NEE) is high even after interpolation of nocturnal respiration. However, summer values of interpolated respiration were high as a result of high soil temperature, therefore the interpolation of nocturnal respiration strongly affected estimated NEE during these periods. Consequently, photosynthesis and respiration were almost in counterpoise during the warmest months. Estimated

values of annual NEE in 2000, 2001, and 2002 were −1.16, −1.40, and −1.13 MgC m^{-2} year^{-1}. At this site, Calculation of NEE highly depends on estimation of nocturnal respiration, because most of the respiration value (about 80%) could be calculated using the estimation equation. Therefore, to evaluate inter-annual changes in NEE and changes in NEE in response to changes in environmental factors, more accurate estimates of nocturnal respiration are required.

4.4. Estimation of NEP from biometric data

4.4.1. Above- and belowground NPP
The carbon pool in aboveground living biomass was 52.18 ± 1.04 MgC ha^{-1} in 1999 and increased annually by 1.08 ± 0.02 MgC ha^{-1} year^{-1}. Errors of living biomass and annual increment of living biomass were calculated by RMSE of allometric estimation. Inaccuracies in the allometric equations are a potential source of error in our estimates, because the equations are highly nonlinear and small errors in the measurements of large trees could have a large impact on our estimates of annual growth. To minimize the impacts of such errors, we used species-specific allometric equations with a strong goodness of fit (mean $r^2 = 0.98$).

Estimated woody root and fine-root biomass values were 9.86 ± 0.79 and 1.84 ± 0.15 MgC ha^{-1}, respectively. In estimating woody root biomass, we used a simple general allometric equation for the relationship between DBH and woody root biomass. Despite the inevitable imprecision in such general-

ized equations, the goodness of fit of this equation was strong ($r^2 = 0.98$). The estimated ratio of aboveground to belowground biomass (the TR-ratio) was 4.36 (i.e., the belowground biomass amounted to 22.9% of the aboveground biomass). Jackson et al. (1996) reported that the midrange root biomass of temperate forests was 42 MgC ha^{-1}, which is much higher than the value in our study, and that the TR-ratio was 4.35, which is close to our value. Because we measured the aboveground biomass in a relatively young forest, whereas the values reported by Jackson et al. (1996) were for mature forests, it is reasonable to expect root biomass to be smaller in our study. The similar TR-ratios probably result from the fact that roots and aboveground biomass must achieve similar balances under similar environmental conditions to ensure that the aboveground biomass can obtain sufficient water and nutrients.

4.4.2. Soil respiration

Estimated annual soil respiration was 5.81 MgC ha^{-1} year^{-1} and ranged from 4.25 to 7.09 MgC ha^{-1} year^{-1}. The RMSE between the calculated and measured soil respiration based on data from 264 soil collar measurements was 1.45 MgC ha^{-1} year^{-1}. Raich and Schlesinger (1992) reviewed soil respiration in temperate broadleaved forests and reported a mean value of 6.46 ± 0.51 MgC ha^{-1} year^{-1}. Thus, mean total soil respiration in our study was slightly smaller than the mean reported by Raich and Schlesinger, possibly because our forest was younger than in their study.

4.4.3. Root respiration and fine-root production

Dannoura et al. (2005b) concluded that annual root respiration estimated using our sampling method amounted to 37% of total soil respiration. This value does not include fine-root turnover. Using an automated chamber method, Dannoura et al. (2006) found that annual root respiration, including fine-root turnover, amounted to 47% of total soil respiration. The difference between these results suggests that fine-root production accounts for 10% of total soil respiration (0.58 MgC ha^{-1} year^{-1}) and heterotrophic respiration (excluding respiration of CWD) amounted to 63% of soil respiration (3.66 MgC ha^{-1} year^{-1}). Scarascia-Mugnozza et al. (2000) studied the tree biomass and growth of European beech (Fagus sylvatica L.) forests, and found that the biomass of coarse roots was 10 times that of fine roots, but that fine roots had growth rates two to five times those of coarse roots owing to their faster turnover. Our result was much smaller than the values reported for a deciduous forest (e.g., Curtis et al., 2002; 1.44–4.92 MgC ha^{-1} year^{-1}). To clarify the role of fine-root production at our study site, a biometric study using equipment such as minirhizotrons will be necessary (Burton et al., 2000).

