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Discussions

Continuous measurement of soil CO_2 efflux in a larch forest by automated chamber and concentration gradient techniques

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Abstract

Winter measurements of soil CO_2 effluxes are few because such measurements are difficult when the ground is snow-covered, limiting the ability of chamber systems to characterize soil CO_2 effluxes accurately year-round. In this study, we used two systems for continuous measurements of soil CO_2 effluxes in a larch forest in northern Japan: (1) a 16-channel automated soil chamber system with eight chambers for measuring soil CO_2 efflux and eight chambers for measuring heterotrophic respiration during snow-free periods, and (2) a soil CO_2 concentration gradient system used year-round, including when the ground was snow-covered. During the warm season, the gradient approach yielded systematically higher CO_2 effluxes than the automated chamber technique, whereas it yielded lower CO_2 effluxes during the cold season. As a result of this bias ($p < 0.001$), the annual soil CO_2 efflux estimated by the automated chamber was 959 g C m^{-2} (of which 57% was contributed by heterotrophic respiration), whereas the efflux estimated by the gradient approach was 1040 g C m^{-2}. Because of the fast-response infrared gas analyzer adopted for the chamber technique, the soil CO_2 efflux response to the onset of rain was detected immediately and the efflux returned to pre-rain values several hours after the rain had stopped. Rain events accounted for about 24 g C m^{-2} (about 2% of the annual soil CO_2 efflux). The gradient system successfully measured the soil CO_2 effluxes when the ground was snow-covered (9 December to 17 April), when they ranged from 0.40 to 0.70 µmol m^{-2} s^{-1}. Total CO_2 efflux from the snowpack estimated by the gradient technique approached 73 g C m^{-2}, corresponding to about 7% of the annual soil CO_2 efflux. The Q_{10} coefficient of the soil CO_2 efflux showed large seasonal variation, mainly because of the large temperature sensitivity of root respiration.

1 Introduction

The world's soils contain about 1550 Pg of organic carbon, which is more than twice the amount in the atmosphere (IPCC, 2007). Forests worldwide contain about 45% of the global carbon stock, a large part of which is in the forest soils. Raich et al. (2002) used a climate-driven regression model to estimate that the soil CO_2 efflux, widely referred to as soil respiration, from global terrestrial ecosystems averaged 80.4 Pg C y^{-1} between 1980 and 1994, which is more than 15 times the rate of fossil fuel combustion (OECD/IEA, 2004), indicating that 20–40% of the atmosphere's CO_2 circulates through soils each year. On the other hand, the soil CO_2 efflux is the largest component of ecosystem respiration and the second largest flux in the global carbon cycle after gross primary production (GPP). It is therefore a key process that is fundamental to our understanding of the terrestrial carbon cycle (Davidson and Janssens, 2006). A relatively small change in the carbon flow into or out of soils can potentially strongly influence global cycles of carbon, nitrogen, and water. For example, it has been reported that positive feedback from enhancement of heterotrophic respiration by global warming would raise the CO_2 concentration in the atmosphere by 20–224 ppm by 2100, and that these higher CO_2 levels would lead to an additional temperature increase ranging between 0.1 and 1.5 $^{\circ}$C (Friedlingstein et al., 2006; IPCC, 2007).

In forest ecosystems, eddy covariance (EC) studies have shown that, on average, ~80% of GPP is respired back to the atmosphere (Law et al., 2002), and the soil CO_2 efflux has been estimated to account for 60–90% of the total ecosystem respiration, with marked temporal as well as spatial variations (Law et al., 1999; Janssens et al., 2000; Liang et al., 2004). Therefore, the soil CO_2 efflux has recently received much attention from researchers and its accurate measurement is critical for developing a reliable model of carbon exchange in forest ecosystems (Jassal et al., 2007; Zhou et al., 2009).

More than half of all terrestrial ecosystems in the Northern Hemisphere experience substantial snow cover during the winter (Sommerfeld et al., 1993). However, little is known about winter soil CO_2 efflux values, particularly those under the snowpack. Because of difficulties of measurement and access, most annual estimates of soil CO_2 efflux have ignored the soil CO_2 winter efflux or have assumed that it is zero (Fahnestock et al., 1999), or the wintertime efflux has been evaluated with simple temperature-driven models (Liang et al., 2004).

FLUXNET has become an effective network for observing carbon sequestration or loss by global terrestrial ecosystems by the EC technique (Luyssaert et al., 2008). Unfortunately, the use of the EC technique for measuring soil CO_2 efflux, especially below forest canopies, is often hampered by relatively low wind speeds (Drewitt et al., 2002) as well as by an abundance of understory vegetation (Lee, 1998; Janssens et al., 2001). Therefore, to validate nocturnal, subcanopy, and bad-weather (e.g., rainy period) EC measurements as well as to partition net ecosystem production (NEP), the flux research community must use automated chamber systems, which can make continuous (i.e., half-hourly or hourly) measurements of the soil CO_2 efflux.

The objectives of this study were to (1) compare the seasonal patterns of soil CO_2 effluxes in a larch forest obtained with a multi-channel automated chamber system and a soil CO_2 concentration gradient measurement system; (2) determine the major environmental and biological factors that control the soil CO_2 efflux in this larch forest; and then (3) evaluate the suitability of these two systems as standard protocols for soil CO_2 efflux measurement.

2 Materials and methods

2.1 Site description

The study site was the Tomakomai flux site (lat 42°44′ N, long 141°31′ E; elevation, 125 m) in Tomakomai National Forest, southern Hokkaido, Japan. The forest is a 45-year-old Japanese larch (*Larix kaempferi* Sarg.) plantation, interspersed with naturally generated Japanese spruce (*Picea jezoensis* Sieb. et Zucc.) and mixed broad-leaved species (*Betula* spp.). In 2001, the stand density was 1087 stems ha^{-1} and the total basal area was 23.2 m^2 ha^{-1}, of which larch accounted for 81%. The forest canopy was about 15 m in height, and the overstory canopy leaf area index (LAI) reached 3.1 during the peak of the growing season. The forest floor was densely covered with perennial buckler fern (*Dryopteris crassirhizoma*) but lacked other understory species and moss. In late June, the average height, biomass, and LAI of the understory were 0.5 m, 1.24 t ha^{-1}, and 2.1 m^2 m^{-2}, respectively. However, leaves of the fern began to fall in the middle of November, and the soil was covered by snow from 0.6 to 1.0 m deep from the end of December to early April.

