Inter-annual variation of soil respiration and its spatial heterogeneity in a cool-temperate young larch plantation in northern Japan

Lifei Sun*,†, Kentaro Takagi*, Munemasa Teramotob, Shintaro Hayakashic and Naishen Liangb

*Teshio Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Horonobe 098–2943, Japan
bCenter for Global Environmental Research, National Institute for Environmental Studies, 16–2, Onogawa, Tsukuba, Ibaraki 305–8506, Japan

Abstract

To understand the magnitudes of temporal variation in soil respiration ($R_s$) and its spatial heterogeneity, and the effect of abiotic and biotic factors to cause the variation in a young plantation recovering after the clear-cutting of a mature forest, we analyzed 8 year $R_s$ microclimate, and vegetation data obtained in a young hybrid larch plantation with dense undergrowth of dwarf bamboo *Sasa* in northern Japan during snow-free periods from 2004 to 2014. $R_s$ was measured by a multichannel automated chamber system and was resolved into two components, temperature sensitivity of respiration, $Q_{10}$, and temperature-normalized basal respiration at 10°C, $R_{10}$. Volumetric soil water content affects both seasonal and inter-annual variation of $R_s$ by suppressing $Q_{10}$, whereas soil temperature affects only its seasonal variation. Vegetation recovery had significant effect on both temporal variation and spatial heterogeneity in $R_s$, although the tree and undergrowth *Sasa* had different contribution to these variations. Increase in the undergrowth *Sasa* PAI (plant area index) recovering after clear-cutting increased the $R_s$ through the increase in $Q_{10}$, whereas the spatial heterogeneity in $R_s$ was increased by the increase in the tree PAI through the increase in $R_{10}$. These results reveal that the soil water and vegetation has strong effect on the inter-annual variation of $R_s$ and its spatial heterogeneity in the recovering young plantation, in spite of the strong exponential relationship of $R_s$ with $T$, in their seasonal variation. Although our results were obtained under the limited range in the inter-annual variation in seasonal mean $T$, (< 2°C), this may not be the unique case only in our study site and gives us a caution when predicting $R_s$ in future warmer environment.

Key words: Basal respiration, Plant area index, $Q_{10}$, *Sasa*, Soil water content

1. Introduction

Soil respiration ($R_s$) is the largest source of carbon (C) flux from terrestrial ecosystems into the atmosphere (Bond-Lamberty and Thomson, 2010) and plays an important role in the global C cycle. Davidson et al. (2006) reported that $R_s$ accounts for 80% of total forest ecosystem respiration; thus, it is important to understand the temporal variation in $R_s$ and its spatial heterogeneity.

Temporal (seasonal and inter-annual) variation in $R_s$ is well understood over different time scales in many ecosystems and is controlled by several environmental factors that include abiotic (soil temperature ($T_s$) and volumetric soil water content (VSWC)) and biotic (plant photosynthesis and biomass) factors. $R_s$ is mainly affected by $T_s$ (Lloyd and Taylor, 1994), and several studies suggest that VSWC or precipitation is also related to $R_s$ in forest or grassland ecosystems (Zhang et al., 2010; Thomey et al., 2011; Hanappattanakit et al., 2015). However, recently, canopy clipping and shading experiments revealed that long-term $R_s$ is directly affected by plant photosynthesis (Wan and Luo, 2003; Jing et al., 2015), which suggests that estimating the long-term $R_s$ from abiotic factors alone could lead to large estimation errors. In contrast, spatial variation in $R_s$ is affected by many factors, such as chemical and physical properties of soil, stand structure, and root distribution (Sce and Buchmann, 2005). Those factors cause large variation, which makes it difficult to obtain a spatial representative to estimate $R_s$ in ecosystem or landscape scale. Shi and Jin (2016) suggested that quantifying and understanding the variability of $R_s$ at different spatial scales can help to reduce errors in the evaluation of landscape-scale $R_s$. Therefore, it is critical to evaluate the magnitude of the temporal (especially inter-annual) and spatial variation in $R_s$ and the abiotic and biotic factors that cause such variation.

$R_s$ can be estimated by the functions using temperature sensitivity of $R_s$ ($Q_{10}$ increase in $R_s$ for a 10°C change in $T$) and soil basal respiration ($R_{10}$, temperature-normalized soil respiration $R_s$ at 10°C). $Q_{10}$ is also affected by several factors, including $T_s$, VSWC, soil carbon content, biomass, root activity, and inputs of labile organic C into soil (Davidson et al., 1998; Zhu et al., 2009). Curiel Yuste et al. (2004) reported that large seasonal variation in $Q_{10}$ was not entirely due to the temperature sensitivities of soil microbes but included the variation in plant activity in temperature forests. Spatial variation in $Q_{10}$ was also described by Luan et al. (2013), who suggested that VSWC and non-capillary porosity was negatively or positively correlated with the magnitude of $Q_{10}$, respectively, in two warm temperature forests. However, studies on the spatial variation in $Q_{10}$ in boreal and cool-temperate forests are still rare. $R_{10}$ may also be influenced by the similar variables mentioned above (Sampson et al., 2007; Cheng et al., 2013), but the temperature-normalized parameter will be more sensitive to
other environmental factors than temperature. Thus, to accurately estimate \( R_e \) and the responses to environmental factors, \( Q_{10} \) and \( R_{10} \) must be concurrently taken into account with environmental changes (Zhou et al., 2013).

