



In situ comparison of four approaches to estimating soil CO₂ efflux in a northern larch (*Larix kaempferi* Sarg.) forest

Naishen Liang^{a,*}, Toshie Nakadai^a, Takashi Hirano^b, Laiye Qu^b,
Takayoshi Koike^c, Yasumi Fujinuma^a, Gen Inoue^a

^a Center for Global Environmental Research, National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan

^b Graduate School of Agriculture, Hokkaido University, Sapporo, Japan

^c Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan

Received 2 February 2003; received in revised form 20 August 2003; accepted 8 October 2003

Abstract

Soil surface CO₂ efflux (F_c) in a 45-year-old northern larch forest was continuously measured, using a multichannel automated chamber system, between June and October, 2001. The results were compared with periodic measurements obtained at the same site with an LI-6400 chamber system and an open-top chamber system, and also with continuous measurements obtained at the same site with a soil CO₂ gradient system. The diurnal and seasonal changes in F_c measured by the automated chamber and soil CO₂ gradient approaches followed the soil temperature patterns. We found only a weak correlation between F_c and soil moisture, probably because the volumetric soil moisture (30–40% at 95% confidence interval) in this larch forest favors microbial and root activities. Among the four approaches, the LI-6400 chamber yielded a substantially higher F_c value than the other three approaches. The open-top chamber gave higher values of F_c than the automated chamber at efflux rates below $3.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ and lower values above this level; however, the results of both these approaches were closely correlated ($R^2 = 0.87$, $n = 105$). Although F_c measured with the soil CO₂ gradient approach was, on average, 45% higher than the results of the automated chamber approach, the correlation between the two techniques was good ($R^2 = 0.77$, $n = 2945$). The annual soil CO₂ efflux estimated by the automated chamber (665 g C m^{-2}) and open-top chamber (720 g C m^{-2}) matched the total annual ecosystem respiration, as estimated by the above-canopy eddy covariance method. However, the LI-6400 chamber and soil CO₂ gradient approaches gave higher values for annual soil CO₂ efflux than the eddy covariance method. © 2003 Elsevier B.V. All rights reserved.

Keywords: AsiaFlux; Automated chamber; Forest ecosystem; Open-top chamber; Soil CO₂ gradient; Soil temperature

1. Introduction

Knowledge of CO₂ emissions from terrestrial soils is critical to estimating future atmospheric CO₂ concentrations and global temperatures, because global warming may trigger positive feedback between the

atmosphere and terrestrial ecosystems via changes in soil and plant respiration (Cox et al., 2000; Prentice et al., 2001). Soil CO₂ efflux (F_c) has been estimated to account for 60–90% of the total ecosystem respiration in temperate forests (Goulden et al., 1998; Valentini et al., 2000; Law et al., 2001). The net ecosystem production is ultimately the result of a delicate equilibrium between the two largest CO₂ fluxes—photosynthesis and F_c —which show strong diurnal, seasonal, and annual variations (Valentini et

* Corresponding author. Tel.: +81-29-8502774;

fax: +81-29-8502960.

E-mail address: liang@nies.go.jp (N. Liang).

al., 2000). Therefore, accurate measurement of F_c is critical for modeling the carbon cycle dynamics of an ecosystem. However, for technical reasons, obtaining valid F_c measurements is difficult (Norman et al., 1997; Janssens et al., 2000; Liang et al., 2003).

Various approaches to measuring F_c have been adopted, including the use of static and dynamic chambers, micrometeorological methods (such as eddy covariance), and soil CO₂ gradient methods. F_c in forests has usually been estimated by one of four chamber-based approaches: (1) static chambers containing either an alkali solution (Kirita, 1971) or soda lime (Biscoe et al., 1975) to absorb the respired CO₂; (2) static chambers from which air samples are taken with a syringe and subsequently analyzed by gas chromatography (Hutchinson and Mosier, 1981); (3) non-steady-state dynamic chambers in which the increase in CO₂ concentration within the chamber headspace is monitored and quantified (Livingston and Hutchinson, 1995); and (4) steady-state dynamic chambers coupled to an infrared gas analyzer (IRGA) (Rayment and Jarvis, 1997), by which the CO₂ concentrations in the air streams entering and exiting the chamber are measured; then F_c is computed as proportional to the products of the concentration difference and the flow rate through the chamber. Some studies have compared measurements obtained with static and dynamic chambers, and the general conclusion is that dynamic chambers are more accurate than static chambers (Rochette et al., 1992; Nakadai et al., 1993; Nay et al., 1994; Janssens et al., 2000) and can be operated in either steady-state or non-steady-state mode. However, both static and non-steady-state techniques give periodic measurements, which are often used to estimate daily and even annual F_c by linear interpolation. Errors can be significant, because changes in F_c between measurements are not always predictable and vary with the time of day (Liang et al., 2003). Because of the temporal variations in F_c , long-term measurement of F_c with automated chamber systems is required (Drewitt et al., 2002; Liang et al., 2003).

Most steady-state and non-steady-state chamber systems measure F_c at only one location, because an IRGA is generally connected to a single chamber (Norman et al., 1997; Janssens et al., 2000). However, high spatial (and temporal) variations in F_c have been found even in relatively uniform agricultural fields (Rochette et al., 1991; Nakadai et al., 1996),

grasslands (McGinn et al., 1998), forests (Kelliher et al., 1999; Liang et al., 2003), and bare soil (Nakadai et al., 1993, 2002), indicating the need for analyzing large numbers of samples to obtain a representative F_c value for an ecosystem. In a forest ecosystem, a critical question concerning measurement of F_c is where should the chamber be placed—near a tree trunk, midway between two neighboring tree trunks, far away from a tree trunk, or randomly on the forest floor?

When a single chamber is used, it is obviously impossible to cover spatial variation (Drewitt et al., 2002; Liang et al., 2003). Several automated systems have been developed for continuous sequential measurement of F_c at several sites within the AmeriFlux (Crill et al., 2000; Law et al., 2001; Drewitt et al., 2002) and CarboEurope networks (John Grace, Edinburgh Univ., pers. commun.), but these systems comprise only 3–6 small (0.06–0.20 m²) chambers. Recently, Liang et al. (2003) reported a multichannel automated chamber system for long-term measuring of F_c within the AsiaFlux network. The system comprises 16 large (0.81 m²) automated chambers and is expected to give simultaneous data on spatial and temporal variations in F_c (Liang et al., 2003).

Another factor to keep in mind is that prolonged continuous measuring of F_c at one location with a chamber may modify the chamber environment relative to ambient conditions of soil moisture and temperature (Norman et al., 1997; Janssens et al., 2000) and alter the CO₂ diffusion gradient within the soil profile (for a review, see Davidson et al., 2002). The soil CO₂ gradient technique (de Jong and Schappert, 1972) and the eddy covariance technique (Baldocchi et al., 1997), which do not modify the microenvironment of the soil surface or the CO₂ concentration gradient within the soil profile, have also been applied to measure F_c . However, successful application of the eddy covariance technique is often limited by the expense of the system and by atmospheric and topographical conditions. In this study, an improved soil CO₂ gradient technique was applied to improve the long-term measurement of F_c .

Larch (*Larix*) forests are the dominant forest type through northeastern Asia to central Siberia. In Hokkaido, Japan, larch plantations (470,000 ha) account for about one third of all forests, because of their high productivity. However, the carbon budget

of larch ecosystems has received little attention, and their F_c is not known. The net ecosystem production (NEP) of a larch forest has been routinely measured by the eddy covariance method at the Tomakomai flux site since the autumn of 2000 (Hirano et al., 2003a). Measurement errors always occur concurrent with rain, snow, and even mist. In addition, stable stratification of the atmosphere at night generally makes the eddy covariance measurement unreliable. Therefore, together with the CO_2 flux measurement over the canopy, appropriate techniques to estimate F_c must be identified and adopted.

The objectives of this study were: (1) to compare four approaches for measuring F_c at the same site; (2) to evaluate the effects of soil temperature and moisture on F_c ; and (3) to choose the most accurate technique for measuring F_c at the Tomakomai flux site. The four approaches for measuring F_c were: (1) a widely used non-steady-state LI-6400 chamber system (LI-COR, Lincoln, NE, USA); (2) a steady-state chamber system with 9 open-top chambers; (3) a steady-state chamber system with 16 automated chambers; and (4) a soil CO_2 gradient system. The eddy covariance method was considered unsuitable for measuring F_c at the Tomakomai flux site because the forest floor is thickly covered with undergrowth (see site description), and the eddy covariance method would underestimate day-time F_c and overestimate night-time F_c because it integrates F_c and understory gas exchange (Norman et al., 1997; Janssens et al., 2000).

2. Materials and methods

2.1. Tomakomai site description

The field study was carried out at the Tomakomai flux site (lat 42°44'N, long 141°31'E, 125 m elevation), Hokkaido, Japan. The forest is a 45-year-old Japanese larch (*Larix kaempferi* Sarg.) plantation, interspersed with Japanese spruce (*Picea jezoensis* Sieb. et Zucc.) and mixed broad-leaved species (*Betula* spp.) in the gaps. In 1999, the stand density of trees with trunk diameter at breast height (DBH, 1.3 m high) larger than 5 cm was 1087 trunks ha^{-1} ; the total basal area was 23.2 $\text{m}^2 \text{ha}^{-1}$, and the trunk volume averaged 151 $\text{m}^3 \text{ha}^{-1}$. The tree canopy was 12.4–15.2 m in height (13.8 m average), with DBH ranging from

6 to 48 cm (18 cm average). The base of the canopy was 7.9 m above the ground, and the overstory canopy leaf area index (LAI; m^2 projected tree leaf area per m^2 ground area) was 2.1 at the maximum, measured with a LI-2000 canopy analyzer (LI-COR) from late June to early September. The forest understory was densely covered by buckler fern (*Dryopteris crassirhizoma*), with occasional bracken (*Dryopteris expansa*) and Japanese spurge (*Pachysandra terminalis* Sieb. et Zucc.). The height and LAI of the understory were 0.5 and 3.0 m, respectively, in late June 2001 (Hirano et al., 2003a). The average biomass of the understory was 1.24 t ha^{-1} .

The site is characterized by a humid continental climate with cold winters and cool summers but without apparent wet or dry seasons. Mean annual precipitation is approximately 1250 mm; and mean annual temperature is 7.3 °C, with the mean monthly temperature ranging from 19.1 °C in August to -3.2 °C in January. The site is essentially flat, with a gentle slope of 1–2°.

The soil is homogeneous, well-drained, arenaceous, and developed from volcanoclastic sediment. The soil is classified as an immature Volcanogenous Regosol (Pumice). The soil is a sparse compacted till at a depth of 15–20 cm. The litter layer is 1–2 cm thick. Below the litter layer is a mat of organic layer between 5 and 10 cm thick and containing abundant fine roots; the next-deepest layer is fragments of porous pumice stone (0.5–3.0 cm in diameter) with some coarse roots. Scarcely any roots are found below a depth of 20 cm. Because of the shallow root distribution, several tens of hectares of trees were blown down by a tornado about 4 km to the east of the flux observation tower in 1998. The root biomass was estimated to be 13.1 t ha^{-1} . The soil is weakly acidic, pH 5.0–6.0, and poor in nutrients.

