

Soil CO₂ efflux of a larch forest in northern Japan

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Abstract. We had continuously measured soil CO₂ 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 CO₂ concentration gradients method to continuously measure soil CO₂ profiles under snowpack in the snowy period and to partition R_s into topsoil (O_a and A horizons) CO₂ efflux (F_t) with a depth of 0.13 m and sub-soil (C horizon) CO₂ efflux (F_c). We found that soil CO₂ 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 CO₂ 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 gC m⁻² during the snowy season for 4 months. The annual R_s was determined at 934 gC 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 CO₂ efflux was consistent with those of soil carbon and root biomass.

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 CO₂ 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 CO₂ 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 CO₂ concentration by 20–224 ppm by 2100 and resulting higher CO₂ 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 CO₂ 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 CO₂ efflux. The objectives of this study are to investigate (1) seasonal variations in soil CO₂ efflux, (2) responses of soil CO₂ efflux to temperature, moisture and rain events, (3) relative contributions of heterotrophic and autotrophic respirations to total R_s , (4) vertical distribution of soil CO₂ 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 CO₂ 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 m² 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 m² 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 m² 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 volcanoclastic 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).

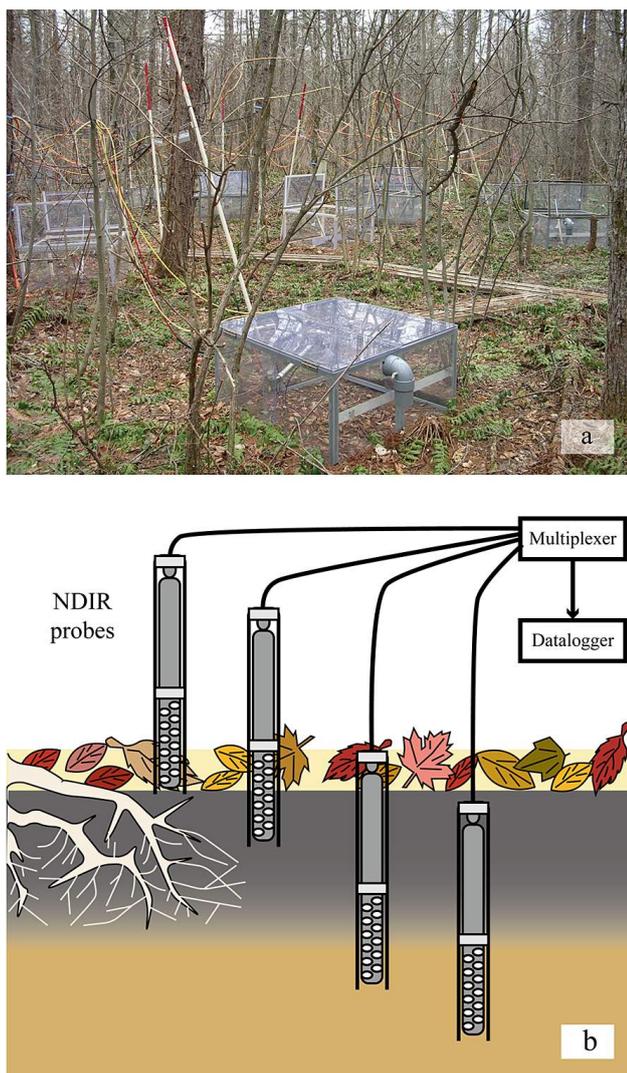


Fig. 2. (a) Image of the multi-channel automated chamber systems installed at the site and (b) a set of infrared gas analyzers (IRGA sensors) vertically installed at different depths of soil.

