

# Change in CO<sub>2</sub> balance under a series of forestry activities in a cool-temperate mixed forest with dense undergrowth

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## Abstract

To evaluate the effects on CO<sub>2</sub> exchange of clearcutting a mixed forest and replacing it with a plantation, 4.5 years of continuous eddy covariance measurements of CO<sub>2</sub> fluxes and soil respiration measurements were conducted in a conifer-broadleaf mixed forest in Hokkaido, Japan. The mixed forest was a weak carbon sink (net ecosystem exchange,  $-44 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), and it became a large carbon source ( $569 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) after clearcutting. However, the large emission in the harvest year rapidly decreased in the following 2 years (495 and  $153 \text{ g C m}^{-2} \text{ yr}^{-1}$ , respectively) as the gross primary production (GPP) increased, while the total ecosystem respiration (RE) remained relatively stable. The rapid increase in GPP was attributed to an increase in biomass and photosynthetic activity of *Sasa* dwarf bamboo, an understory species. Soil respiration increased in the 3 years following clearcutting, in the first year mainly owing to the change in the gap ratio of the forest, and in the following years because of increased root respiration by the bamboo. The ratio of soil respiration to RE increased from 44% in the forest to nearly 100% after clearcutting, and aboveground parts of the vegetation contributed little to the RE although the respiration chamber measurements showed heterogeneous soil condition after clearcutting.

**Keywords:** clearcut harvesting, eddy covariance, gross primary production, hybrid larch, net ecosystem exchange, plant area index, plantation, soil respiration, succession, total ecosystem respiration

Received 9 April 2008; revised version received 7 September 2008 and accepted 26 July 2008

## Introduction

Stand-replacing disturbances such as harvesting, windthrows, and fire have a major impact on CO<sub>2</sub> exchange between forested ecosystems and the atmosphere (Magnani *et al.*, 2007). Comparisons of stand-level CO<sub>2</sub> fluxes measured in early successional forests with those measured at other developmental stages (Schulze *et al.*, 1999; Law *et al.*, 2001; Pypker & Fredeen, 2002; Kowalski *et al.*, 2003, 2004; Litvak *et al.*, 2003; Clark *et al.*, 2004; Kolari *et al.*, 2004; Humphreys *et al.*, 2005, 2006; Machi-

mura *et al.*, 2005; Amiro *et al.*, 2006) have suggested that the effects of a disturbance on CO<sub>2</sub> emission can last from a few years (Clark *et al.*, 2004) to decades (Humphreys *et al.*, 2006). The difference in net ecosystem production among different-aged stands is up to  $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ , which is an order of magnitude greater than measured differences among years within a stand (Humphreys *et al.*, 2006). Thus, age-related differences in the stand structure have important effects on carbon exchange processes. However, few studies of disturbed forests are available, and some were conducted only during the growing season of the year. Moreover, most studies compared different stands during the same study period. Thus, long-term research

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that follows an ecosystem over time is an essential complement to these chronosequence studies, and eddy flux tower data comparing pre- and postharvest conditions are critical (Howard *et al.*, 2004).

On Hokkaido Island in northern Japan, many larch and fir plantations were planted in the 1960s, replacing hardwood forests. As of 2006, the afforested lands accounted for 15 132 km<sup>2</sup>, or about 27% of all forest lands in Hokkaido, and larch forests accounted for 93 826 000 m<sup>3</sup> of wood, or 14% (second largest) of the total wood volume in Hokkaido (Hokkaido Government Department of Fisheries and Forestry, 2006). Because larch is also distributed widely across eastern Eurasia (Gower & Richards, 1990), it is urgent to clarify the carbon sequestration capacity of larch forests.

Previous studies suggested that understory species play an important role in ecosystem carbon sequestration in the first stage of forest development (Kowalski *et al.*, 2003; Machimura *et al.*, 2005). Dwarf woody bamboos are the dominant component of forests and grasslands in parts of Asia and South America (Numata, 1979) and the dwarf bamboo genus *Sasa* is widely distributed and forms dense undergrowth in many forests in Japan. In Hokkaido, *Sasa* covers 89% (50 000 km<sup>2</sup>) of forested areas; its biomass of about 75 Mt, dry weight, accounts for 28% of the wood biomass (Toyooka *et al.*, 1983). The abundant *Sasa* inhibits forest regeneration (Noguchi & Yoshida, 2004) and affects biogeochemical cycles (Fukuzawa *et al.*, 2006, 2007), and it is likely to play an important role in the carbon cycle.

To evaluate the effects of clearcut harvesting and replanting on the CO<sub>2</sub> exchange of a forest, 13.7 ha of trees were clearcut, larch saplings were planted, and the CO<sub>2</sub> exchange between the ecosystem and atmosphere was monitored throughout this process. We compared the CO<sub>2</sub> budget before and after the clearcutting and discuss the contributions of the understory dwarf bamboo and soil respiration on the ecosystem CO<sub>2</sub> budget during the first stage of forest development.

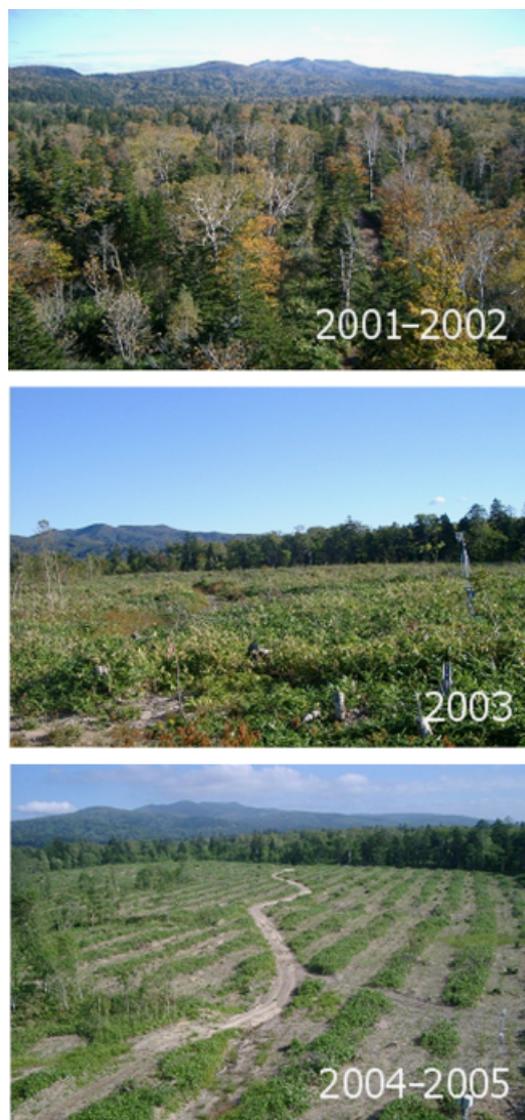
## Materials and methods

### Site description and management

The study site is located on a flat terrace in the Teshio Experimental Forest, Hokkaido University (45°03'N, 142°06'E, 66 m a.s.l.). The soil is a Gleyic Cambisol, and its surface organic horizon is about 10 cm thick. Before clearcutting, the dominant tree species were *Quercus crispula*, *Betula ermanii*, *Abies sachalinensis*, *Betula platyphylla* var. *japonica*, and *Picea jezoensis*. Maximum and mean heights of the tree canopy were about 24 and 20 m, respectively. The basal area of canopy trees was

22 m<sup>2</sup> ha<sup>-1</sup>. Evergreen dwarf bamboos (*Sasa senanensis* and *Sasa kurilensis*) formed dense undergrowth. The seasonal maximum biomass of *Sasa* leaf, culm, and rhizome-root was 1.1 ± 0.04 (SD), 4.8 ± 0.04, and 6.0 ± 1.5 tC ha<sup>-1</sup>, respectively, in the understory and 2.0 ± 0.41, 10.2 ± 1.75, and 13.5 ± 4.69 tC ha<sup>-1</sup> in gaps of the forest.

From January to March 2003 (during the snow-covered period), 13.7 ha of trees were clearcut (Fig. 1). The total biomass volume of trees in this area was 2193 m<sup>3</sup> (Koike *et al.*, 2001), and the logging removed 1203 m<sup>3</sup> (ca. 19 tC ha<sup>-1</sup>) from this ecosystem. *Sasa* bamboos were left intact under the snowpack during the clearcutting; however, bamboos were strip-cut into 4 m wide rows



**Fig. 1** (Upper) Mixed conifer-broadleaved forest, (middle) *Sasa* dwarf bamboo after clearcutting, (lower) site after strip-cutting of *Sasa* bamboo and larch planting.

(half the clearcut area) 7 months after the clearcutting and just before the larch saplings were planted (late October 2003). About 30 000 (2500 ha<sup>-1</sup> or 0.04 t C ha<sup>-1</sup>) 2-year-old hybrid larch (*Larix gmelinii* × *L. kaempferi*) saplings were planted.