2.2. Measurement system description

Four approaches to measurement of F_c were compared in situ at the Tomakomai flux site during the growing season between June and October 2001.

2.2.1. LI-6400 chamber system

We established four 2 m × 2 m plots around the canopy-access tower at the Tomakomai flux site and deployed a commercially available LI-6400 chamber system (LI-COR) to measure F_c (Fig. 1). The

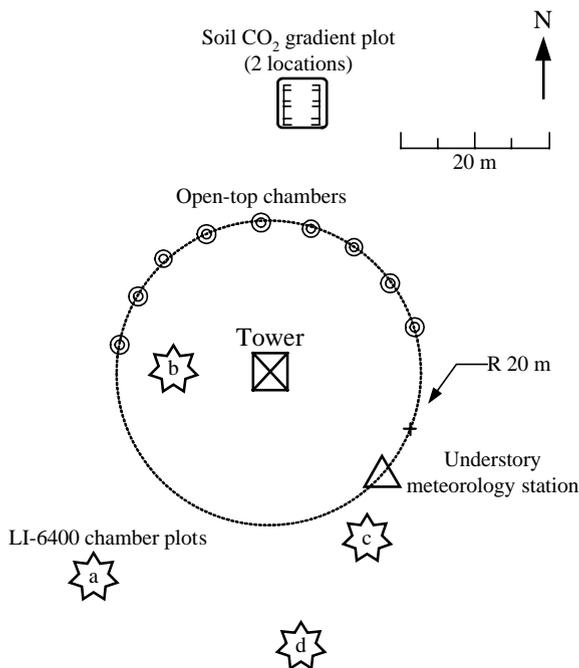


Fig. 1. Layout of soil CO₂ efflux measurements at Tomakomai flux site, showing the locations of the canopy-access tower and the understory meteorological station, as well as the locations of the LI-6400 chambers (plots a, b, c, and d), open-top chambers (9 double circles), automated chambers (16 large chambers), and soil CO₂ gradient system (2 locations). The distances between the tower and the open-top chambers, soil CO₂ gradient plot, and the center of automated chamber plot are 20, 40, and 70 m, respectively.

LI-6400 system is a portable system that utilizes gas-exchange principles to measure photosynthesis in steady-state mode. However, it can instead be used to measure F_c when fitted with a null-balance soil chamber (LI-6400-09) and operated in flow-through, non-steady-state mode. We took 5 samples in each plot, for a total of 20 samples at the site. The measurement errors associated with disturbance of the soil and roots were minimized by permanently inserting chamber collars 3 cm into the soil as an interface between the soil and the chambers. All vegetation was removed from inside the collars prior to the measurements. Mixed chamber air was fed from the top of the chamber to an IRGA, which was attached directly to the chamber, by a micro-blower inside the IRGA housing. Air was returned from the IRGA to the chamber through a manifold near the soil surface

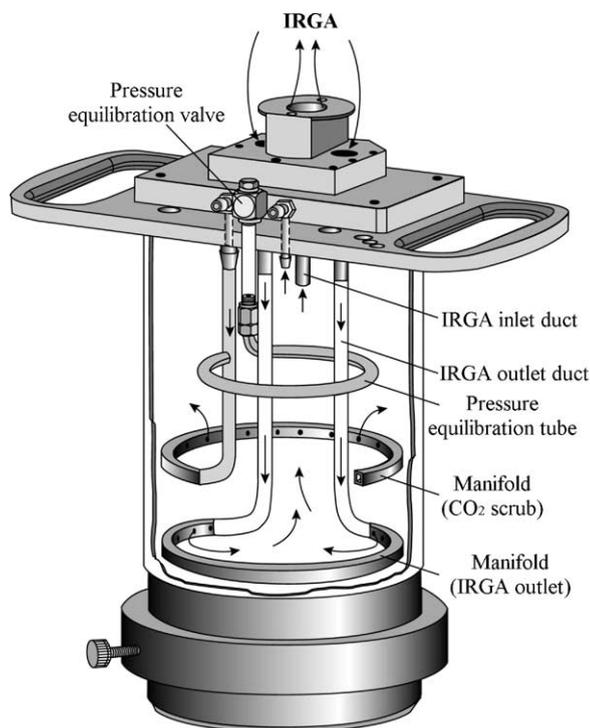


Fig. 2. Diagram of LI-6400 soil CO₂ efflux chamber.

(Fig. 2). F_c was calculated from the increase in CO₂ concentration within the chamber headspace with time. The volume of the entire system was 0.99 l, and the enclosed soil surface area was 71.6 cm². The LI-6400 chamber system employed a pressure equilibration valve so that pressures inside and outside the chamber were in dynamic equilibrium, to minimize the effects of chamber pressurization on the measured F_c (Fig. 2). We sampled F_c about every 4 weeks. Measurement activities typically started at 1230 and ended at 1600. We used the average of the measurements across all 20 samples for analysis.

2.2.2. Open-top chamber system

We developed an open-top chamber system for measuring F_c in forest ecosystems. The system consists of nine open-top chambers, a controller, an IRGA (LI-6262; LI-COR), and a datalogger (CR10X; Campbell Scientific, Logan, UT, USA). The chamber has a flow-through, steady-state design, and F_c is measured as the difference between the CO₂ concentrations entering and exiting the chamber. The

chamber is cylindrical, constructed of opaque PVC pipe with the top open to eliminate the pressure difference between the inside and outside of the chamber. The chamber is similar to that described by Fang and Moncrieff (1998), except that it is larger (diameter: 30 cm; height: 20 cm). Therefore, each chamber can sample about 706 cm² of soil area. Chamber air was sampled from a chimney attached to the top of the chamber. A ring of PVC pipe, 1 cm inside diameter, was fixed to the inner wall of the chamber frame 10 cm from the lower edge. Many small holes (2 mm) were evenly distributed in the pipe for sampling the ambient air. Additional information can be found in Fang and Moncrieff (1998). Both the chamber and ambient air streams were withdrawn at 3.01 min⁻¹; the rate was monitored and controlled by mass flow controllers (SEF-21A; STEC, Tokyo, Japan). The corresponding speed of air movement 2 cm above the soil surface within the chamber was about 0.007 m s⁻¹. A mixing fan was not placed inside the chamber, because it could have induced leakage through the inlet aperture.

Nine chamber collars were installed in early April 2001, after the snow had melted. The collars were placed 6 m away from each other in an arc around the canopy-access tower and about 20 m to its north (Fig. 1). The controller was designed to allow the operation of nine chambers in sequence in a 1 h cycle, each being run for 400 s. In the preliminary study, we observed that after a light rain the soil was wet near the inside edge of the chamber wall but dry in the center of the chamber. Therefore, we did not measure F_c during rain events. Measurements were conducted once a month, and normally began before 1200 and ran continuously for 30 h. All vegetation was removed from inside the collars prior to the measurements. Soil-surface CO₂ efflux (F_c , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated as

$$F_c = (C_S - C_R) \frac{Q \times 10^3}{V_{\text{air}} A} \quad (1)$$

where C_S and C_R are the chamber and ambient CO₂ concentrations ($\mu\text{mol mol}^{-1}$), respectively; Q is the volume flow rate through the chamber ($\text{m}^3 \text{s}^{-1}$); A is the soil surface area covered by the chamber; and V_{air} is the molar volume of air. The values of F_c from the nine chambers were averaged over each 1 h cycle.

2.2.3. Multichannel automated chamber system

We deployed a multichannel automated chamber system intended to measure F_c over entire seasons, as described by Liang et al. (2003). The measurement plot was established approximately 70 m to the southeast of the tower (Fig. 1). The automated chamber system had a flow-through, steady-state design. In brief, the system comprised 16 automated chambers, a 16-channel gas sampler, an IRGA (LI-6262; LI-COR), and a datalogger (CR10X, Campbell Scientific). The automated chambers (0.9 m × 0.9 m × 0.5 m, L × W × H) were constructed of clear PVC (1 mm) glued to a frame of square (30 mm × 30 mm) plastic-coated steel pipe (also see the photograph in Liang et al., 2003). Between measurements, the two sections of chamber lid were raised to allow precipitation and leaf litter to reach the enclosed soil surface, so as to keep the soil conditions as natural as possible. The chamber lids were raised and closed by two pneumatic cylinders (MCM25, Techno Fronto, Hitachi, Japan). When a chamber was closed, approximately 125 l min⁻¹ of well-buffered ambient air was drawn into it through a PVC accordion pipe (25 mm in diameter) by a micro-fan blower (TCF-12, Techno Fronto) located at an inlet on the chamber side wall. Chamber air was exhausted through a 100-mm-diameter downward-pointing elbow opposite the air inlet, resulting in overpressurization of 0.22 Pa. Two mixing fans (KMFH-12B; Nihon Blower, Tokyo, Japan) inside each chamber maintained a wind speed between 0.1 and 0.2 m s⁻¹ at 2 cm above the soil surface, as measured with an anemometer (model 6521, Kanomax Japan, Inc., Osaka, Japan) at 16 points on a 20 cm × 20 cm grid.

The 16 chambers were placed randomly on the forest floor within an area 30 m across. All the vegetation inside the chambers was removed weekly. The length of the polyurethane tubing used to sample air from each chamber was 20 m. Over the course of an hour, the 16 chambers were closed in sequence by a home-made 16-channel gas sampler controlled by the CR10X. In the previous study, the equilibration time of the chamber was found to be 18–20 min (Liang et al., 2003). Therefore, six chambers in this study were closed at the same time, in order to finish a cycle of measurements within 1 h. Ambient air and chamber air were withdrawn continuously from

all 16 chambers, but only the air from the first of the six closed chambers was pumped to the IRGA. Flow rates of both ambient and chamber air were monitored and controlled by mass flow controllers (SEF-21A, STEC). We set the sampling period for each chamber to 225 s. The CR10X acquired output from the LI-6262 at 1 s intervals and averaged and recorded it every 5 s. Because the measurement mode used by the automated chamber system was the same (i.e., steady state) as for the open-top chamber system, we used Eq. (1) to calculate F_c . Forest floor soil CO₂ efflux was averaged from the 16 chambers over each 1 h cycle.

