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Soil warming in a cool-temperate mixed forest with peat soil enhanced heterotrophic and basal respiration rates but Q_{10} remained unchanged

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Abstract

We conducted soil warming experiment in a cool-temperate forest with peat soil in northern Japan, during the snowless seasons of 2007–2009. Our objective was to determine whether or not the heterotrophic respiration rate and the temperature sensitivity would change by soil warming. We elevated the soil temperature by 3 °C at 5 cm depth by means of overhead infrared heaters and continuously measured soil CO_2 fluxes by using a fifteen-channel automated chamber system. Trenching treatment was also carried out to separate heterotrophic respiration and root respiration from the total soil respiration. The fifteen chambers were divided into three groups each with five replications for the control, unwarmed-trenched, and warmed-trenched treatments. We found that heterotrophic respiration contributed 71 % of the total soil respiration with the remaining 29 % accounted to autotrophic respiration. Soil warming enhanced heterotrophic respiration by 74 % (mean 6.11 ± 3.07 S.D. $\mu mol\,m^{-2}\,s^{-1}$) as compared to the unwarmed-trenched treatment (mean $3.52 \pm 1.74\,\mu mol\,m^{-2}\,s^{-1}$). Soil CO_2 efflux, however, was weakly correlated with soil moisture, probably because the volumetric soil moisture (33–46 %) was within a plateau region for root and microbial activities. The enhancement in heterotrophic respiration with soil warming in our study suggests that global warming will accelerate the loss of carbon from forested peatlands more seriously than other upland forest soils. On the other hand, soil warming did not cause significant change in the temperature sensitivity, Q_{10}, (2.79 and 2.74 determined using hourly efflux data for unwarmed- and warmed-trenched, respectively), but increased their basal respiration rate at 0 °C (0.93 and 1.21 $\mu mol\,m^{-2}\,s^{-1}$, respectively). Results suggest that if we predict the soil heterotrophic respiration rate in future warmer environment using the current relationship between soil temperature and heterotrophic respiration, the rate can be underestimated.

1 Introduction

Temperature sensitivity of soil carbon decomposition and the feedback to climate change has recently received considerable interest, because more than twice as much carbon is stored in soils as in the atmosphere (IPCC, 2007) and CO_2 efflux from the soils is the second largest flux in the global carbon cycle after gross primary production, with estimated annual emissions of 98 Pg C yr^{-1} in 2008, which exceeds anthropogenic CO_2 release by an order of magnitude (Bond-Lamberty and Thomson, 2010). Accordingly, relatively small increase in soil respiration would provide strong positive feedback to the atmosphere by increasing the amount of atmospheric CO_2 (Jenkinson et al., 1991; Kirschbaum, 1995; Cox et al., 2000; Knorr et al., 2005). Forests contain about 45 % of the global carbon stock and a large part of which is in the forest soils. Therefore, many soil warming experiments have been conducted in forests to reveal the warming effect on the soil respiration rate and the temperature sensitivity. Several studies reveal that the warming effect decreases after several years of the experiment caused by depletion of substrate availability or acclimation of decomposer community (Rustad et al., 2001; Melillo et al., 2002; Davidson and Janssens, 2006), and the feedback strength is not as large as the prediction obtained by assuming constant temperature sensitivity of decomposition of carbon stocks (Friedlingstein et al., 2006). However, many of these studies are conducted at upland mineral soils, where conditions are generally favorable for decomposition, resulting in relatively low carbon densities (Davidson and Janssens, 2006). On the other hand, Bellamy et al. (2005) have shown that recent losses of soil carbon in England and Wales are likely to have been offsetting absorption of carbon by terrestrial sinks, and peat soils and bogs lost carbon at a faster rate than upland soils. In addition, recent experimental evidence has confirmed that heterotrophic respiration increased in response to warming for at least eight years in a subarctic peatland (Dorrepaal et al., 2009). Thus long-term effect of climate warming on soil carbon is still under debate and more case studies especially for ecosystems with plentiful carbon stock in the soil are required before overlooking the effect (Davidson and Janssens, 2006).

Hence, we conducted soil warming experiment in a cool-temperate mixed forest standing on peat soils, which contain abundant substrates. For precise evaluation of the warming effect on the respiration rate and temperature sensitivity, we adopted multi-channel automated chamber system which enables hourly measurement of soil respiration rate throughout snow-free periods and covers spatial variability with large size and number of chambers (4.05 m^2 in total for each treatment), overhead infrared heaters were added to increase soil temperature by 3 °C. Our results include (1) an observation on the response of soil heterotrophic respiration to elevated temperature and determination of its contribution to the total soil CO_2 efflux during 2007–2009 snow-free seasons; (2) an evaluation of their temperature sensitivities using the empirically-derived Q_{10} values; and (3) a regression analysis to explore how increased temperature affects soil water function as a predictor of soil respiration. While several studies have questioned the validity of using Q_{10}'s (Lloyd and Taylor, 1994; Kirschbaum, 1995; Davidson et al., 2006; Bronson et al., 2008), we used the parameter because it offers a convenient point of comparison to previous studies. A major uncertainty in the future carbon cycle prediction is the assumption that the observed temperature sensitivity of soil respiration under the present climatic condition would hold in a future warmed climate. If there is a change in Q_{10} under warming condition, the model simulations which assume constant Q_{10} would over- or underestimate the soil respiration rate in the future.

2 Materials and methods

2.1 Site description

The experiment was conducted in a flat, low-lying elevation of Teshio Experimental Forest (TEEF), Hokkaido University, Northern Japan (44°55′ N and 142°01′ E). The altitude of the site is about 20 m a.s.l. and the terrain is essentially flat with a gentle slope within 1°. It is a mid-latitude, cool-temperate ecosystem with an annual mean air temperature of 5.7 °C (maximum ~30 °C; minimum ~ −30°C). Annual precipitation is ca. 1000 mm and snow covers from late November to early April. The presence of very thick surface organic matter (~40 cm) in the soil indicates a once peat land site that gone dry ca. 30 yr ago, and surface litter layer is shallow.