4.4.4. CWD carbon budget

Mean annual CWD (stem and branch) input from 2000 to 2004 was 0.61 ± 0.22 MgC ha^{-1} year^{-1}. For that we had identified individual dead tree occurrence for CWD input, estimation error of CWD input was small. But variation of inter-annual CWD input was large and CWD input rate highly depends on measurement year. Therefore, we treated standard deviation of CWD input calculated by four times annual CWD input census held in 2000, 2001, 2003, and 2004 as RMSE of CWD input estimation. Snags comprised 89% of the total CWD input mass.

CWD input equals only 1.2% of the 1999 biomass, but the ratio of CWD input to the annual increment in aboveground biomass amounted to 56%. This difference arises from the fact that the carbon increment from each tree was small, but the carbon loss in a single large dead tree was high. There were many reasons for tree mortality (e.g., disease, windfall), and because of variation in these causes, the annual CWD input rate varied from 0.29 to 0.89 MgC ha^{-1} year^{-1}. Long-term measurement of CWD input rates and estimation of CWD carbon balances thus cannot be ignored when estimating forest NEP from biometric measurements.

The CWD pools in snags and logs equaled 3.69 and 5.61 MgC ha^{-1}, respectively. The total CWD pool was thus equivalent to 18% of the 1999 living wood biomass (Jomura et al., 2007). The annual R_{CWD} for the forest was estimated to be 0.50 ± 0.27 MgC ha^{-1} year^{-1}, with 34% of the total respiration being from snags and 66% from logs. RMSE was estimated from errors of estimated and observed CWD respiration using Eq. (10). Most of the difference between CWD inputs and outputs (through respiration), which equaled 0.11 ± 0.50 MgC ha^{-1} year^{-1}, was probably sequestered as CWD in the forest from 1999 to 2004. However, leaching may also account for some of the difference. Direct measurement of changes in CWD accumulation was difficult and was estimated by the difference between CWD inputs and outputs. Therefore, this value had large variation (error was 4.5 times larger than estimated value).

4.4.5. Litter carbon balance

Based on the historical estimation procedure described in Section 3.2.2, we estimated that the peak P. densiflora aboveground biomass required to provide the measured and calculated present soil carbon storage was about 80 MgC ha^{-1}. 1. The change in soil carbon storage depends on the history of a forest, and especially its succession history (Fig. 11), which in this case was caused by the pine wilt disease. Based on the assumptions described earlier in the text, the mean rate of change in soil organic carbon storage was 0.31 ± 0.11 MgC ha^{-1} year^{-1} from 1994 to 1999, which equals about 12% of the litter input during this period. Because this rate was determined so as to match the measured and calculated present soil carbon storage, it appears to adequately represent the changes in soil carbon storage. However, estimation error in current soil carbon accumulation directly affected with this value. The RMSE of change in soil organic carbon storage was estimated from the RMSE of estimated and observed soil carbon accumulation ($n = 18$).