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 CO₂ mole fraction ($\mu\text{mol mol}^{-1} \text{s}^{-1}$) calculated by the least-square method, and R is the gas constant ($8.314 \text{ Pa m}^3 \text{ K}^{-1} \text{ mol}^{-1}$). 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 CO₂ gradient system

We applied the soil CO₂ gradient method for continuous measurements of topsoil and subsoil CO₂ effluxes (Hirano et

al., 2003b; Liang et al., 2004; Tang et al., 2003). We inserted CO₂ probes (18.5 mm diameter, 155 mm long) of IRGAs (GMT222, Vaisala, Helsinki, Finland) into the soil to directly measure soil CO₂ concentration profiles. The probes were enclosed in polytetrafluoroethylene (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 CO₂ 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 CO₂ 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, CO₂ 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 CO₂ concentration were averaged at each depth and corrected for temperature and pressure accordingly to the manufacturer's instruction and converted to CO₂ molar density ($\mu\text{mol m}^{-3}$). Then, soil CO₂ 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 CO₂ efflux ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), D_s ($\text{m}^2 \text{ s}^{-1}$) is the gaseous CO₂ diffusion coefficient, and $\delta C/\delta z$ is the vertical CO₂ density gradient ($\mu\text{mol m}^{-4}$). Following Hirano et al. (2003b), we calculated soil CO₂ efflux from the soil surface (R_s) and CO₂ efflux from C horizon to A horizon (R_c) every hour from the soil CO₂ 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 CO₂ storage change in the O_a and A horizons for the calculation. In addition, we calculated CO₂ production rate of topsoil (O_a and A horizons) (R_t) by subtracting CO₂ production rate of subsoil (R_c) from R_s . D_s

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

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

where D_0 is the CO₂ diffusion coefficient in air ($1.39 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$) 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 $\text{cm}^2 \text{ s}^{-1}$ with soil temperature and moisture, which is in the middle range of 0.022 to 0.052 $\text{cm}^2 \text{ s}^{-1}$ 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 CO₂ efflux, we performed a regression analysis using an exponential model:

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

where R_s is the CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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

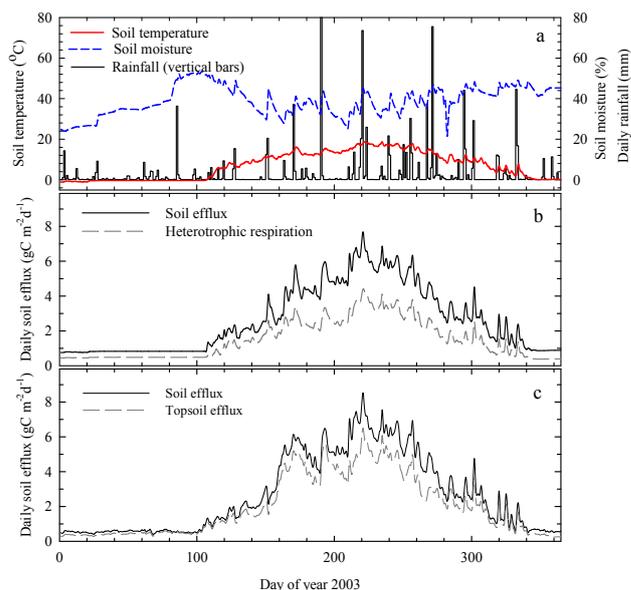


Fig. 3. Seasonal variations in daily means or sums of (a) soil temperature at a depth of 0.05 m (solid line), precipitation (bars) and volumetric soil moisture at a depth of 0.1 m (dashed line), (b) total soil respiration (solid line) and heterotrophic respiration (gray dashed line) measured with the 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 $\text{gC m}^{-2} \text{ d}^{-1}$ 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 $0.50\text{--}0.55 \mu\text{mol m}^{-2} \text{ s}^{-1}$ until mid-March and then gradually increased up to $0.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ with snow melting. Mean R_s for the snowy season of 127 days was $0.56 \pm 0.12 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (mean \pm 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 $0.83 \pm 0.03 \mu\text{mol m}^{-2} \text{ s}^{-1}$. 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.