In late 1970's, an artificial forest was established in the site. To mimic its original vegetation, the site was planted with *Abies sachalinensis, Picea jezoensis, Quercus crispula, Betula ermanii, Betula platyphylla* var. *Japonica* and *Acer mono*. At present, the tree density is 831 stems ha^{-1} and basal area is 20.7 m^2 ha^{-1}. The understory had been dominated by dwarf bamboos (*Sasa senanensis* and *Sasa kurilensis*) for more than 20 yr until October of 2006.

Prior to the conduct of the study, dense *Sasa* bamboos inside the 1480 m^2 fenced experimental site were clear-cut in October, 2006. Cleared forest floor was maintained until the chamber installation in July, 2007 to diminish the influence of residual decomposing roots.

In October 2009 (the 3rd year of the experiment), soil sample cores of 100 cm^3 each were collected near each of 15 chambers for CO_2 efflux measurement, representing the soil organic carbon content of the whole study area. Dry bulk density was obtained by weighing the samples after 4 days of oven-drying at 80 °C. Carbon content was analyzed using an automatic NC analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service, Japan), attached to a gas chromatograph (GC-8A, Shimadzu, Corp., Japan). Three samples were analyzed for each core and the average indicated the carbon content of that soil core. The average carbon content and carbon density at 5 cm surface layer of the study site were 115 ± 37.41 SD gC kg^{-1} and 2.86 ± 0.69 SD kgC m^{-2}, respectively, and there was no significant difference in the carbon content among treatments.

2.2 Experimental layout and soil warming

Using the complete randomized design, the field manipulations consisting of 15 chambers were grouped into five. There were three chambers within each group

that were randomly assigned to one of the three treatments: (1) warmed-trenched; (2) unwarmed-trenched; and (3) served as undisturbed-control chamber (neither trenching nor warming). The use of five chambers for each treatment is within the recommended number of sampling points required to achieve ±20 % degree of precision at 95 % confidence interval (Liang et al., 2004). Warming effect on the heterotrophic respiration can be evaluated by the comparison between treatments (1) and (2), and proportion of heterotrophic respiration rate to soil respiration rate can be elucidated by the comparison between treatments (2) and (3).

We started soil warming on 20 August 2007, 40 days after setting up the chamber systems and trenching. This continued until the snow covered the site. For the following years, warming period were from 22 March to 20 November for 2008, and from 22 April to 20 November for 2009.

The heating treatment was applied to one of the three chambers in each block making the soil temperature at 5 cm depth 3 °C higher than other chambers. They were kept 3 m apart to avoid heat reaching the unwarmed chambers. A frame made of PVC pipes anchored from the two sides of the chamber was installed to hold the 58 cm long, 800 W infrared heating lamps suspended at 1.6 m above the ground. A motion-sensitive device that automatically turns-off the heater in case of troubles, e.g. strong wind, was also installed. Once fell on the ground, heating automatically stops preventing worst cases as forest fire.

We dug a trench ~10 cm away from the sidewalls of the warmed and unwarmed chambers using the hand-held chainsaw. The depth was ~30 cm below the ground surface. We inserted a 4 mm width PVC boards on the trench and backfilled remaining spaces with fine river sand to prevent growth of roots into the trenched plots. Newly emerged seedlings in the chambers were removed every few weeks, making no form of vegetation growing inside the chambers.

2.3 Soil CO_2 efflux and environment measurements

The flow-through, non-steady-state automated chamber system was set-up. The system was originally designed by Liang et al. (2003 and 2004), however was improved to measure the rate of change in CO_2 and water vapor over time in a closed chamber (Takagi et al., 2009; Liang et al., 2010). The system was composed of 15 automated chambers and a control unit. The control unit included 15-channel gas sampler, an IRGA (LI-840, Li-Cor, Lincoln, NE, USA), and a data-logger (CR 1000, Campbell Scientific, Logan, UT, USA). Each of the 15 chambers had a dimension of $0.9 \times 0.9 \times 0.5$ m high. The chambers were made of clear PVC board (2 mm thickness) attached to a 3×3 cm plastic-coated steel pipe square frame. The chambers have PVC lids (4 mm thickness) hinged at the sidewalls. These two lids were automatically opened during non-measurement and closed during measurement by two pneumatic cylinders (SCM-20B, CKD Corp., Nagoya, Japan). The opening of lids during non-measurement allows precipitation and leaf litter reaching the enclosed soil surface so as to maintain the natural condition within it. During measurements, air in the chamber was mixed by two micro fans (MF12B, Nihon Blower Ltd., Tokyo, Japan), air inside the chamber was circulated through the IRGA by a micro-diaphragm pump (5 L min^{-1}; CM-50, Enomoto Ltd., Tokyo, Japan), and the rate of changes in CO_2 and water vapor mole fraction were measured by the IRGA. Over 1 h, the chambers were closed sequentially under the control of the data-logger. The data-logger acquired data output from the IRGA at 20 s intervals within 240 s for each chamber. Consecutively, the CO_2 efflux rate was evaluated every hour for the 15 chambers during the snow-free periods.

Soil temperature at 5 cm depth and volumetric soil water content (SWC) from 3 to 8 cm depth were measured by type-T thermocouples (at 20 s intervals) and soil moisture sensors (ECH$_2$O EC-5, Decagon Devices Inc., Pullman, WA, USA) (at 1 min intervals) inside each chamber. Soil water measurement commenced nearly a month after the start of warming. The 30-min averages of soil and air temperatures, and volumetric soil water content for the 15 chambers were all recorded by the logger.

