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Effects of warming, wetting and nitrogen addition on substrate-induced respiration and temperature sensitivity of heterotrophic respiration in a temperate forest soil

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ABSTRACT

Soil heterotrophic respiration and its temperature sensitivity are affected by various climatic and environmental factors. However, little is known about the combined effects of concurrent climatic and environmental changes, such as climatic warming, changing precipitation regimes, and increasing nitrogen (N) deposition. Therefore, in this study, we investigated the individual and combined effects of warming, wetting, and N addition on soil heterotrophic respiration and temperature sensitivity. We incubated soils collected from a temperate forest in South Korea for 60 d at two temperature levels (15 and 20 °C, representing the annual mean temperature of the study site and 5 °C warming, respectively), three moisture levels (10%, 28%, and 50% water-filled pore space (WFPS), representing dry, moist, and wet conditions, respectively), and two N levels (without N and with N addition equivalent to 50 kg N ha^{-1} $year^{-1}$). On day 30, soils were distributed across five different temperatures (10, 15, 20, 25, and 30 °C) for 24 h to determine short-term changes in temperature sensitivity (Q_{10}, change in respiration with 10 °C increase in temperature) of soil heterotrophic respiration. After completing the incubation on day 60, we measured substrate-induced respiration (SIR) by adding six labile substrates to the three types of treatments. Wetting treatment (increase from 28% to 50% WFPS) reduced SIR by 40.8% (3.77 to 2.23 μg CO_2-C g^{-1} h^{-1}), but warming (increase from 15 to 20 °C) and N addition increased SIR by 47.7% (3.77 to 5.57 μg CO_2-C g^{-1} h^{-1}) and 42.0% (3.77 to 5.35 μg CO_2-C g^{-1} h^{-1}), respectively. A combination of any two treatments did not affect SIR, but the combination of three treatments reduced SIR by 42.4% (3.70 to 2.20 μg CO_2-C g^{-1} h^{-1}). Wetting treatment increased Q_{10} by 25.0% (2.4 to 3.0). However, warming and N addition reduced Q_{10} by 37.5% (2.4 to 1.5) and 16.7% (2.4 to 2.0), respectively. Warming coupled with wetting did not significantly change Q_{10}, while warming coupled with N addition reduced Q_{10} by 33.3% (2.4 to 1.6). The combination of three treatments increased Q_{10} by 12.5% (2.4 to 2.7). Our results demonstrated that among the three factors, soil moisture is the most important one controlling SIR and Q_{10}. The results suggest that the effect of warming on SIR and Q_{10} can be modified significantly by rainfall variability and elevated N availability. Therefore, this study emphasizes that concurrent climatic and environmental changes, such as increasing rainfall variability and N deposition, should be considered when predicting changes induced by warming in soil respiration and its temperature sensitivity.

Key Words: carbon dioxide, decomposition, global warming, soil moisture, soil organic carbon, soil respiration, Q_{10}

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INTRODUCTION

Soil heterotrophic respiration through decomposition of soil organic carbon (C) is a critical component for studying the exchange of carbon dioxide (CO_2) between the atmosphere and terrestrial ecosystems (Allison *et al*., 2010; Bond-Lamberty *et al*., 2018). The effect of temperature on soil heterotrophic respiration has been investigated to enhance understanding of soil respiration and its response to climatic warming (Davidson and Janssens, 2006; Zhong *et al*., 2016). Climatic warming can affect soil microbial activity and its temperature sensitivity, which can directly and indirectly affect the functioning of a wide range of ecosystems (Classen *et al*., 2015; Dutta and Dutta, 2016). On a global level, subtle changes in the temperature sensitivity of soil heterotrophic respiration can have a significant effect on future climatic changes because CO_2 released from the soil under the influence of warming may provide positive feedback to the warming (Kirschbaum, 2000). The temperature dependence of soil organic matter decomposition, which is the major source of soil heterotrophic respiration, has been the subject of intense scientific debate (Kirschbaum, 2006). Many studies have shown that warming over periods of several months or years can lead to a temporary decrease in temperature sensitivity (Q_{10}, change in respiration with 10 °C increase in temperature) of soil heterotrophic respiration (Lloyd and Taylor, 1994; Vanhala *et al*., 2011) and subsequent return to the pre-warming state, because of either substrate reduction or acclimation of soil biota (Melillo *et al*., 2002; Knorr *et*

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al., 2005; Bradford, 2013). Varying responses of soil microbes to warming may result from differences in microbial community composition as well as soil type, C and nitrogen (N) availability, and soil moisture conditions.

In addition to climatic warming, changes in soil moisture because of changing precipitation can also affect the overall rate of soil heterotrophic respiration and its Q_{10} (Moyano *et al*., 2013). However, studies on the effects of soil moisture on Q_{10} have produced variable results. For example, Jiang *et al*. (2013) observed a reduction in the temperature sensitivity of soil respiration in a mixed broad-leaved forest when simulated precipitation was doubled from ambient levels. Craine and Gelderman (2011) found that the highest temperature sensitivity occurred at intermediate soil moisture levels in an upland prairie soil (45% water-holding capacity). Nevertheless, they also reported a positive linear relationship between Q_{10} of soil respiration and soil moisture of the same soil sampled from a lowland prairie area.

Nitrogen deposition has increased in many parts of the world (Kanakidou *et al*., 2016; Ackerman *et al*., 2019), and increased availability of N in the soil coupled with climatic change can further alter the soil C dynamics and soil heterotrophic respiration (Janssens *et al*., 2010). For example, in a weathered tropical soil from Puerto Rico, N-fertilization initially increased the Q_{10} of labile C pools, whereas warming increased the Q_{10} by initiating the decomposition of recalcitrant C pools (Cusack *et al*., 2010). Increased availability of N derived from chronic atmospheric deposition can slow the microbial decomposition of soil organic matter (SOM) due to reduced microbial activity and potential changes in organic matter composition (Ågren *et al*., 2001; Park, 2008), which also affects the rate of soil CO_2 efflux (Bowden *et al*., 2004). Although many studies have found that chronic N deposition can substantially reduce SOM decomposition (Janssens *et al*., 2010), few studies have investigated its effect on the Q_{10} of soil heterotrophic respiration under a warming environment.

Soil microbial heterotrophs, the main players of soil heterotrophic respiration, are sensitive to abiotic factors, such as temperature, moisture, and nutrient availability (Bissett *et al*., 2013). Large seasonal variations in soil temperature or smaller increases in annual temperature caused by global warming may shift the microbial community structure and alter microbial physiological functions (Schindlbacher *et al*., 2011; DeAngelis *et al*., 2015). Climatic warming may create conditions that favor certain groups of microorganisms, reshaping the entire soil microbial community structure (Deslippe *et al*., 2012; Rui *et al*., 2015). Changes in physiological activities in those microorganisms may result in altered rates of respiration, affecting the gaseous exchange between the atmosphere and soil (Allison *et al*., 2010; Bond-Lamberty and Thomson, 2010; Bond-Lamberty *et al*., 2018). Microorganisms can adjust their physiology to warming, by reducing metabolic costs, reducing plant C inputs, or shifting the microbial community composition under a warmer environment (Allison *et al*., 2010). For example, Frey *et al*. (2008) reported increased species diversity and a shift in the microbial community structure in a laboratory warming experiment with soil from a mixed deciduous forest. Soil water content can also have a strong effect on microbial function through soil aeration and substrate availability (Manzoni *et al*., 2012; Moyano *et al*., 2013). In addition, changes in microbial functional capacity and activity were found in soils exposed to chronic N deposition (Chung *et al*., 2007; Frey *et al*., 2008). Previous studies have addressed the main factors controlling the Q_{10} of soil heterotrophic respiration, such as temperature, soil moisture, and nutrient availability. Few studies have assessed the combined effects of multiple factors on the Q_{10} of soil heterotrophic respiration (Davidson *et al*., 1998; Wang *et al*., 2017). A meta-analysis reported a smaller combined effect of temperature and precipitation on soil respiration compared with that of a single factor (Wu *et al*., 2011).