Larch forests are an important forestry resource in northern Japan and only exist as plantations in Hokkaido of northern Japan from the 1960s. Afforested lands account for 14,862 km², or about 27% of all forest lands in Hokkaido, and larch forests account for 91,362,000 m³ of wood, or 12% (second largest) of the total wood volume in Hokkaido (Hokkaido Government Department of Fisheries and Forestry, 2018). Few studies have examined the \( R_e \) in mature larch forests for a long time (Chen et al., 2010; Teramoto et al., 2017), but in young larch forests, such studies are still rare. Therefore, in order to evaluate the biotic and abiotic factors to explain temporal (especially inter-annual) variation of \( R_e \), \( Q_{10} \), and \( R_{10} \) to evaluate the variation of the magnitude of their spatial heterogeneity, we analyzed 8 year \( R_e \) data that were measured by a multichannel automated chamber system in a young larch plantation with dense Sasa undergrowth in northern Hokkaido Japan, with simultaneous observations of abiotic and biotic factors. In northern Japan, dwarf bamboo Sasa grows as very dense understorey vegetation and has a large effect on the C and nutrient cycling in forest ecosystems (Fukuzawa et al., 2006); thus, we separately evaluate the effects of the larch and Sasa on \( R_e \).

2. Materials and methods

2.1 Site description

The study was conducted on a flat terrace inside the Teshio Experimental Forest of Hokkaido University (45°03′N, 142°06′E, 66 m a.s.l.). The soil is a Gleyic Cambisol (Food and Agriculture Organization of the United Nations, 1998), and its surface organic horizon was about 10 cm thick. The site is a young larch plantation, prepared just after clear-cutting of a naturally regenerated mixed forest from January to March 2003 (Aguilos et al., 2014). About 30,000 two-year-old hybrid larch (Larix gmelinii (Rupr.) Kuzen. var. japonica (Maxim. Ex Regel) Pilg. × L. kaempferi (Lamb.) Carrière) saplings were planted in late October 2003 at a density of 2500 ha⁻¹. Before the mixed forest was clear-cut, the forest floor was covered with dense evergreen dwarf bamboo (Sasa senanensis Rehd. and S. kuriensis (Rupr.) Makino et Shibata), which were strip-cut into alternating 4 m-wide cut and uncut rows in the clear-cut area to provide space for planting. In the uncut rows where Sasa remained, its leaf area and biomass increased steeply from 1 year after clear-cutting until 2007 (Aguilos et al., 2014). In the rows where Sasa was strip-cut, to eliminate all Sasa plants growing between the larch trees, above-ground part of Sasa was removed during the first 3 years from 2004. Two years after the last weeding in 2006, Sasa had recovered in the strip-cut rows and the PAI (plant area index; includes the area shaded by stems, branches, culms, and leaves) of these plants was almost the same as that in the surrounding uncut rows, blanketing all gaps between the trees. Conversely, the larch PAI remained relatively small throughout the study period, despite its height growth, and some deciduous broadleaved trees (Betula ermanii Cham., B. platyphylla var. japonica (Miq.) Hara. Maximum, and Quercus crispula Blume) were also naturally regenerating.

2.2 Soil respiration measurement

A multichannel automated chamber system (Liang et al., 2010) was used to measure \( R_e \) during the snow-free period (May to November) from 2004 to 2009 and from 2013 to 2014 for a total of 8 years. The system had a flow-through and non-steady-state design and included a control unit with an IRGA (LI-840; Li-Cor, Lincoln, NE, USA) and a data logger (CR10X; Campbell Scientific, Logan, UT, USA), and eight automated chambers (0.9 m × 0.9 m × 0.5 m high), which were installed at Sasa-cut rows, but adjacent to the Sasa remaining (uncut) rows until 2009. From 2013, the automated chambers were increased to 10 and the setting position was slightly altered. The chambers were constructed from clear PVC board that was glued to a steel pipe frame, and the lids were raised and closed using two pneumatic cylinders. During measurements, one chamber was closed and air in the chamber was mixed using two micro-fans. Chamber air was circulated through the IRGA using a micro-pump. The change in CO₂ concentration and soil temperature at 5 cm depth was measured using the IRGA and thermocouples, respectively. From 2004 to 2009, the chambers were closed sequentially using the data logger over 1 h, and CO₂ concentration was measured at 1 s intervals for 150 s in each chamber, and 10 s averages were recorded using the data logger. Soil respiration rate was evaluated every 1 h in each chamber. In 2013 and 2014, the sampling period and respiration evaluation intervals were changed to 180 s and 0.5 h, respectively. Soil respiration rate (\( R_e; \mu mol CO_2 m^{-2} s^{-1} \)) was calculated as follows:

\[
R_e = \frac{P_t V}{RS (T_e + 273.15)} - \frac{\partial C}{\partial t} \tag{1}
\]

where \( P_t \) is the air pressure (Pa), \( V \) and \( S \) are the effective chamber headspace volume (0.405 m³), and the measured soil surface area (0.81 m²); \( R \) is the universal gas constant (8.314 J K⁻¹mol⁻¹); \( T_e \) is the air temperature (°C) in the chamber; and \( \partial C/\partial t \) is the average rate of change in the CO₂ mole fraction (\( \mu mol CO_2 mol^{-1} s^{-1} \)) during each recording interval. Low-quality \( R_e \) data were removed by checking the stationarity of \( \partial C/\partial t \) following the procedure proposed by Aguilos et al. (2013). In this study, air temperature \( (T_e) \) observed at 3 m height was used for \( T_e \) until 2009, and the air temperature measured inside each chamber was used from 2013. This method produced <2% overestimation of \( R_e \), even when there was a 5°C difference in temperatures.