Climate records between 1979 and 2000 from two weather stations about 10 km around the study site, Tomakomai and Shikotsuko, showed that the mean annual precipitation was approximately 1501 mm, and the mean annual temperature was 7.1 °C, with the mean monthly temperature ranging from −4.5 °C in January to 19.8 °C in August (http://www.data.jma.go.jp/obd/stats/etrn/index.php). The site is essentially flat, with a gentle slope of 1–2°. The soil is a homogeneous, well-drained, arenaceous soil developed from volcaniclastic sediment derived from a volcanic eruption that occurred about 300 years ago. It is classified as an immature Volcanogenous Regosol. There is sparse compacted till at a depth of 15–20 cm. The litter layer (Oie) is 1–2 cm thick and overlies a 5- to 10-cm-thick organic layer containing many fine roots. Beneath this, there is a layer composed of fragments of porous pumice stone (0.5–3 cm in diameter) with some coarse roots. Over 90% of the root biomass is in the top 20-cm-thick soil layer, and the estimated total root biomass is 13.1 t ha^{-1}. As a result, the soil is weakly acidic (pH 5.0–6.0) and poor in nutrients. Total soil organic carbon (SOC) and nitrogen storage are about 22.8 g C kg^{-1} and 1.9 g N kg^{-1}, respectively, and with about 95% of them are estimated to be in the surface layer between 0–10 cm (Sakai et al., 2007).

2.2 Soil CO_2 efflux measurements

2.2.1 Improved automated chamber system

Soil CO_2 efflux is usually measured by chamber-based techniques. Liang et al. (2003) designed a multi-channel automated chamber system that applied a steady-state technique to the measurement of the soil CO_2 efflux throughout the four seasons. However, the pressure inside the chamber was 0.22 Pa higher than that outside the chamber, which is likely to lead to underestimation of the actual soil CO_2 efflux (Fang and Moncrieff, 1998). Therefore, we have modified and improved this system using a flow-through, non-steady-state design. In brief, the system comprises a control unit that is contained within a field access case (0.70 m long × 0.50 m wide × 0.35 m high), and 8 to 24 automated chambers. The main components of the control unit are an infrared gas analyzer (IRGA; LI-840, LI-COR, Lincoln, NE, USA), a datalogger (CR10X, Campbell Scientific Inc., Logan, UT, USA), a gas sampler, and an air compressor (Fig. 1). The automated chambers (0.9 m long × 0.9 m wide × 0.5 m tall) are constructed of clear PVC (1 mm thick) glued to a frame constructed from plastic-coated steel pipe (30-mm square cross-section) (Fig. 2a). Between measurements, the two sections of the chamber lid are raised to allow precipitation and leaf litter to reach the enclosed soil surface, thus keeping the soil conditions as natural as possible. The chamber lids are raised and closed by two pneumatic cylinders (SCM-20B, CKD Corp., Nagoya, Japan) at a pressure of about 0.2 MPa, which is generated by a micro-compressor (M-10, Hitachi Ltd., Tokyo, Japan). During the measurement, the chamber is closed and the chamber air is mixed by two microfans (MF12B, Nihon Blower Ltd., Tokyo, Japan). The chamber air is circulated through the IRGA by a micro-diaphragm pump ($5\,\mathrm{L\,min^{-1}}$; CM-50, Enomoto Ltd., Tokyo, Japan), and the change in the CO_2 concentration is measured by the IRGA. The average power consumption of the whole system is 13 W; thus, the system can be driven by three 75-W solar cells with three 120-A h deep-cycle batteries.

In June 2002, we installed 16 chambers at Tomakomai, at randomly chosen sites on the forest floor within a circular area 40 m in diameter (Fig. 2a). The 16 chambers were divided into two groups, each with 8 chambers. The first group of chambers was used to measure the total soil CO_2 efflux (R_s), and the understory vegetation inside the chambers was clipped periodically during the growing season. Since the major understory species (fern) dies off once the vegetative point is clipped in the growing season, the chambers were installed between individual fern plants. The second group (8 chambers) was used for measuring heterotrophic respiration (R_h), and the chambers were installed in 1×1 m root exclusion plots. Trenches 0.5 to 1 cm-wide and 50 cm deep were dug along the plot boundaries with a root-cutting chainsaw (CSVN671AG, Kioritz Co. Ltd., Tokyo, Japan) and then PVC sheets (4 mm thick) were installed in the trenches to a depth of 50 cm to prevent the growth of roots.

Over the course of an hour, the 16 chambers were closed sequentially by a home-made relay board controlled by the datalogger (Fig. 1). We set the sampling period for each chamber to 225 s. Therefore, the chambers were open 94% of the time: during each 1-h cycle they were open for 56.3 min and closed for 3.7 min. Thus, most of the time rainfall could enter the chambers, and the interior of each chamber had good exposure to any atmospheric turbulence. The datalogger acquired output from the IRGA at 1-s intervals and recorded the averaged values every 5 s. Soil temperature at 5 cm depth and volumetric soil moisture (CS615, Campbell Scientific) at 10 cm depth inside each chamber were recorded by coupling the datalogger with multiplexers (AM25T, Campbell Scientific). Moreover, air pressure at 30 cm height around the chambers was monitored with a pressure transducer (PX2760-800A5V, Omega Engineering, Inc., Stamford, CT, USA). Soil CO_2 efflux (R_s, $\mu\text{mol m}^{-2}\text{ s}^{-1}$) was calculated with Eq. (1)

$$R_s = \frac{VP(1-W)}{RST}\frac{\partial C}{\partial t}, \tag{1}$$

where V is the effective chamber-head volume (m^3), S is the measured soil surface area (m^2), P is the air pressure (kPa), T is the air temperature (K), and W is the water vapor mole fraction (mmol mol^{-1}) inside the chamber; $\partial C/\partial t$ is the initial rate of change in the CO_2 mole fraction (µmol mol^{-1} s^{-1}), and R is the gas constant (8.314 Pa m^3 K^{-1} mol^{-1}).

