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Soil CO_2 efflux of a larch forest in northern Japan

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Abstract. We had continuously measured soil CO_2 efflux (R_s) in a larch forest in northern Japan at hourly intervals for the snow-free period in 2003 with an automated chamber system and partitioned R_s into heterotrophic respiration (R_h) and autotrophic respiration (R_r) by using the trench method. In addition, we applied the soil CO_2 concentration gradients method to continuously measure soil CO_2 profiles under snowpack in the snowy period and to partition R_s into topsoil (O_a and A horizons) CO_2 efflux (F_t) with a depth of 0.13 m and sub-soil (C horizon) CO_2 efflux (F_c). We found that soil CO_2 effluxes were strongly affected by the seasonal variation of soil temperature but weakly correlated with soil moisture, probably because the volumetric soil moisture (30–40% at 95% confidence interval) was within a plateau region for root and microbial activities. The soil CO_2 effluxes changed seasonally in parallel with soil temperature in topsoil with the peak in late summer. On the other hand, the contribution of R_r to R_s was the largest at about 50% in early summer, when canopy photosynthesis and plant growth were more active. The temperature sensitivity (Q_{10}) of R_r peaked in June. Under snowpack, R_s was stable until mid-March and then gradually increased with snow melting. R_s summed up to 79 g C m^{-2} during the snowy season for 4 months. The annual R_s was determined at 934 g C m^{-2} y^{-1} in 2003, which accounted for 63% of ecosystem respiration. The annual contributions of R_h and R_r to R_s were 57% and 43%, respectively. Based on the gradient approach, R_s was partitioned vertically into litter (O_i and O_e horizons) with a depth of 0.01–0.02 m, topsoil and sub-soil respirations with proportions of 6, 72 and 22%, respectively, on an annual basis. The vertical distribution of CO_2 efflux was consistent with those of soil carbon and root biomass.



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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. Recently, Bond-Lamberty and Thomson (2010) estimated that the global soil CO_2 efflux, widely referred to as soil respiration (R_s), was about 98 Pg C y^{-1} in 2008 based on a five-decade record of chamber measurements, which is more than 13 times the rate of fossil fuel combustion (IPCC, 2007), indicating that 20–40% of the atmospheric CO_2 circulates through soils every year. Overall, R_s is the largest component of ecosystem respiration (RE) and the second largest flux in the global carbon cycle after gross primary production (GPP). R_s 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 strongly influence the global carbon cycle. For example, it was reported that the global R_s increased by 0.1 Pg C y^{-1} between 1989 and 2008 (Bond-Lamberty and Thomson, 2010), and that the positive feedback from this enhancement of R_s by global warming would further raise atmospheric CO_2 concentration by 20-224 ppm by 2100 and resulting higher CO_2 levels would lead to an additional temperature increase ranging from 0.1 to 1.5 °C (Friedlingstein et al., 2006; IPCC, 2007).

In forest ecosystems, micrometeorological studies (i.e., eddy covariance) have shown that, on average, about 80% of GPP is respired back to the atmosphere (Law et al., 2002), and R_s has been estimated to account for 60-90% of RE, with marked temporal as well as spatial variations (Law et al., 1999; Janssens et al., 2001a, b; Liang et al., 2004). Therefore, R_s 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).

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Because R_s has high spatial variability and the soil medium is not easily accessible, R_s cannot be measured by large-scale remote sensing. FLUXNET has become an effective network for observing carbon sequestration or loss by global terrestrial ecosystems by the eddy covariance technique (Luyssaert et al., 2008). Unfortunately, the use of the eddy covariance 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., 2001a). Therefore, to validate nocturnal, sub-canopy, and bad-weather (e.g., rainy period) eddy covariance measurements as well as the partition of the net ecosystem production (NEP), the flux research community have used automated chamber systems, which provide continuous (i.e., half-hourly or hourly) measurements of R_s (Gaumont-Guay et al., 2009; Jassal et al., 2007). Moreover, the automated continuous measurements of R_s (Goulden and Crill, 1997; Savage and Davidson, 2003; Liang et al., 2004) provide insights about ecosystem processes, which were not possible to explore before (Vargas et al., 2010).

Although larch forests are an important forest biome in Northeast Eurasian continent (Gower and Richards, 1990), continuous measurements of R_s are quite limited (Liang et al., 2004; Kim et al., 2005a). In this study, we continuously measured R_s at hourly intervals with an automated chamber system and partitioned it into heterotrophic and autotrophic soil respirations using the trench method in a larch forest in northern Japan. In addition, we applied the gradient method to measure R_s under snowpack in the winter season and to determine the vertical distribution of soil CO_2 efflux. The objectives of this study are to investigate (1) seasonal variations in soil CO_2 efflux, (2) responses of soil CO_2 efflux to temperature, moisture and rain events, (3) relative contributions of heterotrophic and autotrophic respirations to total R_s, (4) vertical distribution of soil CO_2 efflux and (5) contribution of R_s to RE, in a larch forest.

2 Site description

The study site is the Tomakomai Flux Site (42°44′ N, 141°31′ E), a larch plantation in Tomakomai National Forest, southern Hokkaido, Japan. The altitude of the site is 125 m and the terrain is essentially flat with a gentle slope of 1–2°. This site was one of the core sites of AsiaFlux network. The tower based eddy CO_2 flux had been measured using both open-path and closed-path systems since August 2000 until the catastrophic damage by a typhoon in September 2004 (Hirano et al., 2003a; Hirata et al., 2007).