From 2006 to 2024, the Korean Meteorological Administration projected that the average temperature of the Korean Peninsula may rise by 0.5 °C ($\pm$ 0.3 °C) in the winter as well as in the summer. Between 2025 and 2049, the average temperature has been projected to rise by 1.2 °C ($\pm$ 0.7 °C) in the summer and 1.2 °C ($\pm$ 0.8 °C) in the winter (KMA, 2014). South Korea is located in East Asia, which experienced 10%–20% increases in precipitation between 1960 and 2003 (Gosling *et al*., 2011). Scientists predict that annual, summer, and winter precipitation in South Korea may increase by 19.1%, 20.5%, and 33.3%, respectively, in the later stages of the 21st century (Oh *et al*., 2016). On the global level, land is estimated to sequester 11% (10%–13%) of annual N inputs (from a baseline of 128 Tg N year^{-1}) (Lee *et al*., 2019). The annual mean total wet N deposition for 1994–1998 was estimated to be about 10.6 kg N ha^{-1} year^{-1} in South Korea (Park and Lee, 2002). The projections suggest that it is important to understand the effects of elevated N on the terrestrial ecosystems in the Korean Peninsula.

This study investigated the combined effects of temperature, soil moisture, and N availability on Q_{10} and substrate-induced respiration (SIR) under controlled laboratory conditions. Incubation experiments under controlled laboratory conditions allowed us to study the combined effects of these three selected factors on Q_{10}, which cannot be tested under field conditions due to the interference of other interacting factors. Therefore, a laboratory incubation experiment was performed using soil collected from a temperate forest in South Korea to investigate the response of SIR and Q_{10} to concurrent changes in temperature, soil moisture, and N addition.

MATERIALS AND METHODS

Study site and soil sampling

Soil samples were collected from a deciduous forest dominated by Mongolian oaks (*Quercus mongolica*) in Bukhan Mountain, South Korea (37°43′27″ N, 126°59′96″ E, and 243 m above sea level). The sampling site has an annual mean air temperature of 12.9 °C and annual precipitation of 1 464 mm (Lee, 2011). The soil type was characterized as acidic sandy loam in the surface soil horizon up to 10 cm; soil pH was 4.8, soil organic C content was 8.8%, and total N content was 1.4 g gk^{-1} (Bae *et al*, 2008). Water-extractable organic C of the soil sample was 4.28 μg g^{-1} soil.

To obtain representative soil samples from the hilly study site, sampling was conducted on a relatively steep ($> 25°$) slope, which is typical in the area. Samples were collected from a top, a mid-slope, and a foothill location of a slope at an equal distance of 5 m. A metal frame with an open inner square (25 cm × 25 cm) was placed on the forest floor. The litter material, composed of freshly fallen or slightly decomposed litter (O_i), moderately decomposed material (O_e), and completely decomposed material (O_a), was cut inside the frame and then collected by hand. Mineral soil in the A-horizon was ploughed to a depth of 10 cm using a trowel. For additional measurements, including bulk density, intact soil samples were collected from the same locations using a soil corer (59 mm in diameter and 61 cm in length) (Giddings Machine Company, USA). Top mineral soils up to 10 cm below the forest floor of the collected intact soil cores were measured for volume and dry weight to calculate bulk density (Nhantumbo and Bennie, 2001).

All soil samples were kept in an icebox during transportation to the laboratory. The litter material was cut using scissors and sieved through a 5-mm mesh. Soils from the three sampling points were mixed thoroughly and sieved through a 2-mm mesh to generate one composite sample for the incubation experiment. Sieved soils were kept at 4 °C before starting the incubation.

Soil incubation experiment

The experiment included two incubation temperatures (15 °C, close to the annual mean temperature at the sampling site (T1) and 20 °C, 5 °C warming (T2)); three soil moisture conditions measured in water-filled pore space (WFPS) (10%, dry (W1); 28%, moist (W2); and 50%, wet (W3)); and two N treatments (0 (N0) and 59.5 mg N kg^{-1} soil (N1)), totalling 12 treatments, T1N0W1, T1N0W2, T1N0W3, T1N1W1, T1N1W2, T1N1W3, T2N0W1, T2N0W2, T2N0W3, T2N1W1, T2N1W2 and T2N1W3. The treatment T1N0W2 was considered the control. Based on the measured ratio of organic litter material to the mineral soil, 2 g of organic horizon materials (O_e and O_a mixed together) underlain by 20 g of mineral soils (dry mass basis) was placed in 120 mL glass vials. Seven replicates per treatment were incubated at two different incubation temperatures: 15 and 20 °C. Soil moisture levels were set up with deionized water, and WFPS (%) was calculated as follows (Linn and Doran, 1984):

$$\text{WFPS} = \frac{\text{Volumetric soil water content}}{\text{Total porosity}} \times 100 \quad (1)$$

where total porosity was calculated as:

$$\text{Total porosity} = 1 - \frac{\text{Soil bulk density}}{\text{Soil particle density}} \quad (2)$$

where soil particle density takes the default value of 2.65 g cm^{-3}.

The two levels of N were created by adding 5 mL water or a 5-mL solution containing 3.4 mg NH_4NO_3 to each soil sample (20 g on dry soil basis). The amount of N added for N1 was equivalent to 50 kg N ha^{-1} $year^{-1}$ based on the surface area of the incubated soil and the incubation period (60 d out of 365 d per year), and it is also approximately five times the global average annual atmospheric N deposition (9–10 kg ha^{-1} $year^{-1}$) projected for 2050 (Lamarque *et al*., 2005; Kanakidou *et al*., 2016).

Throughout the incubation, the moisture level of each soil was maintained constant by adding water when needed. On the 30th day of incubation, seven replicates of each treatment incubated at two temperatures (15 and 20 °C) were randomly placed in incubators set at five different temperatures (10, 15, 20, 25, and 30 °C) for 24 h to determine short-term changes in the temperature sensitivity of soil heterotrophic respiration. Based on the method of Craine *et al*. (2010) with modification, three replicates per treatment were maintained under an appropriate incubation temperature (15 or 20 °C) to determine the accuracy of the measurements (three replicate measurements per incubation temperature), whereas only one soil was incubated at the four other measurement temperatures. The incubation temperatures enabled the microbes to respond to two different temperatures for 30 d. Furthermore, higher than normal temperatures are expected under the effects of climatic warming during the summer months. Therefore, 30 d (equivalent to one month) allowed the microbes to acclimatize to temperatures before they were subjected to short-term temperature treatments (for the estimation of Q_{10}). In other soil incubation studies investigating temperature sensitivity, soil samples were often incubated at five or more different temperatures for 24 h (Meyer *et al*., 2018). According to Meyer *et al*. (2018), the first 12 h of incubation allowed for equilibrium. Soil microbes need a few hours to adapt to new temperatures. The duration varies between studies, ranging from 2 h (Koch *et al*., 2007) to

24 h (Vanhala *et al*., 2011). This design also enabled us to confirm the measurement accuracy within the given time limits. The initial CO_2 efflux from the control soils (without N and at 28% WFPS) incubated at 15 and 20 °C was 25.82 and 37.38 mg CO_2-C m^{-2} h^{-1}, respectively.