2.2.4. Soil CO₂ gradient system

We developed a soil CO₂ gradient system intended for long-term measurements of soil CO₂ effluxes (Hirano et al., 2000, 2001, 2003b). The soil CO₂ gradient technique relies on measurements of CO₂ concentrations at two or more depths within the soil profile. We installed the cylindrical probes (18.5 mm diameter, 155 mm long) of IRGAs (GMT222, Vaisala, Helsinki, Finland) horizontally at depths of 0, 2, 4, 6, 11, and 13 cm. To keep the sensors dry, we enclosed them in polytetrafluoroethylene (PTFE) socks (TB-1419, Sumitomo Electric Fine Polymer, Osaka, Japan). The PTFE sock can keep water outside while allowing gases to diffuse across it. To measure CO₂ concentrations at specific soil depths, we enclosed the probes in acrylic-pipe casings (Fig. 3). The casing was sealed to the probe on the upper side with three rubber gaskets. The opening (1 cm × 7 cm)

on the lower side was covered with a stainless-steel mesh (0.5 mm mesh) to prevent wet soil from entering the casing, but to allow CO₂ molecules to diffuse into the sensor for measurement of the CO₂ concentration.

We made two replications, at two locations 60 cm apart (Fig. 1). This technique was different from the chamber approaches, in that, after burying the probes, we did not disturb the vegetation surrounding them. In a preliminary study, we found that the soil temperature adjacent to the probe could be 1–2 °C higher than that of the surrounding soil, resulting from the heat of the infrared lamp inside the probe. Therefore, all probes in this study were powered on at the 24th minute of each hour, under control of a CR10X datalogger (Campbell Scientific). After the probes were powered on, they were allowed to warm up for 5 min before they recorded the output with the CR10X through a multiplexer (AM25T, Campbell Scientific) at 10 s intervals over the next 2 min. Then the probes were powered off until the 24th minute of the next hour.

Under steady-state conditions, the interlayer soil CO₂ efflux (F_c , $\mu\text{mol m}^{-2} \text{s}^{-1}$) is determined from Fick's Law of diffusion:

$$F_c = -D_s \frac{\partial C}{\partial z} \quad (2)$$

where D_s is the soil gas diffusion coefficient ($\text{m}^2 \text{s}^{-1}$), C is the CO₂ concentration at a given soil depth ($\mu\text{mol m}^{-3}$), and z is the depth (m). The negative sign indicates that the efflux is in the direction of

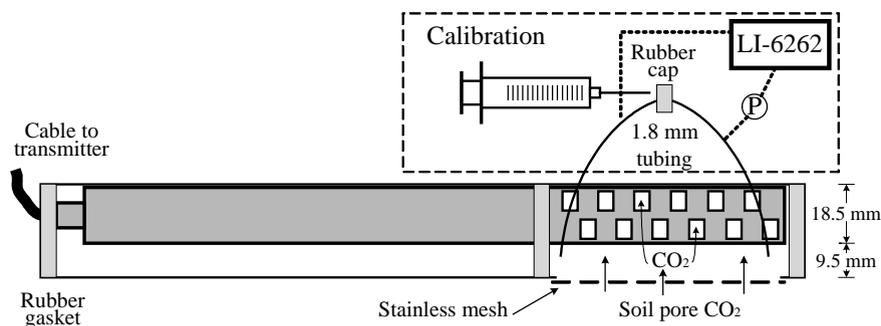


Fig. 3. Schematic of sensor used for measuring CO₂ concentration at specific soil depths. Two calibration methods (in the dashed box): (1) sample is removed from the sensor casing with a 2 ml syringe connected to a nylon tube (1.8 mm outer diameter, 0.8 mm inner diameter) and subsequently analyzed by gas chromatography; (2) CO₂ concentration in the casing is measured in situ by circulating the sample through an analyzer (LI-6262) by means of a micro pump (P) (8 ml min^{-1} , 120SPI, Bio-Chem Valve, Boonton, NJ, USA). See text for other details.

decreasing concentration. The soil gas diffusion coefficient was measured in the laboratory as a function of water content by purging oxygen from a diffusion chamber and measuring the change in oxygen concentration with time.

2.3. Environmental measurements

Inside the open-top and automated chambers, air and soil temperatures were measured with thermocouples, and volumetric soil moisture inside each chamber was measured as follows. For the LI-6400 chambers, one soil moisture sensor was installed in each plot. Volumetric soil moisture was measured by time domain reflectometry (TDR) (CS615 sensors inserted in the soil on an angle; Campbell Scientific).

Half-hourly cumulative rainfall was measured by using tipping buckets with a resolution of 0.1 mm (model 52202; Young, Traverse City, MI, USA); they were located 25 m above the top of the tower and 1 m above the ground at the understory meteorological station (Fig. 1). Soil temperatures at depths of 0, 5, 10, 20, and 50 cm were measured with platinum resistance thermometers (C-PTWP; Climatec, Tokyo, Japan) in four replications at the understory meteorological station. Also, four replications of volumetric soil moisture were measured at depths between 5 and 15 cm. Half-hourly mean wind speeds were measured 1 m above the ground. Ancillary meteorological and soil environmental data were acquired with a CR23X datalogger through AM25T multiplexers (Campbell Scientific).

2.4. Data analysis

Statistical analysis was performed with Version 5.0 of the StatView statistical software package (SAS Institute, Inc., Cary, NC, USA). Individual chambers or sampling points were used as the statistical units for analyzing the spatial variation. The coefficient of variation (CV) was used to represent the spatial variation in F_c . We used averaged data to compare systematic differences among the four approaches. Student's *t*-test was used to test the difference in F_c between the approaches, and regression analysis was used to examine the relationships between F_c and environmental variables. To examine the temperature

response of F_c , we conducted regression analysis using the temperature response function:

$$F_c = a \exp^{bT_{\text{soil}}} \quad (3)$$

where F_c is the CO₂ efflux at soil temperature T_{soil} at 5 cm depth, coefficient a is the efflux rate at temperature zero (i.e., the basal rate), and coefficient b is the sensitivity of F_c to temperature. The b values were also used to calculate the Q_{10} quotient:

$$Q_{10} = \exp^{10b} \quad (4)$$

The Q_{10} coefficient is the relative increase in F_c for a 10 °C change in soil temperature. In a preliminary analysis, we found no significant differences in soil physics, i.e., temperature and moisture, among the four plots. To reduce the uncertainties of systematic error associated with inter-plot variation, we used environmental data obtained at the tower and the understory meteorology station to make comparisons among approaches.

3. Results

3.1. Temporal and spatial variability of forest floor CO₂ efflux

Based on the seasonal changes in hourly soil temperature and moisture (Fig. 4a) and in F_c measured with the automated chamber, open-top chamber, and LI-6400 chamber (Fig. 4b) and soil CO₂ gradient approaches (Fig. 4c), we observed several interesting features.

3.1.1. Seasonal variation

During the entire measurement period, F_c values obtained by all four approaches ranged from 1 to 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and showed significant seasonality, with lower values in the middle of June and at the end of October, and higher values between the first day of July and the middle of September. The mean daily soil temperature at 5 cm depth was about 10 °C in the middle of June and, although fluctuating, increased until the end of June; it remained at a high value of 15–17 °C from the first day of July until the middle of September; then it decreased gradually to below 10 °C by the end of October. However, we found low F_c values during August with the continuous measurements by the

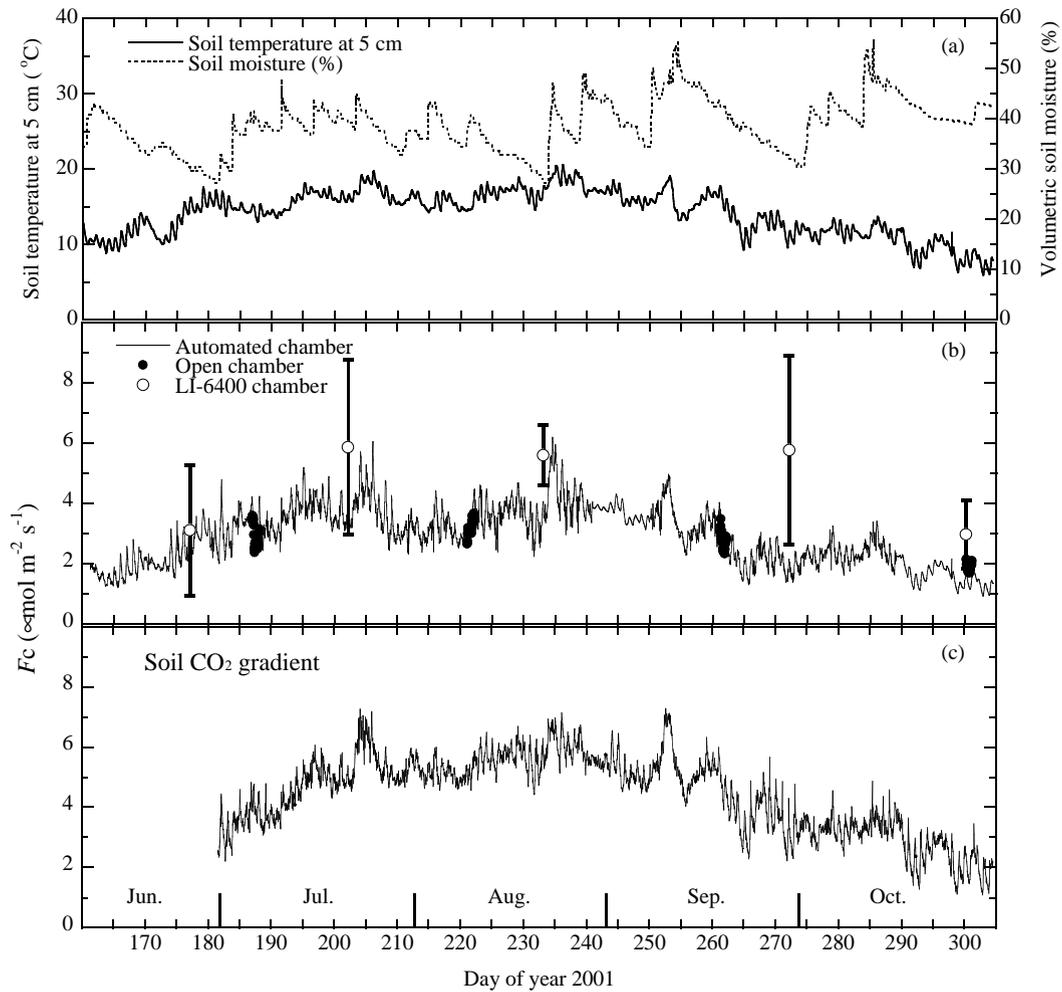


Fig. 4. Seasonal trends in hourly soil temperatures at 5 cm depth (a, solid line) and volumetric soil water content at 5–15 cm depth (a, dashed line), mean soil CO₂ effluxes measured with the automated chambers (b, solid line), LI-6400 chamber (b, open circles with S.D.), open-top chambers (b, closed circles), and soil CO₂ gradient approach (c) in a 45-year-old larch forest ecosystem between June and October 2001.

automated chamber and soil CO₂ gradient approaches. Similarly, relatively lower soil temperatures were observed than expected in August in consequence of the cool summer in the Hokkaido region in 2001.