2.2.2 Modified soil CO_2 concentration gradient system

The soil CO_2 concentration gradient technique for efflux estimation is a procedure that uses measurements of CO_2 concentrations at two or more depths to calculate the CO_2 efflux using Fick's Law. Soil air is generally extracted with gas-tight syringes from tubes inserted into the soil to different depths, and the CO_2 concentrations in the syringes are measured subsequently in the laboratory with an IRGA (Hubbard et al., 2005) or gas chromatograph (Takle et al., 2004), or in the field with an IRGA (Drewitt et al., 2005). The soil CO_2 gradient technique based on syringe samples can provide information on CO_2 production at different soil depths, but it cannot make continuous measurements of the soil CO_2 efflux. Moreover, unavoidable biases usually occur owing to disturbances of the soil environment; the gas extraction, storage, transport, and measurement processes; and the calibration that is necessary to account for changes in porosity with soil depth. In this study, we modified a soil CO_2 gradient system intended for long-term continuous measurements of the soil CO_2 efflux. Briefly, we installed the solid-state sensors (18.5 mm diameter, 155 mm long) of IRGAs (GMT222, Vaisala, Helsinki, Finland) at two depths to directly measure soil CO_2 concentration profiles. To minimize soil disturbance, we installed the sensors vertically (Fig. 2b). To ensure quality measurements, we took the following measures: (1) To keep the sensors dry, we enclosed them in polytetrafluoroethylene (PTFE) socks (TB-1419, Sumitomo Electric Fine Polymer Corp., Osaka, Japan). The PTFE sock excludes liquid water while allowing gases to diffuse freely across it (Liang et al., 2004). (2) To measure CO_2 concentrations at only specific soil depths, we enclosed the sensors in clear PVC (inner diameter 22 mm) casings, and (3) we covered the opening at the bottom end of the casing with a fine (0.5 mm) mesh stainless steel screen to prevent soil particles from entering the casing but to allow CO_2 molecules to diffuse into the sensor for measurement of the CO_2

concentration. Further information about this modified soil CO_2 gradient technique has been reported previously (Hirano et al., 2003; Tang et al., 2003; Liang et al., 2004; Jassal et al., 2005).

In June 2002, we installed two sets of sensors at two locations 60 cm apart at the Tomakomai site. Because of the shallowness of the soil at this site, we set one of the two probes at each location at 0 cm depth and the other at 2 cm depth (measurement range 0–2000 μmol mol^{-1}). We defined 0 cm depth as the soil surface under the surface litter layer. To avoid heating of the soil adjacent to the probe by the infrared lamp inside the probe, all probes in this study were powered on at 24 min past the top of the hour. After the probes were powered on, they were allowed to warm up for 5 min before their output was recorded with a datalogger (CR10X, CSI) through an AM25T multiplexer at 10-s intervals over the next 2 min. Then the probes were powered off until 24 min past the next hour. Soil temperature at 2 and 5 cm depth and volumetric soil moisture at 10 cm depth were also recorded at each location. The probes were removed for drying and calibration every two months.

The CO_2 efflux from the forest floor was calculated with Fick's law using concentrations measured at the surface and at 2 cm depth, under the assumption that the soil was horizontally homogeneous:

$$R_s = -D_s \frac{\partial C}{\partial z} \tag{2}$$

where R_s is the interlayer soil CO_2 efflux ($\mu mol\, m^{-2}\, s^{-1}$), D_s ($m^2\, s^{-1}$) is the gaseous CO_2 diffusion coefficient, and $\partial C/\partial z$ is the vertical CO_2 density gradient ($\mu mol\, m^{-4}$). D_s was calculated using Campbell's function (Campbell, 1985)

$$D_s = D_0 B \left(\frac{T_{soil} + 273.15}{273.15}\right)^{1.75} \left(\frac{1013}{P_s}\right), \tag{3}$$

where D_0 is the CO_2 diffusion coefficient in air ($1.39 \times 10^{-5}\, m^2\, s^{-1}$) at 1013 hPa and 273.15 K, T_{soil} is the average soil temperature (°C) at 2 cm depth, and P_s is the air pressure (hPa). B is the relative soil gaseous diffusion coefficient, which was estimated from

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the air-filled porosity based on the linear relationship between these two parameters; air-filled porosity was determined in the laboratory by the diffusion chamber method (Currie, 1960) in undisturbed soil cores as the residual of the volume fraction of solid and water. More details on the estimation of D_s are given by Hirano et al. (2003).

2.3 Data analysis

The high-frequency data were analyzed as follows: (1) Individual chambers were used as the statistical units for analyzing spatial variation in soil CO_2, which was quantified by the coefficient of variation (CV). (2) Measurements of the eight chambers used for each process (soil CO_2 efflux and heterotrophic respiration) were averaged to obtain the mean efflux. (3) A t-test was used to analyze statistically the difference in magnitude of soil CO_2 effluxes measured by the two approaches. (4) To examine the temperature response of the soil CO_2 efflux, we performed a regression analysis using the temperature response function with data obtained by both the chamber and gradient approaches:

$$R_s = ae^{bT_{\mathrm{soil}}}, \tag{4}$$

where R_s is the CO_2 efflux at soil temperature (T_{soil}) at a depth of 5 cm, a is the efflux at 0 °C (i.e., the basal rate), and b is the sensitivity of the soil CO_2 efflux to temperature. The value of b was also used to calculate the Q_{10} coefficient:

$$Q_{10} = e^{10b} \quad , \tag{5}$$

which is the relative increase in the soil CO_2 efflux with a 10 °C increase in soil temperature.