Soil CO_2 efflux (F_c) was calculated using the equation:

$$F_c = \frac{kPV}{S(T+273.15)}\left(\frac{\Delta C}{\Delta t} + \frac{C}{(1000-W)}\frac{\Delta W}{\Delta t}\right) \tag{1}$$

where k is a constant ($120.28 = 1000/8.314$); V and S are the volume (m^3) and area (m^2) enclosed by the chamber, respectively; P is the atmospheric pressure (constant at 101.325 kPa); T is the average air temperature (°C) in the specific chamber that measured at about 25 cm height in the center of the chamber; C and W are the average CO_2 (µmol mol^{-1}) and water vapor (mmol mol^{-1}) mole fraction, respectively; and $\Delta C/\Delta t$ and $\Delta W/\Delta t$ are the rate of changes in CO_2 and the water vapor mole fraction over time (s), respectively.

2.4 Data processing and analysis

The chamber system automatically records the change in CO_2 and the water vapor mole fraction making it possible for an hourly efflux rate of the 15 chambers to be evaluated. However, the system sometimes failed to get the change correctly, e.g. lid-closing is disturbed by lack of air pressure of the pneumatic cylinders, or by falling branches. In order to detect the quality of the data, we checked the stationarity of the rate of change in CO_2 ($\Delta C/\Delta t$). The data-logger records 12 data for the calculation of the $\Delta C/\Delta t$ (i.e. 20 s interval for 240 s) every 1h for each chamber. We calculated the average $\Delta C/\Delta t$ for three cases: (a) using 10 data except first 2 data just after the change in measured chamber, (b) using 8 data removing both ends of the case (a) data, (c) using 6 data removing both ends of the case (b) data. The $\Delta C/\Delta t$ obtained by these three types of calculations would be the same if they were measured ideally. We evaluated the quality of $\Delta C/\Delta t$ by comparing $\Delta C/\Delta t$ s calculated by the three cases using the following two discriminants;

$$|\Delta C_a/\Delta t_a - \Delta C_b/\Delta t_b|/|\Delta C_a/\Delta t_a| < \beta \tag{2}$$

$$|\Delta C_a/\Delta t_a - \Delta C_c/\Delta t_c|/|\Delta C_a/\Delta t_a| < \beta \tag{3}$$

where the subscripts, *a, b, c* correspond to the three cases, and β is the threshold value. We chose 0.3 for β after repeated trial and error, and the $\Delta C_a/\Delta t_a$ that passed both criteria (Eqs. 2 and 3) was used to evaluate the efflux. This quality checking successfully removed bad quality data (Fig. 1).

To discuss the temperature and soil moisture effect on the heterotrophic respiration or the contribution of heterotrophic respiration rate to the total soil respiration rate, the temperature, soil moisture and efflux data obtained from five chambers were averaged every hour for each treatment. The number of data to be averaged sometimes changed for each time and treatment because some of the five data were removed depending on the result of quality control. However, lack of averaged data was a very rare case. Out of 38 340 data obtained each for soil respiration, soil temperature, and soil water content only 308, 154, 156, respectively were missing. These covered the 20-month measurement period except for soil water content which covered only 19 months as it started late.

To examine temperature sensitivity of soil CO_2 efflux (F_c), we conducted regression analysis using the soil temperature (T_s) as the environmental variable:

$$F_c = a\exp^{bT_s} \tag{4}$$

where coefficients a and b are the basal respiration rate (i.e., F_c at temperature zero) and the sensitivity of F_c to T_s, respectively. The b values were also used to calculate the Q_{10} quotient (relative increase in F_c for a 10 °C change in T_s) as $Q_{10} = \exp^{10b}$.

We also determined the effect of soil moisture on soil CO_2 efflux. In order to eliminate the effect of temperature on each measured soil CO_2 efflux, we used temperature-normalized soil CO_2 efflux, which was calculated as the difference between measured soil CO_2 efflux (F_{cm}) and the estimated efflux at the observed temperature using the regression curve obtained from each treatment ($F_{ce}(t)$) as, $F_{cm} - F_{ce}(t)$.

Repeated measures ANOVA was used to examine treatment effects on CO_2 efflux. Data considered as outliers were not included in the analysis. Statistical analyses were carried out using SPSS (SPSS Science, Birmingham, UK).

3 Results

3.1 Soil temperature and moisture

Soil warming increased soil temperature constantly across the 20-month measurement period (Fig. 2). Annual result revealed a warmer soil in warmed-trenched chambers towards the last year of measurement period (2009) with an average soil temperature of 15.3 °C. This is 1 °C higher compared to the average soil temperature in 2008 (14.3 °C, $p < 0.001$).

During the snowless seasons of 2007–2009, the average soil temperature in warmed chambers was 14.5 °C (ranges from 0.2 to 24.5 °C), this is 3.0 ± 0.92 SD °C higher than the unwarmed-trenched chambers with 11.5 °C (ranges from −0.1 to 21.8 °C), and 3.1 ± 0.87 SD °C higher than the control (neither warming nor trenching) chambers with 11.4 °C ($p < 0.001$).

Soil water content (SWC) inside the warmed-trenched chambers (mean 39 ± 1.6 % S.D., ranging from 33 to 42 %) was drier by 4 and 3 % compared with those in the unwarmed-trenched chambers (43 ± 0.5 % S.D., ranging from 41 to 44 %) and control chambers (42 ± 1.2 % S.D., ranging from 38 to 46 %), respectively ($p < 0.001$). Although SWC differences among treatments were significant, the differences were very small and the average SWC in warmed chambers (39 %) was still high.