#### *Eddy covariance measurements*

Beginning in August 2001, CO<sub>2</sub> fluxes over the mixed forest were evaluated by the closed-path eddy covariance method at 32 m height. A sonic anemometer (DA600-3TV; Kaijo, Tokyo, Japan) and an infrared gas analyzer (IRGA) (LI-7000; Li-Cor, Lincoln, NE, USA) were used for the measurements. The air intake of the IRGA was 15 cm (horizontal) from the center of the anemometer transducers, and air was drawn at a flow rate of 10 L min<sup>-1</sup> through a 1.0 µm filter and into a 6 m Teflon tube. The IRGA reference cell was fed CO<sub>2</sub> gas (300 µmol mol<sup>-1</sup>) at a flow rate of 10–20 mL min<sup>-1</sup>. CO<sub>2</sub> fluctuations were calibrated every day by using two standard CO<sub>2</sub> gases (320 and 420 µmol mol<sup>-1</sup>). The daily calibration (two times for each standard gas and it took 1 min for each calibration during 23:30–24:00 hours) was controlled using a data logger (CR23X; Campbell Scientific, Logan, UT, USA). The reference and calibration gases were manometrically prepared by Japan Fine Products Corp. (Kawasaki, Japan), and were compared two times before and after the usage with a CO<sub>2</sub> standard scale of National Institute for Environmental Studies (the NIES95 scale) prepared using a gravimetric method. The NIES95 scale was compared with a standard CO<sub>2</sub> scale provided by the Climate Monitoring and Diagnostics Laboratory of the National Oceanic and Atmospheric Administration (NOAA/CMDL) in 1996. Differences in CO<sub>2</sub> concentration between the two laboratories were less than 0.12 µmol mol<sup>-1</sup> for a range of values from 343 to 373 µmol mol<sup>-1</sup>. Fluctuation data were sampled at 10 Hz with a digitizing data recorder (DRM3 of TEAC Corp., Tokyo, Japan, until October 2003; and CR5000 of Campbell Scientific, from October 2003) after low-path filtering (cut-off frequency was 5 Hz).

After clearcutting, in addition to the continuous flux monitoring at 32 m, an open-path eddy covariance system was installed in June 2003 and a closed-path system in October 2003 above the *Sasa* canopy at the height of 4.6 m. In the open-path system, a sonic anemometer (DA600-3TV) measured 3-D winds and temperature and an IRGA (OP2; Data Design Group, La Jolla, CA, USA) measured the molar fraction of CO<sub>2</sub>; these instruments were separated by 30 cm (horizontal). In the closed-path system, a LI-7000 IRGA (Li-Cor) was used; the separation distance between the anemometer and the air intake and tube length for air sampling were

5 cm and 15 m, respectively, and air flow rate, gas feed to the IRGA reference cell, calibration, and data sampling frequency were the same as for the system at 32 m. We used flux values obtained at 4.6 m height for almost all the period after the clearcutting (excepting from January to May during and just after the clearcutting and in early October 2003, when there was no available surface flux data).

#### *Ecosystem and micrometeorological measurements*

Meteorological and soil sensors installed in August 2001 were sampled every 5 s, and data were stored as 0.5 h means using three data loggers (two CR23Xs and a CR10X; Campbell Scientific) connected to a PC, which downloads logged data automatically. Meteorological measurements at the 32 m tower included air temperature and relative humidity (HMP45A; Vaisala, Helsinki, Finland), wind speed and direction (010C and 020C; Met One Instruments, Grants Pass, OR, USA), net radiation (CNR-1; Kipp & Zonen, Delft, the Netherlands), photosynthetic photon flux density (PPFD; LI-190SZ, Li-Cor), and precipitation (CYG-52202; RM Young, Traverse City, MI, USA). Except wind direction, these parameters were also monitored just above the undergrowth (ca. 2 m above ground level) by the same type of instruments as those used at 32 m. Snow depth (SR-50; Campbell Scientific) and atmospheric pressure (PTB210-C6C5A; Vaisala) were also measured. The soil temperature profile (at 1, 5, and 10 cm depths) and soil heat flux (2 cm depth) were measured by platinum resistance thermometers and heat flow transducers at five points.

To estimate CO<sub>2</sub> storage in the air layer below the eddy covariance measurement at 32 m, the CO<sub>2</sub> concentration profile within the mixed forest was measured at four (snow-covered period) or five (snow-free period) levels with an IRGA (DX6100; RMT Ltd., Moscow, Russia). From each inlet, air was drawn at a rate of 0.5 L min<sup>-1</sup> through a 1.0 µm filter and into a 50 m nylon tube. Air entering the sample cell was first dried in a thermoelectric cooling module, and then by a fluorine-containing polymer membrane air drier and by Mg(ClO<sub>4</sub>)<sub>2</sub>. Air was drawn from each height for 5 min every 30 min, and the average values over 10 s intervals in the last 2 min were recorded.

The plant area index (PAI; which includes the shade by stems, branches, and culms in addition by leaves) of the tree canopy (until December 2002), *Sasa* canopy (entire study period), and larch saplings (from May 2004) was measured with a LAI-2000 (Li-Cor). The PAI of each component was measured three to five times every 2–4 weeks in the snow-free period. Two reference values (no canopy shade) and 10 sample

values (with canopy shade) were measured to obtain each PAI value.

#### Soil respiration measurements

From June 2002 to November 2003, an LI-6400-09 chamber system (Li-Cor) was deployed to measure soil respiration ( $R_{sL}$ ) every month during snow-free periods. In 2002, four chamber collars were inserted 3 cm into soil beneath the understory and in forest gaps; in 2003, after the clearcut, eight collars were inserted. Soil respiration was measured from about 10:00 to 14:00 hours each day. During each respiration measurement, soil surface temperature beside the chamber was measured by inserting a 10 cm long platinum resistance thermometer into the soil.

From 2003 to 2005, another multichannel automated chamber system to measure soil respiration (design per Liang *et al.*, 2003, 2004) was installed during snow-free periods. The system had a flow-through, non-steady-state design and comprised a control unit and eight automated chambers. The control unit included an IRGA (LI-840; Li-Cor), a data-logger (CR10X; Campbell Scientific), a gas sampler unit, and an air compressor. The chambers (0.9 m × 0.9 m × 0.5 m high) were constructed of clear PVC board glued to a steel-pipe frame. The chamber lids were raised and closed by two pneumatic cylinders. During measurements, the chamber was closed and air in the chamber was mixed by two micro-fans, chamber air was circulated through the IRGA by a micro-pump, and change in CO<sub>2</sub> concentration was measured by the IRGA. Over 0.5 h, the chambers were closed sequentially under the control of the data-logger. The sampling period was 225 s, and the respiration evaluation interval was 30 min. The data-logger acquired output from the IRGA at 1 s intervals and averaged and recorded data every 5 s. In 2004 and 2005, the sampling period, respiration evaluation interval, and data-averaging time were changed to 150 s, 1 h, and 10 s, respectively.

Soil respiration measured by the LI-6400-09 ( $R_{sL}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was calculated as follows:

$$R_{sL} = \frac{kVP}{S(T_c + 273.15)} \left( \frac{\partial C}{\partial t} + \frac{C}{(1000 - W)} \frac{\partial W}{\partial t} \right), \quad (1)$$

where  $k$  is a constant (1.2028);  $V$  and  $S$  are the effective chamber-head volume (991 cm<sup>3</sup>) and measured soil surface area (71.6 cm<sup>2</sup>), respectively;  $P$  and  $T_c$  are the initial pressure (kPa) and air temperature (°C) in the chamber, respectively;  $C$  and  $W$  are the initial CO<sub>2</sub> ( $\mu\text{mol mol}^{-1}$ ) and water vapor ( $\text{mmol mol}^{-1}$ ) mole fraction, respectively; and  $\partial C/\partial t$  and  $\partial W/\partial t$  are the rates of change in CO<sub>2</sub> and the water vapor mole fraction over time (s), respectively. We also used this equation to calculate soil

respiration measured by the automated chamber ( $R_{sM}$ ), but neglecting the effect of soil evaporation on the respiration measurement (i.e.,  $\partial W/\partial t = 0$ ). Data gaps caused by system malfunction were filled by using an Arrhenius-type equation (Lloyd & Taylor, 1994) for each chamber and each year. Soil respiration  $R_s$  can be expressed as

$$R_s = R_{\text{ref}} \times \exp \left[ \frac{E_a}{R} \times \left( \frac{1}{T_{\text{ref}}} - \frac{1}{T} \right) \right], \quad (2)$$

where  $R_{\text{ref}}$  is the respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at the reference temperature ( $T_{\text{ref}} = 283.16 \text{ K}$ );  $E_a$  and  $R$  are the activation energy ( $\text{J mol}^{-1}$ ) and the universal gas constant ( $8.134 \text{ J K}^{-1} \text{ mol}^{-1}$ ), respectively; and  $T$  is the temperature (K) as an independent variable for respiration (we used soil temperature at 5 cm depth). The constants  $E_a$  and  $R_{\text{ref}}$  were fixed throughout the year.