2.3 Measurement of environmental factors

\( T_e \) and precipitation \((P)\) were observed by a platinum resistance thermometer (HMP45A; Vaisala, Helsinki, Finland) and a tipping bucket rain gage (CYG-52202; RM Young, Traverse City, MI, USA), respectively, at a height of 3 m above ground. \( T_e \) and VSWC at 5 cm deep in the soil below the soil surface were measured at five points using horizontally placed platinum resistance thermometers and water content reflectometers (CS615; Campbell Scientific), respectively. These measurements were taken every 5 s, and data were stored as 0.5 h means or sums using a data logger (CR23X; Campbell Scientific). Snow depth (SR-50; Campbell Scientific) was also measured and stored every 0.5 h (CR10X; Campbell Scientific).

PAI of vegetation (tree and Sasa at uncut row) was measured...
at five points every 2 to 4 weeks from June to October every year using a plant canopy analyzer (LAI2000; Li-Cor), and the values were averaged for each year. Difference in the scattered radiation of each of the five groups of zenith angles between above and below the tree or Sasa canopy was used for the PAI estimation for tree and Sasa, respectively. All measurements were conducted near the chamber system throughout the Rs measurement period.

2.4 Data analysis

To explain the seasonal variation in temperature response of Rs, we used an exponential equation as follows:

$$R_s = R_0 \times \exp (\alpha \times T_s)$$

where $R_0$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$) is $R_s$ at 0°C and $\alpha$ is the constant of the regression.

$Q_{10}$ was calculated using the following equation:

$$Q_{10} = \exp (10 \times \alpha)$$

To examine the relationships between $R_s$ and environmental factors (except $T_s$), temperature-normalized soil respiration $R_{10}$ at 10°C ($R_{10}$, µmol CO$_2$ m$^{-2}$ s$^{-1}$) was calculated using the following equation:

$$R_{10} = R_0 \times Q_{10}$$

Daily $R_s$ and $\alpha$ in Eq (2) were determined by the least squares method using hourly or half-hourly $R_s$ and $T_s$ data within a 31 day period (from preceding to succeeding 15 days of the day to determine the parameters) moving window for each of the (eight or 10) chambers for each year. Daily $Q_{10}$ and $R_{10}$ were calculated with the obtained parameters by Eqs (3) and (4), respectively. The

Fig. 1. Inter-annual variations of (a) monthly mean air temperature ($T_a$) and monthly precipitation (TP), (b) daily mean soil temperature ($T_s$) and volumetric soil water content (VSWC) at depth of 5 cm, (c) snow depth and seasonal mean plant area index (PAI) of tree and Sasa, (d) daily mean soil respiration ($R_s$), (e) daily mean temperature sensitivity ($Q_{10}$), and (f) daily temperature-normalized soil respiration at 10°C ($R_{10}$) during measurement period. Error bars in (c) indicate standard deviation of five points. Solid lines in (d), (e), and (f) indicate mean value of eight or 10 chambers, and the coefficient of variation (C.V.) among the chambers is shown as gray line.
coefficient of variation (C.V.) was used to indicate the magnitudes of spatial and inter-annual variation in \( R_s \), \( Q_{10} \), \( R_{10} \), and PAI. C.V. was calculated as the standard deviation of the variation divided by the mean values.

The relationships of \( R_s \), \( Q_{10} \), or \( R_{10} \), or these C.V. values to environmental factors were analyzed using a linear regression model. Coefficients of regression lines between the daily \( R_{10} \) and VSWC were compared among 8 years using an analysis of covariance (ANCOVA; covariate, VSWC). Seasonal mean values from June to October were used to analyze the relationships between inter-annual variation of \( R_s \), \( Q_{10} \) or \( R_{10} \) and environmental factors during 8 year period. All statistical analyses were performed using the R statistical software package (R 3.4.1; The R Foundation for Statistical Computing).