3.2 Soil CO_2 efflux and the warming effect

Soil CO_2 effluxes in all the treatments roughly paralleled to the seasonal variation of soil temperature. Increasing the rate at the start of growing season in spring until summer and decreases towards leaf fall in autumn (Fig. 3). Soil warming increased the heterotrophic respiration rate consistently across the entire measurement period ($p < 0.001$). The efflux rate of control chamber was almost the same with that of warmed-trenched chamber in 2007, but was intermediate between the effluxes of warmed and unwarmed trenched chambers. Annual result revealed a gradually increasing heterotrophic respiration rate in elevated temperature with 4.67, 5.87, and 6.91 (µmol m^{-2} s^{-1}) in average during snow-free periods in 2007, 2008 and 2009, respectively.

Across all seasons within the 3-yr warming period, soil CO_2 efflux was greatest in the warmed-trenched chambers (Table 1 and Fig. 3). Warming increased the efflux by 74 % (or around 25 % per °C) (mean 6.11 ± 3.07 SD µmol m^{-2} s^{-1}) compared with that of the unwarmed-trenched treatments (mean 3.52 ± 1.74 SD µmol m^{-2} s^{-1}) ($p < 0.001$), while the control chambers obtained 4.98 ± 2.44 SD µmol m^{-2} s^{-1}.

An exponential function described the relationship between the soil CO_2 efflux and soil temperature for each treatment using the hourly interval data for the entire study period (Fig. 4). We also plotted the soil CO_2 efflux averaged for every °C against the soil temperature in order to evaluate clearly how soil CO_2 efflux respond to every unit change in temperature (Fig. 5). However, if the total number of data points falling within particular °C is less than 30, we excluded them from the determination of regression curves. The soil CO_2 efflux of warmed-trenched and control chambers was higher than the unwarmed-trenched treatment at the same temperature.

To examine the sensitivity of soil CO_2 efflux to soil temperature, we calculated basal respiration rate and temperature sensitivity (Q_{10}) for the three treatments using, (1) all 1h interval data (Fig. 4), and (2) averaged value for every °C (Fig. 5). For the first case, Q_{10} values in unwarmed-trenched, warmed-trenched and control were 2.79, 2.74, and 2.81, respectively. On the same manner, Q_{10} values for the second case were 2.68, 2.70, and 2.65, respectively. Although the averaging per °C slightly reduced their Q_{10} values, the temperature sensitivity among all the treatments had only small difference for both cases. Meanwhile, basal respiration rate differs among each treatment with a consistently higher initial heterotrophic respiration in warmed-trenched chambers (1.21 and 1.24 µmol m^{-2} $s^{-1}$for the first and second cases, respectively) compared with unwarmed-trenched chambers (0.93 and 0.99 µmol m^{-2} s^{-1}, respectively). Control chambers were the highest (1.33 and 1.41 µmol m^{-2} s^{-1}, respectively) owing to the contribution of root respiration.

Inter-annual variation in temperature sensitivity for the unwarmed-trenched chambers showed slight difference within the three years with Q_{10} equivalent to 2.73, 2.84, and 2.78 for 2007, 2008, and 2009, respectively (Fig. 6). Temperature sensitivity curves for warmed-trenched treatments showed that the efflux rates in 2008 and 2009 were higher than that in 2007, while the reverse thing occurred in the control chambers wherein the efflux rate in 2008 and 2009 was lower than that in 2007, especially in higher temperature range. The Q_{10} values for the warmed-trenched treatments in 2007, 2008, and 2009 were 2.71, 2.85, and 2.64, respectively, while control treatments had 3.09, 2.93, and 2.56, respectively. It must be noted that the differences in the Q_{10}'s between unwarmed-trenched and warmed trenched treatments were very small in 2007 and 2008, hence the Q_{10} obtained in 2009 had most likely caused the entire three year's Q_{10} reduction in warmed-trenched treatment. On the other hand, inter-annual variation of basal respiration rate in 2007, 2008 and 2009 was 0.95, 0.93, and 0.94 µmol m^{-2} s^{-1} for unwarmed-trenched; 1.12, 1.11, and 1.37 µmol m^{-2} s^{-1} for warmed-trenched; and 1.27, 1.26, and 1.45 µmol m^{-2} s^{-1} for control (Fig. 6). Basal respiration rate in unwarmed-trenched treatment did not vary much within the 3-yr period, but the apparent increase in basal respiration rate in both warmed-trenched and control treatments can be observed in 2009. Considering the similar efflux rate at higher temperature range between 2008 and 2009, higher basal respiration rate in the warmed-trenched treatments in 2009 than in 2008 had caused the decrease of Q_{10} in 2009. On the other hand, the decline of Q_{10} in the control treatments in 2009 occurred not only because of its higher basal respiration rate but also due to a decrease in the efflux rate at higher temperature range.

The difference in soil CO_2 efflux between unwarmed-trenched and control chambers showed that heterotrophic respiration contributed 71 % of the total soil respiration and the remaining 29 % was assumed to be the autotrophic respiration (Fig. 7). Autotrophic respiration peaked in advance (June to July) from that of heterotrophic respiration (August) in both 2008 and 2009. For over 20-month period, total soil respiration rate reached 2.74 kgC m^{-2} wherein 1.94 kgC m^{-2} of it had been contributed by heterotrophic respiration. Calculating for an equal period of measurement from 22 April to 19 November for both 2008 and 2009 showed that total soil respiration rate dropped from 1.20 $\mathrm{kgC\,m^{-2}}$ in 2008 to 1.13 $\mathrm{kgC\,m^{-2}}$ in 2009 while soil heterotrophic respiration decreased from 0.86 $\mathrm{kgC\,m^{-2}}$ in 2008 down to 0.81 $\mathrm{kgC\,m^{-2}}$ in 2009. A higher average soil temperature in 2008 (15.5 and 15.6 °C for control and unwarmed-trenched treatment, respectively) than that in 2009 (14.8 and 15.0 °C, respectively) was observed from June to September, and this could cause the decrease in the soil respiration rates in 2009. The rate of decrease in the total soil respiration from 2008 to 2009 (0.07 $\mathrm{kgC\,m^{-2}}$) was primarily driven by the decrease in the soil heterotrophic respiration (0.05 $\mathrm{kgC\,m^{-2}}$).