#### Eddy covariance flux calculation

The sonic rotation angle for planar fit rotation (Wilczak *et al.*, 2001) was determined every day using 30 min averages of wind speed in a 15-day moving window, and a fixed value of the sonic-tube lag time for CO<sub>2</sub> was determined monthly by averaging the lag times determined every 30 min under turbulent conditions (the correlation coefficient between vertical wind velocity and CO<sub>2</sub> concentration at determined lag time is more than 0.26). The time step and range for finding the maximum correlation were 0.1 and 0–10 s, respectively, and the range of the monthly averages was 2.9–6.3 s (4.2 s in average) at 32 m height and 2.7–4.6 s (3.9 s) at 4.6 m. The half-hour CO<sub>2</sub> flux ( $F_c$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was calculated using these angles and lag times. Block averaging was applied and trend removing was not applied to the 10 Hz fluctuation data to calculate the covariances. Effects of cross wind speed and water vapor concentration on the sensible heat flux were corrected following Kaimal & Gaynor (1991) and Hignett (1992), respectively, and then the effect of air density fluctuation on the flux values was corrected (Webb *et al.*, 1980; Leuning & King, 1992). High-frequency losses for open-path signals were corrected by using transfer functions related to the sources of signal damping (Moore, 1986), and losses for closed-path signals (tube attenuation) were corrected following the EUROFLUX methodology (Aubinet *et al.*, 2000, 2001; Kowalski *et al.*, 2003). Co-spectra between vertical winds and scalars (temperature and CO<sub>2</sub> concentration) were normalized according to the covariance integrated over the band-pass range (typically 0.003–0.065 Hz at 32 m) and averaged over periods with similar wind speed under turbulent conditions. The correction factor ( $\epsilon$ ) was determined from the ratio of integrated, normal-

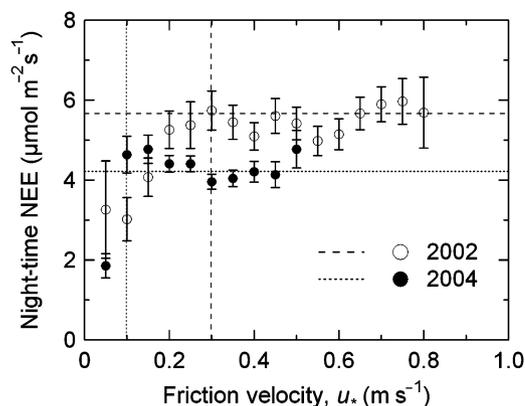
ized co-spectra, using temperature as a reference.  $\varepsilon$  depends on the mean wind speed ( $\bar{u}$ ):  $\varepsilon = a + b\bar{u}$ , where  $a$  and  $b$  are coefficients that were determined every year or upon a change in the system;  $a$  and  $b$  were 1.00 and 0.0343, respectively, in 2002 at 32 m and 0.91–1.11 and 0.152–0.163 in 2003–2005 at 4.6 m.

Before the clearcutting, net ecosystem CO<sub>2</sub> exchange (NEE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was determined as the sum of  $F_c$  and  $F_s$  (negative means downward flux).  $F_s$  is the CO<sub>2</sub> storage change in the air column from the forest floor to the flux measurement height and was calculated from the observed CO<sub>2</sub> profiles, whereas  $F_c$  was directly measured as NEE after clearcutting.  $F_s$  in the mixed forest was calculated every 30 min from the difference in CO<sub>2</sub> storage; however, because CO<sub>2</sub> profile observations were not continuous (127 days in 2002),  $F_s$  in periods with no profile data was estimated by the relationship between the daily  $F_s$  calculated from the profile data ( $F_{sp}$ ) and that calculated from the change in the CO<sub>2</sub> concentration only at 32 m ( $F_{st}$ ) ( $F_{sp} = 1.69F_{st} + 1.05$ ;  $r^2 = 0.61$ ).

#### Quality control of flux data

All raw flux data were checked following the quality-control program proposed by Vickers & Mahrt (1997) and Mano *et al.* (2007), and gaps in raw data caused by removal of noise spikes (more than  $5 \times \text{SD}$  in a series of 3000 overlapping datapoints) were filled by linear interpolation. The stationarity ratio and integral turbulence characteristic tests (Foken & Wichura, 1996) were applied to 30-min averaged flux. Fetch for the flux observation decreased after the clearcutting. The distances between the flux observation point and boundaries of the cut area ranged from 140 to 340 m in the eight cardinal and intercardinal directions. To remove the effect of flux from outside the clearcut, we evaluated the footprint of the observed CO<sub>2</sub> flux using the model developed by Kormann & Meixner (2001), which accounts for thermal stability. We evaluated the cumulative footprint every 30 min up to 2 km and up to the boundaries of the cut area (distance according to wind direction) from the observation point in 1 m steps. The flux data were removed if the ratio of the two cumulative values was  $<0.7$  (i.e., contribution from the cutover was less than about 70%). Open-path flux values during precipitation events ( $0.5 \text{ mm } 30 \text{ min}^{-1}$  and the next 30 min) were removed.

Finally,  $u_*$  (friction velocity) filtering was applied to the remaining NEE data (after summing  $F_c$  and  $F_s$ ). All missing  $u_*$  values after the quality-control procedure were filled before filtration on the basis of the empirical linear relation to wind speed for each snow-free and snow-covered period of each year. The threshold values



**Fig. 2** Night-time net ecosystem exchange (NEE) vs. friction velocity ( $u_*$ ) during snow-free periods. Night-time NEE was split into  $u_*$  classes (each  $0.05 \text{ m s}^{-1}$ ). Average NEE for each  $u_*$  class was compared with that of the highest five  $u_*$  classes (horizontal lines: 5.67 and 4.22 for 2002 and 2004); if the ratio was  $<0.98$ , the class was recognized as below the threshold (vertical lines: 0.3 and  $0.1 \text{ m s}^{-1}$  for 2002 and 2004). Vertical bars represent  $\pm$  standard error of the mean ( $n > 50$ ).

for filtering were set at  $0.3$  and  $0.1 \text{ m s}^{-1}$  for the forest and clearcut, respectively (Fig. 2). However, filtration was not applied during the snow-covered period after clearcutting because the snow surface ( $1.5 \text{ m}$ ) was near the flux observation height ( $4.6 \text{ m}$ ) and wind causes mass transfer of CO<sub>2</sub> in the snowpack (Takagi *et al.*, 2005a). Under such conditions,  $u_*$  filtration overestimated the CO<sub>2</sub> emission from the snow surface when the snow surface was defined as the interface for CO<sub>2</sub> exchange. About half of the 30-min NEE data for each year were rejected based on this quality-control procedure (Table 1).

#### Gap filling of NEE and determination of gross primary production (GPP) and total ecosystem respiration (RE)

We filled the gaps in NEE data mainly by using lookup tables to estimate the annual sum (Falge *et al.*, 2001). Tables were created every 30 days during snow-free periods, and one table was created for the snow-covered period of each year. During the snow-free periods, 30-min NEE values were compiled for each air temperature ( $2^\circ \text{C}$  interval)  $\times$  PPFD ( $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  interval) class. Air temperature at 32 and 2 m was used as the lookup class before and after the clearcutting, respectively. During the snow-covered period, NEE values were compiled for each temperature ( $2^\circ \text{C}$  interval)  $\times$  wind speed at the 32 m ( $1 \text{ m s}^{-1}$  interval) class. Before clearcutting, air temperature at 32 m was used for the temperature class because CO<sub>2</sub> production in soil under the snowpack was related to the air temperature above the snow surface (Takagi *et al.*, 2005a). However, be-

**Table 1** Survived and gap-filled ratio of the 30-min net ecosystem CO<sub>2</sub> exchange data after each quality-control and gap-filling procedure

	Raw data screening	Instationarity ratio and integral turbulence characteristic tests	Footprint checking	$u_*$ filtration	Lookup table filling	MDV filling	Linear interpolation
2001	93	82	–	42	95	100	–
2002	94	85	–	50	96	100	–
2003	87	74	46	44	92	100	100
2004	92	74	65	55	99	100	–
2005	86	67	60	52	96	100	100

Values are percentages of the maximum possible value for each year (i.e., 17 568 for 2004 and 17 520 for the other years). MDV, mean diurnal variation.

cause all plants were under the snow after the clearcutting, soil temperature at 5 cm depth was used instead. Wind accelerated the mass transfer through the snowpack (Takagi *et al.*, 2005a) both before and after clearcutting, so wind speed was used as the environmental factor for the lookup table during the snow-covered period. A few data gaps were not filled by the lookup tables, owing mainly to the lack of environmental data. These gaps were filled by the mean diurnal variation (MDV) approach (Falge *et al.*, 2001), in which missing NEE was replaced by the mean for that time based on the adjacent 9 days. The few remaining gaps were filled by linear interpolation. The ratio of filled data after each gap-filling process is shown in Table 1. In 2001, 2002, and 2004, all the 30-min NEE values were filled after MDV method; on the other hand in 2003 and 2005, there were few gaps (<0.5%) even after the MDV and we applied linear interpolation.

Night-time NEE (PPFD < 1  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in the snow-free period and NEE in the snow-covered period were assumed to be equivalent to RE. In the snow-free period, 30-min values of night-time NEE were compiled for air temperature classes (2 °C interval), and the average NEE for each temperature class was related to the air temperature by using Eqn (2) for each year. The constants  $R_{\text{ref}}$  and  $E_a$  were fixed throughout a snow-free period, and daytime RE was estimated every 30 min by using Eqn (2) and air temperature. GPP was estimated as RE–NEE. The minimum time resolution for GPP and RE was set as the daily sum. If the daily GPP (or RE) was negative, the value was set to zero and the absolute value of the negative value was added to the daily RE (or GPP).