### 3. Results

#### 3.1 Micrometeorology and plant area index

There was clear seasonal variation in \( T_a \) and \( P \), with the warmest month being August and the highest rainfall in July and August, during the 8 year period (Fig. 1a). Snow covered the site from December to April (Fig. 1c). The inter-annual variation in \( T_a \) showed a gradual decrease from 2004 to 2009 (Mann–Kendall test, \( p < 0.01 \), Fig. 1b and Table 1). The highest mean \( T_a \) and \( P \) from June to October were observed in 2013 and 2014, respectively (Table 1). Daily VSWC ranged from 22% to 55% during the 8 year study period (Fig. 1b). The daily VSWC often decreased from May to August and higher rainfall frequency caused higher VSWC, for example, in 2009. The seasonal mean PAI of Sasa increased from 2004 to 2007 after clear-cutting of canopy trees, which may have caused the gradual decrease in \( T_a \) by shading the soil surface (Fig. 1c and Table 1). The seasonal mean PAI of tree was lower than that of Sasa. However, the spatial variation (C.V.) of tree PAI was higher than Sasa PAI, ranging from 8% to 21%, and 5% to 8%, respectively (Table 1). The inter-annual variation in the seasonal mean tree PAI (C.V. = 18%) was also larger than that of Sasa (C.V. = 10%) during the 8 year period.

#### 3.2 Temporal variation in soil respiration

\( R_s \) peaked in August in each year (Fig. 1d) and increased exponentially with \( T_a \). In addition, both \( Q_{10} \) and \( R_{10} \) showed obvious seasonal variation during the 8 year period. The lower \( Q_{10} \) appeared in August, whereas daily \( R_{10} \) tended to be higher in August (Fig. 1e and 1f). As the result, the seasonal variation in daily \( Q_{10} \) negatively related to \( T_a \) (\( p < 0.001, R^2 = 0.24 \) (Fig. 2).

### Table 1. Seasonal averages of air temperature \((T_a)\), soil temperature \((T_s)\), volumetric soil water content \((VSWC)\), plant area index \((PAI)\) of Sasa and tree, soil respiration \((R_s)\), temperature sensitivity \((Q_{10})\), temperature-normalized soil respiration at 10°C \((R_{10})\), and total precipitation \((P)\) from June to October during 8 year study period. \(T_a\) and VSWC were measured at a depth of 5 cm. Values in parentheses are coefficients of variation among chambers (C.V.; %).

|       | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2013 | 2014 |
|-------|------|------|------|------|------|------|------|------|
| \(P\) (mm) | 470  | 446  | 455  | 395  | 268  | 403  | 426  | 541  |
| \(T_a\) (°C) | 15.3 | 15.5 | 15.5 | 14.8 | 15.1 | 14.5 | 16.2 | 15.1 |
| VSWC (%) | 42   | 32   | 39   | 35   | 38   | 46   | 36   | 39   |
| \(T_s\) (°C) | 14.3 | 14.0 | 14.0 | 13.5 | 13.4 | 12.7 | 13.9 | 13.3 |
| PAI of Sasa \((m^2 \cdot m^-2)\) | 4.3(8) | 5.1(5) | 5.6(5) | 6.1(6) | 5.3(5) | 5.5(4) | 5.9(6) | 5.4(7) |
| PAI of tree \((m^2 \cdot m^-2)\) | 0.9(15) | 1.3(8) | 1.4(17) | 1.6(10) | 1.4(11) | 1.3(10) | 1.7(8) | 1.6(21) |
| \(R_s\) \((\mu mol \cdot CO_2 \cdot m^-2 \cdot s^-1)\) | 5.5(36) | 6.4(36) | 6.1(45) | 6.6(48) | 5.8(42) | 5.8(42) | 6.6(58) | 5.7(56) |
| \(Q_{10}\) | 2.1(25) | 2.4(25) | 2.8(23) | 3.1(25) | 3.3(21) | 3.5(27) | 2.7(20) | 2.9(21) |
| \(R_{10}\) \((\mu mol \cdot CO_2 \cdot m^-2 \cdot s^-1)\) | 4.3(36) | 4.6(37) | 3.9(42) | 4.6(52) | 3.8(37) | 3.8(37) | 4.2(61) | 4.2(59) |
Additionally, statistically significant positive relationship was obtained between daily $Q_{10}$ and VSWC ($p < 0.001$); however, the $R^2$ value was small (0.16), and it is hard to detect the clear tendency. Significant negative relationship between the daily $R_{10}$ and VSWC was obtained in each year ($p < 0.001$, Fig. 3). There were significant differences in slopes of the regression lines among years ($p < 0.01$). The slope of the regression lines in the years 2004, 2005, 2006, and 2008 were similar and steeper compared to all other years.

The 8 year average of seasonal mean $R_s$ (average from June to October) was 5.9 µmol CO$_2$ m$^{-2}$ s$^{-1}$, with a small inter-annual variation (C.V. = 15%), although $R_s$ increased from 2004 to 2005 just after clear-cutting (Table 1). The seasonal mean $Q_{10}$ ranged from 2.1 to 3.5 during 8 years and the lowest value was observed in 2004, whereas the seasonal mean $R_{10}$ ranged from 3.8 to 4.6 µmol CO$_2$ m$^{-2}$ s$^{-1}$ and the lowest values appeared in 2008 and 2009.

There was no correlation between seasonal mean $R_s$ and $Ts$ ($p > 0.05$) in their inter-annual variations, whereas the $R_s$ significantly decreased with the increase in VSWC during 8 year period ($p < 0.05$, Fig. 4a). The relationships between two parameters ($Q_{10}$ and $R_{10}$) of $R_s$ and VSWC showed that seasonal mean $R_{10}$ decreased with the increase in VSWC ($p = 0.05$, Fig. 4c), whereas there was no obvious correlation between seasonal mean $Q_{10}$ and VSWC ($p > 0.05$, Fig. 4b). There was no correlation between $R_s$ and its two parameters and TP in the inter-annual variation ($p > 0.05$, data not shown).