3.1.2. Diurnal variation

F_c also showed asymmetric diurnal patterns that followed the same pattern as the diurnal changes in soil temperature (Fig. 5). Generally, the lowest daily F_c occurred just before sunrise (around 0700), as did the minimum soil temperature at 5 cm depth. F_c reached

its highest values in the afternoon, coinciding with the maximum daily soil temperatures. Furthermore, the range of diurnal variation in F_c values, surface soil temperature, and photosynthetic active radiation (PAR) was generally greater on sunny days than on cloudy days (Fig. 6). However, we found no significant difference in total daily efflux between sunny and cloudy days. For example, the magnitude of daily CO₂ efflux was the same, 4.7 g C m⁻² day⁻¹, on the cloudy day of July 24 as on the following sunny day of July 25 (Fig. 6).

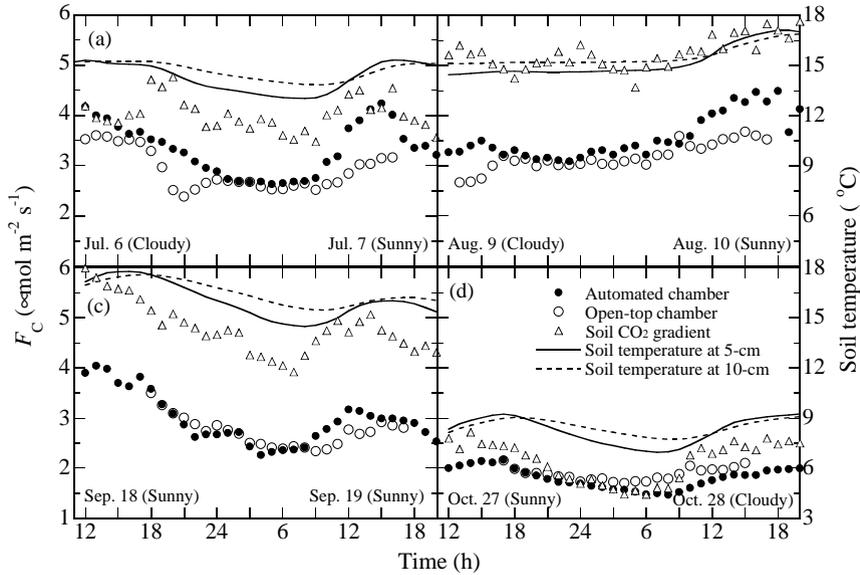


Fig. 5. Hourly soil CO₂ effluxes measured by the automated chambers, open-top chambers, and soil CO₂ gradient technique and soil temperatures at 5 and 10 cm depths. Data of soil CO₂ effluxes and temperatures were collected on the same days (4 days) as the open-top chamber, automated chamber and soil CO₂ gradient approaches were concurrently employed. Data obtained with the LI-6400 chamber are not plotted, because measurements were not made on the same days as with the open-top chambers.

3.1.3. Measurement variation

The absolute estimated F_c values depended on the measurement approach. Throughout the measurement period, a mean F_c value of $2.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ (range: $0.9\text{--}6.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) was observed with the automated chamber approach; and means of 4.7 (range: $3.0\text{--}5.9$), 2.7 (range: $1.7\text{--}3.7$), and 4.4 (range: $1.1\text{--}7.3$) $\mu\text{mol m}^{-2} \text{s}^{-1}$ were obtained with

the LI-6400 chamber, open-top chamber, and soil CO₂ gradient approaches, respectively (Fig. 4).

3.1.4. Spatial variation

The spatial variation in F_c was associated with the size of the chamber. During the entire measurement period, the LI-6400 chamber (size: 71.6 cm^2) system showed an average CV of up to 44%, but the automated

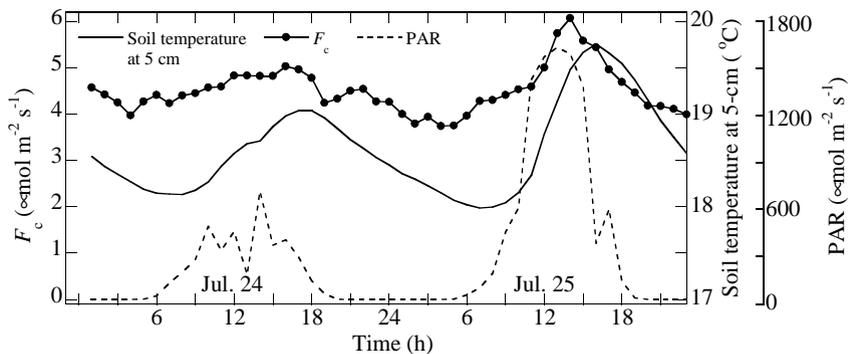


Fig. 6. Asymmetrical diurnal variation in soil CO₂ efflux measured by the automated chambers, in soil temperature at 5 cm depth, and in photosynthetic active radiation (PAR) on a cloudy day of July 24 (left) and sunny day of July 25 (right).

chamber (8100 cm²) system gave an average CV of 16%, and the open-top chamber (706 cm²) system showed an intermediate value of 30%. Moreover, we obtained higher values of F_c with chambers that were located close to tree trunks (<1.5 m) and lower F_c with chambers that were placed farther from tree trunks (>2 m) (data not shown).

3.2. Temperature and moisture responses of forest floor CO₂ efflux

Fig. 7 shows the hourly average F_c values obtained with the different approaches plotted against the soil temperature at 5 cm depth. In general, the relation of F_c to the soil temperature at 5 cm depth is described well by an exponential function (Eq. (3)). Although F_c measured with all four approaches showed an exponential relation to soil temperature, the values of the correlation coefficients (R^2) differed from one another (Fig. 7). R^2 for the automated chamber and soil

CO₂ gradient approaches exceeded 0.84, but R^2 for the LI-6400 chamber was as low as 0.10 and R^2 for the open-top chamber showed an intermediate value R^2 of 0.73. In addition, the soil CO₂ efflux quotient Q_{10} differed significantly among the measurement approaches, with higher Q_{10} for the automated chamber and soil CO₂ gradient (3.0 and 2.8, respectively) approaches and lower Q_{10} for the open-top chamber and LI-6400 chamber (1.9 and 1.6, respectively).

During the 143 consecutive days of measurements, there were 51 rainy days (days with precipitation ≥ 1.0 mm), and the total precipitation was 763 mm. Although the soil moisture changed in a wave pattern associated with the rainfall events, there was no discernible seasonal trend (Fig. 4a). The volumetric soil moisture was between 25 and 55% (95% confidence interval of 30–40%).

To evaluate the roles of soil moisture and temperature on soil CO₂ efflux, the following empirical model based on the soil carbon cycle in Japanese coniferous

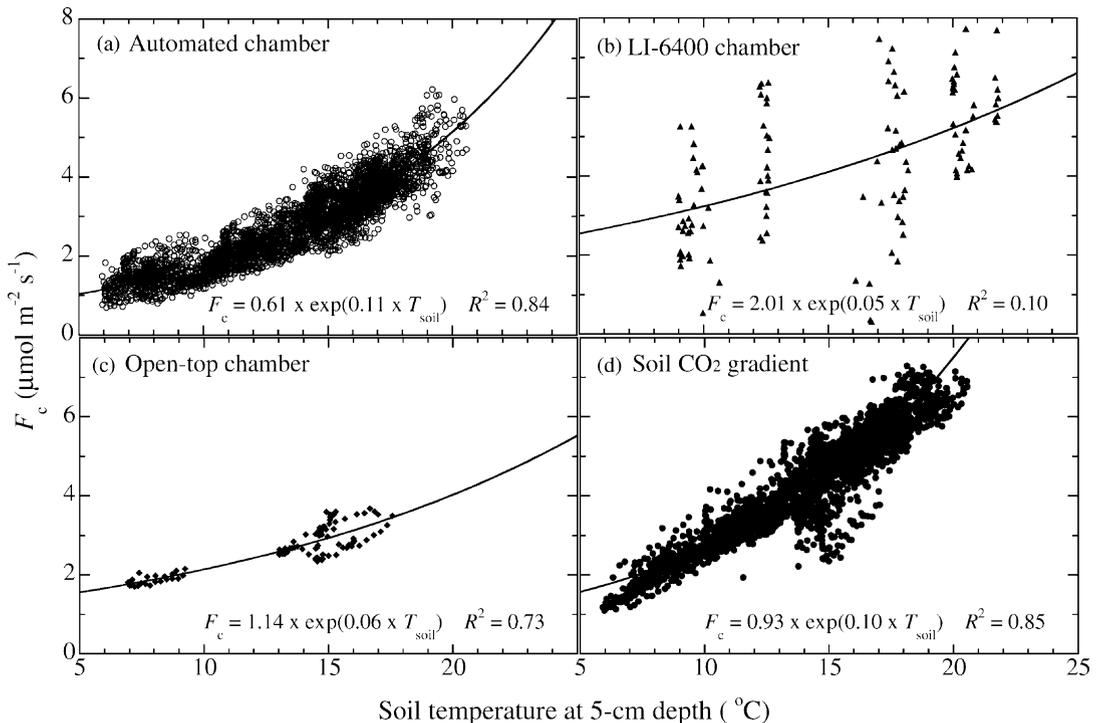


Fig. 7. Effect of soil temperature (5 cm depth) on soil CO₂ effluxes measured with the automated chambers (a), LI-6400 chamber (b), open-top chambers (c), and soil CO₂ gradient technique (d). The data points are all of the data for the whole measurement period. The lines were fit to Eq. (3).

forests was applied (Nakane, 1994):

$$F_c(\theta, T_{\text{soil}}) = a \exp^{bT_{\text{soil}}} \left[1 - \left(1 - \frac{\theta}{c} \right)^2 \right] \quad (5)$$

where T_{soil} is the soil temperature at 5 cm depth, θ is the soil volumetric water content ($\text{m}^3 \text{m}^{-3}$), and a , b , and c are fitted parameters. In the present study, the fitted parameters were estimated by using a constrained nonlinear least-squares parameter-searching procedure (Optimization function of Non-linear Least Squares Solver, S-PLUS, Insightful Corp., Seattle, WA, USA). First, F_c obtained by each approach was normalized according to the best-fit values of $F_c(T_{\text{soil}}) = a \exp^{bT_{\text{soil}}}$ in Eq. (5) and plotted against the soil moisture (Fig. 8). Then the F_c -moisture response curves were established by combining these “temperature normalized” F_c values with Eq. (5). The low correlation coefficients (R^2) shown in Fig. 8 indicate that forest floor CO_2 efflux at the Tomakomai site shows weak agreement with soil moisture throughout the entire growth season.