## Results

### *Interannual variation of micrometeorology and PAI*

In 2002, before the clearcutting, the maximum monthly temperature and annual PPFD were the lowest among the observed years (Table 2). In 2003, annual PPFD was

**Table 2** Interannual variation in micrometeorological parameters

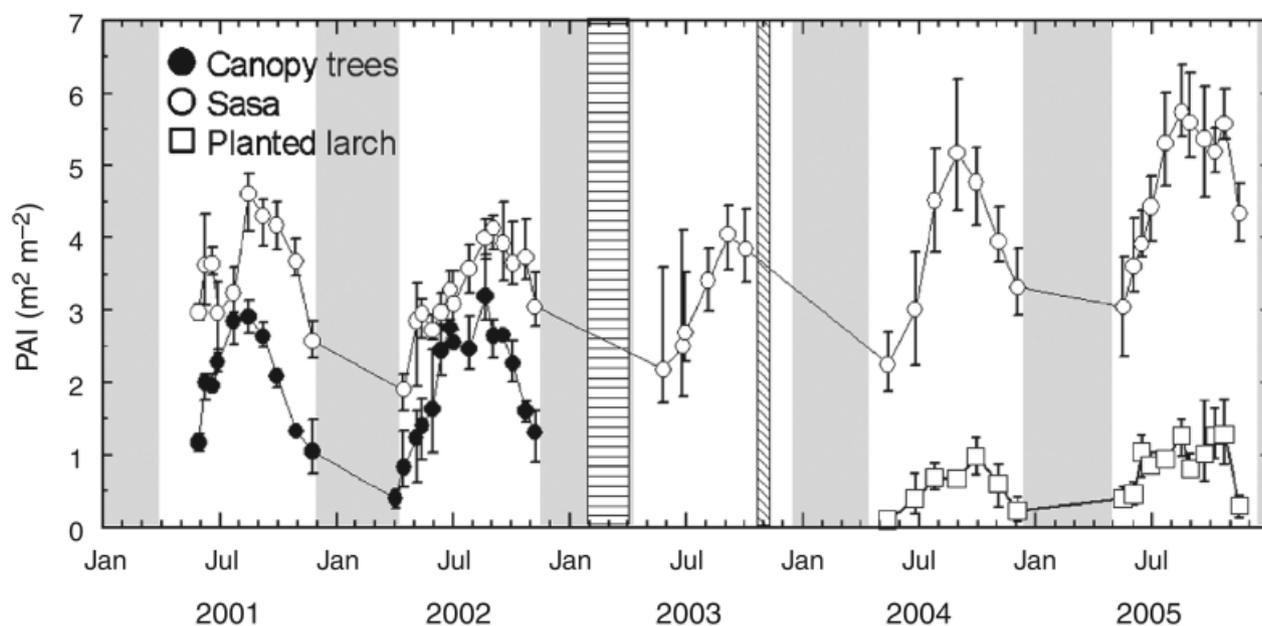
Micrometeorology	2002	2003	2004	2005
Air temperature (°C) at 32 m height				
Annual mean	5.6	5.5	6.3	5.2
Minimum of monthly average	–7.5	–8.4	–6.4	–8.2
Maximum of monthly average	16.1	17.7	18.3	19.8
Annual PPFD (mol m <sup>–2</sup> ) at 32 m height				
Annual precipitation (mm)*	1135	1055	1212	1065

\*Precipitation was the sum of rainfall and snowfall. Rainfall was measured by tipping-bucket rain gauge. Snowfall was measured by snow depth and density at its maximum; the period for evaluation was from the beginning of snow cover in the previous year (November or December) to the beginning of snow cover in the current year.

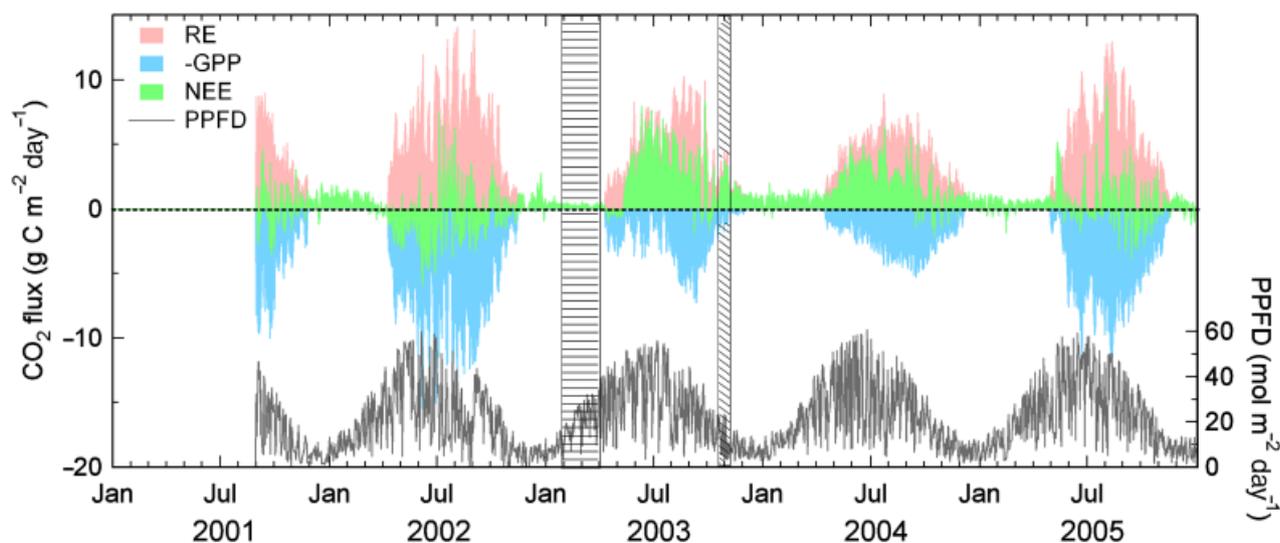
PPFD, photosynthetic photon flux density.

higher and precipitation was lower than in the other years. The highest annual mean temperature and precipitation were observed in 2004. In contrast, the annual mean temperature in 2005 was the lowest, owing to the cold winter. The maximum monthly temperature increased gradually, and high and low precipitation occurred in alternate years during the study period.

PAI values for the understory *Sasa* were higher than those for canopy trees throughout the 2 years in the mixed forest, and the seasonal maximum for canopy trees and *Sasa* was 3.2 and 4.6, respectively (Fig. 3). PAI of both the canopy and understory varied seasonally, and the peak value for *Sasa* lagged that of the canopy by about 1 month. In the rows where it remained, *Sasa* PAI increased from 1 year after the clearcutting, and reached 5.7 in August 2005. Larch saplings were planted in autumn 2003, and the PAI increased gradually (maximum values in 2004 and 2005 were 0.97 and 1.28),



**Fig. 3** Interannual variation of plant area index (PAI). Symbols represent means, and vertical bars denote max/min values. Horizontal and diagonal hatches represent periods of clearcutting and strip-cutting of *Sasa* and planting larch. Gray shading represents snow-covered periods. *Sasa* PAI after the strip cutting was measured in the rows where it remained.



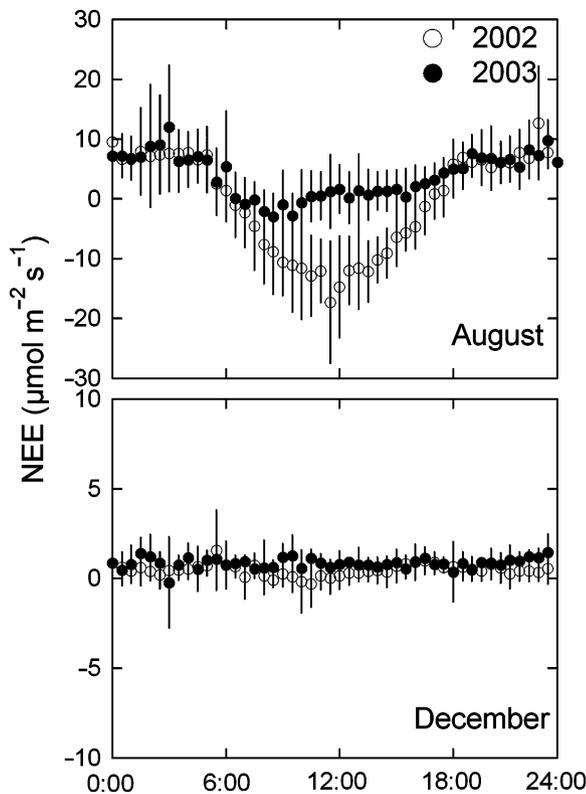
**Fig. 4** Interannual variation of gross primary production (GPP), total ecosystem respiration (RE), net ecosystem CO<sub>2</sub> exchange (NEE), and photosynthetic photon flux density (PPFD). Horizontal and diagonal hatches represent periods of clearcutting and strip-cutting of *Sasa* and planting larch.

although these values remained small compared with those of *Sasa*.

#### *Effect of forestry activities on the carbon budget*

In the mixed forest, daily NEE was mostly negative from April to June, but it often became positive in midsummer caused by the high respiration rate enhanced by high temperature (Figs 4 and 5). The mixed

forest was a weak carbon sink ( $-44 \text{ g C m}^{-2}$ ; Table 3), and annual GPP ( $1439 \text{ g C m}^{-2}$ ) and RE ( $1395 \text{ g C m}^{-2}$ ) were nearly in equilibrium. In 2003, after the clearcutting, *Sasa* bamboos still had a large biomass and the 30-min NEE in the midday was often negative from August to September (Fig. 5). However, because of the large positive values in 30-min NEE in the night-time, which were comparable with those in the mixed forest, the daily NEE was positive throughout most of 2003. In



**Fig. 5** Mean diurnal variations in 30-min net ecosystem  $\text{CO}_2$  exchange (NEE) in August and December 2002 and 2003. Vertical bars indicate 1SD. Data passing quality-control procedure and  $u_*$  screening (and not gap-filled) were used for the averaging.