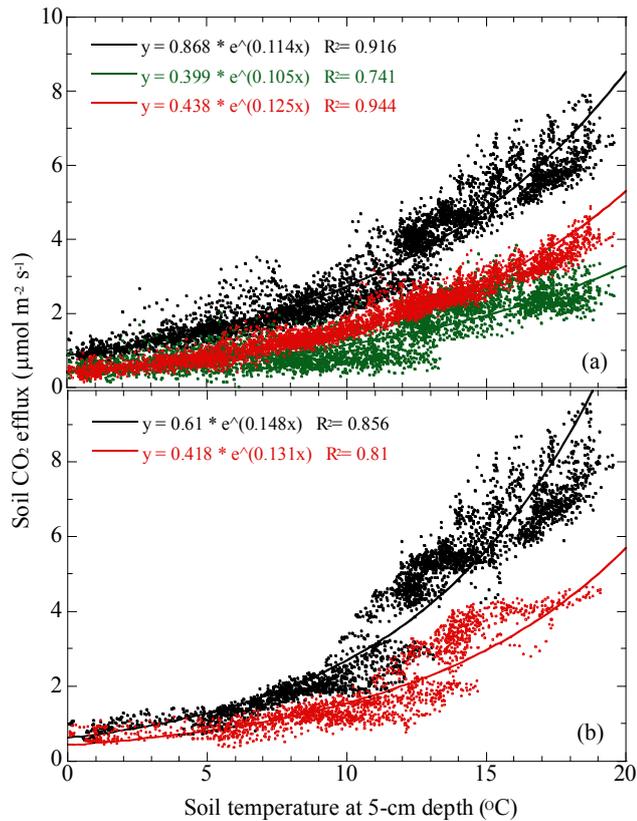


Fig. 4. Relationships between soil temperature at a depth of 0.05 m and (a) total soil CO₂ efflux (black symbols and line), heterotrophic (red symbols and line) and root (green symbols and line) respirations measured by the chamber method, and (b) total soil CO₂ efflux (black symbols and line) and topsoil (O_a and A horizons) CO₂ efflux (red symbols and line) measured by the gradient technique, on an hourly basis. The best-fitted exponential curves are shown.

4.2 Responses of soil CO₂ efflux to soil temperature and moisture

For the snow-free period for 8 month (Fig. 4), soil CO₂ 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

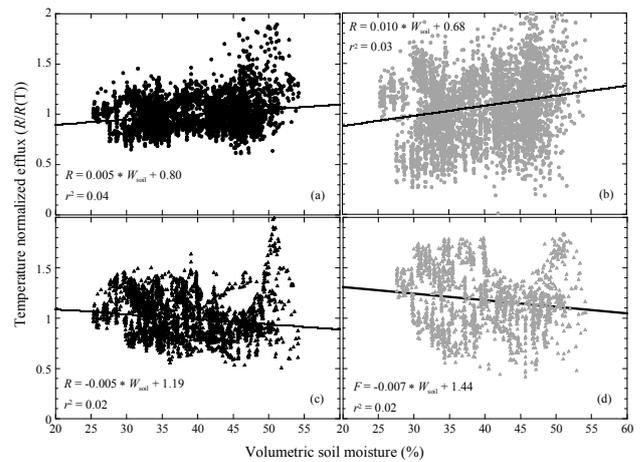


Fig. 5. Temperature normalized soil CO₂ efflux, ratio between measured soil CO₂ efflux (R_s) and its temperature fitted value ($R_s(T)$), versus volumetric soil water content at a depth of 0.1 m. (a) and (b) represent total soil CO₂ efflux and root respiration measured by the automated chamber system, and (c) and (d) represents total soil CO₂ efflux and topsoil (O_a and A horizons) CO₂ efflux measured by the soil CO₂ gradient system.

the high temperature sensitivity of R_h will offset the forest carbon sequestration in the changing world under elevated atmospheric CO₂ 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 CO₂ 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 CO₂ efflux is also controlled by moisture availability. To remove the confounding effect of temperature and evaluate the role of soil moisture on soil CO₂ efflux, we plotted temperature-normalized efflux (i.e., the ratio of observed soil CO₂ 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).

