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Soil Microbial Activities in Beech Forests Under Natural Incubation Conditions as Affected by Global Warming*1

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ABSTRACT

Microbial activity in soil is known to be controlled by various factors. However, the operating mechanisms have not yet been clearly identified, particularly under climate change conditions, although they are crucial for understanding carbon dynamics in terrestrial ecosystems. In this study, a natural incubation experiment was carried out using intact soil cores transferred from high altitude (1 500 m) to low (900 m) altitude to mimic climate change scenarios in a typical cold-temperate mountainous area in Japan. Soil microbial activities, indicated by substrate-induced respiration (SIR) and metabolic quotient (qCO_2), together with soil physical-chemical properties (abiotic factors) and soil functional enzyme and microbial properties (biotic factors), were investigated throughout the growing season in 2013. Results of principal component analysis (PCA) indicated that soil microbial biomass carbon (MBC) and β-glucosidase activity were the most important factors characterizing the responses of soil microbes to global warming. Although there was a statistical difference of 2.82 °C between the two altitudes, such variations in soil physical-chemical properties did not show any remarkable effect on soil microbial activities, suggesting that they might indirectly impact carbon dynamics through biotic factors such as soil functional enzymes. It was also found that the biotic factors mainly controlled soil microbial activities at elevated temperature, which might trigger the inner soil dynamics to respond to the changing environment. Future studies should hence take more biotic variables into account for accurately projecting the responses of soil metabolic activities to climate change.

Key Words: biotic factors, carbon dynamics, metabolic quotient, microbial biomass, soil enzymes, soil respiration

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INTRODUCTION

Global temperatures are predicted to increase by 1.8 to 4.0 °C over the twenty-first century, with greater warming occurring in the higher latitudinal and altitudinal regions (IPCC, 2007). Rising temperature affects almost all biological processes, including soil metabolic processes in terrestrial ecosystems. Those processes involved in soil metabolism (microbial activities) are important indicators of the intensity of organic matter decomposition in an ecosystem, and can be characterized in several ways. Among them, the microbial metabolic quotient (qCO_2), calculated as the amount of soil substrate-induced respiration (SIR) per unit soil microbial biomass carbon (MBC), is estimated for soils with one kind of carbon resource treatment and shows the efficiency of soil microbial biomass in assimilating available C for cell biosynthesis; thus, lower qCO_2 indicates a more efficient physiological status of the soil microbiota (Anderson and Domsch, 1990, 1993). If the sensitivity of microbial activity to warming changes, the current soil respiration temperature sensitivity (Q_{10})-based predications of CO_2 emissions will have to be reconsidered (Bekku *et al.*, 2003).

Many experiments have shown that warming can increase soil metabolic activities (Luo *et al.*, 2001; Knorr *et al.*, 2005; Bond-Lamberty and Thomson, 2010). Nevertheless, a few studies have reported that warming can decrease or has no effect on microbial activities (Zhang *et al.*, 2005; Allison and Treseder, 2008; Lu *et al.*, 2013). These controversies could be ascribed to the procedures of soil respiration, soil enzyme activities, soil microbial activities and community structures, soil dissolved organic matter (DOM), soil nitrogen (N) turnover and transformation, and so on (Rustad *et al.*, 2001; Sardans *et al.*, 2006, 2007, 2008; Allison and Treseder, 2008; Biasi *et al.*, 2008).

Microbes often respond to changing environmental conditions through growing faster or expressing functional genes differently in a given community, which

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leads to changes in community composition and affects enzyme kinetics (Fierer *et al.*, 2003; Collins *et al.*, 2008; Stone *et al.*, 2012). Enzyme activity has been used as a descriptor of soil quality to suggest substrate usage by microbes and nutrient cycling, and to provide a mechanistic understanding of decomposition in natural and disturbed systems (Nannipieri, 1994; Dilly and Nannipieri, 1998; Bandick and Dick, 1999; Sinsabaugh *et al.*, 2009). In particular, extracellular enzyme activities in soil can represent microbial function in a soil ecosystem's response to climate change under natural conditions by revealing the metabolic requirements of the microbial community (Caldwell, 2005).