2.1 Vegetation characteristics

The forest was 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, for trees with breast height diameter (DBH) larger than 0.05 m, stand density was 1087 stems ha^{-1} and basal area density 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 its peak at 5.6 m^2 m^{-2}. 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 species were 0.5 m, 2.7 t ha^{-1}, and 3.6 m^2 m^{-2}, respectively. Defoliation started in mid-October, and the soil was covered by snow for about 4 months from mid-December to mid-April. Snow depth was 0.6 to 1.0 m in midwinter.

2.2 Climate

Climate records between 1979 and 2000 from two weather stations of Japan Meteorology Agency about 10 km away from the study site, Tomakomai and Shikotsuko, showed that the mean annual precipitation was approximately 1500 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.

2.3 Soil characteristics

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. The litter layer (O_i and O_e horizons) is 0.01–0.02 m thick and overlies a 0.1- to 0.15-m-thick organic layer (O_a and A horizons) containing many fine roots. Beneath it, there is a layer composed of fragments of porous pumice stone (0.005–0.03 m in diameter) (C horizon) with some coarse roots. B horizon is lacking. The soil is weakly acidic (pH 5.0–6.0) and poor in nutrients. Sakai et al. (2007) reported that the densities of total and fine root biomass were 24.3 and 6.9 t ha^{-1} and more than 80% of root biomass was distributed in the topsoil with a thickness of 0.15 m. Total soil organic carbon (SOC) and nitrogen storage were about 36 tC ha^{-2} and 300 gN m^{-2}, respectively, and about 90% of SOC accumulated in the surface layer between 0–0.30 m (Sakai et al., 2007).

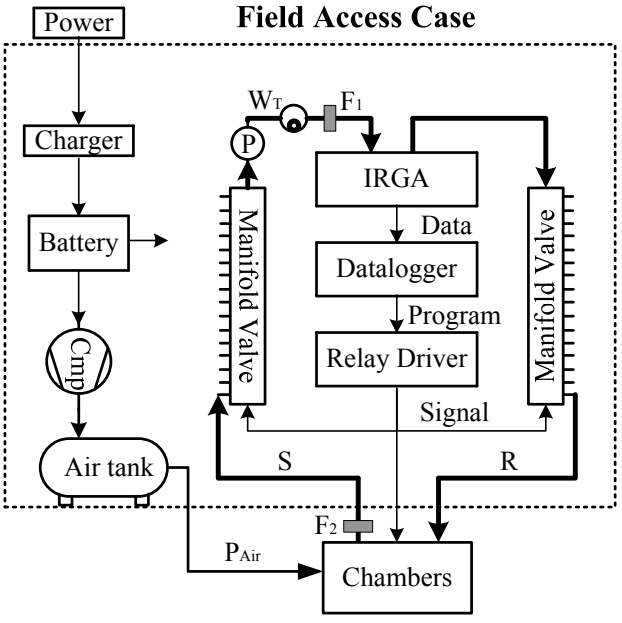


Fig. 1. Schematic illustration of the multi-channel automated chamber system for continuous measurement of soil CO_2 efflux. The dashed square means a water proofed aluminum casing (Field Access Case). Bold arrows indicate the direction of chamber airflow. Abbreviations: Power = DC 12 V or AC 85–240 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.

3 Soil CO_2 efflux measurement

3.1 Automated chamber system

Liang et al. (2003) designed a multi-channel automated chamber system that applied a steady-state technique to continuously measure R_s. 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 R_s (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 waterproof field access case (0.70 m long ×0.50 m wide ×0.35 m high), and can drive maximum 24 automated chambers. The main components of the control unit are an infrared gas analyzer (IRGA, LI-820; 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 vertically 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; Fig. 1). During the measurement, the chamber is closed and the chamber air is mixed by two micro-blowers (MF12B, Nihon Blower Ltd., Tokyo, Japan). The chamber air is circulated through the IRGA by a micro-diaphragm pump (5 L min^{-1}; CM-50, Enomoto Ltd., Tokyo, Japan), and CO_2 concentration is monitored by the IRGA. The average power consumption of the whole system is 13 W; thus, the system can be continuously driven by three 75-W solar cells with three 100-A·h deep-cycle batteries.

In June 2002, we installed 16 chambers at the site randomly 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). Understory vegetation inside the chambers was clipped periodically during the growing season. The second group was used to measure heterotrophic respiration (R_h), and the chambers were installed in 1×1 m root exclusion plots. Trenches with a width of 0.005 to 0.01 m were dug down to 0.5 m along the plot boundaries using 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 0.50 m to prevent root penetration.