Gas sampling and analysis and Q_{10} determination

At the end of the 24 h incubation of the soils at 10, 15, 20, 25, and 30 °C, gas samples were collected twice from the headspace: immediately after closing the incubation vial and 30 min later. Concentration of CO_2 was determined with a gas chromatograph (7890A, Agilent, USA) fitted with a Supelco Hayesep Q column (injector: 200 °C; detector: 250 °C; oven: 60 °C; and makeup gas: N_2). The standard gases used to calibrate the gas chromatograph included four different CO_2 concentrations in the N_2 makeup gas. The standard gas with CO_2 concentration close to the sample range was repeatedly analyzed after every five samples to ensure proper functioning of the gas chromatograph.

The relationship between temperature (T) and soil heterotrophic respiration (SR) can be expressed using an exponential equation:

$$\mathrm{SR}_T = \alpha \mathrm{e}^{\beta T} \tag{3}$$

where SR_T is soil respiration at temperature T and α and β are constants.

Then, Q_{10} was calculated as (Lloyd and Taylor, 1994):

$$Q_{10} = \mathrm{e}^{10\beta} \tag{4}$$

Determination of SIR

To determine the effect of warming coupled with N addition under different soil moisture conditions on the physiological profile and substrate utilization pattern of soil microbial community, soil samples were collected at the end of the 60-d incubation and measured for SIR using MicroResp$^{\mathrm{TM}}$ technique (Macaulay Scientific Consulting Ltd., UK) as described by Campbell *et al*. (2003). A pre-incubation period allows a steady state of microbial activity to be established in the soil (Franzluebbers *et al*., 1999). Previous soil incubation experiments have utilized pre-incubation periods ranging from 3 d to 4 weeks, which enable the reliable determination of SIR from homogenous soil (Creamer *et al*., 2014). However, an extended pre-incubation can reduce the reliability of the steady state of microbial activity, due to a decrease in respiration intensity (Smirnova *et al*., 2016). Six C substrates were selected: glucose, fructose, galactose, oxalic acid, citric acid, and tyrosine based on their widespread availability in soil environments and their lability, which permits an immediate physiological response of active groups in the soil microbial community (Glanville *et al*., 2012). MicroResp$^{\mathrm{TM}}$ consisted of a reaction plate with deep wells, which was filled with soil and C sources, and a detector plate, which detected CO_2 released from the reaction plate. Approximately 0.35 g of soil was put in each well of the reaction plate, and C substrates were added to the wells at a concentration of 30 mg mL^{-1} soil water. A separate control group was included, with only deionized water added. The SIR was calculated as the difference between the respiration of the soil with substrate added and that of the control.

Statistical analysis

Regression significance for the relationship between temperature and respiration was tested using SigmaPlot 10.0 (Systat Software Inc., UK). As only one Q_{10} value was obtained per treatment, treatment effects on Q_{10} were analyzed using single-factor analysis of variance (ANOVA) of SPSS 20 (IBM Inc., USA). For MicroResp$^{\mathrm{TM}}$-based analysis of SIR, one-way ANOVA followed by Tukey's *post-hoc* test ($\alpha = 0.05$) at each WFPS level (10%, 28%, and 50%) under various combinations of incubation temperature and N addition was used.

RESULTS

Treatment effects on SIR

Significant differences ($P < 0.001$) in SIR were found among the 12 treatments (Table I). Increasing the WFPS from 10% to 28% increased the overall SIR by 7.0%; however, increasing WFPS from 28% to 50% reduced the SIR by 41.0%. The warming treatment increased the average SIR by 47.7% (from 3.77 to 5.57 μg CO_2-C g^{-1} h^{-1}). The N addition increased the SIR by 42.0% (from 3.77 to 5.35 μg CO_2-C g^{-1} h^{-1}). When oxalic acid or citric acid was used as substrate, SIR in the W3 treatment was significantly lower ($P < 0.05$) than those in the W1 and W2 treatments for a same temperature and N combination.

Wetting (W3) coupled with warming (T2) did not significantly affect the overall SIR. However, in the T2N0W3 treatment, SIR was significantly higher ($P < 0.05$) than the control (T1N0W2) when glucose and galactose were used as substrate. Warming (T2) coupled with N addition (N1) did not affect the overall SIR, either. However, high SIR was observed when oxalic acid, glucose, and fructose were used as substrate. Nitrogen addition coupled with wetting did not affect the overall SIR. However, SIR was significantly reduced under warming coupled with wetting (T2N0W3) compared to the control (T1N0W2) when oxalic acid and citric acid were used as substrate (from 5.18 to 1.62 μg CO_2-C g^{-1} h^{-1} for oxalic acid; from 7.26 to 1.87 μg CO_2-C g^{-1} h^{-1} for citric acid) and significantly increased when

TABLE I

Soil substrate-induced respiration measured using six substrates in the treatments of different combinations of incubation temperature (T), nitrogen addition (N), and water-filled pore space (W)

Treatment[a)]	Oxalic acid	Citric acid	Tyrosine	Glucose	Galactose	Fructose	Average
	μg CO_2-C g^{-1} soil h^{-1}						
T1N0W1	3.60 ± 0.27[b)]ab[c)]	3.21 ± 0.49a	3.29 ± 0.58abc	3.72 ± 0.47bc	3.51 ± 0.51ab	3.84 ± 0.47bc	3.53 ± 0.25bc
T1N0W2	5.18 ± 1.52bc	7.26 ± 1.85bc	3.48 ± 0.18abc	2.04 ± 0.43a	2.23 ± 0.09a	2.45 ± 0.40a	3.77 ± 0.45c
T1N0W3	1.70 ± 0.12a	1.80 ± 4.27a	2.50 ± 0.14ab	2.37 ± 0.09a	2.77 ± 0.29ab	2.25 ± 0.46a	2.23 ± 0.11a
T1N1W1	3.48 ± 0.32ab	4.27 ± 0.74ab	3.61 ± 0.32abc	3.88 ± 0.45bc	3.80 ± 0.68bc	3.90 ± 0.25bc	3.82 ± 0.23c
T1N1W2	7.83 ± 1.70cd	6.58 ± 2.04bc	4.46 ± 0.85c	4.73 ± 0.45bc	4.06 ± 0.08bc	4.41 ± 0.23c	5.35 ± 0.41d
T1N1W3	1.64 ± 0.02a	1.82 ± 0.04a	4.03 ± 0.33bc	3.13 ± 0.59a	4.66 ± 0.48bc	2.67 ± 0.13ab	2.99 ± 0.22a
T2N0W1	3.70 ± 0.19ab	3.86 ± 1.01ab	3.64 ± 0.84abc	4.35 ± 0.37bc	4.06 ± 0.29bc	4.54 ± 0.33c	4.03 ± 0.20c
T2N0W2	6.25 ± 0.61bcd	9.68 ± 2.14c	3.68 ± 0.14abc	5.02 ± 0.42c	4.16 ± 0.10bc	4.63 ± 0.13c	5.57 ± 0.05d
T2N0W3	1.62 ± 0.00a	1.87 ± 0.02a	3.02 ± 0.74abc	4.21 ± 0.53bc	5.22 ± 1.11c	2.91 ± 0.25ab	3.14 ± 0.11ab
T2N1W1	3.86 ± 0.16ab	3.89 ± 0.68ab	3.31 ± 0.82abc	3.75 ± 0.46bc	3.49 ± 0.70ab	3.08 ± 0.11ab	3.56 ± 0.24bc
T2N1W2	8.44 ± 2.50d	6.92 ± 2.14bc	3.22 ± 0.22abc	3.59 ± 0.61bc	3.19 ± 0.35ab	3.43 ± 0.46bc	4.80 ± 0.16cd
T2N1W3	1.72 ± 0.23a	1.93 ± 0.37a	2.30 ± 0.23a	2.37 ± 0.30a	2.54 ± 0.46ab	2.15 ± 0.17a	2.17 ± 0.13a