When we assume the non-growing season respiration rates to obtain an annual respiration rates by using the soil temperature data throughout the study period (Fig. 1) and temperature-respiration relationships (Fig. 6), the annual total and heterotrophic respirations were 1.43 and 1.03 $\mathrm{kgC\,m^{-2}}$, respectively, in 2008, and 1.39 and 0.98 $\mathrm{kgC\,m^{-2}}$ in 2009. Additional rates were 16 to 19 % of the annual total respiration rates and did not alter the growing season inter-annual tendencies.

Given the Q_{10} values of 2.81 and 2.79 for both control (representing the total soil respiration) and unwarmed-trenched (for heterotrophic respiration) treatments, estimated autotrophic respiration Q_{10} value was 2.75. This was obtained by subtracting the hourly respiration rates in unwarmed-trenched chambers from that of the control chambers during the entire study period. The difference was used to establish a regression line that determines the Q_{10} value of autotrophic respiration.

3.3 Effect of soil moisture on soil CO_2 efflux

Although the soil water content (SWC) of the warmed-trenched chambers was lower than those of the unwarmed-trenched and control chambers, the absolute values were always high for the three treatments and no relationship was observed between normalized CO_2 efflux and the SWC. This trend did not change even in the case of using

monthly averaged data (Fig. 8), which simply implies that soil moisture is not a limiting factor in this study site.

4 Discussion

4.1 Warming effect on soil heterotrophic respiration

Our warming experiment increased heterotrophic respiration rate by 74 % which has proven our assumption that elevated temperature would stimulate heterotrophic respiration. This increase is higher than the work of Melillo et al. (2002) (5 °C increase in the soil temperature in an even-aged mixed forest) who showed a 28 % increase in soil respiration rate over the first 6 yr. Similarly, Rustad et al. (2001) synthesized the soil respiration response to 2 to 5 yr experimental warming (1.5 to 6.0 °C increase in the soil temperature) conducted at 7 forested ecosystems and reported 7 to 46 % rise in soil CO_2 efflux. In addition, Niinistö et al. (2004) reported 27 to 43 % rise in soil CO_2 efflux by a 4-yr warming experiment (3 to 6 °C increase in the air temperature) in a 20-year-old Scots pine forest, and Bronson et al. (2008) revealed 24 and 11 % increase in soil CO_2 efflux at first and second year, respectively, of the warming experiment (5 °C increase in the soil temperature) in a Black spruce forest. Schindlbacher et al. (2009) reported 39 and 45 % increase in the soil heterotrophic respiration rate at first and second year, respectively, of the soil warming (4 °C increase in the soil temperature) in a mature forest dominated by Norway spruce.

In addition to the high increasing ratio of heterotrophic respiration caused by soil warming of this study, we could not observe distinct decrease in the warming effect on the respiration rate within three years of the study period, although the previous studies pointed out a decrease in the warming effect after several years of the experiment caused by depletion of substrate availability or acclimation of decomposer community. Melillo et al. (2002) reported decrease in the warming effect after 6 yr of warming and on the 10th year soil respiration rate showed no significant response. Rustad et al. (2001) suggested that the significant positive effect of warming on soil respiration rate was observed during the initial 3 years, and no significant effect in later years. Bronson et al. (2008) reported that the increase in soil CO_2 efflux by soil warming was diminished over time within two years of the warming experiment. Strömgren (2001) concluded that the rates of soil CO_2 efflux on heated plots were not significantly different from the control plots in the fifth year of warming.

The high increasing ratio throughout the 3 yr of our warming experiment could be attributed to two specific environmental factors in our study site, i.e. large substrate availability and high soil water content. Our study site had been a peatland and was drained ca. 30 yr ago for tree plantation, so there is very thick surface organic layer in the soil and no distinct soil stratification was observed. Assuming that surface 30 cm soil layer had similar carbon content with that in the surface 5 cm layer, the carbon content became 17.2 $\mathrm{kgC\,m^{-2}}$. This value is the same with the mean value for the Japanese peatland soils at surface 30 cm layer (17.2 $\mathrm{kgC\,m^{-2}}$) reported by Morisada et al. (2004) or much higher than the mean global estimate of 11.3 $\mathrm{kgC\,m^{-2}}$ at surface 100 cm layer (Sombroek et al., 1993). The soil heterotrophic respiration rate of 1.94 $\mathrm{kgC\,m^{-2}}$ over the 20-month study period accounts for the 11 % remaining soil carbon content at surface 30 cm soil layer and would not cause serious depletion of available substrate. In addition, it must be noted that litterfall had continuously supplied carbon to the soil. Although we do not have observed data to support this but a study around our site with the same species composition obtained a litterfall rate of 0.13 $\mathrm{kgC\,m^{-2}\,yr^{-1}}$ (Fukuzawa, 2007). Assuming that the same amount of litterfall had been supplied in our study area, a rate of 0.39 $\mathrm{kgC\,m^{-2}}$ for 3 yr would have been added to the prevailing soil carbon content of 17.2 $\mathrm{kgC\,m^{-2}}$, thus reducing the impact of soil heterotrophic emission. In addition, the soil water content had kept constantly high at more than 30 % throughout the study period even at the heated plot, thus microbial activities would not be stressed by soil water deficit.