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 for 94% of the time: during each 1-h cycle each chamber was open for 56.25 minutes and closed for 3.75 minutes. Thus, most of rainfall and leaf litter could enter the chambers, and the interior of each chamber had good exposure to any atmospheric turbulence. Soil temperature at 0.05 m depth inside each chamber was measured with home-made thermocouples and volumetric soil moisture at 0.10 m depth was monitored with TDR sensors (CS615, Campbell Scientific), and recorded by the datalogger via a multiplexers (AM25T, Campbell Scientific). Moreover, air pressure at 0.30 m height around the center of the measurement plots was monitored with a pressure transducer (PX2760, Omega Engineering, Inc., Stamford, CT, USA). The datalogger acquired outputs from the IRGA and the other sensors at 1-s intervals and recorded the averaged values every 5 s. Soil CO_2 efflux (R_s, µmol m^{-2} s^{-1}) was calculated with the following equation:

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

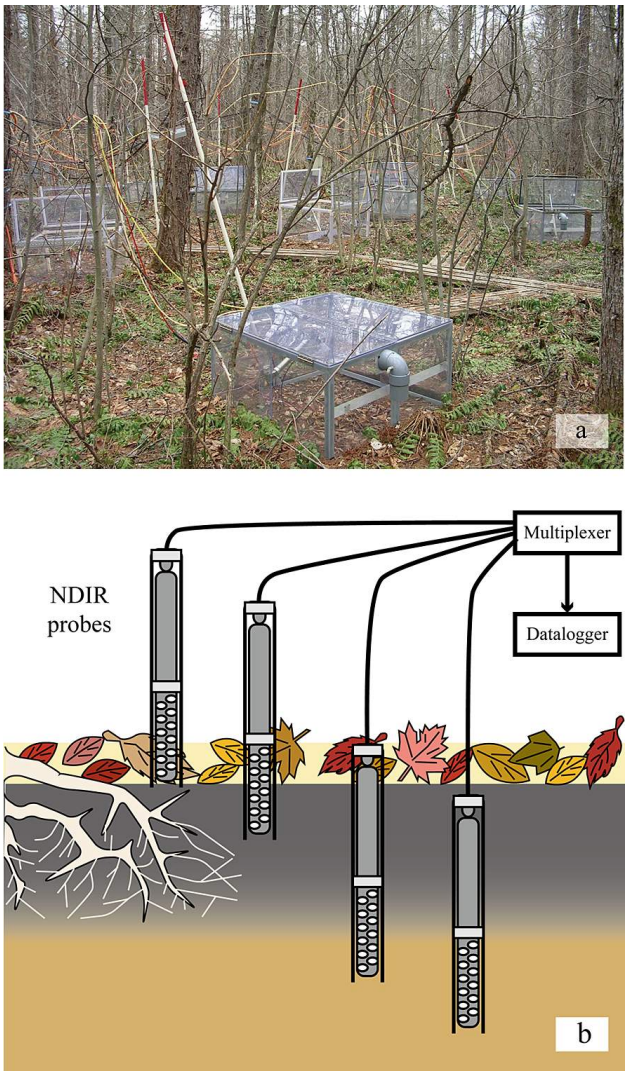


Fig. 2. (a) Image of the multi-channel automated chamber systems installed at the site and **(b)** a set of infrared gas analyzers (IRGA sensors) vertically installed at different depths of soil.

where V is the effective chamber-head volume (m^3), S is the measured soil surface area (m^2), P is the air pressure (hPa), T is the air temperature (K), and W is the water vapor mole fraction (mmol mol^{-1}) inside the chambers; $\delta C/\delta t$ is the rate of change in the CO_2 mole fraction (µmol mol^{-1} s^{-1}) calculated by the least-square method, and R is the gas constant (8.314 Pa m^3 K^{-1} mol^{-1}). Note that the pressure is not the pressure inside the IRGA cell but the pressure inside the chambers and we assumed that there was null pressure difference between the inside and outside of the chambers.

3.2 Soil CO_2 gradient system

We applied the soil CO_2 gradient method for continuous measurements of topsoil and subsoil CO_2 effluxes (Hirano et al., 2003b; Liang et al., 2004; Tang et al., 2003). We inserted CO_2 probes (18.5 mm diameter, 155 mm long) of IRGAs (GMT222, Vaisala, Helsinki, Finland) into the soil to directly measure soil CO_2 concentration profiles. The probes were enclosed in polytetrafluoroehylence (PTFE) socks, which are porous water proofing (Liang et al., 2004), to prevent damage by rainwater, and then they were put into PVC (inner diameter 22 mm) casings to measure CO_2 concentrations at only specific soil depths. A fine (0.5 mm) mesh stainless steel screen was set at the opening at the bottom of the casing to prevent soil particles from entering the casing. In addition, temperature and pressure were measured in each casing with a thermocouple and a pressure transmitter (MPX4115, FreeScale Semiconductor, Austin, Texas, USA) via a plastic tube connected to the casing, respectively.

In June 2002, we installed two sets of sensors each with four CO_2 probes at two locations 0.60 m apart at 0, 0.02, 0.11 and 0.13 m depths. The measuring ranges of the probes were 0–2000 ppm for 0 and 0.02 m and 0-10000 ppm for 0.11 and 0.13 m. The probes were vertically installed to minimize soil disturbance (Fig. 2b). We defined 0 m depth as the soil surface under the litter layer (O_i and O_e horizons). To avoid heating of the soil adjacent to the probes, all probes were powered on hourly at 24 min past the hours, and operated for only 7 min. After warm-up of 5 min, CO_2 concentration was measured for 2 min and recorded every 10 s with a datalogger (CR10X). The temperature and pressure inside the casing were recorded simultaneously. Soil temperature at 0.02, 0.05, 0.10 and 0.15 m depths and volumetric soil moisture at 0.10 m depth were also recorded. The probes were removed for drying and calibration every two months.