4.4.6. Estimation of NEP and ΔC

Annual aboveground NPP (excluding root growth) at the study site was 4.27 ± 0.44 MgC ha^{-1} year^{-1} (Table 1). Kira (1977) reviewed previous studies and reported that the aboveground NPP values in cool-temperate deciduous forests and warm-temperate evergreen broadleaved forests in Japan were 8.74 ± 3.47 ($n = 55$) and 20.65 ± 7.21 MgC ha^{-1} year^{-1} ($n = 33$), respectively. The value for our study site was thus considerably lower than the values reported by Kira. The present forest stand might have a below-average NPP for temperate forests because of its status as a pioneer community that is undergoing secondary succession. Ohtsuka et al. (2005) reported
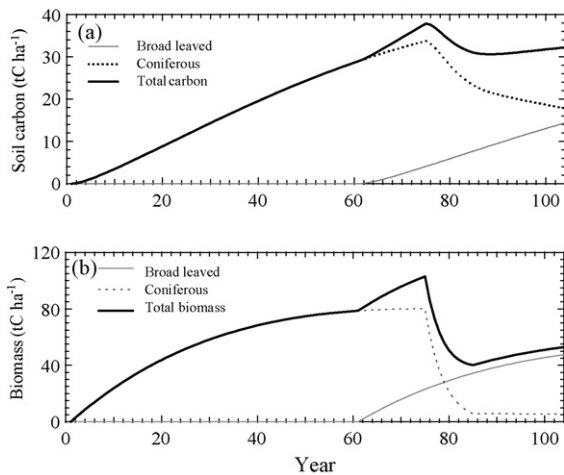
Fig. 11 – (a) Changes in soil carbon storage (bold line) and contribution of coniferous trees (dash line) and broad-leafed trees (thin line) from 1900 (year 0) to 2002 at the study site. Carbon storage was calculated using RothC model (ver. 26.3) and change of above ground biomass (b). (b) Change in total aboveground biomass (bold line), aboveground biomass of coniferous trees (dash line) and broad-leafed trees (thin line) from 1900 (year 0) to 2002 at the study site.

results similar to ours (4.68–5.34 MgC ha^{-1} year^{-1}) in cool-temperate deciduous forests in Japan.

NEP and ΔC estimated using biometric measurements were 0.91 ± 2.13 and 1.72 ± 0.64 MgC ha^{-1} year^{-1}, respectively:

$$NEP = NPP - R_h = NPP - R_h(litter) - R_h(CWD)$$
$$= 5.07 - 3.66 - 0.50 = 0.91 \quad (13)$$

In this calculation, we assumed that the increment lost to herbivory was negligible

$$\Delta C = \Delta W + \Delta S$$
$$= \Delta W_{aboveground} + \Delta W_{woodyroots} + \Delta S_{litter} + \Delta S_{CWD}$$
$$= 1.08 + 0.22 + 0.31 + 0.11 = 1.72 \quad (14)$$

Estimated NEP had large variation (RMSE = 2.13 MgC ha^{-1} year^{-1}) and that was mainly due to RMSE of soil respiration (1.45 MgC ha^{-1} year^{-1}) and estimation error of ΔC was mainly due to RMSE of increment of CWD (ΔS_{CWD}) and was 0.50 MgC ha^{-1} year^{-1}.

This result shows that the increment of live biomass contributed 76% of the total ΔC and that the contribution of ΔS_{litter} was small (18%). Miller et al. (2004) assumed that the capacity of an undisturbed tropical forest soil to store carbon is 0 ± 0.5 MgC ha^{-1} year^{-1}. On the other hand, Ohtsuka et al. (2007) reported large ΔS_{litter} in a cool-temperate deciduous forest (0.8 MgC ha^{-1} year^{-1}; 38% of NEP). Our result was similar to Miller's assumption and might occur as a result of high air temperatures and a humid environment during the summer.