Chamber technique data were missing for the entire snow-covered period, so data for this entire period were calculated by using Eq. (4) and the soil temperature measured at 5 cm depth. Root respiration (R_r) was estimated as the soil CO_2 efflux less the heterotrophic respiration (R_r=R_s-R_h).

3 Results and discussion

3.1 Temporal and spatial variations in the soil CO_2 efflux

Soil CO_2 effluxes measured by both the automated chamber system and the soil CO_2 gradient system showed notable seasonal patterns (Fig. 3). During the snow-covered season, between 9 December and 17 April, soil CO_2 efflux measured by the soil CO_2 gradient technique averaged 0.57 $\mu mol\,m^{-2}\,s^{-1}$, and ranged from 0.40 to 0.70 $\mu mol\,m^{-2}\,s^{-1}$ (Fig. 3c). After the snow melted, the soil CO_2 efflux increased exponentially until day 180 as the soil temperature increased and soil moisture decreased. The soil CO_2 efflux remained high during the summer (between days 180 and 260), on average 5.5 and 6.5 $\mu mol\,m^{-2}\,s^{-1}$ as measured by the automated chamber system and soil CO_2 gradient system, respectively. Then, it decreased steadily with the decreasing soil temperature until the soil was covered by the snow (Fig. 3). In addition, we observed systematically higher CO_2 effluxes by the soil CO_2 gradient approach during the warm season but lower CO_2 effluxes during the cold season compared with those measured by the automated chamber technique. These results are consistent with those that we reported previously (Liang et al., 2004).

The soil CO_2 efflux varied spatially; the coefficient of variation (CV) of the soil CO_2 efflux was 21% and the heterotrophic respiration CV was 20%. Spatial variations in the CO_2 efflux are often observed between measurement plots separated by only a few centimeters, reflecting rock sizes, disturbances by soil fauna, pockets of fine root proliferation, and remnants of decaying organic matter (Davidson et al., 2002; Liang et al., 2004). Furthermore, spatial variation in the soil CO_2 efflux depends on the size of the chamber used for the measurement. In the same forest stand as that used for this study, Liang et al. (2004) reported CVs as high as 44% for data obtained with a standard LI-COR soil chamber (LI-6400-09) with a surface area of 81 cm^2. In contrast, the CV decreased to 30% when the chamber area was increased to 706 cm^2, and they obtained a low CV of 16% when the chamber area was 8100 cm^2. Therefore, Liang et al. (2004) concluded that, for studying spatial variations in soil CO_2 efflux, a system composed of a smaller number of larger chambers would better characterize a site with less labor.

3.2 Responses of the soil CO_2 efflux to soil temperature and moisture

Temperature is the most commonly studied environmental control on soil CO_2 efflux (Lloyd and Taylor, 1994; Davidson and Janssens, 2006; Zhou et al., 2009). We developed functions to evaluate the effect of soil temperature on soil CO_2 effluxes (Fig. 4) by fitting an exponential curve to the relationship between efflux and soil temperature data obtained over the same measurement period (between days 108 and 345). We also calculated Q_{10} coefficients to determine the apparent temperature sensitivity of the soil CO_2 efflux, obtaining values of 3.1 and 4.5 by the chamber and gradient technique, respectively (Fig. 4a, c). Our Q_{10} values were significantly higher than the global mean soil respiration Q_{10} value (reviewed by Zhou et al., 2009). Generally, Q_{10} varies between 1 and 5 and is negatively correlated with temperature and positively correlated with soil moisture (Lloyd and Taylor, 1994). Therefore, we attributed the high Q_{10} values obtained in this study mainly to the high soil moisture at this site and the relatively low average annual temperature. The higher Q_{10} obtained by the gradient technique than by the chamber technique can be attributed to the systematically higher effluxes observed by the gradient technique during the growing season and the lower effluxes observed during the non-growing season (November and December) compared with effluxes observed by the chamber technique.

Soil CO_2 efflux is also controlled by moisture availability. In the present study, to reduce the confounding effect of temperature and evaluate the role of soil moisture on the soil CO_2 efflux, we plotted the temperature-normalized efflux (i.e., the ratio of the observed soil CO_2 efflux to the temperature-fitted efflux) against the volumetric soil moisture (Fig. 5). Temperature-normalized efflux values were around 1.0 throughout the measurement period, and the low correlation coefficients ($r^2 < 0.05$) and gradual slopes (≤ 0.01) of the regression lines indicate that soil CO_2 effluxes at Tomakomai were not sensitive to soil moisture over a wide range of field conditions. The high sensitivity of soil respiration to soil temperature and its low sensitivity to moisture at this site is consistent with the findings of a study conducted in a northern forest in upper Michigan, USA (Tang et al., 2008).

3.3 Seasonal variation of the soil CO_2 efflux Q_{10} coefficient

To investigate the mechanism by which temperature affects the soil efflux, we estimated the Q_{10} coefficient from monthly data sets obtained by the automated chamber system. Figure 6 shows the seasonal changes in Q_{10} values for root respiration, heterotrophic respiration, and the total soil CO_2 efflux in 2003.

The Q_{10} of root respiration peaked in June when productivities of fine roots and the rhizosphere were highest, suggesting that root respiration is controlled mainly by canopy processes through metabolism of recently fixed carbohydrates (Tang et al., 2005; Moyano et al., 2008; Sampson et al., 2007; Irvine et al., 2008). The lowest root respiration Q_{10} was observed in August, during the hottest part of the summer. In contrast, Q_{10} values of heterotrophic respiration remained relatively constant (at around 3.0) across the growing season but increased dramatically from late autumn (October) to early winter (December), accompanied by an extreme decrease in temperature. Precipitation was abundant in the Hokkaido region and no evidence for seasonal drought was observed. Thus, the different seasonality of Q_{10} between root respiration and heterotrophic respiration suggests that the temperature response of root respiration has a different mechanism from that of heterotrophic respiration; when environmental conditions (i.e., temperature and moisture) are favorable for microbial activity, heterotrophic respiration contributes more to the total soil CO_2 efflux, and when they are favorable for root growth, root respiration contributes more. The Q_{10} values of root respiration and heterotrophic respiration averaged over the growing season were 2.8 and 3.4, respectively. Lower Q_{10} of root respiration than of heterotrophic respiration in this larch forest does not agree with the report for a temperate mixed forest at the Harvard Forest, in which the Q_{10} value of root respiration (4.6) was significantly greater than that of soil heterotrophic respiration (2.5) (Boone et al., 1998). Our finding suggests that the high temperature sensitivity of heterotrophic respiration will offset the forest carbon sequestration in the changing world with elevated atmospheric CO_2 concentration.