The two replicates of CO_2 concentration were averaged at each depth and corrected for temperature and pressure accordingly to the manufacturer's instruction and converted to CO_2 molar density (µmol m^{-3}) . Then, soil CO_2 efflux (F_s) was calculated by Fick's first law under the assumption of horizontal homogeneity,

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

where F is the CO_2 efflux (µmol m^{-2} s^{-1}), D_s (m^2 s^{-1}) is the gaseous CO_2 diffusion coefficient, and $\delta C/\delta z$ is the vertical CO_2 density gradient (µmol m^{-4}). Following Hirano et al. (2003b), we calculated soil CO_2 efflux from the soil surface (R_s) and CO_2 efflux from C horizon to A horizon (R_c) every hour from the soil CO_2 concentration profiles. We applied Eq. (2) to the boundary between O_e and O_a horizons (soil surface) and that between A and C horizons at a depth of 0.13 m, and considered CO_2 storage change in the O_a and A horizons for the calculation. In addition, we calculated CO_2 production rate of topsoil (O_a and A horizons) (R_t) by subtracting CO_2 production rate of subsoil (R_c) from R_s. D_s

was calculated using Campbell's function (Campbell, 1985):

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

where D_0 is the CO_2 diffusion coefficient in air (1.39×10^{-5} m^2 s^{-1}) at 1013 hPa and 273.15 K, T_{soil} is the soil temperature (°C) at 0.02 or 0.10 m depth, and P_s is the air pressure (hPa) inside the sensor casing. B is the relative soil gaseous diffusion coefficient, which was determined from air-filled porosity (e) of soil using their power relationship ($B = 0.82e^{2.03}$, $r^2 = 0.94$) (Currie, 1960). The relationship was obtained with undisturbed soil cores by the diffusion chamber method (Currie, 1960). e was determined as residual of the volume fractions of solid and water (θ). The D_s in A horizon fluctuated between 0.015 and 0.045 cm^2 s^{-1} with soil temperature and moisture, which is in the middle range of 0.022 to 0.052 cm^2 s^{-1} for Japanese forest soils (42 ecosystems) (Ishitsuka and Sakata, 2006).

3.3 Data analysis

Hourly measurements of the 8 chambers used for each process (R_s and R_h) were averaged to obtain the mean efflux, and coefficients of variation (CV) were calculated to show spatial variation. To examine the temperature response of soil CO_2 efflux, we performed a regression analysis using an exponential model:

$$R_s = ae^{bT_{soil}}, \quad (4)$$

where R_s is the CO_2 efflux at soil temperature T_{soil} at a depth of 0.05 m, a is the efflux at 0 °C, 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:

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

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

Although chamber data were missing for the snow-covered period for 127 days from January 1 to April 17 and December 12 to December 31 in 2003, more than 95% of data were available for the snow-free period. Also, more than 95% of gradient flux data were available throughout the year. The data gaps were filled with R_s estimated from Eq. (4) by using soil temperature. Root respiration (R_r) was estimated by subtracting R_h from R_s.

4 Results and discussion

4.1 Seasonal variations in soil CO_2 efflux (R_s)

R_s measured by both the chamber and gradient systems showed notable seasonal patterns (Fig. 3). After snow disappearance on 17 April R_s increased rapidly until around DOY

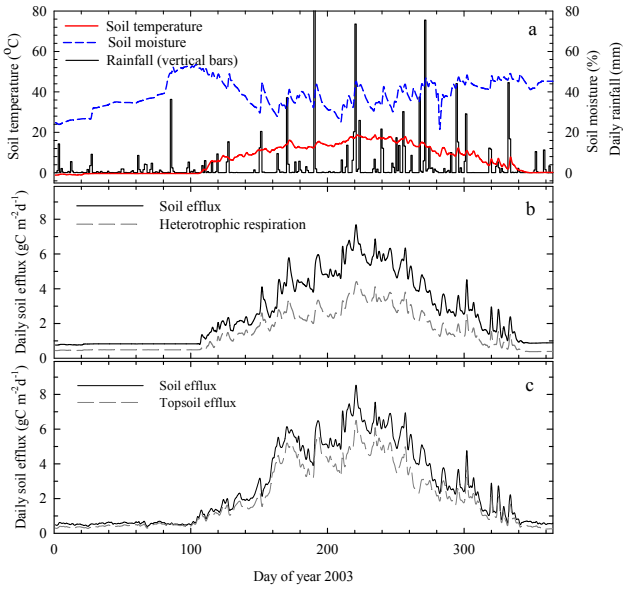


Fig. 3. Seasonal variations in daily means or sums of **(a)** soil temperature at a depth of 0.05 m (solid line), precipitation (bars) and volumetric soil moisture at a depth of 0.1 m (dashed line), **(b)** total soil respiration (solid line) and heterotrophic respiration (gray dashed line) measured with the automated chamber system, **(c)** and total soil respiration (solid line) and topsoil (O_a and A horizons) efflux (gray dashed line) measured with the gradient system. For the chamber method, measurements were conducted between DOY 108 and 345. Other values were estimated by using the Q_{10} function of Eq. (4).

(day of year) 220 with soil temperature. R_s remained high during late summer between DOY 220 and 260. Peak R_s values were about 6 and 7 gC m^{-2} d^{-1} by the chamber and the gradient systems, respectively. Then, R_s decreased steadily with soil temperature until the ground was covered by snow. The pattern in the snow-free season is consistent with that in 2001 (Liang et al., 2004) and RE patterns with the peak in August (Hirata et al, 2007). Heterotrophic respiration (R_h) showed a similar seasonal variation to that of R_s. Also, topsoil respiration (F_t) varied almost in parallel with R_s.