**Table 3** Interannual variation in net ecosystem  $\text{CO}_2$  exchange (NEE), gross primary production (GPP), total ecosystem respiration (RE), RE in snow-free period (RE<sub>g</sub>), and soil respiration using Li-6400-09 ( $R_{sL}$ ) and multichannel chamber system ( $R_{sM}$ )

	2002	2003	2004	2005
NEE	-44 [-92]	569 [577]	495 [473]	153 [150]
GPP	1439 [1428]	481 [367]	540 [655]	1014 [971]
RE	1395 [1336]	1050 [944]	1035 [1128]	1167 [1121]
RE <sub>g</sub>	1301	1010	951	1096
$R_{sL}$	577*	673	-	-
$R_{sM}$	-	852 (289)	1047 (293)	1062 (339)

NEE, GPP, and RE are the annual sums ( $\text{g C m}^{-2} \text{yr}^{-1}$ ), and RE<sub>g</sub>,  $R_{sL}$ , and  $R_{sM}$  are the sums for the snow-free period ( $\text{g C m}^{-2}$ ). Values in square brackets were determined by the FLUXNET approach (see 'Discussion'), and values in parentheses are the SD of the seasonal sum.

\*This value was estimated using soil temperature and Eqn (2) for forest gap and understory, with gaps accounting for 50% of the total study area.

the snow-covered period, there was no distinct change in the diurnal NEE variation between before and after the clearcutting. As a result, the ecosystem became a

large carbon source ( $569 \text{ g C m}^{-2} \text{yr}^{-1}$ ) and the decrease in RE ( $1050 \text{ g C m}^{-2} \text{yr}^{-1}$ ) was smaller than that in GPP ( $481 \text{ g C m}^{-2} \text{yr}^{-1}$ ). The annual NEE ( $495$  in 2004 and  $153 \text{ g C m}^{-2} \text{yr}^{-1}$  in 2005) was positive for the following 2 years, but the emission rate decreased rapidly owing to the increase in GPP.

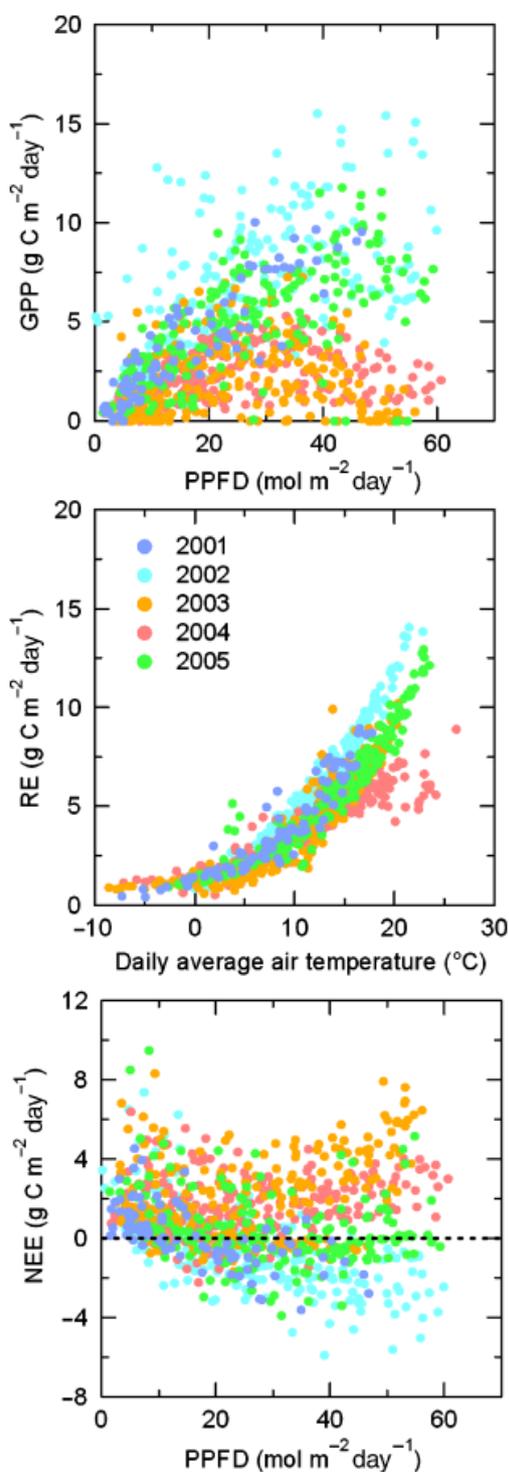
With regard to seasonal variation, in 2002 the maximum daily GPP ( $15.1 \text{ g C m}^{-2} \text{day}^{-1}$ ) was observed in June. In 2003 and 2004, after clearcutting, the daily GPP from April to June decreased and peaks ( $7.3$  and  $5.3 \text{ g C m}^{-2} \text{day}^{-1}$ , respectively) were observed in September. Because of the decrease in RE caused by low temperature, negative daily NEE was observed on several days in September and October 2003 and 2004. In 2005, an increase in daily GPP from April to June was again observed, and the rate during this period ( $251 \text{ g C m}^{-2}$ ) recovered to half that in the forest ( $570 \text{ g C m}^{-2}$ ). The positive spike in NEE ( $52 \text{ g C m}^{-2}$ ) was observed from late October to November 2003, when the *Sasa* was strip-cut and larch saplings were planted, and a relatively high  $\text{CO}_2$  release in the following snow-covered period was observed.

In 2001–2002, in the forest, the daily NEE decreased to about  $-6 \text{ g C m}^{-2}$  with increase in PPFD during the snow-free period (Fig. 6). However, in 2003 and 2004 there was no clear relationship to the daily PPFD, and the daily NEE remained positive throughout the snow-free periods, with the same magnitude but opposite direction to that in the forest. In 2005, daily NEE values converged around zero over the range of the PPFD. The RE–air temperature relationship shows that clearcutting decreased the RE [maxima  $14.1 \text{ g C m}^{-2} \text{day}^{-1}$  (2001–2002),  $10.2 \text{ g C m}^{-2} \text{day}^{-1}$  (2003), and  $8.9 \text{ g C m}^{-2} \text{day}^{-1}$  (2004), and the effect also remained in 2005 ( $12.9 \text{ g C m}^{-2} \text{day}^{-1}$ )]. As a result, daily GPP values decreased in 2003 and 2004 compared with those in 2001–2002; in 2005, the rate recovered to within the range of that in 2001–2002, although the maximum value was still lower than that in the forest.

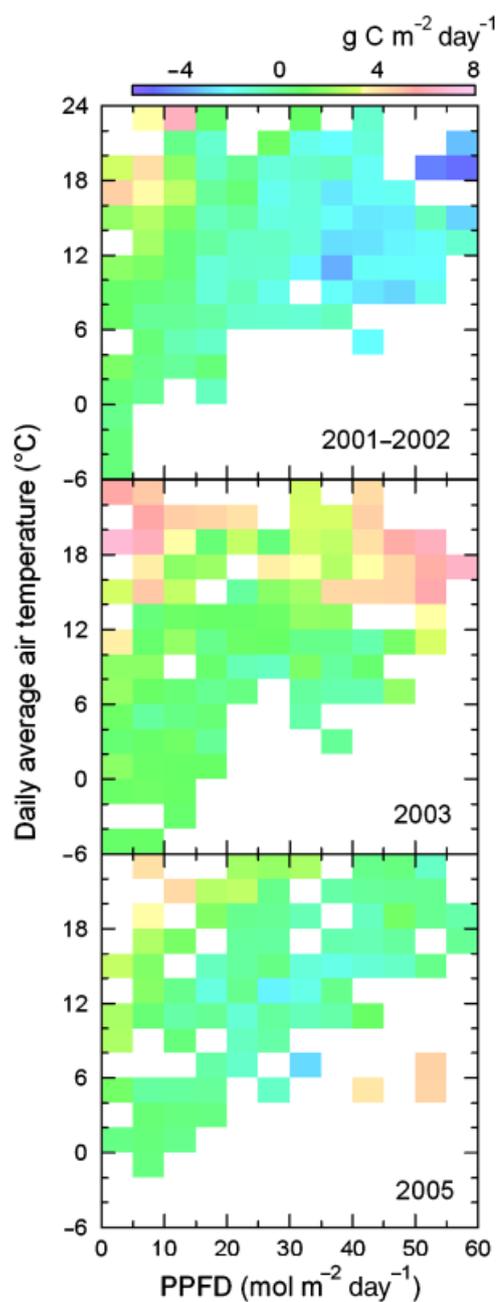
In 2001–2002, the highest sequestration rate was observed under high PPFD and high air temperature (Fig. 7). Just after clearcutting in 2003, high  $\text{CO}_2$  emission was observed at high temperatures regardless of the light condition. The emission strength moderated in 2005, and values were close to zero over a wide range of PPFD and air temperature.

#### Relationship among respirations

In 2002 in the mixed forest, soil respiration in gaps was higher than that in the understory (Fig. 8, Table 4). In 2003, just after clearcutting, soil respiration obtained by both methods (i.e., Li-Cor and multichannel chamber system) showed a similar relationship to soil tempera-

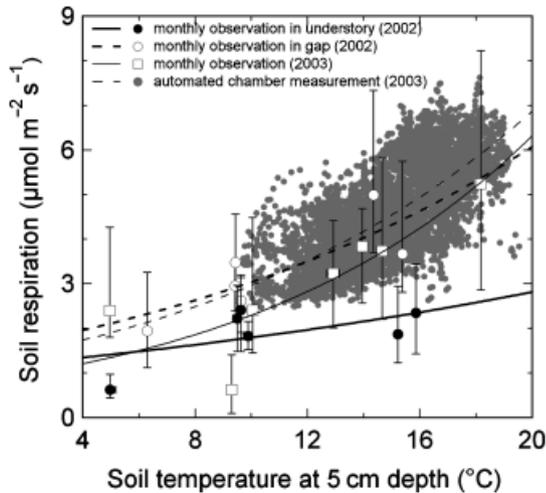


**Fig. 6** Relationship between environmental parameters [photosynthetic photon flux density (PPFD), air temperature] and daily fluxes [gross primary production (GPP), total ecosystem respiration (RE), net ecosystem CO<sub>2</sub> exchange (NEE)] during snow-free periods. Gap-filled data are included in daily values. Air temperature in 2001–2002 and PPFD were measured at 32 m; air temperature in 2003–2005 was measured at 2 m.