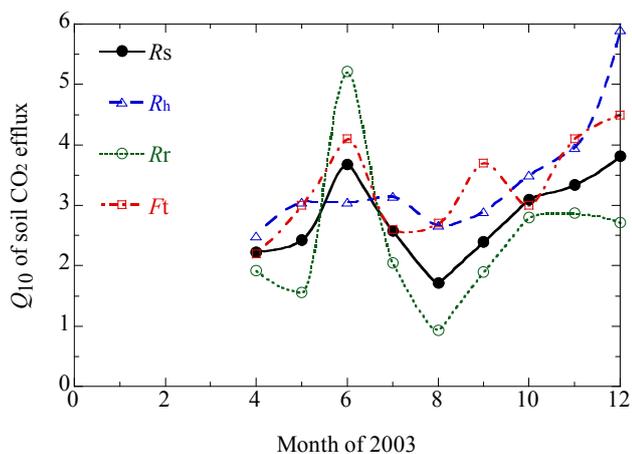


Fig. 6. Seasonal changes in Q_{10} of soil CO₂ efflux (R_s , dots with solid line), heterotrophic respiration (R_h , triangles with dashed line), root respiration (R_r , circles with dotted line), and topsoil CO₂ efflux (F_t , squares with dot-dashed line) for the snow-free season from April through December.

4.3 Seasonal variations in Q_{10} of soil CO₂ efflux

To investigate the mechanism by which temperature affects soil CO₂ 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; Haselquist 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

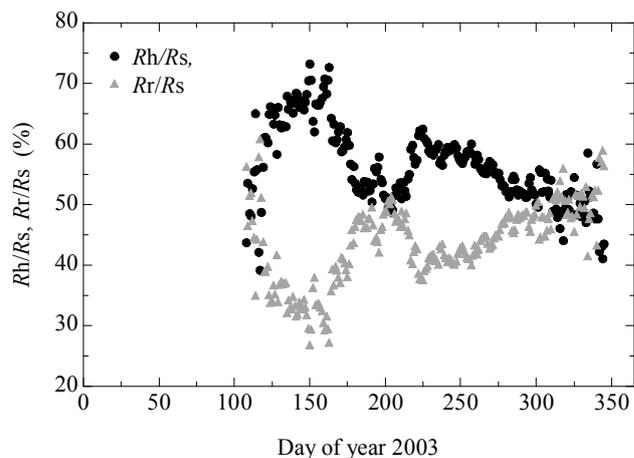


Fig. 7. Seasonal variations in the contributions of heterotrophic respiration (R_h , triangles) and root respiration (R_r , circles) to total soil respiration (R_s) measured by the chamber method on daily basis.

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 CO₂ 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; Inglema et al., 2009; Baldocchi et al., 2006). In this study, both the automated chamber and the gradient approaches revealed episodic CO₂ 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 (Inglema 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 annual sums of soil CO₂ 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 CO₂ efflux from the litter layer (Q_i and Q_e horizons). CO₂ 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 Pingingtha 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 CO₂ 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 estimate winter R_s

by extrapolating Eq. (4) fitted for the snow-free season only, which overestimated the winter R_s 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 grasslands in North China (Wang et al., 2010). In our earlier study (Liang et al., 2004), we obtained an annual R_s of 665 gC 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 CO₂ emitted to the atmosphere. The vertical distribution of CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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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References