Seasional mean $R_s$ increased with the increase in Sasa PAI ($p < 0.05$, Fig. 5a) and marginal positive relationship was obtained between seasonal mean $Q_{10}$ and Sasa PAI ($p = 0.08$, Fig. 5b) in their inter-annual variation; however, there was no correlation between the seasonal mean $R_{10}$ and tree or Sasa PAI ($p > 0.05$, Fig. 5c).

### 3.3 Spatial heterogeneity in soil respiration

Both $R_s$ and $R_{10}$ showed larger spatial (chamber-to-chamber) variations than $Q_{10}$ (Figs. 1d–f). The seasonal mean C.V. among chambers ranged from 36% to 58%, 36% to 61%, and 21% to 27% for $R_{10}$, $R_{10}$, and $Q_{10}$, respectively, during the 8 years (Table 1). Monthly mean C.V. of $R_s$ and $Q_{10}$ tended to decrease during August and September with large inter-annual variation, whereas C.V. of $R_{10}$ tended to decrease during September and October (Fig. 6). We did not observe any significant relationships between the seasonal variations in C.V. of $R_s$, $R_{10}$, and $Q_{10}$ and the environmental factors. However, the inter-annual variation in the seasonal mean C.V. of $R_s$ and $R_{10}$ was significantly and positively related with tree PAI ($p < 0.01$, Fig. 7a and c) during 8 year period, whereas there was no correlation between C.V. of $Q_{10}$ and tree or Sasa PAI ($p > 0.05$, Fig. 7b).
4. Discussion

In addition to the already reported exponential relationship between daily $T_s$ and $R_s$ (Takagi et al., 2009; Aguilos et al., 2014), we observed seasonal variation in daily $Q_{10}$ and $R_{10}$. The $Q_{10}$ changed seasonally and increased with decreasing $T_s$ (Fig. 2a), which is consistent with previous reports (Kirschbaum, 2000; Chen et al., 2010; Teramoto et al., 2016). This may be due to temperature that affects microbial populations more strongly at lower temperatures than at higher temperatures (Andrews et al., 2000). In addition, weak positive relationship between daily $Q_{10}$ and VSWC was obtained during the 8 year period (Fig. 2b). Lower $Q_{10}$ is observed at low VSWC in their seasonal variation in a beech forest (Janssens and Pilegaard, 2003). Chen et al. (2010) showed that the lower VSWC influences the response of $R_s$ to $T_s$ and reduces $Q_{10}$ by inhibiting soil microbial communities and root respiration.

The seasonal variation of $R_{10}$ was negatively related to VSWC in each year ($p < 0.001$, Fig. 3). This tendency contradicts previous studies obtained in several forests in Japan, which

![Fig. 4. Relationships of seasonal mean (a) soil respiration ($R_s$), (b) temperature sensitivity of $R_s$ ($Q_{10}$) and (c) temperature-normalized soil respiration at 10°C ($R_{10}$) with seasonal mean volumetric soil water content (VSWC) from June to October during 8 year period. Symbols and error bars denote the mean and the standard deviation among eight or 10 chambers, respectively. Regression lines are shown with the coefficient of determination and $p$-value if statistical significance is obtained.]

![Fig. 5. Relationships of seasonal mean (a) soil respiration ($R_s$), (b) temperature sensitivity of $R_s$ ($Q_{10}$) and (c) temperature-normalized soil respiration at 10°C ($R_{10}$) with seasonal mean PAI of tree (solid squares) and Sasa (open circles) during 8 year period. Symbols and error bars denote the mean and the standard deviation among eight or 10 chambers, respectively. Regression lines are shown with the coefficient of determination and $p$-value if statistical significance or marginally significance is obtained.]
shows the VSWC range <27% in their seasonal variation. A weak positive relationship between \( R_s \) and VSWC (ranges of about 13% to 27% during May to October) is observed in a Japanese larch forest (Teramoto et al., 2017). Sun et al. (2017) reported that the temperature-normalized \( R_s \) showed neither a linear nor quadratic relation with VSWC (ranges of about 9% to 22% during May to October) in a Japanese red pine forest. On the other hand, similar negative relationship was reported by studies observed at forests with plentiful water in the soil, where soil respiration decreases under anoxic condition formed by excess (>40) in VSWC soil moisture (Sotta et al., 2004; Sundari et al., 2012; Wood et al., 2013). The range of VSWC was from 22% to 55% in our site; thus, the high VSWC may cause the suppression of the respiratory activities and/or reduce diffusion of CO\(_2\) from saturated soils (Linn and Doran, 1984). Slopes of the regression lines between daily \( R_{10} \) and VSWC were significantly different among 8 years \((p < 0.01)\), where the slope in the early years (2004, 2005, 2006, and 2008) were similar and steeper compared to all other years (Fig. 3). Thus, the slopes seem to be gentle according to with the vegetation recovery owing to the higher \( R_{10} \) at high VSWC. Increase in the root respiration might compensate reduction in the microbial respiration under the high VSWC condition (Tomotsune et al., 2013).