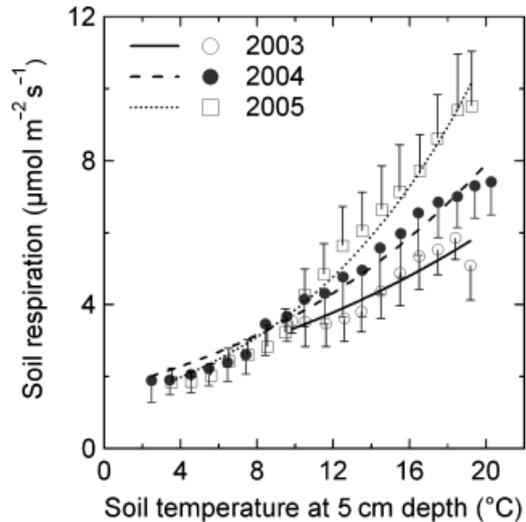


**Fig. 7** Relationship between photosynthetic photon flux density (PPFD), air temperature, and daily net ecosystem CO<sub>2</sub> exchange (NEE) during snow-free periods. Daily NEE was classified into 2 °C classes for air temperature and 5 mol m<sup>-2</sup> day<sup>-1</sup> classes for PPFD for each year; the average for each class is shown. Gap-filled data are included in daily values. See Fig. 6 for measurement heights for PPFD and air temperature.

ture as that in forest gaps, whereas the relationship curves or  $R_{ref}$  and  $E_a/R$  showed a yearly increase in soil respiration from 2003 to 2005 (Fig. 9, Table 4). High  $R_{ref}$  was observed for RE in the mixed forest compared with after-clearcutting, although there was no distinct trend



**Fig. 8** Relationship between soil temperature and soil respiration during snow-free periods in 2002 and 2003. Symbols for monthly observation indicate the averages ( $n = 4$  in 2002 and  $n = 8$  in 2003) and vertical and horizontal bars denote max/min range. Gray dots indicate 30-min averages. Curves were fit by using Eqn (2) (see Table 4 for parameter values).



**Fig. 9** Relationship between soil temperature and soil respiration during snow-free periods in 2003–2005. Respiration data were classified into 1 °C soil temperature classes and the symbols are the average for each temperature class. Vertical bars indicate 1 SD. See Table 4 for parameter values for the regressions.

**Table 4** Respiration parameters for Eqn (2)

	2002	2003	2004	2005
$R_{sL\_gap}$				
$R_{ref}$	3.04 (0.31)	2.29 (0.40)	–	–
$E_a/R$	5750 (2190)	8400 (2470)	–	–
$R_{sL\_can}$				
$R_{ref}$	1.79 (0.26)	–	–	–
$E_a/R$	3770 (2870)	–	–	–
$R_{sM}$				
$R_{ref}$	–	3.35 (0.18)	3.70 (0.09)	3.85 (0.11)
$E_a/R$	–	4900 (690)	6310 (290)	8690 (360)
RE				
$R_{ref}$	4.22 (0.31)	3.07 (0.21)	3.28 (0.30)	3.20 (0.14)
$E_a/R$	7630 (610)	8470 (660)	4260 (720)	8000 (370)

Respiration rate at the reference temperature ( $R_{ref}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and activation energy ( $E_a$ ) were determined as a constant value for each snow-free period. Soil temperature at 5 cm depth and air temperature at canopy height were used to relate the soil respiration and total ecosystem respiration, respectively. Only data that passed the quality-control procedure were used for the regression.  $R_{sL\_gap}$ , soil respiration measured in the gap using Li-6400-09;  $R_{sL\_can}$ , soil respiration measured in the understory using Li-6400-09;  $R_{sM}$ , soil respiration measured using multichannel chamber system; RE, total ecosystem respiration. Values in parentheses are SD.

in  $E_a/R$  during the study period or in  $R_{ref}$  after clearcutting.

In the mixed forest, the ratio of soil respiration to RE was 44% during the snow-free period, and the ratio

increased after clearcutting (Table 3). In 2003, the ratio was 67% for  $R_{sL}$  and  $84 \pm 29\%$  for  $R_{sM}$ . The ratio was  $110 \pm 31\%$  and  $97 \pm 31\%$  in 2004 and 2005, respectively, indicating that the soil respiration rate was similar to the RE and that aboveground parts of the vegetation contributed little to the RE.

## Discussion

### Uncertainty in the annual $\text{CO}_2$ budget

In this study, about 50% of the annual NEE data of each year was rejected by the quality-control procedure (Table 1). Although the survived ratio was within the range of previous studies (Carrara *et al.*, 2003; Humphreys *et al.*, 2005), Falge *et al.* (2001) suggested that large data gaps increase the uncertainty in annual NEE. To validate the estimated annual  $\text{CO}_2$  budgets, we compared our results with those obtained by using an online server (<http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/>) for gap-filling and flux partitioning calculation (Reichstein *et al.*, 2005; Takagi *et al.*, 2007), which is the basic procedure of FLUXNET synthesis activity (Table 3). The  $u_*$  filtration during snow-covered period after clearcutting, and negative values of daily GPP and RE were treated as in our approach. The FLUXNET gap-filling strategy is a combination of several filling methods proposed by Falge *et al.* (2001) and is similar to our approach (except for  $u_*$  threshold determination and the environmental factors for

creating lookup tables, for example), whereas the flux partitioning procedure to obtain RE and GPP differ. Although they use Lloyd & Taylor equation to relate night-time NEE to temperature, the coefficient  $R_{\text{ref}}$  was determined as the time variable by using a 15-day moving window.

The  $u_*$  threshold for the mixed forest was higher in our calculations than according to the FLUXNET approach (0.3 vs. 0.1 m s<sup>-1</sup>), whereas the threshold after clearcutting was the same (0.1 m s<sup>-1</sup>). Owing to the different threshold value, the difference in the annual NEE of the mixed forest between the two approaches (48 g C m<sup>-2</sup>) was larger than that in the following years (3–22 g C m<sup>-2</sup>; Table 3). Hirata *et al.* (2008) applied their own  $u_*$  threshold determination (0 m s<sup>-1</sup>) and gap-filling strategy to compare CO<sub>2</sub> budgets in forest ecosystems across East Asia, and evaluated intermediate value (–70 g C m<sup>-2</sup>) for annual NEE of our mixed forest. Thus, our annual NEE estimation includes at least 50 g C m<sup>-2</sup> uncertainty for the forest and the less for the clearcut caused by the  $u_*$  threshold determination and gap-filling strategy, although these values are comparable with those of previous studies (Falge *et al.*, 2001; Carrara *et al.*, 2003; Humphreys *et al.*, 2005). The FLUXNET approach and Hirata *et al.* (2008) consider the temperature dependency of  $u_*$  to determine threshold values. In addition, FLUXNET approach determines the threshold for each of the four 3-month periods in a year, and chooses the highest value for the filtration. Their threshold values for the forest were lower than our value; however, we chose the highest to avoid underestimation of night-time NEE.

In contrast, annual GPP and RE estimates have larger uncertainty. The difference between the two approaches ranges from 11 to 115 g C m<sup>-2</sup> (average 73 g C m<sup>-2</sup>) (Table 3). This difference arises because both GPP and RE include the uncertainty of the NEE estimation in addition to that of the partitioning procedure. The order of magnitude of the annual fluxes based on the two procedures changed year by year, and there was no trend in the estimated values.

#### *Effect of clearcutting on the CO<sub>2</sub> budget*

The mixed forest was a weak carbon sink, and the annual GPP and RE were nearly in equilibrium, but clearcutting caused large CO<sub>2</sub> emission from the ecosystem (Fig. 4, Table 3). The forest was a naturally regenerated mature forest, and large trees were more than 200-years old (Tsuiji *et al.*, 2006). Thus, maintenance RE was as high as the gross photosynthesis rate and might have decreased the net CO<sub>2</sub> uptake (Howard *et al.*, 2004; Magnani *et al.*, 2007).