3.3. In situ comparisons of measurement approaches

3.3.1. Automated chamber system versus LI-6400 chamber system

In Fig. 9a (as in Fig. 4b), each data point for the LI-6400 chamber represents the mean and standard deviation of 20 sampling points on a measurement date. Furthermore, results obtained with the LI-6400 chamber could approximate only the maximum F_c value, because the measurements were made during the time when the soil was generally at its maximum temperature. Similarly, the data points for the automated chamber are the means of the 16 chambers during the same period of time. We found a significant difference ($P = 0.001$) between results obtained with the automated chamber and the LI-6400 chamber, and then compared with the results obtained with the automated chamber; the LI-6400 chamber usually yielded much higher F_c values, except in June (Fig. 4). Moreover, there was poor correlation between the results obtained by these two approaches ($R^2 = 0.23$, $n = 5$; Fig. 9a).

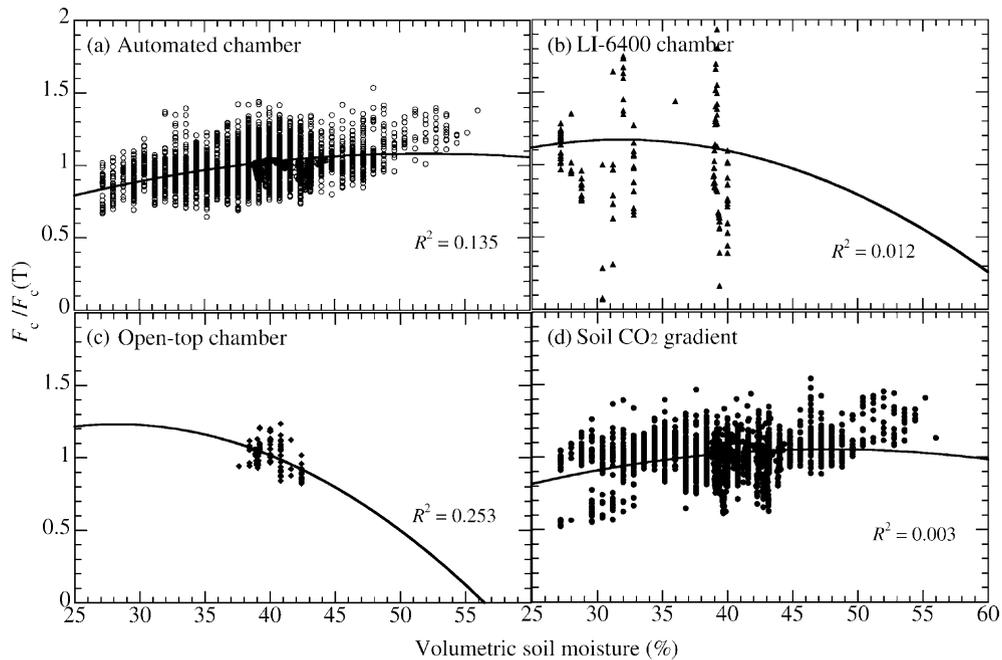


Fig. 8. Hourly soil CO_2 effluxes obtained with the automated chambers (a), LI-6400 chamber (b), open-top chambers (c), and soil CO_2 gradient technique (d), normalized according to the best-fit line of Eq. (3) and plotted against the volumetric soil water content. The solid line in each plot is the nonlinear least-squares best fit of the θ terms of Eq. (5).

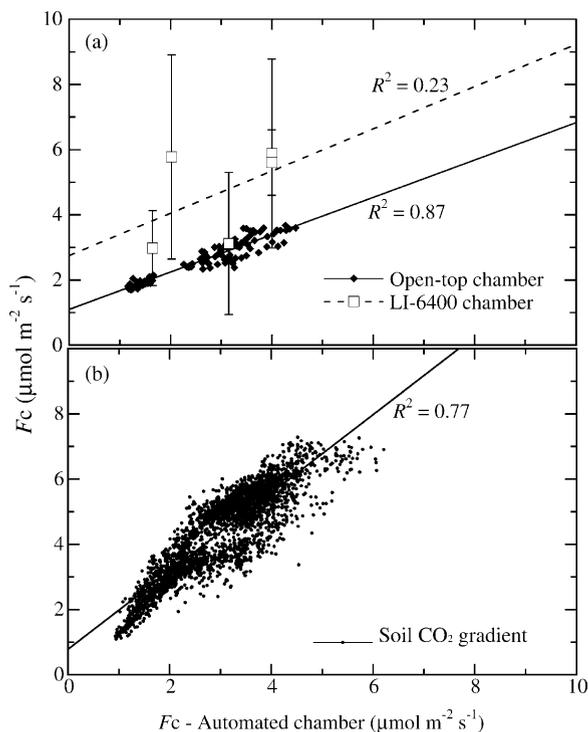


Fig. 9. Same-site comparison of soil CO₂ efflux values measured in automated chambers with results obtained from (a) the LI-6400 chamber and open-top chambers and (b) the soil CO₂ gradient technique.

3.3.2. Automated chamber system versus open-top chamber system

Measurements of soil CO₂ efflux obtained with the open-top chamber also were significantly different ($P = 0.048$) from those measured with the automated chamber. The open-top chamber system yielded higher values of F_c than the automated chamber at efflux values (automated chamber) below about $3.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ and yielded lower values than the automated chamber at efflux values above this level. However, the results from both the systems were closely correlated ($R^2 = 0.87$, $n = 105$; Fig. 9a).

3.3.3. Automated chamber system versus soil CO₂ gradient system

The results obtained with the two continuous measurement systems—automated chamber and soil CO₂ gradient—differed significantly ($P < 0.001$). F_c measured by the CO₂ gradient approach was, on

average, 45% higher than the results of the automated chamber approach. In particular, the soil CO₂ gradient approach yielded much higher F_c values than the automated chamber approach during the warmest season (15 July through 15 September) when the efflux rates were high. However, the results obtained from the two approaches showed similar patterns of diurnal and seasonal changes (Figs. 4 and 5) and had a relatively significant linear relationship ($R^2 = 0.77$, $n = 2945$; Fig. 9b).

4. Discussion

4.1. Forest floor CO₂ efflux and its variation

During the warmer season (July–September), the mean soil CO₂ effluxes measured in the Tomakomai larch forest with our automated chamber ($3.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) and open-top chamber ($3.0 \mu\text{mol m}^{-2} \text{s}^{-1}$) approaches fell in the middle of the values found for Siberian coniferous forests ($2.8\text{--}4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$; Kelliher et al., 1999) and temperate coniferous forests ($1\text{--}6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$; Law et al., 1999; Xu and Qi, 2001). In contrast, the mean soil CO₂ effluxes we measured with the LI-6400 chamber ($5.7 \mu\text{mol m}^{-2} \text{s}^{-1}$) and soil CO₂ gradient ($5.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) approaches fell in the upper range of values for Siberian and temperate coniferous forests.

The soil CO₂ efflux showed diurnal and seasonal changes and even changed quickly in response to sudden changes in environmental variables, such as rainfall (Fig. 4). The diurnal changes in soil CO₂ efflux in parallel with changes in the soil temperature, as found in the present study (Figs. 4 and 6), are consistent with results of previous studies (Davidson et al., 1998; Xu and Qi, 2001; Drewitt et al., 2002). The asymmetric diurnal pattern suggests that measurements taken during a short period in the day-time, especially if during the colder morning or warmer afternoons, cannot be assumed to represent the daily (day-time + night-time) mean soil CO₂ efflux and would tend to underestimate or overestimate the soil CO₂ efflux.

Seasonal variations in soil CO₂ efflux are generally attributed to changes in soil temperature and moisture (Davidson et al., 1998; Kelliher et al., 1999; Xu and Qi, 2001; Drewitt et al., 2002). In the present study, variations in soil CO₂ efflux were found to depend strongly

on changes in soil temperature. However, there was no evidence for seasonal drought at this site, because rainfall usually occurred once or twice a week. Thus, in contrast to previous reports, we did not find soil CO₂ efflux and soil moisture to be positively correlated at low soil moisture (<19%) or negatively correlated at high soil moisture (>19%) (Davidson et al., 1998; Xu and Qi, 2001). Abundant precipitation at our study site, coupled with good soil drainage, resulted in a volumetric soil moisture, usually 30–40%, that was uniformly favorable to microbial activity and root respiration throughout the growing season. These results suggest that, for the larch forests in the Hokkaido region, the environmental variable with the greatest influence on temporal variations in soil CO₂ efflux is the soil temperature.

Some publications show a close link between soil CO₂ efflux and tree phenology (Högberg et al., 2001; Janssens et al., 2001). It is possible that the rapid increase in soil CO₂ efflux in the spring and early summer (until about 15 July) did not result only from an increase in soil temperature but also was at least partly the result of an increase in foliage photosynthesis. Högberg et al. (2001) argued that seasonal patterns of soil CO₂ efflux in a boreal Scots pine ecosystem are driven by both current photosynthesis and photosynthate allocation to roots. At our site, Hirano et al. (2003a) observed that the gross primary production (GPP) increased significantly from the leaf-flushing season of spring until early summer. On the other hand, coniferous ecosystems usually show increases in root growth in the latter part of the growing season, resulting from higher allocation of photosynthate, i.e., starch, to the roots (Högberg et al., 2001; Drewitt et al., 2002). In our study, soil CO₂ efflux at the same soil temperature was greater in the late summer to autumn (end of August–middle of October) than in the spring to early summer (before 15 July), which may be partly due to increased root respiration in the autumn.

The soil CO₂ efflux quotients ($Q_{10} = 3.0$ with automated chamber and 2.8 with soil CO₂ gradient approach) we found are in the middle of the range (1.3–5.6) for a variety of forest soils (reviewed by Xu and Qi, 2001). The lower Q_{10} values we obtained with the open-top chamber (1.9) and LI-6400 chamber (1.6) may not reflect the true relationship between CO₂ efflux and soil temperature, because the periodic measurements by these two approaches were conducted

only once a month and thus ignored the wide changes in soil temperature and moisture that occurred between measurement dates (Figs. 7 and 8).