[a)] T1 = 15 °C; T2 = 20 °C; N0 = 0 mg N kg^{-1} soil; N1 = 59.5 mg N kg^{-1} soil; W1 = 10% water-filled pore space (WFPS); W2 = 28% WFPS; W3 = 50% WFPS.

[b)] Mean ± standard error ($n = 7$).

[c)] Values followed by different letters are significantly different for a same substrate at $P < 0.05$.

galactose was used as substrate (from 2.23 to 5.22 μg CO_2-C g^{-1} h^{-1}). Warming coupled with N addition and wetting reduced the overall SIR by 42.4% (Table I). Significant reductions were observed on oxalic acid (from 5.18 to 1.72 μg CO_2-C g^{-1} h^{-1}) and citric acid (from 7.26 to 1.93 μg CO_2-C g^{-1} h^{-1}) under the treatment of warming coupled with N addition and wetting.

Treatment effects on Q_{10}

Warming had a negative effect on Q_{10} (Fig. 1, Table II). The warming treatment reduced Q_{10} by 37.5% (from 2.4 to 1.5) and by 23.0% (from 3.0 to 2.3) for soils with 28% and 50% WFPS, respectively. A negative effect of N addition was also observed. Under incubation at 15 °C, the addition of N reduced the Q_{10} by 16.7% at 28% WFPS (2.4 to 2.0) and reduced Q_{10} by 33.3% at 50% WFPS (from 3.0 to 2.0). In contrast, wetting increased the Q_{10} by 25% (from 2.4 to 3.0, $P < 0.05$, Table II) while 10% WFPS reduced the Q_{10} by 58% (2.4 to 1.0). Increasing the moisture from 10% to 50% WFPS increased the Q_{10} by 200% (1.0 to 3.0).

The addition of N coupled with wetting (from 28% to 50% WFPS) did not affect the Q_{10} (Table II). Wetting (from 28% to 50% WFPS) coupled with the warming treatment did not affect the Q_{10} (4% decrease). Wetting treatment (from 28% to 50% WFPS) coupled with the N addition reduced the Q_{10}. The combination of warming, wetting (from 28% to 50%), and N addition increased the Q_{10} by 12.5% compared with the control (T1N0W2) ($P < 0.05$).

DISCUSSION

Responses of SIR to the different treatments

Warming increased SIR, with significantly higher individual SIRs for the simple sugars, such as glucose, galactose, and fructose, compared with the control (T1N0W2). Generally, microbes can acclimatize to warming (Bradford *et al*., 2008); therefore, the catabolic properties adjust to the warmed environment. However, microbes can be reactivated in response to the increased availability of externally added labile substrates (Bradford, 2013; Frey *et al*., 2013).

After a 60-d incubation, SIR decreased under the wettest condition (50% WFPS) compared with the control moisture condition (28% WFPS). The wettest condition in our study may have hindered the diffusion of gas produced by decomposition of the added substrates. The addition of the labile substrates (glucose, galactose, fructose, oxalic acid, citric acid, and tyrosine) may have increased respiration to the maximum rate through a priming effect. However, the added substrate solution coupled with the already wet condition (50% WFPS) appears to have reduced the rate of gas diffusion, limiting O_2 availability for aerobic respiration (Lin and Brookes, 1999).

In our study, we found that N addition increased the overall SIR. Previous studies have shown that N addition increased short-term microbial activity (Crecchio *et al*., 2001). In a nutrient-poor mineral forest soil, roots provide nutrients such as N, which enhance the SIR of microbes in the planted areas (Priha *et al*., 1999). It was reported that N addition stimulates microbes to efficiently use the recalcitrant C pool once the labile C pool is depleted (Jiang *et al*., 2014). In our study, we also observed a significant increase in the utilization of simple sugars, like glucose, galactose, and fructose. Following the addition of simple sugars, C accessibility increases, leading to changes in microbes or microbial activity (Kuzyakov *et al*., 2000). Microorganisms whose activities are limited by N availability might become stimulated following the addition of N; the

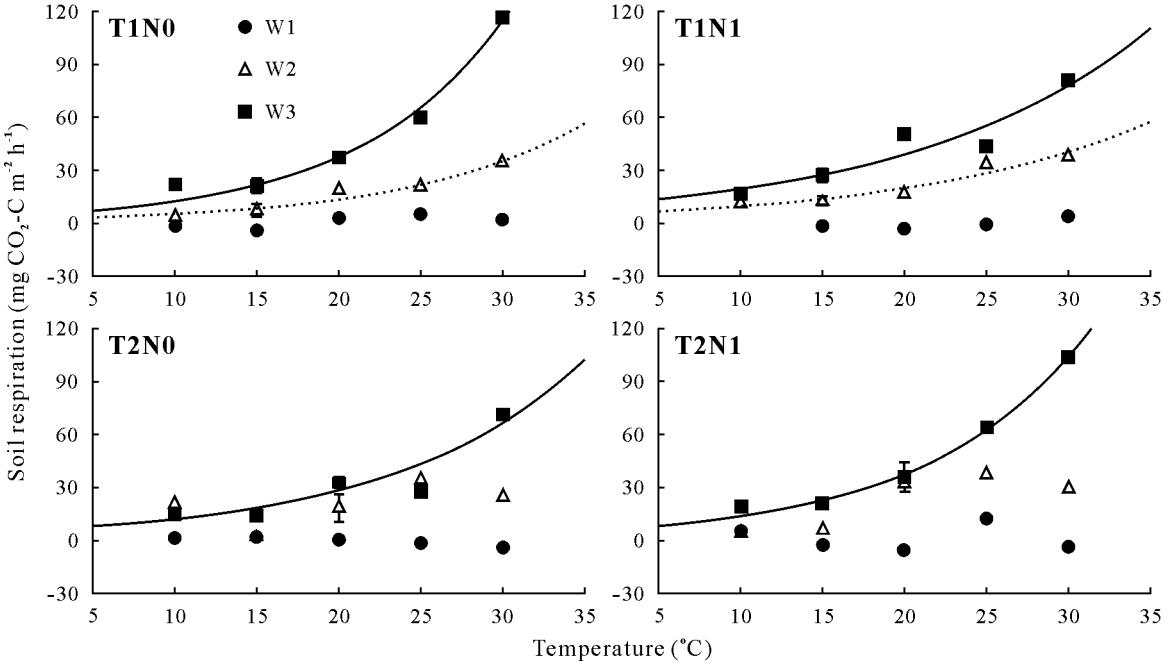

Fig. 1 Short-term (24 h) temperature response of soil respiration on the 30th day of incubation at different combinations of temperature (T), nitrogen addition (N), and water-filled pore space (W). Error bars shown for two measurements in each subfigure indicate standard deviations ($n = 3$). Only significant ($P < 0.05$) regressions are indicated by best-fit lines. T1 = 15 °C; T2 = 20 °C; N0 = 0 mg N kg^{-1} soil; N1 = 59.5 mg N kg^{-1} soil; W1 = 10% water-filled pore space (WFPS); W2 = 28% WFPS; W3 = 50% WFPS.