During the snowy season, R_s measured by the gradient method was stable at 0.50–0.55 µmol m^{-2} s^{-1} until mid-March and then gradually increased up to 0.8 µmol m^{-2} s^{-1} with snow melting. Mean R_s for the snowy season of 127 days was 0.56±0.12 µmol^{-2} s^{-1} (mean±SD). The seasonal variation and the mean value are very similar to those measured in a neighboring deciduous broadleaf forest using the gradient method (Hirano, 2005). On the other hand, R_s can be also estimated from soil temperature using Eq. (4) fitted to chamber data. The mean and SD of the estimated value was 0.83±0.03 µmol m^{-2} s^{-1}. However, compared to the patterns of the gradient method, there was no variation during the snow-melting season. This stable R_s is due to the stable soil temperature under snowpack.

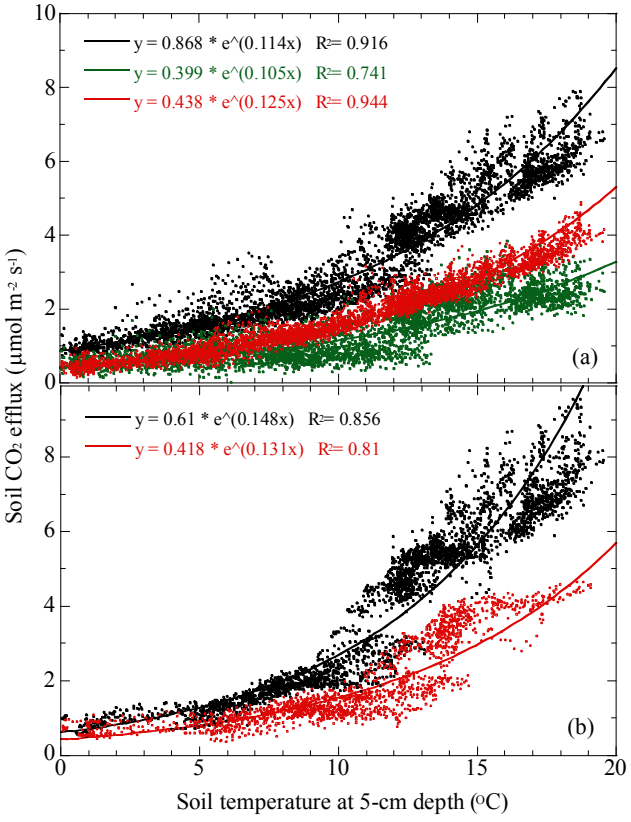


Fig. 4. Relationships between soil temperature at a depth of 0.05 m and **(a)** total soil CO_2 efflux (black symbols and line), heterotrophic (red symbols and line) and root (green symbols and line) respirations measured by the chamber method, and **(b)** total soil CO_2 efflux (black symbols and line) and topsoil (O_a and A horizons) CO_2 efflux (red symbols and line) measured by the gradient technique, on an hourly basis. The best-fitted exponential curves are shown.

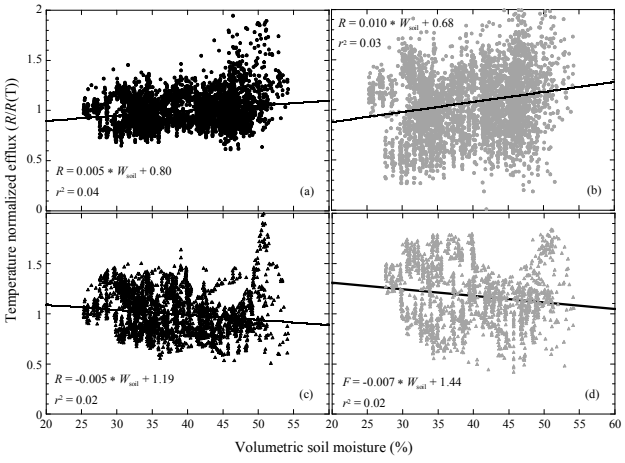


Fig. 5. Temperature normalized soil CO_2 efflux, ratio between measured soil CO_2 efflux (R_s) and its temperature fitted value ($R_s(T)$), versus volumetric soil water content at a depth of 0.1 m. **(a)** and **(b)** represent total soil CO_2 efflux and root respiration measured by the automated chamber system, and **(c)** and **(d)** represents total soil CO_2 efflux and topsoil (O_a and A horizons) CO_2 efflux measured by the soil CO_2 gradient system.

4.2 Responses of soil CO_2 efflux to soil temperature and moisture

For the snow-free period for 8 month (Fig. 4), soil CO_2 effluxes increased exponentially with temperature and Q_{10} value was estimated to be about 3.1, 3.5, 2.9 and 3.6 for R_s, R_h, R_r and F_t, respectively. The Q_{10} of R_s was quite larger than the global mean Q_{10} of R_s (ranging 1.43–2.03; Raich et al., 2002; 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, the high Q_{10} is attributable mainly to high soil moisture, ranging between 25 and 55% with 95% confidence interval of 30–40%, and relatively low air temperature with an annual mean of 7.1°C. The Q_{10} was lower for R_r than for R_h in this site. The result is inconsistent with the report for a temperate mixed forest at the Harvard Forest, in which the Q_{10} of R_r (4.6) was significantly greater than that of R_h (2.5) (Boone et al., 1998). Our finding suggests that the high temperature sensitivity of R_h will offset the forest carbon sequestration in the changing world under elevated atmospheric CO_2 concentration (Bond-Lamberty and Thomson, 2010). The Q_{10} of F_t from O_a and A horizons with a depth of 0.13 m was almost the same as that of R_h, whereas it was larger than that of R_s. R_s includes CO_2 efflux from litter layer (O_e and O_i layers) with low Q_{10} values around 2 (Kim et al., 2005b) and that from C horizon, which is almost independent of temperature at a depth of 0.5 m (Hirano et al., 2003b). This fact can explain the difference in Q_{10} between R_s and F_t.