Recent field studies have also observed significant seasonal changes in Q_{10} values of the soil CO_2 efflux (Chen et al., 2009; Liu et al., 2006). By partitioning soil CO_2 efflux into root respiration and heterotrophic respiration, we showed that the seasonality of the soil CO_2 efflux Q_{10} value was similar to that of the root respiration Q_{10} (Fig. 6), a finding consistent with previous report about the total soil CO_2 efflux, in which Janssens and Pilegaard (2003) suspected that low summertime Q_{10} values were caused by summer drought stress. The similar seasonality that we found between the root respiration Q_{10} and the total soil CO_2 efflux Q_{10} suggests that large seasonal changes in root respiration dominate the seasonal pattern of the soil CO_2 efflux, especially during the growing season. However, the relative stability of the heterotrophic respiration Q_{10} is consistent with both laboratory results and theoretical predictions (Davidson and Janssens, 2006). The seasonal Q_{10} variation indicates that a Q_{10} function (e.g., Eq. 4) based on annual data will under- or overestimate the soil CO_2 efflux on shorter timescales; thus, empirical models should be parameterized at a time resolution similar to that required by the output of the model.

3.4 Root respiration and heterotrophic respiration

Distinguishing root respiration from heterotrophic respiration is an important first step in interpreting measurements and modeling, as autotrophic and heterotrophic respiration can respond differently to the environment and to environmental disturbances (Ryan and Law, 2005; Cisneros-Dozal et al., 2007; Scott-Denton et al., 2003; Moyano et al., 2008; Irvine et al., 2008). In this larch forest, the relative contributions of root respiration and heterotrophic respiration to the total soil CO_2 efflux showed distinct seasonal patterns (Fig. 7), consistent with the suggestion of Hanson et al. (2000) that the proportion of the soil CO_2 efflux derived from root and heterotrophic respiration may vary seasonally and among ecosystems.

Heterotrophic respiration accounted for most of the soil CO_2 efflux (65–70%) between 30 April and 9 June (days 120 to 160), probably because the rapid increase in soil temperature in the spring after the snow melted enhanced decomposition of the recently accumulated litterfall, as well as because the decreasing soil moisture led to increased oxygenation, which stimulated microbial activity. As a result, the contribution of heterotrophic respiration to the total efflux increased and that of autotrophic respiration decreased. Once the canopy began to leaf out, from 25 May (days 145), photosynthesis increased exponentially and was maintained at a high rate, presumably providing substrate for root and associated rhizosphere respiration, which eventually matched or exceeded the contribution of heterotrophic respiration (Tang et al., 2005; Moyano et al., 2008). Thus, autotrophic respiration contributed more (around 50%) to the soil CO_2 efflux between 10 June and 3 August (days 161 to 215), when the plants were growing rapidly. In midsummer, from early August to mid-September (days 216 to 258), high temperatures probably both inhibited photosynthesis and enhanced decomposition of litterfall, allowing the heterotrophic contribution to reach a second peak. As the temperature decreased from the beginning of September, the heterotrophic respiration contribution decreased but the contribution from root respiration remained at a relatively high level owing to the higher allocation of photosynthate (i.e., starch) to the roots (Liang et al., 2004; Liu et al., 2006; Kurganova et al., 2007).

During the whole growing season, between 15 May (day 135) and 15 October (day 288), the average contribution of heterotrophic respiration to the total soil CO_2 efflux was 58%. During the non-growing season, root respiration and heterotrophic respiration each accounted for roughly half of the soil CO_2 efflux. Hanson et al. (2000) reviewed that, in forests, heterotrophic contributions were ranging from 40% during the growing season to 54% annually. The root exclusion method (trenching) used in this study to distinguish autotrophic from heterotrophic respiration might overestimate heterotrophic respiration in the short term (e.g., within one year) owing to the decomposition of dead roots, but it might underestimate heterotrophic respiration in the long term (e.g., over one year) because no new fine root litter is supplied.

3.5 Bias in the annual soil CO_2 efflux

The soil CO_2 efflux at this site was influenced mainly by soil temperature, so we used hourly soil temperature data (Fig. 3) and the best-fit parameter values of soil CO_2 efflux (Eq. 4) to derive missing data for estimation of the annual soil efflux. The annual soil CO_2 efflux estimated by the automated chamber approach was 959 g C m^{-2}, with 57% contributed by heterotrophic respiration. In contrast, the annual soil CO_2 efflux obtained by the soil CO_2 gradient technique was 1040 g C m^{-2}, about 8% higher than that determined with the automated chamber system. However, if we derive the annual soil CO_2 efflux by using the continuously measured soil temperature values and the Q_{10} functions (the solid lines in Fig. 4), then we obtain annual soil CO_2 effluxes of 933 and 992 g C m^{-2} by the automated chamber and soil CO_2 gradient technique, respectively, a bias toward higher values by 59 g C m^{-2} (6.1% of the mean) for the gradient technique. If litter decomposition were taken into account, this bias would be larger because the upper probe of the gradient system was installed under the surface litter layer.

In our previous study, we obtained an annual soil CO_2 efflux of 665 g C m^{-2} with a steady-state chamber system at this site in 2001 (Liang et al., 2004). If we ignore temperature and precipitation differences between 2001 and 2003, the bias toward higher values of 294 g C m^{-2} of the 2003 chamber system suggests that the positive pressure of 0.22 Pa inside the chamber in the steady-state system may have led to underestimation of the soil CO_2 efflux by about 36%. The results are consistent with those of previous laboratory tests that a pressure difference of a few tenths Pa will cause several-fold variation in measured soil CO_2 efflux (Fang and Moncrieff, 1998).