Stand-level CO<sub>2</sub> fluxes have been measured in early successional forests in Europe (Kowalski *et al.*, 2003, 2004; Kolari *et al.*, 2004), Canada (Pypker & Fredeen, 2002; Litvak *et al.*, 2003; Humphreys *et al.*, 2005, 2006; Amiro *et al.*, 2006), the United States (Law *et al.*, 2001; Clark *et al.*, 2004), and Siberia (Schulze *et al.*, 1999; Machimura *et al.*, 2005). All these studies showed that disturbance converts forests from carbon sinks to sources with a wide range of emission rates (tens to thousands of g C m<sup>-2</sup> yr<sup>-1</sup>); however, in most studies that started observations within 1 year after the disturbance, a high emission rate was observed. Clark *et al.* (2004) observed the highest reported emission rate (1269 g C m<sup>-2</sup> yr<sup>-1</sup>) after clearcutting of *Pinus elliotii* var. *elliottii* in north Florida, while Machimura *et al.* (2005) observed the lowest (296 g C m<sup>-2</sup>) reported rate during 5 months of the growing season at a cutover of *L. gmelinii*. Kowalski *et al.* (2004) reported a high carbon emission rate (591 g C m<sup>-2</sup> yr<sup>-1</sup>) during 9 months after the harvest of *Quercus cerris* in Italy and estimated that the annual NEE would approach 1000 g C m<sup>-2</sup> if the emission immediately following the harvest was taken into account. Kowalski *et al.* (2003) observed an annual carbon loss of 200–340 g C m<sup>-2</sup> in a French *Pinus pinaster* forest following clearcutting. The annual GPP and RE at the cutover were one-third and two-thirds of the values in a nearby mature forest, respectively, and the decreasing ratios in GPP and RE caused by clearcutting were similar to our observations. Humphreys *et al.* (2005) reported that following clearcutting of a *Pseudotsuga menziesii* var. *menziesii* stand on Vancouver Island, 520–620 g C m<sup>-2</sup> yr<sup>-1</sup> was emitted for 3 years, and this emission rate is comparable with our results (569 g C m<sup>-2</sup> yr<sup>-1</sup>). In most cases, the emission rate tended to decrease with time after the disturbance. Thus, observations during the event are necessary to evaluate precisely the effects of disturbance on ecosystem CO<sub>2</sub> exchange.

A large CO<sub>2</sub> emission in the harvest year rapidly decreased in the following years, caused by an increase in GPP, whereas the RE was relatively stable (Fig. 4, Table 3). The decreasing trend in the emission rate suggests that the ecosystem will likely become a carbon sink within the next few years. Studies of Canadian boreal forests (Litvak *et al.*, 2003; Humphreys *et al.*, 2006; Fredeen *et al.*, 2007), Siberian (Schulze *et al.*, 1999) and northern European (Kolari *et al.*, 2004) *Pinus sylvestris* forests, and *Pinus ponderosa* forests in the United States (Law *et al.*, 2001) suggested that carbon emissions last for 8–20 years after harvesting. In contrast, Clark *et al.* (2004) reported a rapid decrease in the emission rate and predicted that the annual NEE would be negative within 3–4 years following harvesting owing to the rapid biomass accumulation by planted saplings. Ma-

chimura *et al.* (2005) also observed a rapid decrease in the emission rate during 3 years after clearcutting as a result of recovery of the surface vegetation.

At our site, larch saplings were planted in the *Sasa* strip-cut lines, and the growth rate was normal for this region (ca. 0.6 m in height from 2003 to 2005). However, the larch PAI is still small compared with that of the remaining *Sasa*. Even in the forest, the *Sasa* PAI was higher than that of the canopy trees (Fig. 3), and it began to increase within 1 year after clearcutting. The increase in *Sasa* PAI, and thus in photosynthesis, was likely the major contributor to the GPP increase immediately after the disturbance, as seen in the seasonal variation of GPP. In 2003 and 2004, GPP from April to June decreased (121 and 108 g C m<sup>-2</sup>, respectively) compared with that in 2002 (570 g C m<sup>-2</sup>), and the seasonal maximum was observed in September. *Sasa* developed new leaves from July to August and PAI increased 1–3 months after the PAI increase of the canopy trees (Fukuzawa *et al.*, 2007), which would explain the peak shift in the GPP after clearcutting. The GPP decrease in early summer can be attributed to the removal of the canopy trees. By 2005, however, the GPP rate had recovered to half that in the forest, reflecting the contribution of larch photosynthesis to GPP 2 years after planting.

#### Soil respiration and its contribution to RE

Soil respiration in forest gaps was higher than that in the understory before clearcutting (Fig. 8). *Sasa* biomass in gaps was twice that below the canopy, and bamboos are connected by well-developed rhizomes that account for about 50% of total biomass both in gaps and understory. Thus, the large *Sasa* root biomass might explain the high soil respiration rate in the gaps. In addition, Lei & Koike (1998) reported that *S. senanensis* growing in gaps attained a higher photosynthesis rate per unit leaf area than understory bamboos. The higher photosynthetic capacity in gaps would lead to a higher soil respiration rate than in the understory.

The soil respiration rate increased after clearcutting (Table 3). The temperature sensitivity of the respiration rate in 2003 was similar to that in the forest gaps (Fig. 8), and the dense *Sasa* stands prevented a change in soil temperature before and after clearcutting (Takagi *et al.*, 2005b). Therefore, changes in the gap area (50% and 100% of the site in 2002 and 2003, respectively) and the temperature sensitivity of soil respiration in the former understory was likely the main cause for the increase in respiration in 2003, rather than a change in soil temperature or in the temperature sensitivity in forest gaps. Soil respiration increased every year from 2003 (Fig. 9, Table 3) with the increase in *Sasa* biomass. All newly

developed *Sasa* seedlings in the respiration chambers were removed, but there was no barrier to prevent underground root invasion. Fukuzawa *et al.* (2006) revealed that *Sasa* expands its root distribution and replaces the space for the tree roots within 1 year after tree cutting. Thus, the increase in soil respiration from 2003 to 2005 can be attributed to an increase in *Sasa* root biomass.

The annual soil respiration rate was assumed to be the sum of the RE rate during the snow-covered period and the soil respiration rate during snow-free period in Table 3. The estimated annual rate was 671 g C m<sup>-2</sup> in 2002, 713 ( $R_{sL}$ ) or 892 ( $R_{sM}$ ) g C m<sup>-2</sup> in 2003, 1131 g C m<sup>-2</sup> in 2004, and 1133 g C m<sup>-2</sup> in 2005. The annual rate in the forest was close to the average value in Japanese forests [ $669 \pm 264$  (SD) g C m<sup>-2</sup> yr<sup>-1</sup>, range 203–1290; Lee *et al.*, 2006] and in temperate broad-leaved and mixed forests worldwide ( $647 \pm 272$  g C m<sup>-2</sup> yr<sup>-1</sup>, range 304–1414; Raich & Schlesinger, 1992). After the clearcutting, however, the rate reached the higher end of these reported ranges. Several studies of Japanese forests with dense *Sasa* understories have also reported high annual soil respiration rates (1060, 854, 1008 g C m<sup>-2</sup>, respectively, by Lee *et al.*, 2005; Mo *et al.*, 2005; Yanagihara *et al.*, 2006), so *Sasa* ecosystems can be characterized as having a high soil respiration rate.

Clearcutting raised the contribution of soil respiration to the RE (Table 3). A quantitative discussion is difficult, however, because of the large variance in the soil respiration rate among chambers after clearcutting. The chamber system has many replicates, high measurement frequency, and a large area covered by each chamber, so the large variance is likely caused by heterogeneous soil conditions after clearcutting. In 2004 and 2005, the contribution of soil respiration to RE was nearly 100% (SD about 30%). Although RE ( $R_{sM}$ ) may have been underestimated (overestimated), respiration from aboveground parts of the vegetation clearly made only a small contribution after clearcutting. Nishimura *et al.* (2004) evaluated carbon budgets of a forest floor *S. senanensis* community in central Japan and revealed that the leaf and culm respiration of *Sasa* (103 g C m<sup>-2</sup> yr<sup>-1</sup> in average) was 23–37% of the root respiration (357 g C m<sup>-2</sup> yr<sup>-1</sup>) and 13–16% of the soil (including root) respiration (715 g C m<sup>-2</sup> yr<sup>-1</sup>). In addition, they showed that root respiration rate per dry weight was ca. 3.8 times higher than that of the aboveground part. Although *Sasa* biomass in their study site (3.0 and 2.7 t C ha<sup>-1</sup> for above- and belowground, respectively) was ca. one-fourth of that in the forest gap of our study site, their results indicate that the root respiration rate is much higher than the leaf and culm respiration and it is likely that the respiration rate from the aboveground part was less than 20–30% of the soil

respiration observed in this study and within the large standard deviation of the annual soil respiration rate.

## Conclusions

Clearcutting of a mixed forest turned the ecosystem from a weak carbon sink to a large carbon source. However, the large emission in the harvest year rapidly decreased in the following 2 years, caused by a rapid increase in GPP attributed to increases in the PAI and photosynthetic activity of the former *Sasa* understory. Considering the decreasing trend in the carbon emission rate, the ecosystem will likely become a carbon sink within the next few years. Clearcutting increased soil respiration in the following 3 years. The ratio of soil respiration to RE increased from 44% in the forest to nearly 100% after clearcutting, and aboveground parts of the vegetation contributed little to the RE after clearcutting.

## Acknowledgements

We are grateful to two anonymous reviewers for helpful comments and suggestions. This research was a collaboration between Hokkaido University, National Institute for Environmental Studies, and Hokkaido Electric Power Co., through the project 'CC-LaG Experiment,' and was partly supported by Global Environment Research Fund (B-073) from Ministry of the Environment, and grants-in-aid for scientific research (nos. 13760109, 18710002) from the Japanese Ministry of Education, Culture, Sports, Science and Technology. We thank N. Saigusa, S. Yamamoto, and M. Reichstein for technical advice and M. Takada, K. Inukai, M. Maebayashi, M. Mizuno, and the staff of the Teshio Experimental Forest for their support.