Supporting our consideration, repeated soil inventories in England and Wales over the last 25 yr have shown that peat soils and bogs lost C at a faster rate than upland

soils (Bellamy et al., 2005). In addition, Dorrepaal et al. (2009) revealed that approximately 1 °C warming accelerated total ecosystem respiration rates on average by 60 % in spring and by 52 % in summer in a subarctic peatland and that this effect was sustained for at least eight years. They also found that at least 69 % of the increase in respiration rate originated from carbon in subsurface peat towards the bottom (25 to 50 cm) of the active layer above the permafrost. Ise et al. (2008) reported high sensitivity of peat decomposition to warming temperature in boreal old black spruce and fen sites of the Northern Study Area of the Boreal Ecosystem-Atmosphere Study (BOREAS), and their simulation revealed that experimental warming of 4 °C causes a 40 % loss of soil organic carbon from the shallow peat and 86 % loss from the deep peat, concluding that peatlands will quickly respond to the expected warming in this century by losing labile soil organic carbon during dry periods. However, in any case, our results were obtained only from 3 yr experiment, although Strömgren (2001), Rustad et al. (2001), and Melillo et al. (2002) reported depression of the warming effect after at least 3 yr of the experiment. These results have challenged us to continue our work and assess whether this effect will be sustained beyond three years.

4.2 Temperature sensitivity

Our warming experiment slightly decreased Q_{10}, when the value was determined using hourly data (2.79 and 2.74 for unwarmed and warmed treatments, respectively), however the opposite result was obtained when we used averaged efflux rate for every °C (2.68 and 2.70). The difference between treatments was small for both cases, thus we can conclude that soil warming did not cause the significant change in the Q_{10} value. On the other hand, we observed 25 (hourly data) and 30 (bin average for every °C) % increase in the basal respiration rate (efflux rate at 0 °C) by soil warming throughout the three years. This trend was also true for the value determined each year. Reductions in the Q_{10} under induced temperature were observed in a tallgrass prairie (Luo et al., 2001), suggesting acclimation of respiration to climate warming and/or alteration of substrate supply. Strömgen (2001) and Bronson (2008) also reported a lower Q_{10}'s for the heated than the control treatments. On the other hand, Niinistö et al. (2004) could not find significant difference in the Q_{10} values between warming and control treatments during the four years experiment (although Q_{10} was smaller for the warming plots than that for control), and reported significant difference in the basal respiration rate in the final year of the experiment, which supports our results. Large substrate availability and high soil moisture condition in our study site helped in keeping a high temperature sensitivity during the whole three years of the experiment, and rather increased the soil respiration rate at low temperature range. The large enhancement in soil heterotrophic respiration rate (74 %) was realized by the increase in temperature by 3 °C without change in the Q_{10} (36 % increase for $Q_{10} = 2.8$) and increase in the basal respiration rate (25 to 30 %). It is difficult to explain the reason for the increase in the basal respiration rate by soil warming, however, enhancement of the soil microbial activities or change in the composition would be attributed. Further investigation is still needed to verify these accounts.

Our results (stimulation in basal respiration rate without depletion of Q_{10}) suggest a greater carbon release and a weakening carbon sequestration potential in future warmer climate for ecosystems with high substrate availability and soil moisture, and prediction model with no change in the basal respiration rate would cause an underestimation of carbon release from the soil to the atmosphere in future warmer environment. Gorham (1991) estimated that total release of carbon by drainage of boreal and subarctic peatlands could be 8.5 to 42 TgC yr^{-1}. Accordingly, 74 % increase in soil heterotrophic respiration rate would correspond to an increased release of 6 to 31 Tg C yr^{-1}. This is 10 % of Japan's current industrial CO_2 emission of 330 Tg C yr^{-1} in 2008 (GIO and CGER- NIES, 2010), and could provide a strong positive feedback to global atmospheric CO_2 concentrations and, consequently, warming.

4.3 Contribution of heterotrophic respiration to the total soil respiration

The temperature-response curve of control (total soil respiration) is higher than the unwarmed-trenched (heterotrophic respiration) owing to the presence of live and/or

decomposing roots compared to the root-lacking trenched chambers. Our result showed that heterotrophic respiration rate (not associated with warming) governs the total soil respiration rate given its 71 % contribution. Those who agree with this result include: 67 % for a mixed hardwood forest in Massachusetts (Bowden et al., 1993); 77 % for a lowland old-growth beech (*Nothofacus*) in New Zealand (Tate et al., 1993); >70 % for *Picea abies* stands in Northeast Bavaria, Germany (Buchmann, 2000); and 56 to 69 % for a subalpine forest dominated by lodgepole pine (*Pinus contorta*) trees in Niwot Ridge, Colorado (Scott-Denton et al., 2006). On the other hand, root respiratory contribution in our case only held the 29 % fraction of the total soil respiration, although this is lower than those of previous studies reporting 90 % for a oak-hornbeam forest in Belgium (Thierron and Laudelout, 1996); 54 % for a boreal forest in Saskatchewwan, Canada (Uchida et al., 1998); 52 to 56 % for a boreal Scots pine (*Pinus sylvestris* L.) forest (Högberg et al., 2001); and 78 % for a mixed mountain forest in Switzerland (Ruehr and Buchmann, 2010). Temperature sensitivity also showed that root respiration had almost similar Q_{10} value (2.75) with 2.79 for heterotrophic respiration, thus disputing the notions made by Boone et al. (1998), Grogan and Jonasson (2005), and Ruehr and Buchmann (2010) who explained that root respiration was more temperature sensitive than bulk soil respiration.

5 Conclusions

The large positive increase (74 %) in soil heterotrophic respiration with 3 °C elevated soil temperature in our study suggests that warming accelerates a loss of carbon from soils in forested peatlands more seriously than other upland soils. But whether this response lasts will be revealed by further monitoring. Soil warming increased the basal respiration rate with Q_{10} remained unchanged, thus if we predict the soil heterotrophic respiration rate in future warmer environment using the current relationship between soil temperature and heterotrophic respiration, the rate can be underestimated.

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Table 1. Parameters and average soil CO_2 efflux with different treatments.