TABLE II

Relationships (Eq. 3) between soil heterotrophic respiration (SR) and incubation temperature (T) and temperature sensitivity (Q_{10}, change in respiration with 10 °C increase in temperature) of SR at different combinations of incubation temperature (T), nitrogen addition (N), and water-filled pore space (W)

Treatment[a)]	Constant of Eq. 3		R^2	P value	Q_{10}
	α	β			
T1N0W1	−0.26	3.27×10^{-11}	0.00	> 0.05	1.0
T1N0W2	2.03	0.09	0.97	< 0.001	2.4
T1N0W3	4.11	0.11	0.91	0.001	3.0
T1N1W1	−1.03	1.04×10^{-11}	0.00	> 0.05	1.0
T1N1W2	4.80	0.07	0.90	0.001	2.0
T1N1W3	9.70	0.06	0.89	0.001	2.0
T2N0W1	2.72	6.73×10^{-11}	0.00	> 0.05	1.0
T2N0W2	8.40	0.04	0.25	> 0.05	1.5
T2N0W3	5.13	0.08	0.83	0.005	2.3
T2N1W1	−4.80	0.01	0.00	> 0.05	1.2
T2N1W2	9.74	0.04	0.44	> 0.05	1.6
T2N1W3	4.92	0.10	0.96	< 0.001	2.7

[a)] T1 = 15 °C; T2 = 20 °C; N0 = 0 mg N kg^{-1} soil; N1 = 59.5 mg N kg^{-1} soil; W1 = 10% water-filled pore space (WFPS); W2 = 28% WFPS; W3 = 50% WFPS.

stimulated microorganisms can then decompose labile C substrates, such as glucose (Frey *et al*., 2013; Li *et al*., 2017).

The combined treatment of wetting, N addition, and warming reduced the overall SIR. The results suggest that moisture confounded the effect of N availability and temperature on SIR. Soil moisture controls substrate availability in soil aggregates, further constraining the activity of the microbial population (Chen *et al*., 2007). For example, Zhou *et al*. (2013) found that six years of warming and elevated precipitation reduced SIR. They also found a marginally positive effect of N availability on SIR. Although in our study the addition of labile substrates may have increased the respiration to the maximum rate through a priming effect, the added solution coupled with the already wet condition (50% WFPS) appears to have reduced the rate of gas diffusion, leading to the limited availability of O_2 for aerobic respiration (Lin and Brookes 1999). The effect of this combined treatment was particularly pronounced in the case of carboxylic acids, *i.e*., oxalic acid and citric acid. Carboxylic acids are low molecular labile C sources in forest soils, which are released as root exudates and during decomposition of leaves and other litter (Strobel, 2001) and function as a source of labile C for soil heterotrophs (Van Hees *et al*., 2003a, b; Daté *et al*., 2018). As noted, the addition of these labile organic acid substrates might have enhanced respiration, leading to a reduction in gas diffusion.

Although only six C substrates were utilized in our study, all three major groups of C sources have been included: carbohydrates, amino acids, and carboxylic acids. A duration of 6 h was used for SIR measurement using the Microresp^{TM}, which may not be long enough to detect any long-term changes in catabolic diversity (Daté *et al*., 2018). A longer duration of MicroResp^{TM} assessment may reveal a shift in the catabolic profile of soil microbial communities.

Responses of Q_{10} to the different treatments

We found that warming had a negative effect on Q_{10} (Table II), consistent with the results of previous studies (Knorr *et al*., 2005; Subke and Bahn, 2010). A review summarizing 27 warming experiments found inconsistent responses of soil respiration, but a decline in Q_{10} at temperatures above 25 °C (Carey *et al*., 2016). Although warming briefly enhances soil respiration (Subke and Bahn, 2010), after the initial phase, soil microorganisms become acclimated to the warmer temperature and less temperature-sensitive (Crowther and Bradford, 2013). Decrease in microbial enzyme activities, once their physiological thermal limit is reached, may explain the reduced Q_{10} under warmer conditions (Carey *et al*., 2016). Conant *et al*. (2008) found that the effect of warming on Q_{10} may change over time, because the decomposition of the labile C pool is less sensitive to temperature than that of the recalcitrant C pool (Conant *et al*., 2008). Therefore, the negative warming effects on Q_{10} may indicate that the labile C pool is sufficient for fueling heterotrophic respiration in the warmed soil.

Similar to the effects of warmings, N addition also reduced Q_{10}. Previous studies have reported contrasting effects of N addition on Q_{10} in soils from various ecosystems. For example, in an incubation experiment with a pastoral soil from a Tibetan alpine meadow (Song *et al*., 2010), N addition did not affect the Q_{10}, while in a laboratory incubation with tropical soil from Puerto Rico, N addition enhanced the Q_{10} of both labile and recalcitrant C pools (Cusack *et al*., 2010). In both a wetland soil and a cultivated soil, a high N level (240 kg N ha^{-1}) reduced the Q_{10} (Jin *et al*., 2010). The contrasting findings of the previous studies could be attributed to the heterogeneity of biome types, N application rates, soil conditions, environmental conditions, and experimental methods (Zhong *et al*., 2016). The addition of N can change the quantity and quality of substrate inputs, soil environmental conditions, and the activity of soil microbial communities (Liu *et al*., 2016). After N addition, less N-demanding microbial species are replaced by more N-demanding species (Janssens *et al*., 2010). Nitrogen becomes so abundant that N becomes a less limiting factor for soil microbial organisms (Schimel and Weintraub, 2003). The shifting of the microbial community composition towards more N-demanding species could be one of the reasons for the observed reduction in Q_{10}, because N-demanding species might require less energy to obtain N in N-enriched soils (Janssens *et al*., 2010). Wei *et al*. (2017) observed a decrease in Q_{10} under N-fertilization of a soil from a broad-leaved forest and suggested that recalcitrant organic materials are the major N sources for soil microorganisms. The addition of N inhibited specific microbial groups and changed the substrate preference from recalcitrant organic matter to labile organic matters. This led to a decrease in Q_{10} due to the lower temperature sensitivity of labile organic materials.

The present results are consistent with those of previous studies, since wetting increased the Q_{10}. Generally, soil microbial activity increases with WFPS increase from 30% to 60% (Linn and Doran, 1984; Winkler *et al*., 1996; Qi *et al*., 2002). Linn and Doran (1984) found that soil respiration rate had a linear relationship with soil moisture at 30%–60% WFPS. Below 30% and over 60% WFPS, soil respiration decreased. Generally, soil respiration is most sensitive to temperature at intermediate moisture levels and becomes less sensitive at low and high moisture levels (Illeris *et al*., 2004; Reichstein *et al*., 2005; Gabriel and Kellman, 2011).