Larch forests are widely distributed throughout the Northern Hemisphere (e.g., >40% of Russian forests) and are thus a globally important forest biome. Our results indicate that regional and global soil respiration are probably significantly over- or underestimated by upscaling data obtained by a single-method approach.

3.6 Impact of rainfall events on the soil CO_2 efflux

Several studies have detected large ecosystem respiration pulses during pulse rain events in arid ecosystems (Lee et al., 2004; Xu et al., 2004; Liang et al., 2003, 2004; Kelliher et al., 2004; Chen et al., 2009; Inglima et al., 2009). In this study, both the automated chamber and soil CO_2 gradient approaches revealed episodic emissions (Fig. 3b, c); the soil CO_2 efflux increased by approximately 70% following rain events with >20 mm of precipitation (Fig. 3b). The soil CO_2 efflux responded rapidly and instantaneously to the onset of rain and returned to the pre-rain rate several hours after the rain had stopped. Our results are consistent with the findings of rain simulation studies (Lee et al., 2004; Chen et al., 2009), and field observations (Inglima et al., 2009; Xu et al., 2004). A 170-mm rainstorm has been reported to enhance the soil CO_2 efflux up to fivefold, and the efflux returns to the pre-rain value usually <1 h after the rain has stopped, showing no sign of a post-wetting efflux pulse (Lee et al., 2004). Kelliher et al. (2004) reported that in a young ponderosa pine forest, soil CO_2 efflux increased threefold with a simulated rain event that increased the soil water holding capacity of previously dry soil to 60%, and then it returned to pre-watering levels within 24 h of the pulse event. However, automated chamber measurements in the same forest (Irvine and Law, 2002) showed that the intensity of rain events had a substantial effect on interannual variation in soil respiration because heavy rain events resulted in prolonged elevation of the soil CO_2 efflux (e.g., 7 days).

The rapid response of the soil CO_2 efflux to pulse rain events suggests that continuous measurements by automated chamber and soil CO_2 gradient systems are important for accurate, quantitative estimates of the contribution of the soil CO_2 efflux to the carbon balance in a particular ecosystem. Periodic manual chamber measurements made only under fine-weather conditions undoubtedly underestimate soil CO_2 effluxes in rainy weather because the pulse signals are missed, which may strongly affect the estimated ecosystem carbon balance (Lee et al., 2004; Xu et al., 2004; McCulley et al., 2007). For instance, if we derive the parameters of a soil temperature-dependent

Q_{10} function (Eq. 4) using the CO_2 efflux values and soil temperatures observed only on the fine days (daily rainfall = 0 mm) of this study and then apply them to rainy days (daily rainfall ≥1 mm), then the estimated annual soil CO_2 efflux decreases by 24 g C m^{-2}, accounting for about 2% of annual soil CO_2 efflux in this larch ecosystem.

3.7 The significance of soil efflux during the snow-covered season

Hirano (2005) used small CO_2 sensors for in situ measurements of soil CO_2 profiles, and showed that soil CO_2 effluxes under a snowpack showed a definite seasonal pattern; they were relatively constant between the beginning of winter and midwinter, but increased dramatically in late winter as the snow melted. In the present study, using the soil temperature-dependent efflux equation (Eq. 4), we estimated the total soil CO_2 efflux during the snow-covered period (between 12 December and 17 April) to be 105 g C m^{-2} by the automated chamber technique, which corresponds to about 11% of the annual soil efflux. Over the same period, however, we measured the soil CO_2 efflux as about 73 g C m^{-2} by the soil CO_2 gradient approach. A bias toward lower values by 32 g C m^{-2} for the gradient approach compared to the chamber technique could cause a difference of about 15% in the annual NEP estimate for this forest ecosystem (Hirata et al., 2007). Brooks et al. (2005) also demonstrated that the failure to account for the winter soil efflux would, on average, result in an overestimation of annual NEP by 71% in deciduous forests and 111% in coniferous forests.

A few studies have demonstrated that both fungal (Schadt et al., 2003) and bacterial (Lipson et al., 2000) biomass values are higher in snow-covered soils than in the same soils in summer, suggesting that the soil CO_2 efflux continues throughout the snow-covered period and constitutes an important part of the annual carbon budget in snowy ecosystems. Intercomparison studies of chamber, soil CO_2 gradient, and micrometeorological techniques might clarify the bias in soil CO_2 efflux measurements between the chamber and soil CO_2 gradient techniques.

4 Conclusions

This study investigated two systems for accurate measurement of soil CO_2 effluxes: a multi-channel automated soil chamber system usable only during snow-free periods, and a soil CO_2 concentration gradient system, which can be used throughout the year, even when the ground is snow-covered.

1. Annual soil CO_2 effluxes of 959 and 1040 g C m^{-2} were obtained with the automated chamber system and by the soil CO_2 gradient technique, respectively. With the chamber-based measurements, the estimated annual mean contribution of heterotrophic respiration to the soil CO_2 efflux was about 57%.
2. The relatively high Q_{10} values (between 3.1 and 4.5) and the low moisture sensitivity of the soil CO_2 efflux demonstrated that temperature was the most importance environmental factor driving the soil CO_2 efflux in this forest.
3. The fast-response chamber technique showed that temporarily higher fluxes following rain events were responsible for about 2% of the annual soil CO_2 efflux. On the other hand, during the snow-covered season, the gradient approach measured the soil CO_2 effluxes ranged from 0.40 to 0.70 $\mu mol\,m^{-2}\,s^{-1}$. Our results suggest that high-resolution continuous measurements are important for accurate quantitative estimation of the contribution of the soil CO_2 efflux to the ecosystem carbon balance.
4. The seasonality of the root respiration Q_{10} was dominantly responsible for the seasonal pattern of the soil CO_2 efflux Q_{10}.
5. The significant difference in soil CO_2 efflux estimates between the two measurement techniques indicates that additional intercomparison studies (for instance, a field campaign using the eddy covariance measurement method) are essential to validate annual soil CO_2 efflux estimates.