Both the automated chamber and soil CO₂ gradient approaches revealed irregularities in soil CO₂ efflux—when effluxes suddenly increased to very high values—during rainfall events. However, the higher effluxes returned to the usual, lower levels several hours after each rainfall. Kelliher et al. (1999) and Law et al. (2001) also reported only a 14–24 h effect of rain in increasing soil CO₂ effluxes from semiarid soils beneath pine forests in central Siberia and western America. The quantity of rainfall-induced CO₂ efflux is difficult to estimate from the volume of precipitation, because the magnitude of the increase in CO₂ efflux was positively correlated with the volume of precipitation and also negatively correlated with frequency of rainfalls. For instance, after 12 consecutive sunny days, the mean soil CO₂ efflux (measured with the automated chambers) increased immediately to a maximum value of 5.5–6.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the rainfall between 2100 of day 234 and 0500 of day 235 (Fig. 4). This value was about 40% higher than the maximum CO₂ efflux (4.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 1400) on day 233. However, on day 236, the maximum CO₂ efflux rate returned to 4.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Although 50 mm of rain fell again on day 239, 3 days later, the CO₂ efflux rate did not show much increase (4.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Although dynamic patterns of soil CO₂ efflux in response to rainfall have not been well characterized in natural ecosystems, Liu et al. (2002) reviewed the evidence that rainfall-induced soil CO₂ efflux can be attributed to a few mechanisms, including (1) additional water fills soil pores and replaces CO₂ highly concentrated air, which usually happens within minutes (artificial irrigation) and may last up to a few hours (rainfall); (2) addition of water to an extremely dry soil activates microbial activity, which begins within several hours to days; and (3) addition of water to a dry soil also activates the respiration of living roots, which remains high for several days to weeks. However, the site we examined receives considerable, frequent precipitation, and our results resemble those of our previous measurements with the automated chamber system in a temperate pine forest (Liang et al., 2003) and suggest that the rapid increases in soil CO₂ efflux following rainfalls are caused mainly by the physical displacement of gasses, including CO₂,

from soil spaces by rainwater, as well as activation of microbial activity. Our results also suggest that continuous measurements are important for accurately estimating the quantitative contribution of soil CO₂ efflux to the forest carbon balance; using periodic measurements of soil CO₂ efflux only on sunny or cloudy days would undoubtedly overestimate or underestimate the longer-term soil CO₂ efflux.

4.2. LI-6400 chamber system

During the comparative field measurements, soil CO₂ efflux obtained with all four systems showed distinct seasonal changes (Fig. 4). The LI-6400 chamber recorded substantially higher soil CO₂ effluxes than the other three approaches, except in June. McGinn et al. (1998) and Law et al. (2001) also reported that a LI-COR chamber overestimated soil CO₂ effluxes relative to their larger automated chambers (0.09–0.21 m²). Theoretically, the positive pressure of 0.2–0.3 Pa inside the LI-6400 chamber (Le Dantec et al., 1999) should result in underestimation of soil CO₂ efflux compared to the open-top chamber and soil CO₂ gradient approach. Therefore, the overestimation of soil CO₂ efflux by the LI-6400 chamber could derive from the influence of higher wind speeds inside the chamber. At 1 cm above the soil surface, the wind speed within the LI-6400 chamber is 0.4 m s⁻¹, higher than the field turbulence above the soil surface in forests. A high wind speed inside the chamber would decrease the high boundary layer over the soil surface, hence promoting exhaust of the CO₂ from underneath the respiration chamber and lateral diffusion of CO₂ from the surrounding area toward the chamber (Hanson et al., 1993; Le Dantec et al., 1999). Proper measurement of soil CO₂ efflux can be achieved by maintaining the wind speed inside the chamber below 0.4 m s⁻¹, as pointed out by Le Dantec et al. (1999). Indeed, at the Tomakomai site, the average wind speed 2 cm above the forest floor is about 0.1 m s⁻¹ in the growth season and 0.3 m s⁻¹ in the non-growth season (Liang et al., unpublished data). Moreover, the LI-6400 chamber measurements were usually begun 15 μmol mol⁻¹ below the ambient CO₂ concentration; this artificially lower CO₂ concentration inside the chamber would also favor overestimation of soil CO₂ efflux (Conen and Smith, 2000; Davidson et al., 2002).

Spatial variations of CO₂ efflux relevant to chamber measurements are often on the scale of centimeters, reflecting the sizes of rocks, disturbances by soil fauna, pockets of fine root proliferation, and remnants of decaying organic matter (Davidson et al., 2002). In the present study, the CV was as high as 44% with the LI-6400 chamber and decreased with increasing chamber size, suggesting that the spatial variation at our site is on a small scale and that larger chambers average the small-scale heterogeneity by covering greater areas. Further, the area covered by a chamber influences the number of chambers required to estimate representative forest floor CO₂ efflux.

To estimate the number of sampling points required for each approach at various degrees of precision at a specific confidence level, the following equation was applied:

$$n = \left[\frac{ts}{D} \right]^2 \quad (6)$$

where n is the sampling point requirement, t is the t -statistic for a given confidence level (i.e., 95%) and degrees of freedom, s is the standard deviation of the full samples of measurement, and D is the desired interval about the full sample mean in which a smaller sample mean is expected to fall (i.e., ±10% of the full sample mean). The results in Table 1 demonstrate that 5, 16, and 89 sampling points are required for the automated chamber, open-top chamber, and LI-6400 chamber approaches, respectively, to obtain an experimental mean that falls within ±20% of the full sample mean with 95% confidence interval; and 18, 65, and 355 sampling points are required, respectively, to achieve ±10% with 95% confidence interval. Our estimates of sampling points required are larger than the sampling point requirement reported by Yim et al. (2003), whose research was conducted at the same site. Yim et al. (2003) used 50 relatively small chambers (125 cm²) to measure soil CO₂ efflux by the alkali absorption method and estimated that 8 and 30 sampling points were required, respectively, to achieve means within ±20% and ±10% of the full sample mean with 95% confidence interval. However, the number of sampling points required, as estimated by Yim et al. (2003), is significantly less than the sampling points required as reported by Davidson et al. (2002), who made 36 soil CO₂ efflux measurements with relatively larger chambers (500 cm²) in

Table 1

Number of sampling points required for the automated chamber, open-top chamber, and LI-6400 chamber approaches to achieve different degrees of precision (within $\pm 10\%$ to within $\pm 20\%$ of the full sample mean) with 95% confidence interval

Chamber type	No. of sampling points actually measured	CO ₂ efflux (mean + S.D.) (mg C m ⁻² h ⁻¹)	No. of sampling points required for measurements	
			Within $\pm 10\%$	Within $\pm 20\%$
Automated	16	126 \pm 20	18	5
Open-top	9	118 \pm 35	65	16
LI-6400	20	202 \pm 90	355	89

Calculation is based on results averaged for the entire measurement period.

the Harvard forest in Connecticut, USA. Our results indicate that, to accurately estimate the ecosystem level of soil CO₂ efflux, a large number of sampling points with small chambers or relatively fewer sampling points with larger chambers are needed. In our experience, the automated and open-top chamber systems can be expanded to include up to 24 chambers. However, for studying temporal variations in soil CO₂ efflux, an automated system with a smaller number of larger chambers would better characterize a site with less labor (Liang et al., 2003).

The LI-6400 chamber system is likely to be accepted as “standard” methodology by many research groups. The greatest advantages of the LI-6400 chamber system are its portability and low power consumption. Therefore, measurements at many locations within a short time are possible, leading to good estimation of spatial variability. The disadvantages of the LI-6400 chamber design are its small area (only 71.6 cm²) and its inability to be used for continuous measurements. In other words, intensive temporal sampling (e.g., over a diurnal cycle) is labor intensive.

4.3. Open-top chamber system

Chamber-based measurements may impose substantial artifacts and biases on the estimated soil CO₂ effluxes. The pressure difference between the inside and outside of a chamber designed for steady-state measurements can cause mass flow between the pore spaces within the soil and the outside air, resulting in underestimation (at overpressurization) or overestimation (at underpressurization) of soil CO₂ efflux. Nevertheless, an increase in CO₂ concentration in the headspace of a chamber designed for non-steady-state measurements can alter the CO₂

diffusion gradient within the soil underneath the chamber, resulting in 10–15% underestimation of soil CO₂ efflux (for a review, see Davidson et al., 2002). The steady-state-designed open-top chamber should minimize the influence of pressure differences on the measured CO₂ efflux and yield estimated CO₂ efflux values close to the true CO₂ efflux of undisturbed soil (Fang and Moncrieff, 1998). However, because the sample air stream is sucked from the chamber, the corresponding slight underpressurization (even if not detectable) inside the open-top chamber might lead to an overestimation of soil CO₂ efflux during a calm night, when efflux rates are generally very low. In contrast, because the flow rate (31 min⁻¹) of the sampling air stream resulted in almost no air movement (<0.01 m s⁻¹) inside the chamber, the boundary layer over the soil surface inside the chamber was higher than in the surrounding area during the day-time, when higher turbulence generally occurred at the forest floor (0.1–0.3 m s⁻¹ at 2 cm above the soil surface). This strengthened boundary layer inside the chamber could reduce the diffusion of CO₂ from the soil underneath the respiration chamber, thus resulting in underestimation of soil CO₂ efflux (Le Dantec et al., 1999). In addition, an additional underestimation of soil CO₂ efflux at higher efflux rates (>3 $\mu\text{mol m}^{-2} \text{s}^{-1}$) is associated with leakage of respired CO₂ from the round aperture of the chamber, induced by horizontal wind near the forest floor. Fang and Moncrieff (1998) sampled air at a flow rate of 81 min⁻¹ from their small chamber and found that a gentle wind of > 0.5 m s⁻¹ could cause serious leakage of respired CO₂ from the open-top chamber.

The open-top chamber system used in our study combines the advantages of lower pressurization and

multiple chambers. Moreover, our open-top chamber covers an area (706 cm^2) about 10 times larger than the LI-6400 chamber, and the whole system can sample a total soil area of 0.64 m^2 . The system is relatively simple, and installation takes only 1–2 h in the field. Thus, the system can be used in different ecosystems to evaluate spatial and temporal variation of soil CO_2 efflux simultaneously. However, controlling manifold valves and running two pumps to extract the reference and sample air streams means that our open-top chamber system consumes about twice the electrical power (25 W) of the LI-6400 chamber system.

The open-top chamber is opaque and shades the enclosed soil surface from sunlight. Rainwater flows to the inner edge of the chamber through narrow apertures distributed around the inner wall, and leaf litter cannot drop into it. Thus, the chamber environment may become modified during long-term measurements. However, our open-top chamber system can be used during intervals between rainfalls for short-term monitoring of diurnal trends in forest floor CO_2 efflux, for instance, for periods from a day to a week.

4.4. Automated chamber system

Liang et al. (2003) recently showed that the automated chamber system can be applied for continuous measurements of forest floor CO_2 efflux, even on snowy and rainy days. With growing interest in determining the role of soils in the global carbon cycle, our automated chamber system is likely to be of some interest to carbon-flux researchers, because long-term and continuous measurements of soil CO_2 efflux can help us to calibrate net ecosystem carbon flux as measured by the eddy covariance method. The Fluxnet–Canada network recently adopted an automated chamber system as a standard system for continuous measurements of soil CO_2 efflux; the system comprises six 0.20 m^{-2} automated chambers (Drewitt et al., 2002). Our automated chamber system has several advantages over previous chamber systems: (1) Each chamber in the system is 113 and 11.5 times larger in area than the LI-6400 chamber and open-top chamber, respectively, which minimizes problems associated with small-scale spatial variability. (2) The system has a large number of chambers that can

integrate the sample area, which enables evaluation of spatial variation. Thus, measurements with our system can enhance the reliability of a model when chamber measurements of soil CO_2 efflux are scaled up to an ecosystem level. (3) Between measurements the chamber lids are raised vertically to allow precipitation and leaf litter to reach the enclosed soil surface. Therefore, the automated chamber system can make long-term measurements of soil CO_2 efflux with minimal modification of the chamber environment relative to ambient conditions, e.g., soil moisture status and temperature. (4) The cost of the system is low, because a single CO_2 analyzer can be used for all 16 chambers.