In the inter-annual variation, \( R_s \) was not significantly affected by precipitation \((p > 0.05)\) but controlled by VSWC through altering \( R_{10} \) instead of \( Q_{10} \) (Fig. 4). Both of the negative relationships between seasonal or inter-annual variation in \( R_{10} \) and VSWC could be explained as the VSWC exceeded the optimum water content for soil (heterotrophic) respiration.

Development of the vegetation was another main factor to drive the inter-annual variation in \( R_s \) because the seasonal mean \( R_s \) and \( Q_{10} \) significantly increased with the increase in \( Sasa \) PAI in this study \((p < 0.05, \text{Fig. 5a and b})\). Because root respiration is considered to be more sensitive to \( T_s \) than microbial respiration (Boone et al., 1998), increase in the \( Sasa \) biomass and its root respiration might cause the increase in the seasonal mean \( R_s \) through the increase in \( Q_{10} \), whereas negative relationship between seasonal mean \( R_{10} \) and VSWC (Fig. 4c) might mask the effect of the PAI on the \( R_{10} \).

Pumpanen et al. (2004) suggested that an increase in \( R_s \) after clear-cutting may have been due to higher \( T_s \) and VSWC, which enhanced the decomposition of a large amount of logging residue in the young stands. However, seasonal mean \( T_s \) gradually decreased after clear-cutting until 2009 and was not significantly correlated with \( R_s \) in our study. The reason for the decreasing trend in the seasonal mean \( T_s \) after clear-cutting may have been

---

Fig 6. Seasonal variations of monthly mean coefficient of variation (C.V.) of soil respiration \( (R_s) \), temperature sensitivity of \( R_s \) \( (Q_{10}) \), and temperature-normalized \( R_s \) \( (R_{10}) \) among chambers. Symbols and error bars denote the mean and the standard deviation among 8 years, respectively.

Fig 7. Relationships of seasonal mean C.V of \( (a) \) soil respiration \( (R_s) \), \( (b) \) temperature sensitivity of \( R_s \) \( (Q_{10}) \), and \( (c) \) temperature-normalized soil respiration at 10°C \( (R_{10}) \) with seasonal mean PAI of tree (solid squares) and \( Sasa \) (open circles) during 8 year period. Regression lines are shown with the coefficient of determination and \( p \)-value if statistical significance is obtained.
due to the decreased intensity of sunlight with increasing Sasa biomass (Aguilos et al., 2014). The root respiration of Sasa is considered to increase with its biomass increase and to cause opposite inter-annual trends in $T_r$ (decrease) and $R_r$ (increase) during the first 4 years (2004–2007).

Large spatial variation was observed in $R_r$ in this study (C.V. ranged from 36% to 58%), which was consistent with previous studies. Khomik et al. (2006) reported that the spatial C.V. of $R_r$ ranges from 4% to 74% in the seasonal variation in a boreal mixed wood forest in central Ontario. Luo et al. (2012) reported that the spatial C.V. of $R_r$ ranges from 12% to 89% in six sites of different successional stages of vegetation in south-eastern fringe of Tibetan Plateau. Because the magnitude and the seasonal variation in spatial C.V. of $R_{10}$ were similar to those of $R_r$ (Fig. 6), the spatial variation in $R_r$ was mainly caused by the basal respiration ($R_{10}$), not by the temperature sensitivity ($Q_{10}$). Although several studies have shown that spatial variation in $R_r$ was mainly caused by the spatial heterogeneity in tree and root biomass, species composition, or soil C content, C:N ratio, or bulk density (Khomik et al., 2006; Luan et al., 2012; Dore et al., 2014), we could not determine the main cause of the spatial variation because of the lack of such information for each chamber. However, because the seasonal mean spatial C.V. of $R_r$ and $R_{10}$ increased with tree PAI (Fig. 7), we can infer that the magnitude of the spatial heterogeneity in $R_r$ depends on the spatial heterogeneity in the tree distribution, thus its root distribution, which may have been caused by the tree growth through the change in the basal respiration $R_{10}$.

5. Conclusions

We analyzed 8 year $R_r$ data measured by a multichannel automated chamber system in a young larch plantation with dense Sasa undergrowth in northern Hokkaido Japan. Soil water affects both seasonal and inter-annual variation of $R_r$ by suppressing $R_{10}$, whereas soil temperature affects only its seasonal variation. Vegetation recovery had significant effect on the temporal variation in $R_r$ and its spatial heterogeneity, although the tree and undergrowth Sasa had different contributions to these variations. Increase in the undergrowth Sasa biomass recovery after clear-cutting increased the $R_r$ through the increase in $Q_{10}$, whereas the spatial heterogeneity in $R_r$ was increased by the increase in the tree biomass through the increase in $R_{10}$. These results suggest that the soil water and vegetation has strong effect on the inter-annual variation of $R_r$ and its spatial heterogeneity in the studied site, in spite of the strong exponential relationship of $R_r$ with $T_r$ in their seasonal variation.