Our study found that N addition coupled with war- ming reduced the Q_{10}. Liu *et al*. (2016) found a negative effect of N and temperature on Q_{10} in a cold temperate forest in northeastern China. The authors stated that in the summer season, microbes responsible for heterotrophic respiration compete with roots for available nutrients, including N. This leads to the suppression of microbial respiration and its temperature sensitivity. In an incubation experiment, Wei *et al*. (2017) reported reduction in Q_{10} due to N addition (100 kg N ha^{-1}). Treseder (2008) argued that reduction in substrates due to thermal acclimation under warming could be compensated by the availability of externally added N.

In our study, the combined treatment of wetting, warming, and N addition increased the Q_{10}. Considering that both N addition and warming reduced the Q_{10}, while wetting increased the $Q_{10,}$ our results suggest that the effect of wetting might be greater than that of warming and N addition. The overriding effect of wetting can be explained as discussed above. Since N addition may increase the availability of labile substrates, soil moisture may facilitate substrate accessibility (Suseela *et al*., 2012). Soluble and labile organic compounds are products of the microbial decomposition of soil organic matter. The higher availability of N can induce significant changes in the soil microbial activity and thus, increase C mineralization per unit of microbial biomass (Lagomarsino *et al*., 2006).

Overall, the results of our study suggest that soil moisture may become increasingly important for Q_{10} when climatic warming coincides with changes in precipitation (Hursh *et al*., 2017). In addition to forest soils, a strong influence of soil moisture on Q_{10} has also been reported in grassland soils (Craine and Gelderman, 2011). Given the synergistic effects of soil moisture on the response of Q_{10} to warming and N enrichment, more attention should be paid to widely varying soil moisture conditions when assessing the effects of warming and N enrichment on the Q_{10} of forest soils under monsoon climates. Moreover, we used a well-drained sandy loam soil from a steep slope, which usually has a WFPS

lower than 50%. The results from this experiment may not be applicable to soils that have greater pore-spaces and therefore hold more water. However, in the short-term, even a well-drained soil might possess soil moisture exceeding 50% WFPS, especially during recurrent extreme precipitation events. Our study focused on short-term changes in the temperature sensitivity of soil heterotrophic respiration under varying soil moisture conditions. The number of days with intense rainfalls has increased by 17% per century and 38% over the 227 years of instrumental recorded history in Seoul, South Korea (Wang *et al*., 2006). The recorded data show that there is a strong positive relationship between soil moisture level and precipitation during the summer months (Cho *et al*., 2016).

CONCLUSIONS

Although this short-term laboratory study cannot fully represent complex field conditions, it provides some insights into the differential short-term responses of SIR and Q_{10} to the individual and combined effects of warming, wetting, and N addition. Notably, the results reveal the concurrent moderating effect of soil moisture and N availability on the warming-induced alteration of SIR and Q_{10}. The overall results suggest that considering warming effects alone might result in substantial errors in the estimation of soil heterotrophic respiration under climate change scenarios, because the actual rates of SIR and Q_{10} can be substantially affected by concurrent environmental changes, including soil N enrichment and changing soil moisture regimes. While we acknowledge that results obtained under controlled laboratory conditions cannot be applied directly to more complex field conditions, we predict that warming coupled with N addition may sustain soil heterotrophic respiration at higher rates compared to the individual effects of warming and N addition, particularly under favorable soil moisture conditions (e.g., 50% WFPS in this experiment), which often occur during the summer monsoon period in forest ecosystems across East Asia. Further studies including multiple climatic and environmental factors under controlled conditions are required to investigate the effects of temperature on soil respiration for better prediction of site-specific soil microbial heterotrophic respiration. In addition, longer experiments should be conducted with various soils of different textures to understand variations in the composition and activity of microbial communities in response to changing environmental conditions. As indicated by the altered SIR rates at the end of the incubation, which did not reflect Q_{10} changes in the middle of incubation, simultaneous measurements of soil microbial properties, such as Q_{10}, SIR, and soil microbial biomass, are essential to understand and corroborate concomitant changes in the microbial physiological profile and temperature sensitivity of soil respiration.

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REFERENCES

Ackerman D, Millet D B, Chen X. 2019. Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochem Cycles*. **33**: 100–107.

Ågren G I, Bosatta E, Magill A H. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia*. **128**: 94–98.

Allison S D, Wallenstein M D, Bradford M A. 2010. Soil-carbon response to warming dependent on microbial physiology. *Nat Geosci*. **3**: 336–340.

Bae K K, Kwon Y H, Park J H, Lee Y J, Lee H J. 2008. Measurement of soil properties and soil organic carbon sequestration of *Quercus mongolica* forest in Mt. Gwanak, Mt. Nam and Mt. Bukhan in Seoul. *In* Korean Forest Society (ed.) Proceedings of the 2008 Annual Meeting of the Korean Forest Society, Seoul. pp. 127–128.

Bissett A, Brown M V, Siciliano S D, Thrall P H. 2013. Microbial community responses to anthropogenically induced environmental change: Towards a systems approach. *Ecol Lett*. **16**: 128–139.

Bond-Lamberty B, Bailey V L, Chen M, Gough C M, Vargas R. 2018. Globally rising soil heterotrophic respiration over recent decades. *Nature*. **560**: 80–83.

Bond-Lamberty B, Thomson A. 2010. Temperature-associated increases in the global soil respiration record. *Nature*. **464**: 579–582.

Bowden R D, Davidson E, Savage K, Arabia C, Steudler P. 2004. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard forest. *Forest Ecol Manage*. **196**: 43–56.

Bradford M A. 2013. Thermal adaptation of decomposer communities in warming soils. *Front Microbiol*. **4**: 333.

Bradford M A, Davies C A, Frey S D, Maddox T R, Melillo J M, Mohan J E, Reynolds J F, Treseder K K, Wallenstein M D. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol Lett*. **11**: 1316–1327.

Campbell C D, Chapman S J, Cameron C M, Davidson M S, Potts J M. 2003. A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Appl Environ Microbiol*. **69**: 3593–3599.

Carey J C, Tang J W, Templer P H, Kroeger K D, Crowther T W, Burton A J, Dukes J S, Emmett B, Frey S D, Heskel M A, Jiang L F, Machmuller M B, Mohan J, Panetta A M, Reich P B, Reinsch S, Wang X, Allison S D, Bamminger C, Bridgham S, Collins S L, de Dato G, Eddy W C, Enquist B J, Estiarte M, Harte J, Henderson A, Johnson B R, Larsen K S, Luo Y Q, Marhan S, Melillo J M, Peñuelas J, Pfeifer-Meister L, Poll C, Rastetter E, Reinmann A B, Reynolds L L, Schmidt I K, Shaver G R, Strong A L, Suseela V, Tietema A. 2016. Temperature response of soil respiration largely unaltered with experimental warming. *Proc Natl Acad Sci USA*. **113**: 13797–13802.

Chen M, Zhu Y G, Su, Y H, Chen, B D. 2007. Effects of soil moisture and plant interactions on the soil microbial community structure. *Eur J Soil Sci*. **43**: 31–38.

Cho E, Zhang A Q, Choi M. 2016. The seasonal difference in soil moisture patterns considering the meteorological variables throughout the Korean Peninsula. *Terr Atmos Ocean Sci*. **27**: 907-920

Chung H, Zak D R, Reich P B, Ellsworth D S. 2007. Plant species richness, elevated CO_2, and atmospheric nitrogen deposition alter soil microbial community composition and function. *Global Change Biol*. **13**: 980–989.