It should also be noted that all the biochemical processes such as respiration, enzyme activity and the microbial community structure are closely related to substrate supply (Liu, 2013). Microbes utilize organic C as a source of energy and biosynthetic precursor while releasing CO_2 and contributing to long-term soil C storage (Burgin *et al.*, 2011). Because of the enormous C flux they generate, microorganisms become the main drivers of the global C cycle (Schindlbacher *et al.*, 2011; Lu *et al.*, 2013).

The aforementioned biotic and abiotic factors at work in biophysical or biochemical environments may have complex relations with each other, as noted by several researchers (Wardle and Ghani, 1995; Ros *et al.*, 2003; Goberna *et al.*, 2006; Allison *et al.*, 2010). However, the relative contributions of abiotic and biotic factors to explain soil microbial activity changes remain poorly studied (Baker, 1995; Kurz *et al.*, 1995; Dale *et al.*, 2001; Luo *et al.*, 2001).

Numerous approaches, including controlled-climate laboratory studies (Whitby and Madritch, 2013; Ziegler *et al.*, 2013), field-based experimental manipulations using plastic enclosures as well as external heat inputs (Schindlbacher *et al.*, 2011) and ecosystem simulation modeling (Hart, 2006) have been applied to investigate the potential effects of global warming on terrestrial ecosystems and all have their own advantages and limitations (Hart, 2006). Alternatively, using natural temperature gradients resulting from changes in altitude or aspect, coupled with direct manipulation (soil or plant-soil transfer), has been proposed as a surrogate experimental approach. This approach has advantages over controlled laboratory studies in that ecosystem components are subjected to micro-environmental dynamics that are hard, if not impossible, to emulate in the laboratory. In addition, altitudinal soil translocation is relatively inexpensive, allowing more replications, which is not possible when climate is manipulated using external heating (Shaver *et al.*, 2000). Therefore, compared with the former approaches, natural incubation (without artificial warming) may provide a powerful, cost-effective and convenient tool for assessing the potential impact of climate change on terrestrial ecosystems (Hart and Perry, 1999; Hart, 2006; Zhang *et al.*, 2010).

The objectives of this study were thus: 1) to investigate the responses of qCO_2, Q_{10} and SIR to elevated temperature and 2) to understand how the abiotic (soil physical-chemical properties) and biotic (soil functional enzymes and microbial properties) factors contribute to the responses of microbial activity in deciduous forests. We hypothesized that: 1) soil microbial activity increases with naturally elevated temperature and 2) biotic variables control soil metabolic processes under natural warming. This study grew from a natural incubation experiment which was carried out on Mt. Naeba, a typical cold-temperate mountain in Japan where beech dominates at altitudes of 550 to 1 500 m.

MATERIALS AND METHODS

Study sites

Our study was conducted at two permanent sites, 900 m (36°51′ N, 138°40′ E) and 1 500 m (36°50′ N, 138°43′ E), located on the northern slope of Mt. Naeba, Japan (Fig. 1). The bedrock in the study area is predominantly basalt, and moist brown forest soils have developed on it. The upper layer of the canopy mainly consists of beech (*Fagus crenata*), which is widely distributed throughout Japan, and is a dominant species in typical cold-temperate deciduous forests. Occasionally, it is mixed with *Quercus mongolica* var. *grosseserrata* and *Magnolia obovata* at the 900 m site, and *Betula grossa* and *Betula ermanii* at the 1 500 m site. In addition, the prevalence of evergreen bamboo (*Sasa kurilensis*) increases with height to > 90% cover at the 1 500 m site (Zhao *et al.*, 2009).

Climatically, this region along the coast of the Japan Sea is characterized by high precipitation (*ca.* 2 000 mm year^{-1}), with large quantities of precipitation falling as snow in winter and producing 3 to 4 m of snow cover that lasts until mid-May (Zhao *et al.*, 2009, 2011). In 2013, the mean soil temperature from July to August was 20.47 and 17.69 °C and the average soil water content (SWC) was 218.7 and 287.4 g kg^{-1} at the 900 m site and the 1 500 m site, respectively. The snow remains until the beginning of May at the 900 m site. At the 1 500 m site, snowmelt occurs in early June. During the study period, soil total organic carbon (TOC) was 17.60 and 0.74 mg g^{-1}, soil total