In the Yamashiro Experimental Forest, mean NEP was markedly smaller than ΔC. This tendency was also noted by Curtis et al. (2002), who reported that NEP was smaller than ΔC at four of five sites. Because our study site is located in complex terrain with steep slopes, soil respiration exhibited large spatial variation. Based on the minimum soil respiration, estimated NEP was larger than ΔC (1.89 MgC ha^{-1} year^{-1} vs. 1.72 MgC ha^{-1} year^{-1}, respectively). Dannoura et al. (2006) reported that the ratio of fine-root respiration to total soil respiration ranged from 25 to 60% over the course of the year. We hypothesize that the temporal variation in this ratio might be caused by changes in the biomass available to support heterotrophic respiration. In first half of the year, enough leaf litter to support heterotrophic respiration exists on the forest floor, but this substrate gradually decreases in midsummer and fall, therefore the ratio of fine-root respiration to soil respiration was higher in the fall than in the spring. Temporal variations also affect the role of soil respiration in evaluations of NEP. The role of fine-root production is more controversial. Our estimates included many uncertainties, thus more accurate measurement of fine-root turnover is required. We also found a high efflux of volatile organic compounds from Q. serrata (mainly isoprene; Okumura et al., 2006). In estimating NEP, future models should estimate this component as well and evaluate the corresponding uncertainties (e.g., spatial and temporal variation). Because ΔC involves fewer measurements (thus, fewer uncertainties) than NEP, greater confidence might be expected in measurements of annual carbon storage based on ΔC (Curtis et al., 2002). However, in estimating ΔC, the estimation of changes in soil carbon is also controversial. Malhi et al. (1999) reported large increments of soil carbon in tropical and temperate forests (3.60 and 3.96 MgC ha^{-1} year^{-1}, respectively). On the other hand, Curtis et al. (2002) reported little or no change (with no change at three of five sites) in soil carbon over a 1-year period. We estimated ΔS using the RothC model and site-specific boundary conditions for the initial soil carbon pool and historical changes in forest biomass, but this method might not be feasible in every forest. Thus, improvements in the general estimation method for soil carbon accumulation processes in forests are required.

In the present study, very simple estimates of ΔW and ΔS that allocated W and S linearly as a function of stand age ($\Delta W'$, about 50 year) and similar estimates of soil carbon accumulation (ΔS, about 100 year) agreed well with estimated ΔW and ΔS:

$$\Delta W' = \frac{W}{50} = \frac{72.01}{50} = 1.44 \quad (15)$$

$$\Delta S' = \frac{30.0}{100} = 0.30 \quad (16)$$

These very basic estimates may still provide useful information about forest site characteristics.

4.5. Comparison of the biometric and eddy-covariance methods

Estimated ΔC and mean NEP were 1.72 and 0.91 MgC ha^{-1} year^{-1}, respectively. Estimated mean NEE was

Table 1 – Pools (MgC ha^{-1}), fluxes (MgC ha^{-1} year^{-1}) and variation (RMSE) of the major components of NPP and of net ecosystem carbon storage for the study site

	Pool		Flux	
	(MgC ha^{-1})	RMSE	(MgC ha^{-1} year^{-1})	RMSE
Aboveground				
(a) Wood	48.40	1.04	1.08	0.02
(b) Leaves	3.78	0.21	2.58	0.20
(c) CWD	9.30	0.23	0.61	0.22
Belowground				
(d) Woody roots	9.86	0.79	0.22	0.01
(e) Fine roots	1.84	0.15	0.58	0.15
(f) NPP (a + b + c + d + e)			5.07	0.60
(g) Total soil respiration (mean)			5.81	1.45
(h) (max.)			7.09	1.78
(i) (min.)			4.25	1.50
(j) Heterotrophic respiration in soil respiration (mean)			3.66	0.92
(k) (max.)			4.47	1.12
(l) (min.)			2.68	0.67
Respiration from CWD (m + n)	9.30	0.23	0.50	0.27
(m) Logs	5.61	0.14	0.17	0.09
(n) Snags	3.69	0.09	0.33	0.18
Soil carbon				
(o) litter	31.00	11.16	0.31	0.11
(p) CWD	9.30	0.23	0.11	0.50
NEP (mean) (f-j-m-n)			0.91	2.13
(max.) (f-l-m-n)			1.89	2.43
(min.) (f-k-m-n)			0.10	2.33
ΔC (a + d + o + p)			1.72	0.64
NEE			−1.23	

Annual net carbon storage was calculated both as NEP and as the change in carbon pool size (ΔC). Net ecosystem exchange (NEE) was derived from the eddy-covariance data using a u^* threshold of 0.4 m s^{-1}. A negative flux indicates carbon gain in NEE and a positive flux indicates carbon gain in ΔC and NEP.