Classen A T, Sundqvist M K, Henning J A, Newman G S, Moore J A M, Cregger M A, Moorhead L C, Patterson C M. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*. **6**: 1–30.

Conant R T, Steinweg J M, Haddix M L, Paul E A, Plante A F, Six J. 2008. Experimental warming shows that decomposition temperature sensitivity increases with soil organic matter recalcitrance. *Ecology*. **89**: 2384–2391.

Craine J M, Fierer N, McLauchlan K K. 2010. Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nat Geosci*. **3**: 854–857.

Craine J M, Gelderman T M. 2011. Soil moisture controls on temperature sensitivity of soil organic carbon decomposition for a mesic grassland. *Soil Biol Biochem*. **43**: 455–457.

Creamer R E, Schulte R P O, Stone D, Gal A, Krogh P H, Lo Papa G, Murray P J, Pérès G, Foerster B, Rutgers M, Sousa J P, Winding A. 2014. Measuring basal soil respiration across Europe: Do incubation temperature and incubation period matter? *Ecol Ind*. **36**: 409–418.

Crecchio C, Curci M, Mininni R, Ricciuti P, Ruggiero P. 2001. Short-term effects of municipal solid waste compost amendments on soil carbon and nitrogen content, some enzyme activities and genetic diversity. *Biol Fertil Soils*. **34**: 311–318.

Crowther T W, Bradford M A. 2013. Thermal acclimation in widespread heterotrophic soil microbes. *Ecol Lett*. **16**: 469–477.

Cusack D F, Torn M S, McDowell W H, Silver W L. 2010. The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biol*. **16**: 2555–2572.

Daté V, Nwaishi F C, Price J S, Andersen R. 2018. Short-term exposure to oil sand process-affected water does not reduce microbial potential activity in three contrasting peatland types. *Wetlands*. **38**: 769–778.

Davidson E A, Janssens I A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*. **440**: 165–173.

Davidson E C A, Belk E, Boone R D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol*. **4**: 217–227.

DeAngelis K M, Pold G, Topçuoğlu B D, van Diepen L T A, Varney R M, Blanchard J L, Melillo J, Frey S D. 2015. Long-term forest soil warming alters microbial communities in temperate forest soils. *Front Microbiol*. **6**: 104.

Deslippe J R, Hartmann M, Simard S W, Mohn W W. 2012. Long-term warming alters the composition of arctic soil microbial communities. *FEMS Microbiol Ecol*. **82**: 303–315.

Dutta H, Dutta A. 2016. The microbial aspect of climate change. *Energy, Ecol Environ*. **1**: 209–232.

Franzluebbers A J, Haney R L, Hons F M, Zuberer D A. 1999. Assessing biological soil quality with chloroform fumigation-incubation: Why subtract a control? *Can J Soil Sci*. **79**: 521–528.

Frey S D, Drijber R, Smith H, Melillo J. 2008. Microbial biomass, functional capacity, and community structure after 12 years of soil warming. *Soil Biol Biochem*. **40**: 2904–2907.

Frey S D, Lee J, Melillo J M, Six J. 2013. The temperature response of soil microbial efficiency and its feedback to climate. *Nat Climate Change*. **3**: 395.

Gabriel C E, Kellman L. 2011. Examining moisture and temperature sensitivity of soil organic matter decomposition in a temperate coniferous forest soil. *Biogeosciences*. **8**: 1369–1409.

Glanville H, Rousk J, Golyshin P, Jones D L. 2012. Mineralization of low molecular weight carbon substrates in soil solution under laboratory and field conditions. *Soil Biol Biochem*. **48**: 88–95.

Gosling S N, Dunn R, Carrol F, Christidis N, Fullwood J, de Gusmao D, Golding N, Good L, Hall T, Kendon L, Kennedy J, Lewis K, McCarthy R, McSweeney C, Morice C, Parker D, Perry M, Stott P, Willett K, Allen M, Arnell N, Bernie D, Betts R, Bowerman N, Brak B, Caesar J, Challinor A, Dankers R, Hewer F, Huntingford C, Jenkins A, Klingaman N, Lewis K, Lloyd-Hughes B, Lowe J, McCarthy R, Miller J, Nicholls R, Noguer M, Otto F, van der Linden P, Warren R. 2011. Climate: Observations Projections and Impacts. UK Met Office, Nottingham.

Hursh A, Ballantyne A, Cooper L, Maneta M, Kimball J, Watts J. 2017. The sensitivity of soil respiration to soil temperature, moisture, and carbon supply at the global scale. *Global Change Biol*. **23**: 2090–2103.

Illeris L, Christensen T R, Mastepanov M. 2004. Moisture effects on temperature sensitivity of CO_2 exchange in a subarctic heath ecosystem. *Biogeochemistry*. **70**: 315–330.

Janssens I A, Dieleman W, Luyssaert S, Subke J A, Reichstein M, Ceulemans R, Ciais P, Dolman A J, Grace J, Matteucci G, Papale D, Piao S L, Schulze E D, Tang J, Law B E. 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nat Geosci*. **3**: 315–322.

Jiang H, Deng Q, Zhou G, Hui D, Zhang D, Liu S, Chu G, Li J. 2013. Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. *Biogeosciences*. **10**: 3963–3982.

Jiang X, Cao L, Zhang R. 2014. Changes of labile and recalcitrant carbon pools under nitrogen addition in a city lawn soil. *J Soils Sediments*. **14**: 515–524.

Jin X B, Bai J H, Zhou Y K. 2010. Temperature sensitivity of soil respiration is affected by nitrogen fertilization and land use. *Acta Agric Scand Sect B Soil Plant Sci*. **60**: 480–484.

Kanakidou M, Myriokefalitakis S, Daskalakis N, Fanourgakis G, Nenes A, Baker A R, Tsigaridis K, Mihalopoulos N. 2016. Past, present, and future atmospheric nitrogen deposition. *J Atmos Sci*. **73**: 2039–2047.

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

Kirschbaum M U F. 2006. The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biol Biochem*. **38**: 2510–2518.

Knorr W, Prentice I C, House J I, Holland E A. 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature*. **433**: 298-301.

Koch O, Tscherko D, Kandeler E. 2007. Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. *Global Biogeochem Cycles*. **21**: GB4017.

Korea Meteorological Administration (KMA). 2014. Korean Climate Change Assessment Report 2014. Korea Meteorological Administration, Seoul.

Kuzyakov Y, Friedel J K, Stahr K. 2000. Review of mechanisms and quantification of priming effects. *Soil Biol Biochem*. **32**: 1485–1498.

Lagomarsino A, Moscatelli M C, De Angelis P, Grego S. 2006. Labile substrates quality as the main driving force of microbial mineralization activity in a poplar plantation soil under elevated CO_2 and nitrogen fertilization. *Sci Total Environ*. **372**: 256–265.

Lamarque J F, Kiehl J T, Brasseur G P, Butler T, Cameron-Smith P, Collins W D, Collins W J, Granier C, Hauglustaine D, Hess P G, Holland E A, Horowitz L, Lawrence M G, McKenna D, Merilees P, Prather M J, Rasch P J, Rotman D, Shindell D, Thornton P. 2005. Assessing future nitrogen deposition and carbon cycle feedback using a multimodel approach: Analysis of nitrogen deposition. *J Geophys Res: Atmos*. **110**: D19303

Lee M, Shevliakova E, Stock C A, Malyshev S, Milly P C D. 2019. Prominence of the tropics in the recent rise of global nitrogen pollution. *Nat Commun*. **10**: 1437.

