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Different responses of soil, heterotrophic and autotrophic respirations to a 4-year soil warming experiment in a cool-temperate deciduous broadleaved forest in central Japan

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ABSTRACT

The responses of soil respiratory components to global warming are poorly understood particularly in high altitude forest ecosystems. To examine the different responses of soil respiration (R_S) components, i.e., autotrophic (R_A) and heterotrophic (R_H) respirations, in a mountainous temperate forest to elevated temperature, we conducted an open-field soil warming experiment combined with trenching treatments in a 60-year-old cool-temperate deciduous broadleaved forest in central Japan. Here we particularly focused on the temporal variations of respirations under remarkable seasonal change of air and soil temperatures in the region. R_S was divided into R_A and R_H by trenching method in both warmed and control plots (three subplots for each treatment). We installed heating cables at 5 cm below the soil surface to increase soil temperature by 3.0 °C during snow-free seasons in the four experimental years from 2012 to 2015. The soil warming significantly increased R_S, however, the soil warming did not alter fine root biomass, carbon concentrations nor nitrogen availability in the soils, which were positively related to R_S. The magnitude of the warming effects on R_H was negatively correlated to both soil temperature and soil moisture content. In this cool-temperate forest characterized by monsoon climate in summer, the high soil moisture level may not be a limiting factor for the soil warming effect on R_H. The effect of soil warming on R_S did not vary throughout the daytime, but the effect on R_S varied seasonally because R_H showed more sensitive response to soil warming in the late-growing season when compared to other seasons. We demonstrated that the season-specific Q_{10} model is able to quantify the warming impacts on annual respiration rates more accurately than apparent annual Q_{10} model. The soil warming increased annual R_S, R_H, and R_A for the second year by 18.1%, 25.6%, and 5.3%, respectively, but the magnitude of those increments declined in the fourth year to 9.9%, 19.5%, and −2.8%, respectively. Our results suggest that soil warming did not alter the temperature sensitivity of R_H in this forest soil, but might have induced thermal acclimation of R_A. This 4-year soil warming study in a mountainous forest contributes to the better understanding of the different responses of R_H and R_A to changing soil temperature conditions, and we highlight that the seasonal variations in the warming effects on R_H and R_A to future climate conditions should be taken into consideration in projecting the future soil carbon cycle.

1. Introduction

Soil respiration (R_S) is the second largest carbon flux in the terrestrial carbon cycle. The global R_S was estimated at 98 PgC yr^{-1} in 2008 with the increase of 0.1 PgC yr^{-1} since 1989 (Bond-Lamberty and Thomson, 2010). On-going global warming would potentially stimulate the soil carbon loss due to the general temperature dependency of R_S and the magnitude of soil carbon stocks in terrestrial ecosystems (Carey et al., 2016). The latest study based on 49 field warming experiments estimated that 2 °C of warming over the next 35 years would drive the loss of 55 PgC from the upper soil horizon, and the stimulation in global soil carbon loss could accelerate climate change (Crowther et al., 2016). However, the considerable uncertainties in predictions of global carbon-climate feedback should be eliminated by taking into account the responses of separated components of the ecosystem carbon cycles and more data from unexplored ecosystems (Chen et al., 2016; Crowther et al., 2016).

Many studies have addressed the effect of increasing soil

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temperature on R_S in various forest ecosystems (e.g., Carey et al., 2016; Lu et al., 2013), but very limited studies investigated respective effects on heterotrophic respiration (R_H) and autotrophic respiration (R_A) (Noh et al., 2016a; Schindlbacher et al., 2009; Vogel et al., 2014). R_S is composed of R_H and R_A associated with soil organic matter decomposition and root respiratory activity, respectively (Kuzyakov and Gavrichkova, 2010). Therefore, the effect of warming on R_S is determined by the responses of R_H and R_A to increasing temperature. The increasing temperature is generally expected to stimulate R_S, by accelerating R_A, R_H or both, but their responses to warming may not be the same (Noh et al., 2016a; Wang et al., 2014). The warming-induced stimulation in R_S, which reflects the positive or negative responses of plant and soil microbes, could be explained by the changes in belowground carbon fluxes and pools as well as by the site-specific environmental conditions such as soil carbon substrate quality and quantity, litterfall, root biomass and exudates, soil moisture and nutrient availability (Giardina et al., 2014; Hopkins et al., 2014; Leppälammi-Kujansuu et al., 2014). However, meta-analyses show no consensus in the magnitudes and directions of the responses of these various components to warming (Lu et al., 2013; Wang et al., 2014).

The temperature responses of R_S across biomes were not largely altered by experimental warming (Carey et al., 2016). However, the warming could decrease the temperature sensitivities of R_S for specific biomes (e.g. grassland, boreal forests) (Luo et al., 2001; Carey et al., 2016). For example in a cool-temperate deciduous forest located at lowland in northern Japan, the temperature sensitivity of R_S decreased by experimental warming probably due to the thermal acclimation of plant root respiration (Noh et al., 2016a). There are growing needs to consider thermal acclimations of plants and microbes in assessing terrestrial carbon cycle feedbacks to global warming (Eliasson et al., 2005; Ito et al., 2007; Smith et al., 2016). In our previous study using a process-based ecosystem model we estimated that R_S would increase by 17.0% under future climate, projected by a regional climate model under the Special Report on Emissions Scenario A1B greenhouse gas scenario, around 2085 in a cool-temperate deciduous forest of the present study (Kuribayashi et al., 2017). The study also suggested that incorporating thermal acclimation processes of respirations into ecosystem models should improve the prediction.