- Baldocchi, D., Tang, J. W., and Xu, L. K.: How switches and lags in biophysical regulators affect spatial-temporal variation of soil respiration in an oak-grass savanna, *J. Geophys. Res.*, 111, G02008, doi:10.1029/2005JG000063, 2006.
- Bond-Lamberty, B. and Thomson, A.: Temperature-associated increases in the global soil respiration record, *Nature*, 464, 579–582, doi:10.1038/nature08930, 2010.
- Boone, R. D., Nadelhoffer, K. J., Canary, J. D., and Kaye, J. P.: Roots exert a strong influence on the temperature sensitivity of soil respiration, *Nature*, 396, 570–572, 1998.
- Campbell, G. S.: *Soil Physics with BASIC: Transport Models for Soil-Plant Systems*, Elsevier, New York, USA, 150 pp., 1985.
- Chen, J. M., Huang, S. E., Ju, W., Gaumont-Guay, D., and Black, T. A.: Daily heterotrophic respiration model considering the diurnal temperature variability in the soil, *J. Geophys. Res.*, 114, G01022, doi:10.1029/2008JG000834, 2009a.
- Chen, S. P., Lin, G. H., Huang, J. H., and Jenerette, G. D.: Dependence of carbon sequestration on the differential responses of ecosystem photosynthesis and respiration to rain pulses in a semiarid steppe, *Global Change Biol.*, 15, 2450–2461, 2009b.
- Cisneros-Dozal, L. M., Trumbore, S. E., and Hanson, P. J.: Effect of moisture on leaf litter decomposition and its contribution to soil respiration in a temperate forest, *J. Geophys. Res.*, 112, G01013, doi:10.1029/2006JG000197, 2007.
- Currie, J. A.: Gaseous diffusion in porous media Part 1. – A non-steady state method, *Br. J. Appl. Phys.*, 11, 314–317, 1960.
- Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, 440, 165–173, 2006.
- Drewitt, G. B., Black, T. A., Nestic, Z., Humphreys, E. R., Jork, E. M., Swanson, R., Ethier, G. J., Griffis, T., and Morgenstern, K.: Measuring forest floor CO₂ fluxes in a Douglas-fir forest, *Agr. For. Meteorol.*, 110, 299–317, 2002.
- Fang, C. and Moncrieff, J. B.: An open-top chamber for measuring soil respiration and the influence of pressure difference on CO₂ efflux measurement, *Func. Ecol.*, 12, 319–325, 1998.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr,