Acknowledgments

This research was supported by the Environment Research and Technology Development Fund (2-1705) of the Environmental Restoration and Conservation Agency, the Global Environment Research Fund (B-073) and Global Environment Research Coordination System (Evaluation of the potential effect of global warming on soil carbon emission of Japanese forest ecosystems) of the Ministry of the Environment, Government of Japan. This research was also financially supported by the Grants-in-Aid for Scientific Research (nos 25241002, 26292076 and 16K14934) from the Ministry of Education, Culture, Sports, Science and Technology, Japan. This study was also partly supported by the Global Environmental Monitoring Program and the Climate Change Research Program of the National Institute for Environmental Studies. The study site was maintained as a collaboration study of Teshio Experimental Forest, Hokkaido University and Center for Global Environmental Research, National Institute for Environmental Studies, JP. We thank the staff of the Teshio Experimental Forest for their support.

References

Aguilos M, Takagi K, Liang N, Ueyama M, Fukuzawa K, Nomura M, Kishida O, Fukazawa T, Takahashi H, Kotsuka C, Sakai R, Ito K, Watanabe Y, Fujinuma Y, Takahashi Y, Murayama T, Saigusa N, Sasa K, 2014: Dynamics of ecosystem carbon balance recovering from a clear-cutting in a cool-temperate forest. Agricultural and Forest Meteorology 197, 26–39.

Aguilos M, Takagi K, Liang N, Watanabe Y, Teramoto M, Goto S, Takahashi Y, Mukai H, Sasa K, 2013: Sustained large stimulation of soil heterotrophic respiration rate and its temperature sensitivity by soil warming in a cool-temperate forestal peatland. Tellus Series B: Chemical and Physical Meteorology 65, 20792. http://dx.doi.org/10.3402/tellusb.v65i020792.

Andreas JA, Matamala R, Westover KM, Schlesinger WH, 2000: Temperature effects on the diversity of soil heterotrophs and the δ13C of soil-respired CO2. Soil Biology & Biochemistry 32, 699–706.

Bond-Lamberty B, Thomson A, 2010: A global database of soil respiration data. Biogeosciences 7, 1915–1926.

Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP, 1998: Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Chen B, Liu S, Ge J, Chu J, 2010: Annual and seasonal variations of $Q_{10}$ soil respiration in the sub-alpine forests of the Eastern Qinghai-Tibet Plateau, China. Soil Biology & Biochemistry 42, 1735–1742.

Cheng F, Peng X, Zhao P, Yuan J, Zhong C, Cheng Y, Cui C, Zhang S, 2013: Soil microbial biomass, basal respiration and enzyme activity of main forest types in the Qinling Mountains. PLoS ONE 8, e67353. https://doi.org/10.1371/journal.pone.0067353.

Curiel Yuste J, Janssens IA, Carrara A, Ceulemans R, 2004: Temperature effects on the diversity of soil heterotrophs and its soil respiration rate and its temperature sensitivity. Global Change Biology 10, 161–169.

Davidson EA, Belk E, Boone RD, 1998: Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4, 217–227.

Davidson EA, Richardson AD, Savage KE, Hollinger DY, 2006: A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. Global Change Biology 12, 230–239.

Dore S, Fry DL, Stephens SL, 2014: Spatial heterogeneity of soil CO2 efflux after harvest and prescribed fire in a California mixed conifer forest. Forest Ecology and Management 319, 150–160.

Food and Agriculture Organization of the United Nations (FAO), 1998: World Reference Base for Soil Resources, Rome.

Fukuzawa K, Shibata H, Takagi K, Nomura M, Kurima N, Fukazawa T, Satoh F, Sasa K, 2006: Effects of clear-cutting on nitrogen leaching and fine root dynamics in a cool-temperate
forested watershed in northern Japan. *Forest Ecology and Management* **225**, 257–261.

Hanpattanakit P, Leclerc MY, Mcmillan AMS, Limtong P, Maeght JL, Panuthai S, Imabushi K, Chidtahasong A, 2015: Multiple timescale variations and controls of soil respiration in a tropical dry dipterocarp forest, western Thailand. *Plant and Soil* **390**, 167–181.

Hokkaido Government Department of Fisheries and Forestry (2018) Statistics of Forest and Forestry in Hokkaido, 2016. http://www.pref.hokkaido.lg.jp/sr/sum/kcs/rin-toukei/28rtk.htm (2018/12/26) (in Japanese)

Janssens IA, Filegaard K, 2003: Large seasonal changes in $Q_{10}$ of soil respiration in a beech forest. *Global Change Biology* **9**, 911–918.

Jing Y, Guan D, Wu J, Wang A, Jin C, Yuan F, 2015: An experimental comparison of two methods on photosynthesis driving soil respiration: Girdling and defoliation. *PLoS ONE* **10**, e0132649. https://doi.org/10.1371/journal.pone.0132649

Khomik M, Arain MA, McCaughey JH, 2006: Temporal and spatial variability of soil respiration in a boreal mixedwood forest. *Agricultural and Forest Meteorology* **140**, 244–250.

Kirschbaum MUF, 2000: Will changes in soil organic carbon storage act as a positive or negative feedback on global warming? *Biogeochemistry* **48**, 21–51.

Liang N, Hirano T, Zheng ZM, Tang J, Fujimuna Y, 2010: Soil CO$_2$ efflux of a larch forest in northern Japan. *Biogeosciences* **7**, 3447–3457.