Lee N Y. 2011. Estimation of carbon storage in three cool-temperate broad-leaved deciduous forests at Bukhansan National Park, Korea. *J Natl Park Res*. **2**: 53–57.

Li Q R, Tian Y Q, Zhang X Y, Xu X L, Wang H M, Kuzyakov Y. 2017. Labile carbon and nitrogen additions affect soil organic matter decomposition more strongly than temperature. *Appl Soil Ecol*. **114**: 152–160.

Lin Q, Brookes P C. 1999. An evaluation of the substrate-induced respiration method. *Soil Biol Biochem*. **31**: 1969–1983.

Linn D M, Doran J W. 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Sci Soc Am J*. **48**: 1267–1272.

Liu B Q, Mou C C, Yan G Y, Xu L J, Jiang S L, Xing Y J, Han S J, Yu J H, Wang Q G. 2016. Annual soil CO_2 efflux in a cold temperate forest in northeastern China: Effects of winter snowpack and artificial nitrogen deposition. *Sci Rep*. **6**: 18957.

Lloyd J, Taylor J A. 1994. On the temperature dependence of soil respiration. *Funct Ecol*. **8**: 315–323.

Manzoni S, Schimel J P, Porporato A. 2012. Responses of soil microbial communities to water stress: Results from a meta-analysis. *Ecology*. **93**: 930–938.

Melillo J M, Steudler P A, Aber J D, Newkirk K, Lux H, Bowles F P, Catricala C, Magill A, Ahrens T, Morrisseau S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science*. **298**: 2173–2176.

Meyer N, Meyer H, Welp G, Amelung W. 2018. Soil respiration and its temperature sensitivity (Q_{10}): Rapid acquisition using mid-infrared spectroscopy. *Geoderma*. **323**: 31–40.

Moyano F E, Manzoni S, Chenu C. 2013. Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models. *Soil Biol Biochem*. **59**: 72–85.

Nhantumbo A D J Da C, Bennie A T P. 2001. A procedure for determining the minimum bulk density of soils. *South African J Plant Soil*. **18**: 44–46.

Oh S G, Suh M S, Lee Y S, Ahn J B, Cha D H, Lee D K, Hong S Y, Min S K, Park S C, Kang H S. 2016. Projections of high resolution climate changes for South Korea using multiple-regional climate models based on four RCP scenarios. Part 2: Precipitation. *Asia-Pacific J Atmos Sci*. **52**: 171–189.

Park J H. 2008. Changing C-N interactions in the forest floor under chronic N deposition: Implications for forest C sequestration. *J Ecol Environ*. **31**: 167–176.

Park S U, Lee Y H. 2002. Spatial distribution of wet deposition of nitrogen in South Korea. *Atmos Environ*. **36**: 619–628.

Priha O, Grayston S J, Pennanen T, Smolander A. 1999. Microbial activities related to C and N cycling and microbial community structure in the rhizospheres of *Pinus sylvestris*, *Picea abies* and *Betula pendula* seedlings in an organic and mineral soil. *FEMS Microbiol Ecol*. **30**: 187–199.

Qi Y, Xu M, Wu J G. 2002. Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: Nonlinearity begets surprises. *Ecol Modell*. **153**: 131–142.

Reichstein M, Subke J A, Angeli A C, Tenhunen J D. 2005. Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biol*. **11**: 1754–1767.

Rui J P, Li J B, Wang S P, An J X, Liu W T, Lin Q Y, Yang Y F, He Z L, Li X Z. 2015. Responses of bacterial communities to simulated climate changes in alpine meadow soil of the Qinghai-Tibet plateau. *Appl Environ Microbiol*. **81**: 6070–6077.

Schimel J P, Weintraub M N. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: A theoretical model. *Soil Biol Biochem*. **35**: 549–563.

Schindlbacher A, Rodler A, Kuffner M, Kitzler B, Sessitsch A, Zechmeister-Boltenstern S. 2011. Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biol Biochem*. **43**: 1417–1425.

Smirnova E V, Giniyatullin K G, Okunev R V, Valeeva A A, Guseva I A. 2016. The effect of pre-incubation duration of soil-biochar model mixtures on the results of determination the intensity of substrate-induced respiration (methodological aspects of study). *Res J Pharmaceut, Biol Chem Sci*. **7**: 1360–1366.

Song M H, Jiang J, Cao G M, Xu X L. 2010. Effects of temperature, glucose and inorganic nitrogen inputs on carbon mineralization in a Tibetan alpine meadow soil. *Eur J Soil Biol*. **46**: 375–380.

Strobel B W. 2001. Influence of vegetation on low-molecular-weight carboxylic acids in soil solution—a review. *Geoderma*. **99**: 169–198.

Subke J A, Bahn M. 2010. On the 'temperature sensitivity' of soil respiration: Can we use the immeasurable to predict the unknown? *Soil Biol Biochem*. **42**: 1653–1656.

Suseela V, Conant R T, Wallenstein M D, Dukes J S. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biol*. **18**: 336–348.

Treseder K K. 2008. Nitrogen additions and microbial biomass: A meta-analysis of ecosystem studies. *Ecol Lett*. **11**: 1111–1120.

Van Hees P A W, Jones D L, Godbold D L. 2003a. Biodegradation of low molecular weight organic acids in a limed forest soil. *Water, Air Soil Pollut: Focus*. **3**: 121–144.

Van Hees P A W, Vinogradoff S I, Edwards A C, Godbold D L, Jones D L. 2003b. Low molecular weight organic acid adsorption in forest soils: Effects on soil solution concentrations and biodegradation rates. *Soil Biol Biochem*. **35**: 1015–1026.

Vanhala P, Karhu K, Tuomi M, Björklöf K, Fritze H, Hyvärinen H, Liski J. 2011. Transplantation of organic surface horizons of boreal soils into warmer regions alters microbiology but not the temperature sensitivity of decomposition. *Global Change Biol*. **17**: 538–550.

Wang B, Ding Q H, Jhun J G. 2006. Trends in Seoul (1778–2004) summer precipitation. *Geophys Res Lett*. **33**: L15803.

Wang R, Sun Q Q, Wang Y, Liu Q F, Du L, Zhao M, Gao X, Hu Y X, Guo S L. 2017. Temperature sensitivity of soil respiration: Synthetic effects of nitrogen and phosphorus fertilization on Chinese loess plateau. *Sci Total Environ*. **574**: 1665–1673.

Wei H, Chen X M, He J H, Zhang J E, Shen W J. 2017. Exogenous nitrogen addition reduced the temperature sensitivity of microbial respiration without altering the microbial community composition. *Front Microbiol*. **8**: 2382.

Winkler J P, Cherry R S, Schlesinger W H. 1996. The Q_{10} relationship of microbial respiration in a temperate forest soil. *Soil Biol Biochem*. **28**: 1067–1072.

Wu Z T, Dijkstra P, Koch G W, Peñuelas J, Hungate B A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biol*. **17**: 927–942.

Zhong Z M, Shen Z X, Fu G. 2016. Response of soil respiration to experimental warming in a highlanḅarley of the Tibet. *SpringerPlus*. **5**: 137.

Zhou X, Chen C, Wang Y, Smaill S, Clinton P. 2013. Warming rather than increased precipitation increases soil recalcitrant organic carbon in a semiarid grassland after 6 years of treatments. *PLOS ONE*. **8**: e53761.