However, because our automated chamber system was operated in steady-state mode, its use for long-term continuous measurements of soil CO_2 efflux was accompanied by several disadvantages: (1) The chamber took up to 20 min to achieve steady state, resulting in exclusion of some rainwater and leaf litter as well as an increase in air temperature, particularly in the chambers placed in forest gaps. (2) A small overpressurization ($\leq 0.22\text{ Pa}$) inside the chambers means that the soil CO_2 effluxes estimated by our automated chamber approach were theoretically lower than results obtained with the open-top chambers and systematically lower than those of the soil CO_2 gradient approach. However, the automated chamber approach yielded larger soil CO_2 effluxes than the open-top chamber at efflux values $> 3\ \mu\text{mol m}^{-2}\text{ s}^{-1}$, perhaps due to leaks through the opening of the open-top chambers as mentioned in Section 4.3. (3) The whole system has high power consumption (70 W), which is impossible to maintain without an external electricity supply. However, Liang et al. (2003) suggested that these disadvantages can be minimized or avoided by operating the system in non-steady-state mode. In the non-steady-state mode, the closure time for each chamber can be shortened to 2–3 min; the pressure difference can be eliminated by fitting the chambers with a pressure-equilibration tube; and the mean power consumption can be decreased to $< 15\text{ W}$.

4.5. Soil CO_2 gradient system

Under laboratory steady-state conditions, soil CO_2 effluxes obtained by the soil CO_2 gradient approach

correlated well with those of LI-6400 chamber measurements. However, under non-steady-state conditions in the field, soil CO₂ effluxes estimated by the soil CO₂ gradient approach were not as well correlated with the LI-6400 chamber measurements (S. Jones and D. Or, Utah State University, unpublished data). We obtained similar results. Diurnal and seasonal variations in the soil CO₂ efflux estimated by the soil CO₂ gradient approach showed a high correlation with soil temperature ($R^2 = 0.85$), and the Q_{10} value (2.8) matched the common range for various forests, indicating that our simple soil CO₂ gradient system is a good alternative approach for continuous measurement of soil CO₂ efflux under field conditions (also see Hirano et al., 2000, 2001, 2003b). Although we do not clearly understand why the soil CO₂ effluxes estimated by the soil CO₂ gradient approach were systematically higher than those of the automated and open-top chamber approaches, the soil CO₂ gradient approach does not disturb the soil, vegetation, or boundary layer around the sensors, which consequently do not cause overestimation or underestimation of soil CO₂ efflux. However, as measurements by the soil CO₂ gradient approach were only made at two locations which were only 60 cm apart, the higher soil CO₂ effluxes might be due to specific microsite characteristics.

The soil CO₂ gradient approach has several strengths over the chamber-based methods—(1) Once installed, it does not alter the diffusion gradient within the soil profiles and there is no need to clip vegetation around the sensors. (2) It can continuously monitor CO₂ concentrations at several soil depths and estimate the associated soil CO₂ efflux. (3) The system is very easy to maintain. In our opinion, the best sensors (i.e., small, commercially available, and inexpensive) for the soil CO₂ gradient approach are the Vaisala GMT222 sensors. Unfortunately, the Vaisala sensor is not very accurate ($\pm 2\%$ of reading corresponds to $\pm 20 \mu\text{mol CO}_2 \text{ mol}^{-1}$), and it can be damaged by the soil microenvironment (constant 100% humidity). Also, the practical difficulties of measuring or modeling an accurate soil CO₂ diffusion coefficient for heterogeneous forest soils hinder the reliability of the estimated soil CO₂ efflux. However, these sources of error can be partly eliminated by frequent measurements of the soil CO₂ diffusion coefficient and calibration of the sensors.

4.6. Annual forest floor CO₂ efflux

The annual net ecosystem productivity of forests is reported to relate generally to the soil CO₂ efflux (Law et al., 1999; Valentini et al., 2000; Janssens et al., 2001; Drewitt et al., 2002). However, most previous studies used periodic manual measurements to make predictions of annual CO₂ efflux, and thus obtained substantially different results even for similar coniferous forest ecosystems, ranging from 687 to 1700 g C m⁻² y⁻¹ (Law et al., 1999; Moncrieff and Fang, 1999; Rayment and Jarvis, 2000; Morén and Lindroth, 2000; Widén, 2002). Recently, the annual soil CO₂ efflux in a very productive Douglas-fir forest in British Columbia, Canada, was estimated to be 1920 g C m⁻² y⁻¹, based on automated chamber measurements (Drewitt et al., 2002). In the present study, because the soil CO₂ efflux was found to be influenced mainly by the soil temperature and less by the soil moisture, we used hourly soil temperature data (Fig. 10a) and the best-fit parameter values for $F_c(T_{\text{soil}}) = a \exp^{bT_{\text{soil}}}$ in Eq. (5) to calculate the annual net forest floor CO₂ efflux according to the four approaches. The best-fit parameters used here for each approach are those shown in Fig. 7. Fig. 10b,c shows the derived hourly mean soil CO₂ efflux for each approach. The average annual soil CO₂ effluxes are 665, 1153, 720, and 902 g C m⁻² for the automated chamber, LI-6400 chamber, open-top chamber, and soil CO₂ gradient approach, respectively. The soil CO₂ efflux in this larch forest falls the lower range of values reported for most forests (Law et al., 1999; Moncrieff and Fang, 1999; Rayment and Jarvis, 2000; Drewitt et al., 2002), which is likely due to the shallow soil and the deficiency of forest floor organic matter. Among the four approaches, the LI-6400 chamber yielded much higher values because it overestimated the soil CO₂ efflux in the winter (Fig. 10b). Estimates of annual soil CO₂ efflux by the automated chamber and open-top chamber approaches matched the total annual ecosystem respiration of 659–786 g C m⁻² estimated by the above-canopy eddy covariance method, and the soil CO₂ gradient approach yielded higher values than the eddy covariance method (Hirano et al., 2003). Although disagreements thus exist between the chamber- and tower-based measurements, our results indicate that soil CO₂ efflux dominates ecosystem respiration in this larch forest.

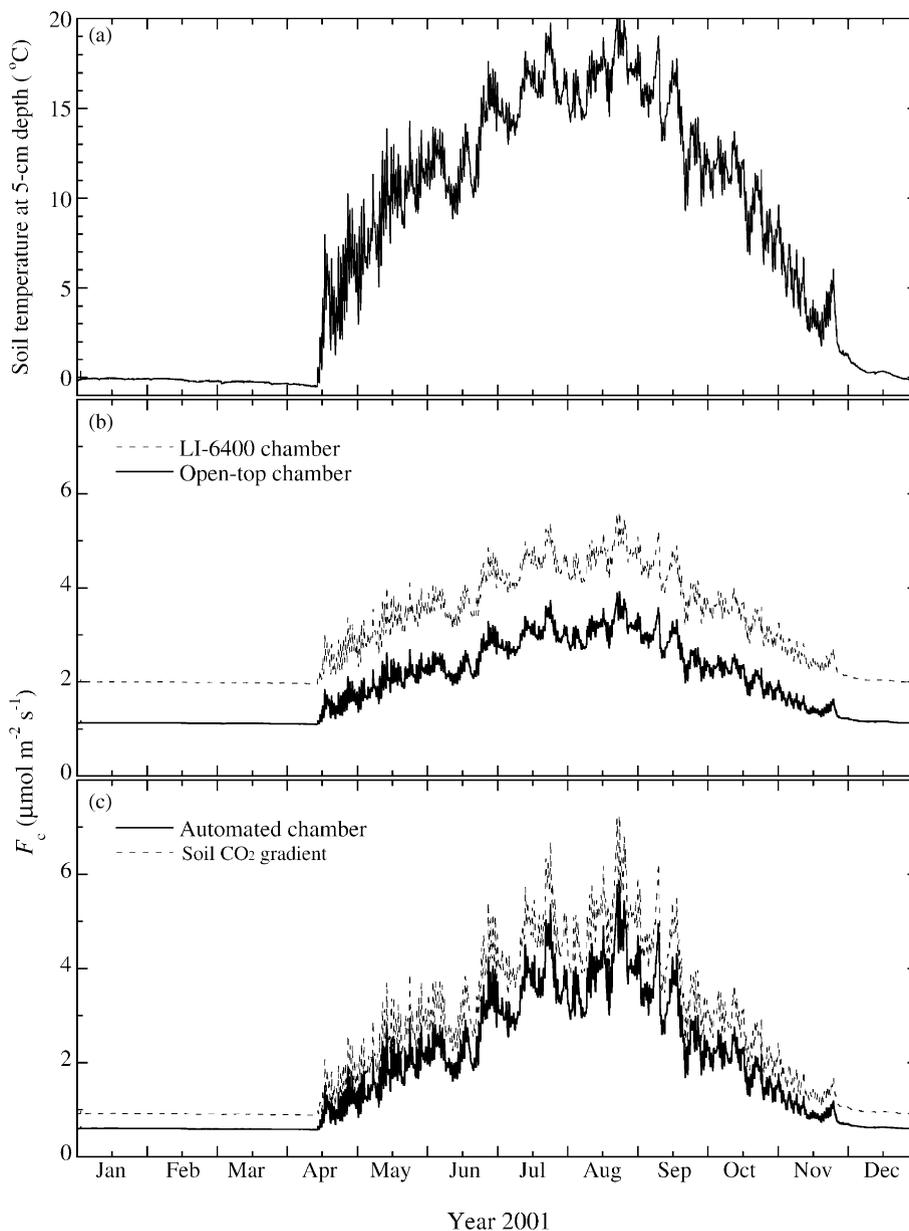


Fig. 10. (a) Hourly soil temperature at 5 cm depth. Calculated hourly soil CO₂ effluxes (b) for the LI-6400 chamber and open-top chambers and (c) for the automated chamber and soil CO₂ gradient technique, using the soil temperature data and best-fit parameters shown in Fig. 7.

5. Conclusions

The choice of measuring approach depends on the objective. If one wants to quantify the contribution

of soil CO₂ efflux to the total ecosystem CO₂ fluxes recorded above the canopy, then the measuring approach for estimating soil CO₂ efflux should have the following performance characteristics:

- The pressure difference between the inside and outside of the chamber should be low (at least <0.3 Pa, or even better, <0.1 Pa) and the CO_2 concentration difference should be equally low.
- The wind speed inside the chamber should match the ambient (for forests, usually between 0.1 and 0.2 m s^{-1} at 2 cm above the soil surface).
- It should be able to measure a large number of sampling points or a large sampling area.
- The chamber environmental conditions, such as soil moisture status and temperature, should not change during the time period of interest.