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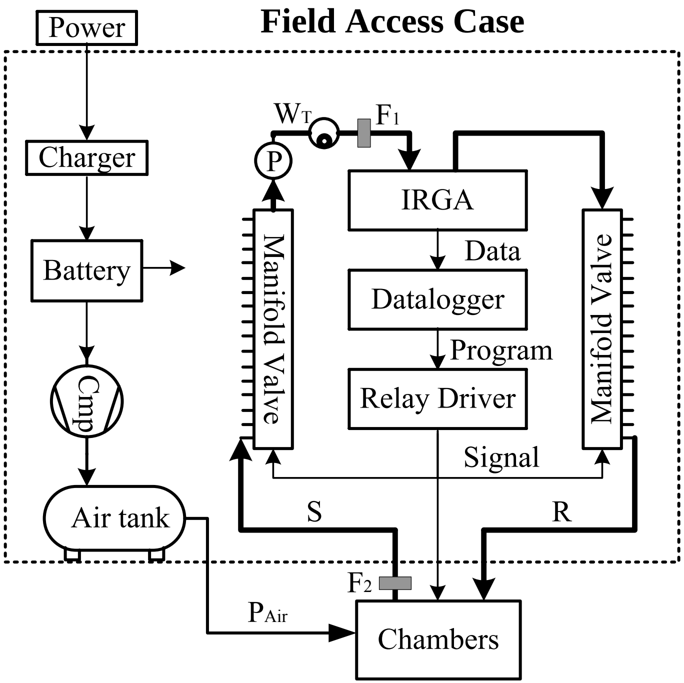

Fig. 1. Schematic illustration of the multi-channel automated chamber system for continuous measurement of soil CO_2 efflux. The dashed square means a water proofed aluminum casing (Field Access Case). Bold arrows indicate the direction of chamber airflow. Abbreviations: Power = DC 12 V or AC 85–240 V for the system; Charger = AC-DC convert for charging and controlling a 12 V (7.2 A h) lead-acid battery that drives the system; Cmp = air compressor; P_{Air} = compressed air from the air tank to the pneumatic cylinders for opening and closing the chamber lids; F_2 = air filter (0.5 mm mesh); S = sample air from the chamber; P = sample pump; W_T = water trap; F_1 = air filter (1 μF mesh); IRGA = infrared gas analyzer; R = sampled air returned to the chamber.

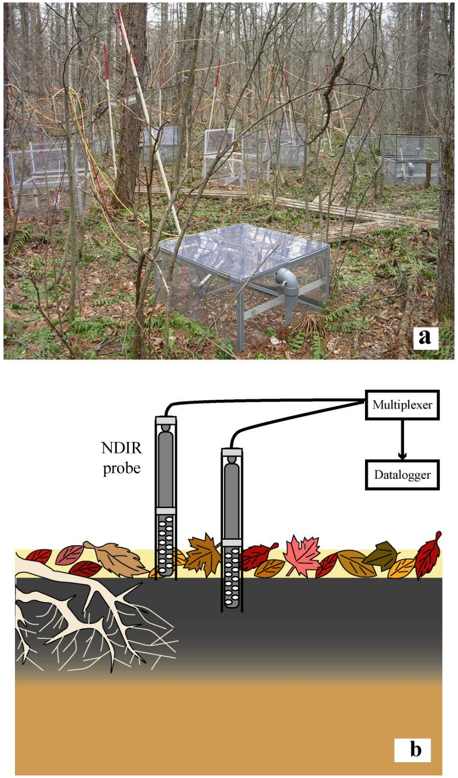

Fig. 2. Image of the multi-channel automated chamber systems installed at the Tomakomai site **(a)** and a set of solid state, non-dispersive infrared gas analyzers (NDIR sensor) vertically installed at different depths of soil **(b)**.

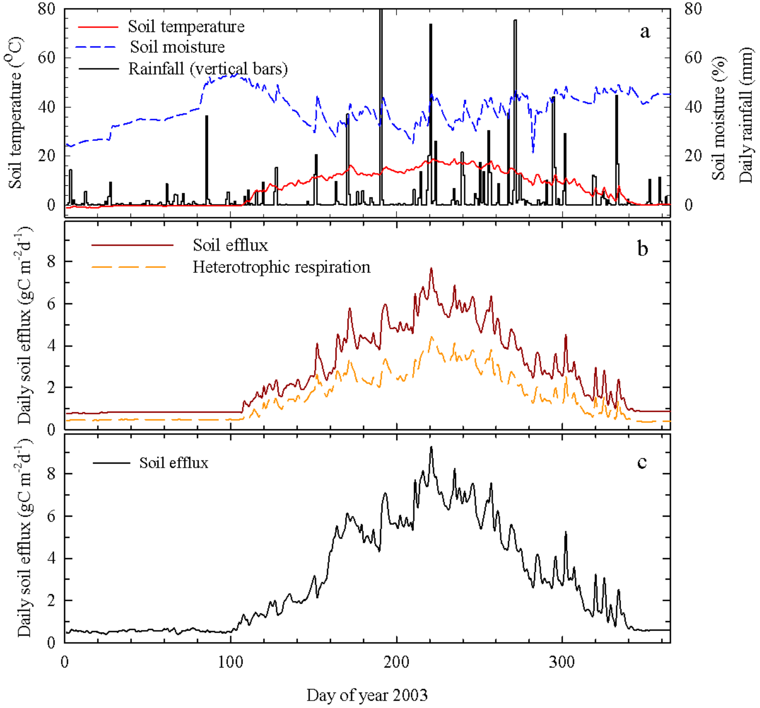

Fig. 3. Seasonal changes in **(a)** hourly soil temperature at 5 cm depth (solid line), daily rainfall (bars), hourly volumetric soil moisture (dashed line), **(b)** soil CO_2 efflux (solid line) and heterotrophic respiration (dashed line) measured by the automated chamber system, and soil CO_2 efflux measured by the soil CO_2 gradient system **(c)** in larch forest at Tomakomai flux site in 2003. For the chamber approach, measurements were conducted between day 108 and day 345, other values were estimated by using the Q_{10} function of Eq. (4).