	Unwarmed-trenched			Warmed-trenched			Control		
	R_0	Q_{10}	R_{mean}	R_0	Q_{10}	R_{mean}	R_0	Q_{10}	R_{mean}
2007	0.95	2.73	2.91 ± 1.44	1.12	2.71	4.67 ± 2.27	1.27	3.09	4.46 ± 2.71
2008	0.93	2.84	3.56 ± 1.87	1.11	2.85	5.87 ± 3.11	1.26	2.93	4.97 ± 2.60
2009	0.94	2.78	3.71 ± 1.63	1.37	2.64	6.91 ± 3.05	1.45	2.56	5.18 ± 2.10

R_0 and R_{mean} are basal respiration rate at 0 °C and mean soil CO_2 efflux during observation period, respectively. R_0 and Q_{10} are evaluated using bin averages of efflux rates per every °C (see Fig. 6). R_{mean} values are shown with the S.D.

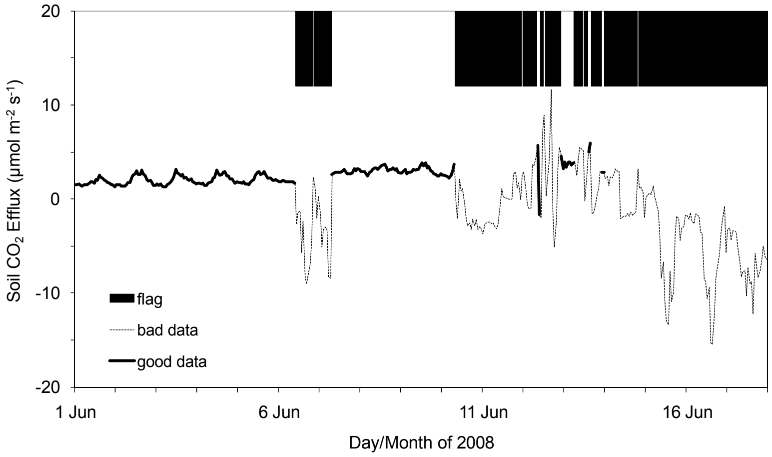

Fig. 1. A sample of the quality checking by two discriminants (Eqs. 2 and 3). Outlying data are flagged.

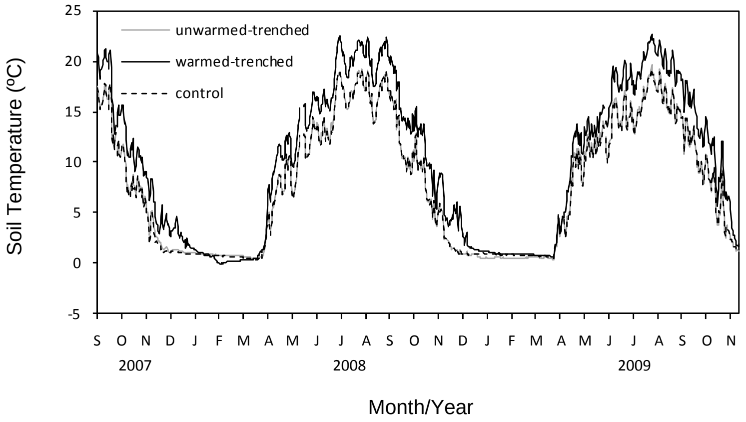

Fig. 2. Inter-annual variation of soil temperature in unwarmed-trenched, warmed-trenched, and control during the study period in 2007–2009. All data are daily averages.

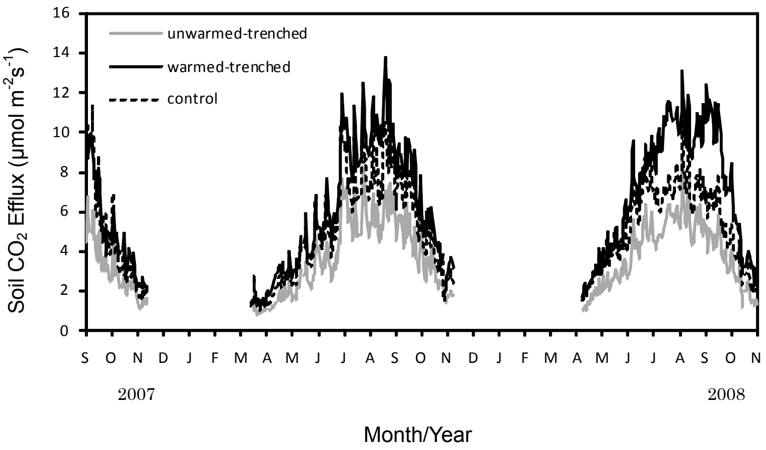

Fig. 3. Interannual variation in soil CO_2 efflux during the snow-free seasons in 2007–2009.

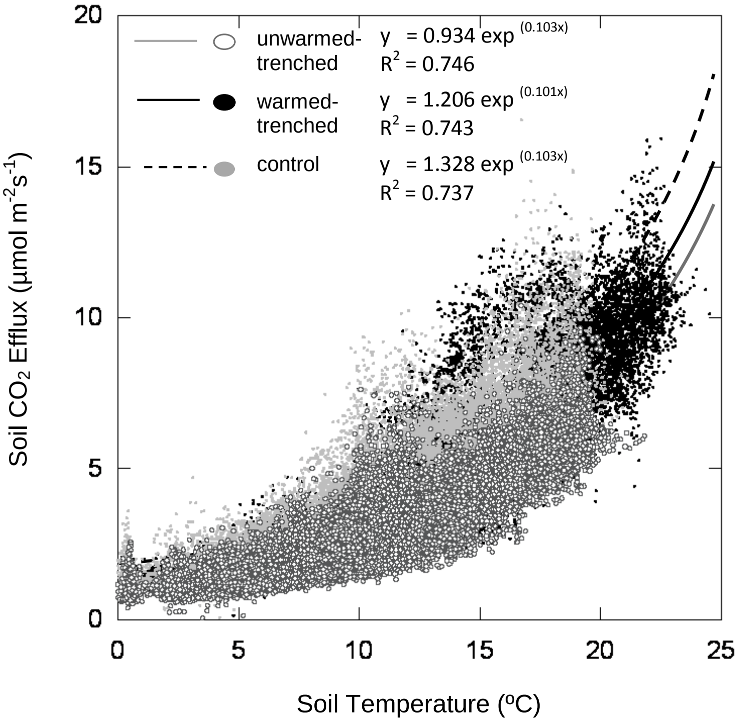

Fig. 4. Exponential correlation of soil CO_2 efflux with soil temperature across the 3-yr snow-free seasons of 2007–2009. All data are hourly averages.