Therefore, the modified automated chamber system (run in non-steady-state mode) and the soil CO_2 gradient system seem to be the most appropriate for long-term monitoring of soil CO_2 efflux in forest ecosystems. Currently, a non-steady-state-mode automated chamber system with 16 chambers and a soil CO_2 gradient system with six replicates are being used at the Tomakomai site for long-term continuous measurements of soil CO_2 efflux. In addition, for more accurate measurements, a direct in situ comparison of the automated chamber approach with the soil CO_2 gradient approach is underway: Vaisala CO_2 sensors are buried horizontally at 0, 2, and 4 cm depths in the center of four automated chambers.

However, the LI-6400 chamber system and the open-top chamber system, with their advantages of portability and lower power consumption, are more effective for estimating spatial variations in soil CO_2 efflux at a specific site.

The significant differences between results obtained by different approaches in the present study may suggest that inter-site comparisons and modeling of regional or global soil CO_2 effluxes should be based on data obtained by the same measurement approach.

Acknowledgements

We thank Mr. Koh Inukai and Mr. Yasuyuki Kitamori (Econix, Hokkaido), who very efficiently managed the Tomakomai flux site. We thank LI-COR, Inc., for providing a high quality diagram of the LI-6400 chamber. We thank Dr. Ming Xu (Rutgers University) for critically reviewing the manuscript. Two anonymous reviewers are acknowledged for their valuable

comments. This work is part of the Global Environmental Monitoring Program of the National Institute for Environmental Studies, Japan.

References

- Baldocchi, D.D., Vogel, C.A., Hall, B., 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agric. For. Meteorol.* 83, 147–170.
- Biscoe, P.V., Scott, R.K., Monteith, J.L., 1975. Barley and its environment. III. Carbon budget of the stand. *J. Appl. Ecol.* 12, 269–291.
- Conen, F., Smith, K.A., 2000. An explanation of linear increases in gas concentration under closed chambers used to measure gas exchange between soil and the atmosphere. *Eur. J. Soil Sci.* 51, 111–117.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled model. *Nature* 408, 184–187.
- Crill, P.M., Keller, M., Weitz, A., Grauel, B., Veldkamp, E., 2000. Intensive field measurements of nitrous oxide emissions from a tropical agricultural soil. *Glob. Biogeochem. Cycl.* 14, 85–95.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol.* 4, 217–228.
- Davidson, E.A., Savage, K., Verchot, L.V., Navarro, R., 2002. Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agric. For. Meteorol.* 113, 21–37.
- de Jong, E., Schappert, J.V., 1972. Calculation of soil respiration and activity from CO_2 profiles in the soil. *Soil Sci.* 113, 328–333.
- Drewitt, G.B., Black, T.A., Nestic, Z., Humphreys, E.R., Jork, E.M., Swanson, R., Ethier, G.J., Griffis, T., Morgenstern, K., 2002. Measuring forest floor CO_2 fluxes in a Douglas-fir forest. *Agric. For. Meteorol.* 110, 299–317.
- Fang, C., Moncrieff, J.B., 1998. An open-top chamber for measuring soil respiration and the influence of pressure difference on CO_2 efflux measurement. *Funct. Ecol.* 12, 319–325.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279, 214–217.
- Hanson, P.J., Wullschlegel, S.D., Bohlman, S.A., Todd, D.E., 1993. Seasonal and topographic patterns of forest floor CO_2 efflux from upland oak forest. *Tree Physiol.* 13, 1–15.
- Hirano, T., Setoyama, H., Tanaka, Y., Kim, H., 2000. Diffusive CO_2 efflux from the soil surface of a deciduous broad-leaved forest in Hokkaido, Japan, In: *Proceedings: International workshop for advanced flux network and flux evaluation*. Center for global Environmental Research, National Institute for Environmental Studies, Japan, pp. 113–118.
- Hirano, T., Kim, K., Tanada, Y., 2001. Seasonal variation in CO_2 efflux from the soil surface of a cool-temperate deciduous forest. In *Extended Abstract: 6th International Carbon Dioxide*

- Conference. Organizing Committee of the 6th International Carbon Dioxide Conference, Sendai, Japan, pp 420–423.
- Hirano, T., Hirata, R., Fujinuma, Y., Saigusa, N., Yamamoto, S., Harazono, Y., Takada, M., Inukai, K., Inoue, G., 2003a. CO₂ and water vapor exchange of a larch forest in northern Japan. *Tellus* 55B, 244–257.
- Hirano, T., H., Tanaka, Kim, K. 2003b. Long-term continuous measurements of soil CO₂ concentration and soil respiration in a deciduous forest. *J. Geophys. Res.*, (in press).
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Edblad, A., Högberg, M.N., Nyberg, G., Ottensson-Löfvenius, M., Read, D.A., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 789–792.
- Hutchinson, G.L., Mosier, A.R., 1981. Improved soil cover method for field measurement of nitrous oxide fluxes. *Soil Sci. Soc. Am. J.* 45, 311–316.
- Janssens, I.A., Kowalski, A.S., Longdoz, B., Ceulemans, R., 2000. Assessing forest soil CO₂ efflux: an in situ comparison of four techniques. *Tree Physiol.* 20, 23–32.
- Janssens, I.A., Lanckreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7, 269–278.
- Kelliher, F.M., Lloyd, J., Arneeth, A., Luhker, B., Byers, J.N., McSeveny, T.M., Milukova, I., Grigoriev, S., Panfyorov, M., Sogatchev, A., Varlargin, A., Ziegler, W., Bauer, G., Wong, S.-C., Schulze, E.-D., 1999. Carbon dioxide efflux density from the floor of a central Siberian pine forest. *Agric. For. Meteorol.* 94, 217–232.
- Kirita, H., 1971. Re-examination of the absorption method of measuring soil respiration under field conditions. IV. An improved absorption method using a disc of plastic sponge as absorbent holder. *Jpn. J. Ecol.* 21, 119–127.
- Law, B.E., Baldocchi, D.D., Anthoni, P.M., 1999. Below-canopy and soil CO₂ fluxes in a ponderosa pine forest. *Agric. For. Meteorol.* 94, 171–188.
- Law, B.E., Kelliher, F.M., Baldocchi, D.D., Anthoni, P.M., Irvine, J., Moore, D., Van Tuyl, S., 2001. Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. *Agric. For. Meteorol.* 110, 27–43.
- Le Dantec, V., Epron, D., Dufrêne, E., 1999. Soil CO₂ efflux in a beech forest: comparison of two closed dynamic systems. *Plant and Soil* 214, 125–132.
- Liang, N., Inoue, G., Fujinuma, Y., 2003. A multichannel automated chamber system for continuous measurement of forest soil CO₂ efflux. *Tree Physiol.* 23, 825–832.
- Liu, X., Wan, S., Su, B., Hui, D., Luo, Y., 2002. Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant and Soil* 240, 213–223.
- Livingston, G.P., Hutchinson, G.L., 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. In: Matson, P.A., Harriss, R.C. (Eds.), *Biogenic Trace Gases: Measuring Emissions from Soil and Water*. Blackwell Scientific Publications, Oxford, pp. 14–51.
- McGinn, S.M., Akinremi, O.O., McLean, H.D.J., Ellert, B., 1998. An automated chamber system for measuring soil respiration. *Can. J. Soil Sci.* 78, 573–579.
- Moncrieff, J.B., Fang, C., 1999. A model for soil CO₂ production and transport. Part 2. Application to a Florida *Pinus elliotte* plantation. *Agric. For. Meteorol.* 95, 237–256.
- Morén, A.-S., Lindroth, B.A., 2000. CO₂ exchange at the floor of a boreal forest. *Agric. For. Meteorol.* 101, 1–14.
- Nakadai, T., Koizumi, H., Usami, Y., Satoh, M., Oikawa, T., 1993. Examination of the methods for measuring soil respiration in cultivated land: effect of carbon dioxide concentration on soil respiration. *Ecol. Res.* 8, 65–71.
- Nakadai, T., Koizumi, H., Bekku, Y., Totsuka, T., 1996. Carbon dioxide evolution of an upland rice and barley, double cropping field in central Japan. *Ecol. Res.* 11, 217–227.
- Nakadai, T., Yokozawa, M., Ikeda, H., Koizumi, H., 2002. Diurnal changes of carbon dioxide flux from bare soil in agricultural field in Japan. *Appl. Soil Ecol.* 19, 161–171.
- Nakane, K., 1994. Modeling the soil carbon cycle of pine ecosystems. *Ecol. Bul.* 43, 161–172.
- Nay, S.M., Mattson, K.G., Bormann, B.T., 1994. Biases of chamber methods for measuring soil CO₂ efflux demonstrated with a laboratory apparatus. *Ecology* 75, 2460–2463.
- Norman, J.M., Kucharik, C.J., Gower, S.T., Baldocchi, D.D., Grill, P.M., Rayment, M., Savage, K., Striegl, R.G., 1997. A comparison of six methods for measuring soil-surface carbon dioxide fluxes. *J. Geophys. Res.* 102, 28771–28777.
- Prentice, I.C., Farquhar G.D., Fasham M.J.R., Goulden M.L., Heimann M., Jaramillo V.J., Khesghi H.S., Le Quere C., Scholes R.J., Wallace D.W.R. 2001. The carbon cycle and atmospheric carbon dioxide. In: Houghton, J.T., Ding Y., Griggs D.J., Noguier M., van der Linden P.J., Dai X., Maskell K., Johnson C.A. (Eds.), *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, pp. 183–238.
- Rayment, M.B., Jarvis, P.G., 1997. An improved open chamber system for measuring soil CO₂ effluxes in the field. *J. Geophys. Res.* 102, 28779–28784.
- Rayment, M.B., Jarvis, P.G., 2000. Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest. *Soil Biol. Biochem.* 32, 35–45.
- Rochette, P., Desjardins, R.L., Pattey, E., 1991. Spatial and temporal variability of soil respiration in agricultural fields. *Can. J. Soil Sci.* 71, 189–196.
- Rochette, P., Gregorich, E.G., Desjardins, R.L., 1992. Comparison of static and dynamic closed chambers for measurement of soil respiration under field conditions. *Can. J. Soil Sci.* 72, 605–609.
- Valentini, R., Matteucci, G., Dolman, A.J., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–865.

- Widén, B., 2002. Seasonal variation in forest–floor CO₂ exchange in a Swedish coniferous forest. *Agric. For. Meteorol.* 111, 283–297.
- Yim, M.–H., Joo, S.–J., Shutou, K., Nakane, K., 2003. Spatial variability of soil respiration in a larch plantation: estimation of the number of sampling points required. *For. Ecol. Manage.* 175, 585–588.
- Xu, M., Qi, Y., 2001. Soil–surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol.* 7, 667–677.