Soil CO_2 efflux is also controlled by moisture availability. To remove the confounding effect of temperature and evaluate the role of soil moisture on soil CO_2 efflux, we plotted temperature-normalized efflux (i.e., the ratio of observed soil CO_2 efflux to temperature-fitted efflux) against volumetric soil moisture (Fig. 5). Temperature-normalized values were largely scattered around 1.0 throughout the snow-free period. Low coefficients of determination ($R^2 < 0.04$) and slight slopes (≤ 0.01) of regression lines suggest that, soil moisture of 30–40% at 95% confidence interval favored root and microbial activities. For this forest, there was indeed no clear correlation between soil moisture and GPP or RE that was observed based on the flux tower measurement (Hirata et al., 2007). However, the larger deviations at high soil moisture were probably induced by the rain events (Fig. 5). Results are consistent with the findings in relative humid forest ecosystems (Tang et al., 2008; Ruehr et al., 2010; Klimek et al., 2009).

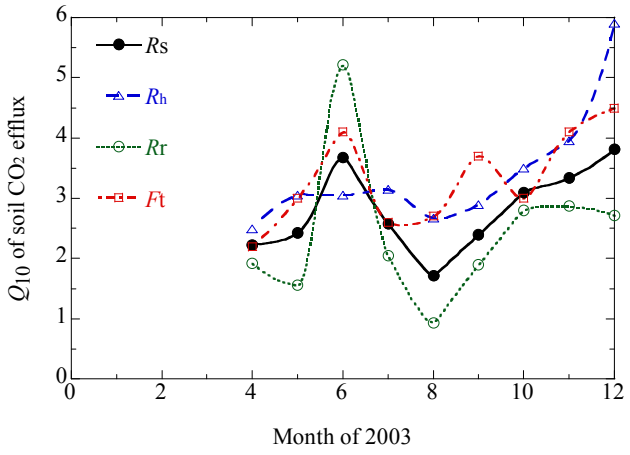


Fig. 6. Seasonal changes in Q_{10} of soil CO_2 efflux (R_s, dots with solid line), heterotrophic respiration (R_h, triangles with dashed line), root respiration (R_r, circles with dotted line), and topsoil CO_2 efflux (F_t, squares with dot-dashed line) for the snow-free season from April through December.

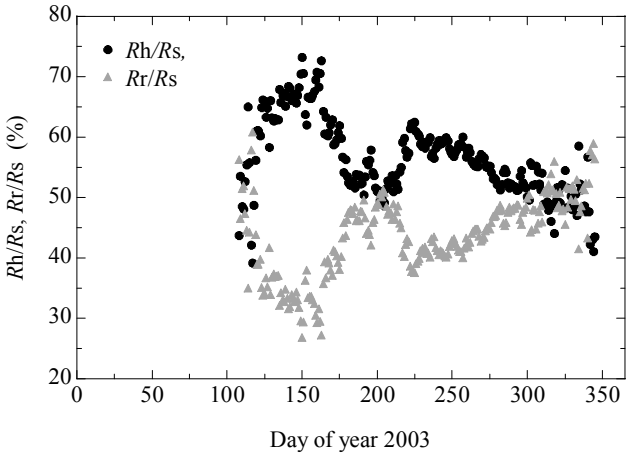


Fig. 7. Seasonal variations in the contributions of heterotrophic respiration (R_h, triangles) and root respiration (R_r, circles) to total soil respiration (R_s) measured by the chamber method on daily basis.

4.3 Seasonal variations in Q_{10} of soil CO_2 efflux

To investigate the mechanism by which temperature affects soil CO_2 efflux, we determined Q_{10} values monthly. Figure 6 shows seasonal variations in Q_{10} of R_s, R_h, R_r and F_t. The Q_{10} of R_r peaked in June when productivities of fine roots and the rhizosphere were highest, suggesting that R_r is controlled mainly by canopy processes (e.g. photosynthesis) through metabolism of recently fixed carbohydrates (Tang et al., 2005; Moyano et al., 2008; Sampson et al., 2007; Irvine et al., 2008; Baldocchi et al., 2006; Yuste et al., 2004; Hasselquist et al., 2010). The fact that ecosystem photosynthesis (GPP) of this larch forest also peaked in June (Hirata et al., 2007) supports this suggestion. R_r showed the lowest Q_{10} in August (i.e., midsummer). In contrast, the Q_{10} of R_h remained relatively constant at around 3 throughout the growing season but increased drastically from late autumn (October) to early winter (December), accompanied by a large decrease in temperature. The increase in Q_{10} of R_h in late autumn was attributable to fresh litter supply through defoliation (Kim et al., 2005a). Precipitation was abundant for the growing season in this site, and no evidence for seasonal drought was observed. Thus, the different seasonality of Q_{10} between R_r and R_h suggests that the temperature response of R_r has a different mechanism from that of R_h.