−1.23 MgC ha^{-1} year^{-1} using a u^* threshold of 0.4 m s^{-1}. Estimated NEE was 35% larger than mean NEP. However, soil respiration varied greatly, and estimates of heterotrophic respiration, soil respiration, and root production had many uncertainties. Our previous research has found that cutting of roots near the soil surface leads to underestimation of soil respiration in the Yamashiro Experimental Forest (data not shown). Therefore, underestimation of soil respiration and fine-root production might have caused the underestimation of NEP. On the other hand, estimated ΔC was 39% larger than NEE even though the difference between these rates was less than 1.0 MgC ha^{-1} year^{-1}. This high ratio and small difference were also found in the NEE estimation. NEE estimated using a u^* threshold of 0.2 m s^{-1} was −1.93 MgC ha^{-1} year^{-1}; at 0.4 m s^{-1}, it was −1.23 MgC ha^{-1} year^{-1}. The ratio of NEE ($u^* \geq 0.4$) to NEE ($u^* \geq 0.2$) was 64%, thus NEE was relatively sensitive to changes in u^* even though the difference between the two NEE values was only 0.7 MgC ha^{-1} year^{-1}.

5. Conclusion

The eddy-covariance method has commonly been used to study NEE of CO_2 in forest ecosystems (Baldocchi et al., 2001). However, uncertainties in the long-term carbon uptake arise from systematic underestimation of nocturnal flux measurements (Goulden et al., 1996). Horizontal advection and drainage flow when mixing of air is poor are also assumed to occur and may be significant in sloping terrain unless barriers to both processes exist. The resulting errors are significant, especially in forests situated in complex terrain. Moreover, a high rate of respiration occurred at high temperatures, causing a large nocturnal efflux. In turn, this increases the effect of the u^* filter on the calculation of annual net flux, which decreases confidence in the tower-based estimates of NEP (Miller et al., 2004). Therefore, the choice of a u^* filter and the u^* threshold have many uncertainties at warm temperatures and in complex terrain. Unfortunately, forests that meet this description are common in Japan, suggesting a need for more research to resolve these uncertainties.

In the present study, we evaluated ΔC and NEP from biometric measurements and NEE using the eddy-covariance method in a warm-temperate deciduous forest in Japan. Estimated NEE using a u^* threshold of 0.4 m s^{-1} showed a good relationship with NEP. However, estimated ΔC was 86% larger than NEP. In addition, estimated ΔC showed a high dependency of total ΔC on the change in live biomass caused by a high decomposition rate. The present study thus provides important insights into the relationship between the two estimation methods and identifies priorities for future

research, because there have been few (e.g. Miller et al., 2004; Curtis et al., 2002) studies that compared NEE calculated based on the eddy-covariance method with NEP calculated based on the biometric method. More such comparisons are required to provide a better understanding of carbon budgets and permit comparisons between studies that used different methods.

Acknowledgements

REFERENCES

Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., Laitat, E., 2001. Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. Agric. Forest Meteorol. 108, 293–315.

Baldocchi, D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biol. 9 (4), 479–492.

Baldocchi, D., Vogel, A., Hall, B., 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. Forest Meteorol. 83, 147–170.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, Ch., Davis, K., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Mahli, Y., Meyers, T., Munger, W., Oechel, W., Paw, U.K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82, 2415–2434.

Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutyra, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294, 1688–1691.

Black, T.A., Denhartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., Staebler, R., Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. Global Change Biol. 2, 219–229.

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.

Carrara, A., Kowalski, A.S., Neirynck, J., Janssens, I.A., Curiel Yuste, J., Ceulemans, R., 2003. Net ecosystem CO_2 exchange of mixed forest in Belgium over 5 years. Agric. Forest Meteorol. 119, 209–227.

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. Agric. Forest Meteorol. 113, 3–19.

Dannoura, M., Kominami, Y., Goto, Y., Kanazawa, Y., 2005a. Estimation of root biomass and root surface area of a broad-leaved secondary forest in the southern part of Kyoto prefecture. J. Jpn. For. Sci. 88 (2), 120–125 (In Japanese with English summary).