- W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K. G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison, *J. Climate*, 19, 3337–3353, 2006.
- Gaumont-Guay, D., Black, T. A., McCaughey, H., Barr, A. G., Krishnan, P., Jassal, R. S., and Nescic, Z.: Soil CO₂ efflux in contrasting boreal deciduous and coniferous stands and its contribution to the ecosystem carbon balance, *Glob. Change Biol.*, 15, 1302–1319, 2009.
- Goulden, M. L. and Crill, P. M.: Automated measurements of CO₂ exchange at the moss surface of a black spruce forest, *Tree Physiol.*, 17, 537–542, 1997.
- Gower, S. T. and Richards, J. H.: Larches: deciduous conifers in an evergreen world, *BioScience*, 40, 818–826, 1990.
- Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration: A review of methods and observations, *Biogeochemistry*, 48, 115–146, 2000.
- Hasselquist, N. J., Vargas, R., and Allen, M. F.: Using soil sensing technology to examine interactions and controls between ectomycorrhizal growth and environmental factors on soil CO₂ dynamics, *Plant Soil*, 331, 17–29, 10.1007/s11104-009-0183-y, 2010.
- Hirano, T., Hirata, R., Fujinuma, Y., Saigusa, N., Yamamoto, S., Harazono, Y., Takada, M., Inukai, K., and Inoue, G.: CO₂ and water vapor exchange of a larch forest in northern Japan, *Tellus*, 55B, 244–257, 2003a.
- Hirano, T., Kim, H., and Tanaka, Y.: Long-term half-hourly measurement of soil CO₂ concentration and soil respiration in a temperate deciduous forest, *J. Geophys. Res.*, 108, 4631, doi:4610.1029/2003JD003766, 2003b.
- Hirano, T.: Seasonal and diurnal variations in topsoil and subsoil respiration under snowpack in a temperate deciduous forest, *Global Biogeochem. Cy.*, 19, 2005.
- Hirano, R., Hirano, T., Saigusa, N., Fujinuma, Y., Inukai, K., Kitamori, Y., Takahashi, Y., and Yamamoto, S.: Seasonal and interannual variations in carbon dioxide exchange of a temperate larch forest, *Agric. For. Meteorol.*, 147, 110–124, 2007.
- Inglisma, I., Alberti, G., Bertolini, T., Vaccari, F. P., Gioli, B., Miglietta, F., Cotrufo, M. F., and Peressotti, A.: Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO₂ efflux, *Global Change Biol.*, 15, 1289–1301, 2009.
- IPCC: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L., Cambridge University Press, Cambridge, UK and New York, NY, USA, 996 pp., 2007.
- Irvine, J. and Law, B. E.: Contrasting soil respiration in young and old-growth ponderosa pine forests, *Global Change Biol.*, 8, 1183–1194, 2002.
- Irvine, J., Law, B. E., and Kurpius, M. R.: Coupling of canopy gas exchange with root and rhizosphere respiration in a semi-arid forest, *Biogeochemistry*, 73, 271–282, 2005.
- Irvine, J., Law, B. E., Martin, J. G., and Vickers, D.: Interannual variation in soil CO₂ efflux and the response of root respiration to climate and canopy gas exchange in mature ponderosa pine, *Global Change Biol.*, 14, 2848–2859, 2008.
- Ishitsuka, S. and Sakata, T.: Estimate equation of gas diffusion coefficient of forest soils in Japan, (in Japanese with English abstract), *Jpn. J. For. Environ.*, 48, 9–15, 2006.
- Janssens, I. A., Kowalski, A. S., and Ceulemans, R.: Forest floor CO₂ fluxes estimated by eddy covariance and chamber-based model, *Agric. For. Meteorol.*, 106, 61–69, 2001a.
- Janssens, I. A., Lankreijer, M., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pielegard, K., Kutsch, W., Longdoz, B., Grunbald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibron, A., Moncrieff, J., Aubinet, M., Berhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Global Change Biol.*, 7, 269–278, 2001b.
- Janssens, I. A. and Pilegaard, K.: Large seasonal changes in Q_{10} of soil respiration in a beech forest, *Glob. Change Biol.*, 9, 911–918, 2003.
- Jassal, R. S., Black, T. A., Cai, T. B., Morgenstern, K., Li, Z., Gaumont-Guay, D., and Nescic, Z.: Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand, *Agric. For. Meteorol.*, 144, 44–57, 2007.
- Kelliher, F. M., Ross, D. J., Law, B. E., Baldocchi, D. D., and Rodda, N. J.: Limitations to carbon mineralization in litter and mineral soil of young and old ponderosa pine forests, *For. Ecol. Manage.*, 191, 201–213, 2004.
- Kim, H., Hirano, T., Koike, T., and Urano, S.: Contribution of litter CO₂ production to total soil respiration in two deciduous forests, *Phyton*, 45, 385–388, 2005a.
- Kim, H., Hirano, T., and Urano, S.: Seasonal variation in CO₂ production of leaf litter from different deciduous forests at the early decomposition stage, *J. Agric. Meteorol.*, 61, 91–104, 2005b.
- Klimek, B., Choczynski, M., and Juskiewicz, A.: Scots pine (*Pinus sylvestris* L.) roots and soil moisture did not affect soil thermal sensitivity, *Euro. J. Soil Biol.*, 45, 442–447, doi:10.1016/j.ejsobi.2009.06.008, 2009.
- Kurganova, I. N., Yermolaev, A. M., de Gerenyu, V. O. L., Larionova, A. A., Kuzyakov, Y., Keller, T., and Lange, S.: Carbon balance in the soils of abandoned lands in Moscow region, *Eurasian Soil Sci.*, 40, 51–58, 2007.
- Law, B. E., Ryan, M. G., and Anthoni, P. M.: Seasonal and annual respiration of a ponderosa pine ecosystem, *Glob. Change Biol.*, 5, 169–182, 1999.
- Law, B. E., Falge, E., Gu, L., Baldocchi, D. D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A. J., Falk, M., Fuentes, J. D., Goldstein, A., Granier, A., Grelle, A., Hollinger, D., Janssens, I. A., Jarvis, P., Jensen, N. O., Katul, G., Mahli, Y., Matteucci, G., Meyers, T., Monson, R., Munger, W., Oechel, W., Olson, R., Pilegaard, K., Paw, K. T., Thorgeirsson, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, *Agric. For. Meteorol.*, 113, 97–120, 2002.
- Lee, X.: On micrometeorological observations of surface-air exchange over tall vegetation, *Agric. For. Meteorol.*, 91, 39–49, 1998.