There is an increasing evidence that Q_{10} of R_s is not seasonally constant and tends to increase with decreasing temperature and increasing soil moisture (Chen et al., 2009a). Recent field studies have also observed significant seasonal variations in Q_{10} of R_s (Chen et al., 2009a; Janssens and Pilegaard, 2003; Liu et al., 2006b; Phillips et al., 2010; Xu and Qi, 2001). By partitioning R_s into R_r and R_h, we found that the seasonality of the Q_{10} of R_s was almost parallel with that of the Q_{10} of R_r (Fig. 6). The summer depression in Q_{10} was also reported by Janssens and Pilegaard (2003), whereas they suspected that the depression was caused by summer drought stress. The similar seasonal variations in the Q_{10} of R_s and R_r suggest that the large seasonal change in R_r dominates the seasonal pattern of R_s during the growing season. The relative stability of the Q_{10} of R_h is consistent with both laboratory results and theoretical predictions (Davidson and Janssens, 2006). The seasonal Q_{10} variation indicates that a Q_{10} function based on annual data will under- or overestimate R_s on shorter timescales. Thus, empirical models should be parameterized at a time resolution similar to that required by the output of each model.

4.4 Root respiration (R_r) and heterotrophic respiration (R_h)

Distinguishing R_r from R_h is an important first step in interpreting field measurements, because R_r and R_h can respond differently to the environment (Cisneros-Dozal et al., 2007; Moyano et al., 2008; Irvine et al., 2008; Ryan and Law, 2005). In this larch forest, the relative contributions of R_r and R_h to R_s showed distinct seasonal patterns (Fig. 7), which is consistent with the suggestion of Hanson et al. (2000) that the proportions of R_r and R_h to R_s vary seasonally and among ecosystems.

R_h accounted for most of R_s (65–70%) between late April and early June (DOY 120 to 160), probably because a rapid increase in soil temperature after the thaw enhanced decomposition of the leaf litter accumulated in the last autumn, as well as because the decreasing soil moisture led to increase soil oxygenation, which stimulated microbial activity. As a result, the contribution of R_h to R_s increased, and that of R_r decreased in this period. After the canopy began to leaf out, from early May, GPP rapidly increased and was maintained

at a high rate from early June through mid-August (Hirata et al., 2007), which probably provided substrate for root and associated rhizosphere (Vargas et al., 2010; Tang et al., 2005; Moyano et al., 2008; Hasselquist et al., 2010). Thus, R_r contributed more (around 50%) to R_s between early June and early August (DOY 161 to 215), when the plants grew rapidly. From early August to mid-September (DOY 216 to 258), high temperatures probably both inhibited photosynthesis and enhanced decomposition of organic matter, allowing the heterotrophic contribution to reach a second peak. As the temperature decreased from the beginning of September, the R_h contribution decreased but the R_r contribution remained at a relatively high level owing to the higher allocation of photosynthate (i.e., starch) to roots and ectomycorrhizal fungi (Liang et al., 2004; Liu et al., 2006a; Kurganova et al., 2007; Hasselquist et al., 2010). In the end of September, the contributions of R_r and R_h became equal, which lasted until December. On the other hand, the contribution of F_t to R_s showed a simpler seasonal variation (data are not shown). The F_t contribution linearly increased from 60% to 90% by late April for 4 months and gradually decreased to 70% by late November. During December, it decreased to 45%. The seasonal variation is similar with that in a neighboring deciduous broadleaf forest (Hirano et al., 2003b; Hirano, 2005).

During the whole growing season for 5 months, between DOY 135 and 288, the average contribution of R_h to R_s was 57%. During the non-growing season, R_r and R_h each accounted for roughly half of R_s. 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 by trenching, which was used in this study to distinguish R_r from R_h, can overestimate R_h in the short term (e.g., within the first treatment year) owing to the decomposition of dead roots, whereas it can underestimate R_h in the long term (e.g., over one year) because no new fine root litter is supplied.

4.5 Impact of rainfall events on soil CO_2 efflux

Several studies have detected a sudden increase in soil respiration during pulsed rain events especially in arid ecosystems (Lee et al., 2004; Xu et al., 2004; Irvine et al., 2005; Kelliher et al., 2004; Chen et al., 2009b; Inglima et al., 2009; Baldocchi et al., 2006). In this study, both the automated chamber and the gradient approaches revealed episodic CO_2 emissions (Fig. 3). R_s rapidly responded to the onset of rain and increased by approximately 70% following a rain event with more than 20 mm of precipitation. After the rain, R_s returned to the pre-rain rate in several hours. Our results are consistent with the findings of rain simulation studies (Lee et al., 2004; Chen et al., 2009b), and field observations (Inglima et al., 2009; Xu et al., 2004; Baldocchi et al., 2006). Lee et al. (2004) reported that a 170-mm rainstorm enhanced R_s up to fivefold, and R_s returns to the pre-rain level within one hour after the rain. Kelliher et al. (2004) reported that, in a young ponderosa pine forest, R_s was increased threefold by a simulated rain event and returned to the pre-rain levels within 24 h after the rain. In the same forest, Irvine and Law (2002) showed that the intensity of rain events had a substantial effect on interannual variation in R_s, because heavy rain events resulted in prolonged elevation of R_s.