Dannoura, M., Kominami, Y., Tamai, K., Goto, Y., Jomura, M., Kanazawa, Y., 2005b. Short-term evaluation of the contribution of root respiration to soil respiration in a broad-leaved secondary forest in the southern part of Kyoto Prefecture. J. Agric. Meteorol. 62 (1), 15–20 (in Japanese with English summary).

Dannoura, M., Kominami, Y., Tamai, K., Jomura, M., Miyama, T., Goto, Y., Kanazawa, Y., 2006. Development of an automatic chamber system for long-term measurements of CO_2 flux from roots. Tellus 58B, 502–512.

Foken, T., Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. Agric. Forest Meteorol. 78, 83–105.

Goto, Y., Kominami, Y., Miyama, T., Tamai, K., Kanazawa, Y., 2003. Aboveground biomass and net primary production of a broad-leaved secondary forest in the southern part of Kyoto prefecture, central Japan. Bull. For. For. Prod. Res. Inst. 387, 115–147 (in Japanese with English summary).

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C., Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271, 1576–1578.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distribution for terrestrial biomes. Oecologia 108, 389–411.

Jenkinson, D.S., Coleman, K., 1994. Calculating the annual input of organic matter to soil from measurements of total organic carbon and radiocarbon. Eur. J. Soil Sci. 45, 167–174.

Jenkinson, D.S., Hart, P.B.S., Rayner, J.H., Parry, L.C., 1987. Modelling the turnover of organic matter in long-term experiments at Rothamsted. Intecol. Bull. 15, 1–8.

Jomura, M., Kominami, Y., Kanazawa, Y., 2005. Long-term measurements of the CO_2 flux from coarse woody debris using an automated chamber system. J. Jpn. For. Soc. 87 (2), 138–144 (in Japanese with English summary).

Jomura, M., Kominami, Y., Tamai, K., Miyama, T., Goto, Y., Dannoura, M., Kanazawa, Y., 2007. The carbon budget of coarse woody debris in a temperate broad-leaved secondary forest in Japan. Tellus 59B (2), 211–222.

Kaimal, J.C., Wyngaard, J.C., Haugen, D.A., 1968. Deriving power spectra from a three-component sonic anemometer. J. Appl. Meteorol. 7, 827–837.

Kimoto, A., Mizuyama, T., Okano, K., 2002. Spatial and temporal changes of vegetation cover in granite mountains in central Japan: a GIS-based approach. Land Degrad. Dev. 13, 345–357.

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.

Knohl, A., Schulze, E.D., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agric. Forest Meteorol. 118, 151–167.

Kominami, Y., Miyama, T., Tamai, K., Nobuhiro, T., Goto, Y., 2003. Characteristics of CO_2 flux over a forest on complex topography. Tellus 55B, 313–321.

Kominami, Y., Miyama, T., Tamai, K., Jomura, M., Dannoura, M., Goto, Y., 2005. Evaluation of nighttime eddy CO_2 flux using automated chamber measurements. J. Agric. Meteorol. 60, 745–748.

Loescher, H.W., Law, B.E., Mahrt, L., Hollinger, D.Y., Campbell, J., Wofsy, S.C., 2006. Uncertainties in, and interpretation of,

carbon flux estimates using the eddy covariance technique. J. Geophys. Res. 111 D21S90.

Malhi, Y., Baldocchi, D.D., Jarvis, P.G., 1999. The carbon balance of tropical, temporal and boreal forests. Plant Cell Environ. 22, 715–740.

McMillen, R.T., 1988. An eddy correlation technique with extended applicability to non-simple terrain. Boundary-Layer Meteorol. 43, 231–245.

Miller, S., Goulden, M., Menton, M., Rocha, H., Freitas, H., Figueira, H., Sousa, C., 2004. Biometric and micrometeorological measurements of tropical forest carbon balance. Ecol. Appl. 14 (4), S114–S126.

Miyama, T., Kominami, Y., Tamai, K., Nobuhiro, T., Goto, Y., 2003. Automated foliage chamber method for long-term measurement of CO_2 flux in the uppermost canopy. Tellus 55B, 322–330.