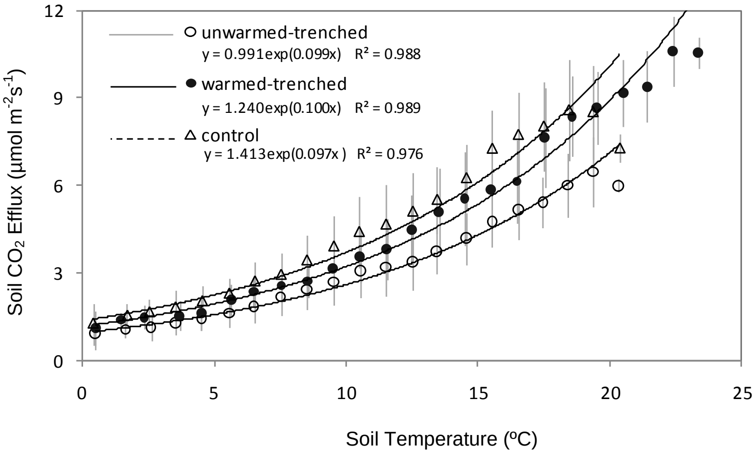

Fig. 5. Exponential relationship of soil CO_2 efflux per ˚C change in soil temperature. Symbols are bin averages and error bars represent ±1 SD.

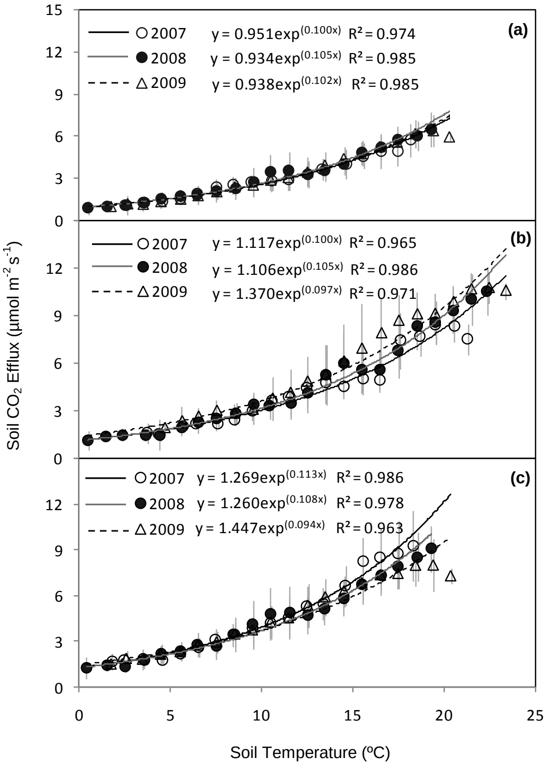

Fig. 6. Interannual variation in temperature dependency of soil CO_2 efflux for **(a)** unwarmed-trenched, **(b)** warmed-trenched, and **(c)** control chambers. Symbols are bin averages and error bars represent ±1 SD.

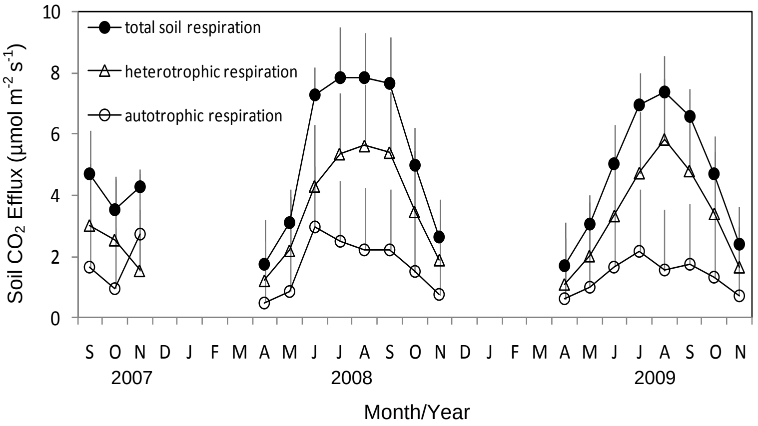

Fig. 7. Contributions of heterotrophic and autotrophic respiration to the total soil respiration over 20-month period. Symbols are monthly averages and error bars represent 1 SD.

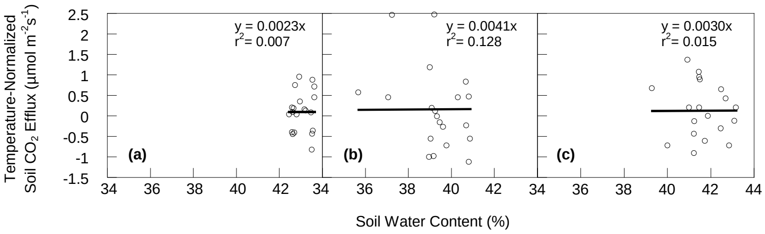

Fig. 8. Relationship of soil CO$_2$ efflux and soil water content using the temperature-normalized efflux for **(a)** unwarmed-trenched, **(b)** warmed-trenched, and **(c)** control treatments. All data are monthly averages across the 20-month snow-free seasons.