The rapid response of R_s to pulsed rain events suggests that continuous measurements are crucial for accurate, quantitative assessment of R_s (Vargas et al., 2010). Periodic measurements by the manual chamber method, which are generally conducted only under fine-weather conditions, undoubtedly underestimate R_s under rainy conditions, because the pulse signals of R_s are missed. The underestimation can strongly affect ecosystem carbon balance (Lee et al., 2004; Xu et al., 2004; McCulley et al., 2007). For instance, if we estimate annual R_s from soil temperature using two exponential models (Eq. 4) fitted to data on all days and no-rain days, respectively, the latter model ignoring rainy data underestimates annual R_s by 24 $gC\,m^{-2}$ or 2%, which is equivalent to 11% of the annual NEE of this forest (Hirata et al., 2007).

4.6 Seasonal and annul sums of soil CO_2 efflux (R_s)

R_s measured with the chamber system summed up to 855 $gC\,m^{-2}$ for about 8 months of the snow-free season. The seasonal sum of R_s measured by the gradient method for the same period was 896 $gC\,m^{-2}$, whereas it must be underestimated, because the gradient method could not measure CO_2 efflux from the litter layer (Q_i and Q_e horizons). CO_2 efflux from the litter layer at this site can be estimated at 60 $gC\,m^{-2}$ for the snow-free season in 2002 from the results of Kim et al. (2005a). If its interannual variation is negligible, R_s comes to 956 $gC\,m^{-2}$ by adding the litter contribution, which is larger than that by the chamber method by 12%. The overestimation by the gradient method is consistent with the result in 2001 (Liang et al., 2004). However, it is worth noting that the difference between the two methods is considerably smaller than those reported by, for example, Vargas et al. (2008) and Pingintha et al. (2010), who showed that the gradient effluxes were 23% and 90% larger than that by the chamber method, respectively. In contrast, Baldocchi et al. (2006) reported that gradient effluxes were only 77% of chamber measurements. Because each hourly R_s by the gradient method always fell within the range of 8 measurements of R_s by the chamber method, the difference between the two methods is attributable to spatial variation in R_s; the coefficient of variation (CV) was 21% for R_s and 20% for R_h on average.

For 4 months of the snowy season, the gradient-based R_s summed up to 73 $gC\,m^{-2}$, which is almost the same as that in a neighboring deciduous broadleaf forest (Hirano, 2005). By adding litter CO_2 efflux (Kim et al., 2005a), R_s under snowpack is estimated to be 89 $gC\,m^{-2}$. On the other hand, the chamber-based R_s may be used to estimated winter R_s

by extrapolating Eq. (4) fitted for the snow-free season only, whith overestimated the winter R_s by by 26 gC m^{-2}. As a result, when the chamber method and the gradient method are adopted for the snow-free and snowy seasons, respectively, the annual R_s is determined to be 934 gC m^{-2} y^{-1}. The annual R_s stands in the middle class of that of temperate forest (Bond-Lamberty and Thomson, 2010). The winter R_s for 4 months accounted for 8.5% of the annual R_s. In a neighboring broadleaf forest, the winter R_s accounted for 8–10% of the annual R_s (Hirano 2005; Kim et al., 2005a). The contribution of the winter R_s was slightly larger than those of forests, shrubs and meadow glasslands in North China (Wang et al., 2010). In our earlier study (Liang et al., 2004), we obtained an annual R_s of 665 g C m^{-2} y^{-1} with a steady-state chamber system at this site in 2001. The large difference of 269 gC m^{-2} in the annual R_s may be attributed to the positive pressure of 0.22 Pa inside the steady-state chamber system, which led to a systematic underestimation of R_s (Fang and Moncrieff, 1998; Widen and Lindroth, 2003).

Based on the gradient measurement, the relative contribution to the annual R_s from topsoil, subsoil, and litter was 72, 22 and 6%, respectively. Such a proportion indicates that the organic soil layer with a depth of 0.13 m produced 72% of total CO_2 emitted to the atmosphere. The vertical distribution of CO_2 efflux can be explained by those of soil carbon content and root biomass, which were localized in surface soil (Sakai et al., 2007). The annual ecosystem respiration (RE) of this site was 1493 gC m^{-2} y^{-1} in 2003 (Hirata et al., 2007). The annual R_s of 934 gC m^{-2} y^{-1} accounted for 63% of the RE. The ratio of R_s to RE is compatible with those of European forests (Janssens et al., 2001b). Liang et al. (2005) reported that the annual sum of the stem respiration of larch trees was 78–80 gC m^{-2} y^{-1} in this forest in 2002. Considering the contribution of broadleaf species, the total stem respiration may be estimated to be about 100 gC m^{-2} y^{-1}. Then, we can attribute the residual of RE (i.e., 459 gC m^{-2} y^{-1}) to the aboveground respiration of tree canopy and understory species as well as the decomposition of coarse woody debris.

5 Conclusions

The concurrent employment of gradient method along with chamber method provide not only the soil effluxes during the snow-covered period but also further insight into their partitioning. Soil CO_2 effluxes of the larch forest, including total soil respiration (R_s), heterotrophic respiration (R_h), autotrophic (root) respiration (R_r) and top soil respiration (F_t), were strongly affected by soil temperature. Overall, no constraints of soil moisture on any soil CO_2 efflux were found, whereas soil respiration showed pulsed increase after rain events. The contribution of R_r to R_s changed seasonally, and peaked in early summer when canopy photosynthesis and plant growth were active. The vertical distribution of soil CO_2 efflux reflected those of soil carbon content and root biomass. On an annual basis, R_r accounted for 43% of R_s, and R_s accounted for 63% of ecosystem respiration measured by the eddy covariance technique.

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