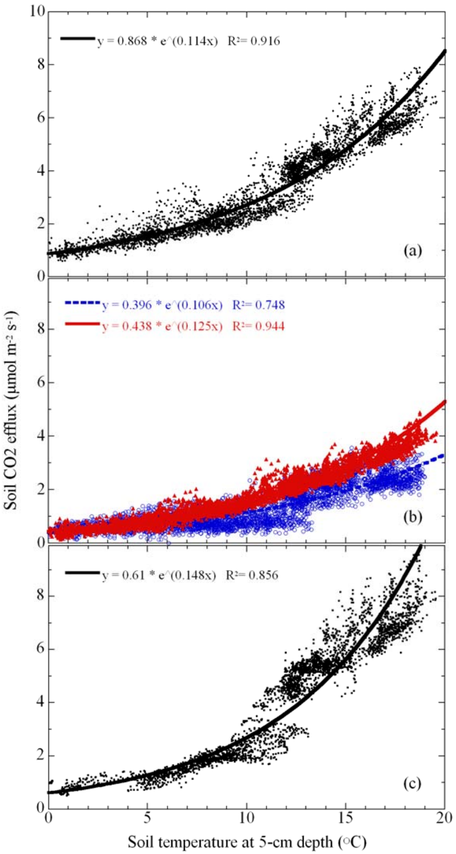

Fig. 4. Effect of soil temperature at a depth of 5 cm on **(a)** soil CO_2 efflux, **(b)** heterotrophic (red triangles) and root respiration (blue circles) measured by the automated chamber system, and **(c)** soil CO_2 efflux measured by the soil CO_2 gradient system. Data points represent the hourly efflux averaged over eight chambers or two gradient plots. The solid line represents the best fitting curve of temperature-dependent Q_{10} function.

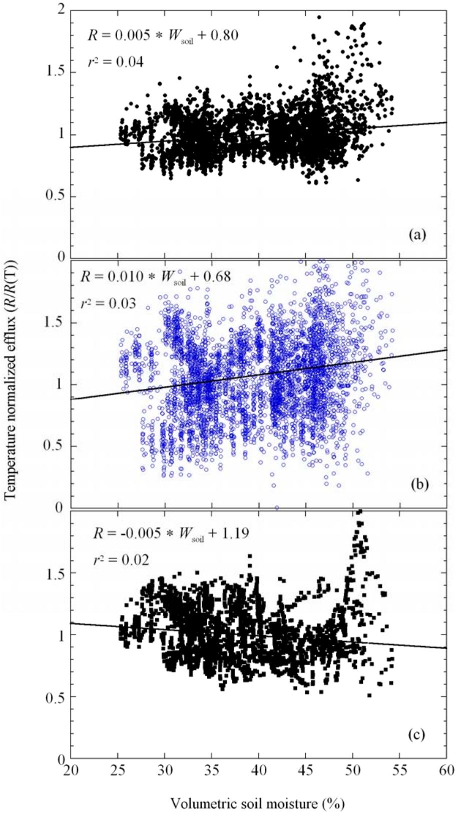

Fig. 5. Temperature normalized soil CO_2 efflux, ratio between measured soil CO_2 efflux (R_s) and its temperature fitted value ($R_s(T)$), versus volumetric soil water content. **(a)** and **(b)** represent soil CO_2 efflux and root respiration measured by the automated chamber system, and **(c)** represents soil CO_2 efflux measured by the soil CO_2 gradient system.

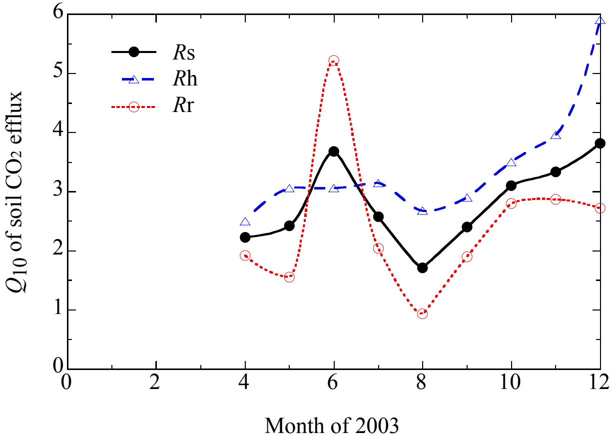

Fig. 6. Seasonal changes in Q_{10} of soil CO_2 efflux (dots with solid line), heterotrophic respiration (triangles with dashed line) and root respiration (circles with dotted line). Respiration data were obtained with the automated chamber system. Root respiration was estimated as soil CO_2 efflux minus heterotrophic respiration. We could not derive the Q_{10} during the snow covered season even from datasets obtained with the soil CO_2 gradient technique, due to the fact that soil temperature was maintained very stable under the snowpack (Fig. 3a).

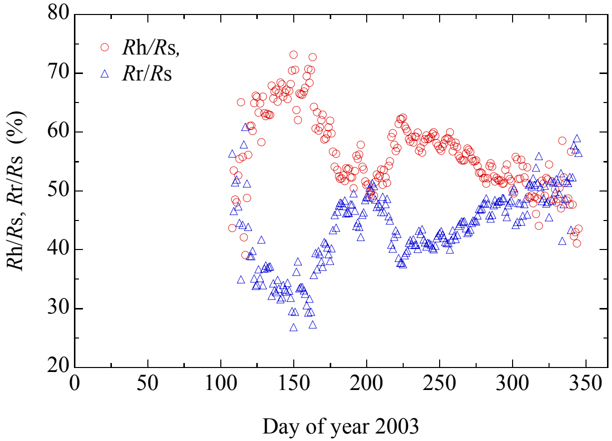

Fig. 7. Seasonal change in the contributions of heterotrophic respiration (triangles) and root respiration (circles) to the total soil CO_2 efflux. Respiration data were obtained with the automated chamber system. Root respiration was estimated as soil CO_2 efflux minus heterotrophic respiration.