Miyama, T., Kominami, Y., Tamai, K., Goto, Y., Kawahara, T., Jomura, M., Dannoura, M., 2006. Components and seasonal variation of night-time total ecosystem respiration in a Japanese broad-leaved. Tellus B 58, 550–559.

Nobuhiro, T., Tamai, K., Kominami, Y., Miyama, T., Goto, Y., Kanazawa, Y., 2003. Development of the IRGA enclosed-chamber system for soil CO_2 efflux measurement and its application to a spatial variation measurement. J. Jpn. For. Res. 8, 297–301.

Ohkubo, S., Kosugia, Y., Takanashia, S., Mitania, T., Tani, M., 2007. Comparison of the eddy covariance and automated closed chamber methods for evaluating nocturnal CO_2 exchange in a Japanese cypress forest. Agric. Forest Meteorol. 142 (1), 50–65.

Ohtsuka, T., Akiyama, T., Hashimoto, Y., Inatomi, M., Sakai, T., Jia, S., Mo, W., Tsuda, S., Koizumi, H., 2005. Biometric based estimates of net primary production (NPP) in a cool-temperate deciduous forest stand beneath a flux tower. Agric. Forest Meteorol. 134, 27–38.

Ohtsuka, T., Mo, W., Satomura, T., Inatomi, M., Koizumi, H., 2007. Biometric based carbon flux measurements and net ecosystem production (NEP) in a temperate deciduous broad-leaved forest beneath a flux tower. Ecosystems 10 (2), 324–334.

Okumura, M., Tani, A., Kominami, Y., Kosugi, Y., Takanashi, S., Tohno, S., 2006. Isoprene emission from *Quercus serrata* in the deciduous broad-leaved forest. In: International Workshop on Flux Estimation over Diverse Terrestrial Ecosystems in Asia—AsiaFlux Workshop. p. 50.

Perala, D.A., Alban, D.H., 1994. Allometric Biomass Estimators for Aspen-Dominated Ecosystems in the Upper Great Lakes. USDA Forest Service, St. Paul, MN, Research Paper NC-134, p. 38.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B (2), 81–99.

Richardson, A.D., Hollinger, D.Y., Burba, G.G., Davis, K.J., Flanagan, A.B., Katul, G.G., Munger, J.W., Ricciuto, D.M., Stoy, P.C., Suyker, A.E., Verma, S.B., Wofsy, S.C., 2006. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. Agric. Forest Meteorol. 136 (1/2), 1–18.

Ruimy, A., Jarvis, P.G., Baldocchi, D.D., Saugier, B., 1995. CO_2 fluxes over plant canopies and solar radiation. Rev. Adv. Ecol. Res. 26, 1–68.

Scarascia-Mugnozza, G., Bauer, G.A., Persson, H., Matteucci, G., Masc, 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.

Subke, J.W., Schlesinger, W.H., 2003. Explaining temporal variation in soil CO_2 efflux in a mature spruce forest in Southern Germany. Soil Biol. Biochem. 35, 1467–1483.

Tamai, K., Kominami, Y., Miyama, T., Goto, Y., 2005. The estimation of time series data for soil respiration based on soil temperature and soil moisture content ratio and its spatial variations in a small mountainous catchment: in the case of weathered granite region in southern Kyoto prefecture. J. Jpn. For. Sci. 87, 331–339 (in Japanese with English summary).

Vickers, D., Mahrt, L., 1996. Quality control and flux sampling problems for tower and aircraft data. J. Atmos. Oceanic Technol. 14, 512–526.

Waring, R.H., Schlesinger, W.H., 1985. Forest Ecosystems: Concepts and Management. Academic Press, New York.

Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapor transfer. Quart. J. R. Meteorol. Soc. 106, 85–100.

Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO_2 in a mid-latitude forest. Science 260, 1314–1317.

Yasuda, Y., Watanabe, T., Ohtani, Y., Nakayama, K., 1998. Seasonal variation of CO_2 flux over a broadleaf deciduous forest. J. Jpn. Soc. Hydrol. Water Resour. 11 (6), 575–585.