Linn DM, Doran JW, 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nottilted soils. *Soil Science Society of America Journal* **48**, 1267–1272.

Lloyd J, Taylor JA, 1994: On the temperature dependence of soil respiration. *Functional Ecology* **8**, 315–323.

Luan J, Liu S, Wang J, Zhu X, 2013: Factors affecting spatial variation of annual apparent $Q_{10}$ of soil respiration in two warm temperate regions. *PLoS ONE* **8** e64167. https://doi.org/10.1371/journal.pone.0064167

Luan J, Liu S, Zhu X, Wang J, Liu K, 2012: Roles of biotic and abiotic variables in determining spatial variation of soil respiration in secondary oak and planted pine forests. *Soil Biology & Biochemistry* **44**, 143–150.

Luo J, Chen Y, Wu Y, Shi P, She J, Zhou P, 2012: Temporal-spatial variation and controls of soil respiration in different primary succession stages on glacier forefield in Gongga Mountain, China. *PLoS ONE* **7**, e24354. https://doi.org/10.1371/journal.pone.0042354

Pumpinan J, Westman CJ, Ilvesniemi H, 2004: Soil CO$_2$ efflux from a podzolic forest soil before and after forest clear-cutting and site preparation. *Boreal Environment Research* **9**, 199–212.

Sampson DA, Janssens IA, Curiel Yuste J, Cavelmans R, 2007: Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. *Global Change Biology* **13**, 2008–2017.

Shi B, Jin G, 2016: Variability of soil respiration at different spatial scales in temperate forests. *Biology and Fertility of Soils* **52**, 561–571.

Soe ARB, Buchmann N, 2005: Spatial and temporal variations in soil respiration in relation to stand structure and soil parameters in an unmanaged beech forest. *Tree Physiology* **25**, 1427–1436.

Sotta ED, Meir P, Malhi Y, Nobre AD, Hodnett M, Grace J, 2004: Soil CO$_2$ efflux in a tropical forest in the central Amazon. *Global Change Biology* **10**, 601–617.

Sun L, Teramoto M, Liang N, Yazaki T, Hirano T, 2017: Comparison of litter-bag and chamber methods for measuring CO$_2$ emissions from leaf litter decomposition in a temperate forest. *Journal of Agricultural Meteorology* **73**, 59–67.

Sundari S, Hirano T, Yamada H, Kusin K, Limin S, 2012: Effect of groundwater level on soil respiration in tropical peat swamp forests. *Journal of Agricultural Meteorology* **68**, 121–134.

Takagi K, Fukuzawa K, Liang N, Kayama M, Nomura M, Hojyo H, Sugata S, Shibata H, Fukazawa T, Takahashi Y, Nakaji T, Oguma H, Mano M, Akibayashi Y, Murayama T, Koike T, Sasa K, Fujinuma Y, 2009: Change in CO$_2$ balance under a series of forestry activities in a cool-temperate mixed forest with dense undergrowth. *Global Change Biology* **15**, 1275–1288.

Teramoto M, Liang N, Takagi M, Zeng J, Grace J, 2016: Sustained acceleration of soil carbon decomposition observed in a 6-year warming experiment in a warm-temperate forest in southern Japan. *Scientific Reports* **6**, 35563. doi:10.1038/srep35563

Teramoto M, Liang N, Zeng J, Saigusa N, Takahashi Y, 2017: Long-term chamber measurements reveal strong impacts of soil temperature on seasonal and inter-annual variation in understory CO$_2$ flux in a Japanese larch *Larix kaempferi Sarg.* forest. *Agricultural and Forest Meteorology* **247**, 194–206.

Thomey ML, Collins SL, Vargas R, Johnson JE, Brown RF, Natvig DO, Friggens MT, 2011: Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology* **17**, 1505–1515.

Tomotsune M, Masuda R, Yoshitake S, Anzai T, Koizumi H, 2013: Seasonal and inter-annual variations in contribution ratio of heterotrophic respiration to soil respiration in a cool-temperate deciduous forest. *Journal of Geography* **122**, 745–754.

Wan S, Luo Y, 2003: Substrate regulation of soil respiration in a tallgrass prairie: Results of a clipping and shading experiment. *Global Biogeochemical Cycles* **17**, 1054. https://doi.org/10.1029/2002GB001971

Wood TE, Detto M, Silver WL, 2013: Sensitivity of soil respiration to variability in soil moisture and temperature in a humid tropical forest. *PLoS ONE* **8**, e80965. https://doi.org/10.1371/journal.pone.0080965

Zhang LH, Chen YN, Zhao RF, Li WH, 2010: Significance of groundwater level on soil respiration in tropical peat swamp forest. *Journal of Agricultural Meteorology* **68**, 121–134.

Zhou Z, Guo C, Meng H, 2013: Temperature sensitivity and basal rate of soil respiration and their determinants in temperate forests of North China. *PLoS ONE* **8**, e81793. https://doi.org/10.1371/journal.pone.0081793

Zhu J, Yan Q, Fan A, Yang K, Hu Z, 2009: The role of environmental, root, and microbial biomass characteristics in soil respiration in temperate secondary forests of Northeast China. *Trees - Structure and Function* **23**, 189–196.