The warming might affect soil carbon fluxes differently among seasons, particularly in deciduous forests, because of their remarkably different seasonal behaviours in tree canopy photosynthesis and respirations (Migliavacca et al., 2015; Muraoka et al., 2010; Noda et al., 2015) as well as R_S associated with substrate availability (Tucker et al., 2013). Specifically, seasonal variations in substrate availability might affect the magnitude of warming effects on R_H through the limitation and supply of labile substrates for organic carbon decomposition (Fissore et al., 2013; Kirschbaum, 2013). In addition, seasonal lags in relationships between gross primary production and ecosystem respiration or R_S have been reported (Reichstein et al., 2005; Vargas et al., 2010), because allocation of the canopy photosynthate to belowground is variable with a certain time lag (Kuzyakov and Gavrichkova, 2010; Tang et al., 2005). Thus understanding of season-specific temperature response functions of respirations and the clarification of the seasonal response of R_S to warming is crucial for more realistic projection of future carbon cycle under climate change (Contosta et al., 2013; Savage et al., 2009).

Terrestrial ecosystems in high altitude and mid- to high latitude regions might have large impacts on soil carbon fluxes by climate change, due to their great labile soil carbon stocks and high temperature sensitivity of R_H (IPCC, 2013; Kirschbaum, 1995, 2013). However, in spite of world-wide distribution of deciduous broadleaved forests in those regions, there is no study on the warming impacts on R_H and R_A in forests in those regions. To our knowledge, this is the first study to examine the warming effects on both R_H and R_A in a mountainous cool-temperate deciduous broadleaved forest. In this study we investigated the temporal variations of the warming effects on both R_H and R_A using soil warming and trenching treatments, and then quantified the increments of the annual respiration rates using season-specific relationships between temperature and respiration rates by a 4-year warming experiment in a cool-temperate deciduous broadleaved forest in central Japan. We hypothesized 1) the respirations would be more responsive to experimental warming in early and late growing seasons which have higher temperature sensitivity than in mid growing season, 2) the season-specific temperature response curves could better estimate the annual respiration rates under future climate, and 3) the warming effects on R_S would be explained by increases in R_H and changes in fine root biomass, soil carbon and nitrogen availability.

Table 1
Annual mean air and soil temperatures, soil water content, and annual precipitation from 2012 to 2015. The numbers in parenthesis represent the mean values during snow-free season (May to November).

	2012	2013	2014	2015
Air temperature (°C)[a]	6.60 (12.88)	7.06 (13.67)	6.65 (13.28)	7.62 (13.43)
Soil temperature (°C)[b]	8.20 (12.65)	8.46 (13.02)	8.22 (12.51)	8.55 (12.99)
Soil water content (vol %)[c]	29.2 (28.7)	28.7 (28.3)	28.7 (28.6)	29.0 (28.8)
Precipitation (mm y^{-1})[a]	2117 (1275)	2183 (1637)	2296 (1287)	2274 (1355)

[a] The data were collected at 3 m height by AWS at TKY Field Station.
[b] Measured by thermocouples at 5 cm depth soil ($n = 9$).
[c] Measured by CS616 TDR at 0–10 cm depth soil ($n = 3$).

2. Materials and methods

2.1. Study sites

This study was conducted at the Takayama field station (TKY, 36°08′N, 137°25′E, 1420 m a.s.l.) of Gifu University, Japan. The study site is located on a plat ridge at a southwest-facing mid-slope position in a mountainous region under cool-temperate climate of central Japan (Table 1). Annual mean air temperature and precipitation were 6.4 °C and 2075 mm (1994–2008), respectively. The snow-free period is usually from mid-April to November, and the maximum snow depth is usually 1.0–1.5 m. The study site is a deciduous broadleaved forest dominated by ~60-year-old *Quercus crispula* Blume with a canopy height of about 20 m. Co-dominant tree species are *Betula ermanii* Cham. and *Betula platyphylla* var. *japonica* Hara. The shrub layers are dominated by *Hydrangea paniculata* Sieb. and *Viburnum furcatum* Blume ex Maxim. The forest floor is covered with an evergreen dwarf bamboo grass (*Sasa senanensis*). The soil type is a Dystric Cambisol and the depth is 1.5–2.0 m. Additional details of the sites are given by Ohtsuka et al. (2005). Long-term carbon cycling and budgets in these forests are being monitored using the eddy covariance method and biometric techniques (Ohtsuka et al., 2009). This study site is contributing to JapanFlux (part of the AsiaFlux Network, http://www.asiaflux.net/), JaLTER (Japan Long-term Ecological Research Network, http://www.jalter.org/) and J-BON (Japan Biodiversity Observation Network).

2.2. Experimental warming and environmental parameters

Experimental plots with three control subplots and three warming subplots (each 4 m × 5 m) were established in November 2011. In preliminary observation made on 2nd October 2011, before the warming system was installed, we confirmed that there was no significant difference in soil temperature (°C, mean ± one S.E., $n = 9$) between the control (12.3 ± 0.1) and warmed plots (12.2 ± 0.1) ($p > 0.05$). Electric heating cables were inserted horizontally into the soil at the depth of 5 cm with intervals of 15–20 cm in each warming subplot. The soil in the control plots was also cut using a flat-bladed