## References

- Amiro BD, Barr AG, Black TA *et al.* (2006) Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. *Agricultural and Forest Meteorology*, **136**, 237–251.
- 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. *Agricultural and Forest Meteorology*, **108**, 293–315.
- Aubinet M, Grelle A, Ibrom A *et al.* (2000) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Advances in Ecological Research*, **30**, 113–175.
- Carrara A, Kowalski AS, Neiryneck J, Janssens IA, Yuste JC, Ceulemans R (2003) Net ecosystem CO<sub>2</sub> exchange of mixed forest in Belgium over 5 years. *Agricultural and Forest Meteorology*, **119**, 209–227.
- Clark KL, Gholz HL, Castro MS (2004) Carbon dynamics along a chronosequence of slash pine plantations in north Florida. *Ecological Applications*, **14**, 1154–1171.
- Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, **107**, 43–69.
- Foken T, Wichura B (1996) Tools for quality assessment of surface-based flux measurements. *Agricultural and Forest Meteorology*, **78**, 83–105.
- Fredeen AL, Waughal JD, Pypker TG (2007) When do replanted sub-boreal clearcuts become net sinks for CO<sub>2</sub>? *Forest Ecology and Management*, **239**, 210–216.
- Fukuzawa K, Shibata H, Takagi K *et al.* (2006) Effects of clearcutting on nitrogen leaching and fine root dynamics in a cool-temperate forested watershed in northern Japan. *Forest Ecology and Management*, **225**, 257–261.
- Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa K (2007) Vertical distribution and seasonal pattern of fine-root dynamics in a cool-temperate forest in northern Japan: implication of the understory vegetation, *Sasa* dwarf bamboo. *Ecological Research*, **22**, 485–495.
- Gower ST, Richards JH (1990) Larches: deciduous conifers in an evergreen world. *BioScience*, **40**, 818–826.
- Hignett P (1992) Corrections to temperature measurements with a sonic anemometer. *Boundary-Layer Meteorology*, **61**, 175–187.
- Hirata R, Saigusa N, Yamamoto S *et al.* (2008) Spatial distribution of carbon balance in forest ecosystems across East Asia. *Agricultural and Forest Meteorology*, **148**, 761–775, doi: 10.1016/j.agrformet.2007.11.016.
- Hokkaido Government Department of Fisheries and Forestry (2006) *Statistics of Forest and Forestry in Hokkaido, 2005*. Hokkaido Government, Sapporo, Japan, 110 pp. (in Japanese).
- Howard EA, Gower ST, Foley JA, Kucharik CJ (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biology*, **10**, 1267–1284.
- Humphreys ER, Black TA, Morgenstern K, Cai T, Drewitt GB, Nestic Z, Trofymow JA (2006) Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agricultural and Forest Meteorology*, **140**, 6–22.
- Humphreys ER, Black TA, Morgenstern K, Li Z, Nestic Z (2005) Net ecosystem production of a Douglas-fir stand for 3 years following clearcut harvesting. *Global Change Biology*, **11**, 450–464.
- Kaimal JC, Gaynor JE (1991) Another look at sonic thermometry. *Boundary-Layer Meteorology*, **56**, 401–410.
- Koike T, Hojo H, Naniwa A *et al.* (2001) Basic data for CO<sub>2</sub> flux monitoring of a young larch plantation: current status of a mature, mixed conifer-broadleaf forest stand. *Eurasian Journal of Forest Research*, **2**, 65–79.
- Kolari P, Pumpanen J, Rannik Ü, Ilvesniemi H, Hari P, Berninger F (2004) Carbon balance of different aged Scots pine forests in southern Finland. *Global Change Biology*, **10**, 1106–1119.
- Kormann R, Meixner FX (2001) An analytical footprint model for non-neutral stratification. *Boundary-Layer Meteorology*, **99**, 207–224.
- Kowalski AS, Loustau D, Berbigier P *et al.* (2004) Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. *Global Change Biology*, **10**, 1707–1723.

- Kowalski AS, Sartore M, Burlett R, Berbigier P, Loustau D (2003) The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. *Global Change Biology*, **9**, 1051–1065.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology*, **7**, 755–777.
- Lee M-S, Mo WH, Koizumi H (2006) Soil respiration of forest ecosystems in Japan and global implications. *Ecological Research*, **21**, 828–839.
- Lee M-S, Nakane K, Nakatsubo T, Koizumi H (2005) The importance of root respiration in annual soil carbon fluxes in a cool-temperate deciduous forest. *Agricultural and Forest Meteorology*, **134**, 95–101.
- Lei TT, Koike T (1998) Functional leaf phenotypes for shaded and open environments of a dominant dwarf bamboo (*Sasa senanensis*) in northern Japan. *International Journal of Plant Sciences*, **159**, 812–820.
- Leuning R, King KM (1992) Comparison of eddy-covariance measurements of CO<sub>2</sub> fluxes by open- and closed-path CO<sub>2</sub> analysers. *Boundary-Layer Meteorology*, **59**, 297–311.
- Liang NS, Inoue G, Fujinuma Y (2003) A multichannel automated chamber system for continuous measurement of forest soil CO<sub>2</sub> efflux. *Tree Physiology*, **23**, 825–832.
- Liang NS, Nakadai T, Hirano T, Qu L, Koike T, Fujinuma Y, Inoue G (2004) In situ comparison of four approaches to estimating soil CO<sub>2</sub> efflux in a northern larch (*Larix kaempferi* Sarg.) forest. *Agricultural and Forest Meteorology*, **123**, 97–117.
- Litvak M, Miller S, Wofsy SC, Goulden M (2003) Effect of stand age on whole ecosystem CO<sub>2</sub> exchange in the Canadian boreal forest. *Journal of Geophysical Research*, **108**, 8225, doi: 10.1029/2001JD000854.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Machimura T, Kobayashi Y, Iwahana G, Hirano T, Lopez L, Fukuda M, Fedorov AN (2005) Change of carbon dioxide budget during three years after deforestation in eastern Siberian larch forest. *Journal of Agricultural Meteorology*, **60**, 653–656.
- Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–850.
- Mano M, Miyata A, Yasuda Y *et al.* (2007) Quality control for the open-path eddy covariance data. *Journal of Agricultural Meteorology*, **63**, 125–138 (in Japanese with English abstract and figure captions).
- 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 in Japan. *Agricultural and Forest Meteorology*, **134**, 81–94.
- Moore CJ (1986) Frequency response corrections for eddy correlation systems. *Boundary-Layer Meteorology*, **37**, 17–35.
- Nishimura N, Matsui Y, Ueyama T *et al.* (2004) Evaluation of carbon budgets of a forest floor *Sasa senanensis* community in a cool-temperate forest ecosystem, central Japan. *Japanese Journal of Ecology*, **54**, 143–158 (in Japanese with English abstract and figure captions).
- Noguchi M, Yoshida T (2004) Tree regeneration in partially cut conifer-hardwood mixed forests in northern Japan: roles of establishment substrate and dwarf bamboo. *Forest Ecology and Management*, **190**, 335–344.
- Numata M, ed (1979) *Ecology of Grasslands and Bamboos in the World*. W. Junk, The Hague, the Netherlands.
- Pypker TG, Fredeen AL (2002) Ecosystem CO<sub>2</sub> flux over two growing seasons for a sub-boreal clearcut 5 and 6 years after harvest. *Agricultural and Forest Meteorology*, **114**, 15–30.
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44B**, 81–99.
- Reichstein M, Falge E, Baldocchi D *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.
- Schulze E-D, Lloyd J, Kelliher FM *et al.* (1999) Productivity of forests in the Euro Siberian boreal region and their potential to act as a carbon sink: a synthesis. *Global Change Biology*, **5**, 703–722.
- Takagi K, Lee D, Tamai K (2007) Report on the FLUXNET synthesis workshop 2007. *AsiaFlux Newsletter*, **21**, 1–6.
- Takagi K, Nomura M, Ashiya D *et al.* (2005a) Dynamic carbon dioxide exchange through snowpack by wind-driven mass transfer in a conifer-broadleaf mixed forest in northernmost Japan. *Global Biogeochemical Cycles*, **19**, GB2012, doi:10.1029/2004GB002272.
- Takagi K, Nomura M, Fukuzawa K *et al.* (2005b) Deforestation effects on the micrometeorology in a cool-temperate forest in northernmost Japan. *Journal of Agricultural Meteorology*, **60**, 1025–1028.
- Toyooka H, Satoh A, Ishizuka M (1983) *Distribution Map of the Sasa Group in Hokkaido, Explanatory Note*. Forestry and Forest Products Research Institute, Hokkaido Branch, Sapporo, Japan, 36 pp. (in Japanese).
- Tsuji H, Nakatsuka T, Takagi K (2006)  $\delta^{18}\text{O}$  of tree-ring cellulose in two species (spruce and oak) as proxies of precipitation amount and relative humidity in northern Japan. *Chemical Geology*, **231**, 67–76.
- Vickers D, Mahrt L (1997) Quality control and flux sampling problems for tower and aircraft data. *Journal of Atmospheric and Oceanic Technology*, **14**, 512–526.
- Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, **106**, 85–100.
- Wilczak JM, Oncley SP, Stage SA (2001) Sonic anemometer tilt correction algorithms. *Boundary-Layer Meteorology*, **99**, 127–150.
- Yanagihara Y, Shibata H, Matsuura Y, Koike T (2006) Effects of soil and vegetation types on soil respiration rate in larch plantations and a mature deciduous broadleaved forest in northern Japan. *Eurasian Journal of Forest Research*, **9**, 79–95.