- Lee, X., Wu, H. J., Sigler, J., Oishi, C., and Siccama, T.: Rapid and transient response of soil respiration to rain, *Glob. Change Biol.*, 10, 1017–1026, 2004.
- Liang, N., Inoue, G., and Fujinuma, Y.: A multichannel automated chamber system for continuous measurement of forest soil CO₂ efflux, *Tree Physiol.* 23, 825–832, 2003.
- Liang, N., Nakadai, T., Hirano, T., Qu, L. Y., Koike, T., Fujinuma, Y., and Inoue, G.: In situ comparison of four approaches to estimating soil CO₂ efflux in a northern larch (*Larix kaempferi* Sarg.) forest, *Agric. For. Meteorol.*, 123, 97–117, 2004.
- Liang, N., Fujinuma, Y., and Inoue, G.: Measurement of wood CO₂ efflux using a multichannel automated chamber system, *Phyton*, 45, 109–115, 2005.
- Liu, H. S., Li, L. H., Han, X. G., Huang, J. H., Sun, J. X., and Wang, H. Y.: Respiratory substrate availability plays a crucial role in the response of soil respiration to environmental factors, *Appl. Soil Ecol.*, 32, 284–292, 2006a.
- Liu, Q., Edwards, N. T., Post, W. M., Gu, L., Ledford, J., and Lenhart, S.: Temperature-independent diel variation in soil respiration observed from a temperate deciduous forest, *Glob. Change Biol.*, 12, 2136–2145, 2006b.
- Lloyd, J. and Taylor, J. A.: On the Temperature-Dependence of Soil Respiration, *Func. Ecol.*, 8, 315–323, 1994.
- Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmoller, D., Law, B. E., Ciais, P., and Grace, J.: Old-growth forests as global carbon sinks, *Nature*, 455, 213–215, 2008.
- McCulley, R. L., Boutton, T. W., and Archer, S. R.: Soil respiration in a subtropical savanna parkland: Response to water additions, *Soil Sci. Soc. Am. J.*, 71, 820–828, 2007.
- Moyano, F. E., Kutsch, W. L., and Rebmann, C.: Soil respiration fluxes in relation to photosynthetic activity in broad-leaf and needle-leaf forest stands, *Agric. For. Meteorol.*, 148, 135–143, 2008.
- Phillips, S. C., Varner, R. K., Frolking, S., Munger, J. W., Bubier, J. L., Wofsy, S. C., and Crill, P. M.: Interannual, seasonal, and diel variation in soil respiration relative to ecosystem respiration at a wetland to upland slope at Harvard Forest, *J. Geophys. Res.*, 115, G02019, doi:10.1029/2008JG000858, 2010.
- Pingintha, N., Leclerc, M. Y., Beasley, J. P., Zhang, G. S., and Senthong, C.: Assessment of the soil CO₂ gradient method for soil CO₂ efflux measurements: comparison of six models in the calculation of the relative gas diffusion coefficient, *Tellus*, 62B, 47–58, doi:10.1111/j.1600-0889.2009.00445.x, 2010.
- Raich, J. W., Potter, C. S., and Bhagawati, D.: Interannual variability in global soil respiration, 1980–94, *Glob. Change Biol.*, 8, 800–812, 2002.
- Ruehr, N. K., Knohl, A., and Buchmann, N.: Environmental variables controlling soil respiration on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland, *Biogeochemistry*, 98, 153–170, doi:10.1007/s10533-009-9383-z, 2010.
- Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, *Biogeochemistry*, 73, 3–27, doi:10.1007/s10533-004-5167-7, 2005.
- Sakai, Y., Takahashi, M., and Tanaka, N.: Root biomass and distribution of a *Picea-Abies* stand and a *Larix-Betula* stand in pumiceous Entisols in Japan, *J. For. Res.*, 12, 120–125, 2007.
- Sampson, D. A., Janssens, I. A., Yuste, J. C., and Ceulemans, R.: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest, *Glob. Change Biol.*, 13, 2008–2017, 2007.
- Savage, K. E. and Davidson, E. A.: A comparison of manual and automated systems for soil CO₂ flux measurements: trade-offs between spatial and temporal resolution, *J. Exp. Botany*, 54, 891–899, 2003.
- Tang, J., Baldocchi, D. D., Qi, Y., and Xu, L. K.: Assessing soil CO₂ efflux using continuous measurements of CO₂ profiles in soils with small solid-state sensors, *Agric. For. Meteorol.*, 118, 207–220, 2003.
- Tang, J., Baldocchi, D. D., and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal basis, *Glob. Change Biol.*, 11, 1298–1304, 2005.
- Tang, J. W., Bolstad, P. V., Desai, A. R., Martin, J. G., Cook, B. D., Davis, K. J., and Carey, E. V.: Ecosystem respiration and its components in an old-growth forest in the Great Lakes region of the United States, *Agric. For. Meteorol.*, 148, 171–185, 2008.
- Vargas, R. and Allen, M. F.: Dynamics of fine root, fungal rhizomorphs, and soil respiration in a mixed temperate forest: Integrating sensors and observations, *Vadose Zone J.*, 7, 1055–1064, doi:10.2136/vzj2007.0138, 2008.
- Vargas, R., Detto, M., Baldocchi, D. D., and Allen, M. F.: Multi-scale analysis of temporal variability of soil CO₂ production as influenced by weather and vegetation, *Glob. Change Biol.*, 16, 1589–1605, doi:10.1111/j.1365-2486.2009.02111.x, 2010.
- Wang, W., Peng, S., Wang, T., and Fang, J.: Winter soil CO₂ efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China, *Soil Biol. Biochem.*, 42, 451–458, 2010.
- Widen, B., and Lindroth, A.: A calibration system for soil carbon dioxide efflux measurement chambers: Description and application, *Soil Sci. Soc. Am. J.*, 67, 327–334, 2003.
- Xu, L. K., Baldocchi, D. D., and Tang, J. W.: How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature, *Glob. Biogeochem. Cycles*, 18, GB4002, doi:10.1029/2004GB002281, 2004.
- Xu, M. and Qi, Y.: Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevada forest, *Glob. Biogeochem. Cy.*, 15, 687–696, 2001.
- Yuste, J. C., Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity, *Glob. Change Biol.*, 10, 161–169, 2004.
- Zhou, T., Shi, P. J., Hui, D. F., and Luo, Y. Q.: Global pattern of temperature sensitivity of soil heterotrophic respiration (Q_{10}) and its implications for carbon-climate feedback, *J. Geophys. Res.*, 114, G02016, doi:10.1029/2008JG000850, 2009.