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Soil Microbial Biomass, Respiration Rate, and Temperature Dependence on a Successional Glacier Foreland in Ny-Ålesund, Svalbard

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Abstract

We examined soil microbial activities, i.e., biomass, respiration rate, and temperature dependence of the respiration on a glacier foreland in Ny-Ålesund, Svalbard, Norway. We collected soil samples from 4 study sites that were set up along a primary succession (Site 1, the youngest, to Site 4, the oldest). Microbial biomass measured with the SIR method increased with successional age (55 to 724μg $C_{biomass}$ g^{-1} soil d.w. from Site 1 to Site 4). The microbial respiration rate of the soil was measured in a laboratory with an open-flow infrared gas-analyzer system, changing the temperature from 2° to 20°C at 3–4° intervals. The microbial respiration rate increased exponentially with the temperature at all sites. The temperature dependence (Q_{10}) of the microbial respiration rate ranged from 2.2 to 4.1. The microbial respiration rates at a given temperature increased with succession as a step change (0.48, 0.43, 1.26, and 1.29μg C g^{-1}soil h^{-1} at 8°C from Site 1 to Site 4, respectively). However, the substrate-specific respiration rate (respiration rate per gram soil carbon) decreased with successional age (0.034 to 0.006μg C $mg^{-1}C_{soil}$ h^{-1} from Site 1 to Site 4). A comparison of these respiratory properties with other ecosystems suggested that soil microorganisms in arctic soils have a high potential for decomposition when compared to those of other temperate ecosystems.

Introduction

Predicted future global warming due to the anthropogenic release of greenhouse gases would have a great effect on the decomposition processes of soil organic matter, especially in the arctic region (Oechel and Billings, 1992; Oechel and Vourlitis, 1994). Elevated temperatures may enhance the activities of soil microorganisms and decomposition rates of soil organic matter stored in permafrost because of the ensuing thawing and lowering of the water table, which results in greater soil aeration (Billings et al., 1983; Nadelhoffer et al., 1992; Oechel and Billings, 1992; Oechel and Vourlitis, 1994). The increase in the decomposition rates could result in changes to the nutrient and carbon cycles, which would affect the structure and function of arctic ecosystems. Thus, in order to predict the impact of climate change on the arctic ecosystems, it is important to clarify the effects of warming on decomposition based on a mechanistic understanding of its processes.

Decomposition rates can be understood as a function of three parameters: microbial biomass, microbial respiration rate, and their dependency on environmental factors. For a mechanistic understanding, the responses of these parameters to environmental factors, such as temperature, soil water content, substrate quality, and quantity, should be elucidated. However, there are only a few reports of soil microbial biomass in low-arctic ecosystems (Bunnell et al., 1980; Cheng and Virginia, 1993) and even fewer in the high-arctic (Jones et al., 2000). In addition, limited information exists on the temperature dependence of respiration in arctic soils (Flanagan and Bunnell, 1980; Heal et al., 1981; Nadelhoffer et al., 1991). Especially, little is known about soil microbial biomass and temperature dependence of microbial respiration in primary successional series on high-arctic glacier foreland. Under the current increase of deglaciation in polar and high-altitude areas, an increasing understanding of soil respiration and soil microbial biomass in the high-arctic glacier foreland is becoming more important for evaluating how arctic ecosystems might respond to future global warming.

In this study, we report the soil microbial biomass and temperature dependence of the respiration rate at different stages in the primary succession at a glacier foreland in Ny-Ålesund, Svalbard. We discuss the attributes of soil respiration in high-arctic soils by comparing them to other ecosystems. This study is part of a larger study examining the process and function of carbon cycling in the arctic primary succession (Nakatsubo et al., 1998; Bekku et al., 1999; Uchida et al., 2002; Muraoka et al., 2002; Bekku et al., 2003; Bekku et al., 2004).

Materials and Methods

STUDY SITE

The study area is located at the front of East Brøgger Glacier in Ny-Ålesund, Svalbard, in Norway (79°N, 12°E). The annual mean air temperature and annual precipitation in this area are –5.7°C and 487 mm, respectively (Department of Meteorology, Norwegian Polar Institute). Four study sites were set up along a primary successional series on different-aged moraines in the deglaciated area of the East Brøgger Glacier. Site 1, immediately in front of the glacier toe, became ice free only recently (within the last 30 yr). The coverage of vascular plants is very small (<1%), but black crusts of cyanobacteria and several species of bryophytes partially cover the ground. Site 2 is located on a moraine with a few scattered patches of vegetation (mainly *Saxifraga oppositifolia* L., *Poa alpina* L., and *Draba* spp.). The plant coverage is still low (<10%). Site 3 is located on a small moraine that became ice free more than 2000 yr ago. This site is characterized by patterned ground composed of small polygons. The central part of the polygons is bare ground (17%). The marginal part of the polygons is covered with cyanobacteria and lichens (30%) and a mixed community

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TABLE 1

Characteristics of soils in the study sites

	Thickness of O-horizon (cm)	Soil C content[a] (%)	Soil N content[a] (%)	C/N[a]	Soil pH (H_2O)	Mean soil surface temperature [c] (°C)	Soil water content[a,d] (%)
Site 1	0	1.42 (0.02)[b]	0.03 (0.01)[b]	47 (13.2)[b]	6.7 (0.06)[b]	8.3 (3.4)[b]	6–19
Site 2	0	2.1 (0.03)	0.08 (0.01)	26 (0.27)	6.7 (0.00)	7.7 (2.7)	18–21
Site 3	0–3	10.1 (1.67)	0.61 (0.08)	17 (1.11)	5.8 (0.21)	7.8 (1.9)	68–92
Site 4	1–3	21.9 (0.53)	1.29 (0.04)	17 (0.38)	5.7 (0.21)	6.6 (1.6)	100–170

[a] Average of 0–3 cm layer.

[b] The values indicate means of 6 samples with SE in parentheses.

[c] Means soil surface temperature during period from late July to mid-August 1996.

[d] (Fresh weight − Dry weight)/Dry weight; determined several times in late July to early August in 1995 and 1996.

Data was modified from Bekku et al. (1999) and Nakatsubo et al. (1998).

of bryophytes and vascular plants (53%), such as *Salix polaris* Wahlenb., *Luzula confusa* Lindeb., and *Poa alpina*. Site 4 is on the oldest moraine, which is similar to Site 3 except that a black crust of cyanobacteria and lichens entirely covers the central part of the polygons. The coverage of bryophytes and vascular plants is 45% and that of cyanobacteria and lichens 55%. A more detailed description is given by Nakatsubo et al. (1998) and Minami et al. (1996). The soils are regosolic cryosols. The soil characteristics and environments are summarized in Table 1. The thickness of the O-horizon, soil carbon, and nitrogen contents in the 0–3-cm layer increased with successional age (Table 1). Conversely, the carbon-to-nitrogen ratio (C/N) in soil decreased from 47 at Site 1 to 17 at Site 4. At Site 1, the mean of the soil surface temperatures from late July to mid-August was slightly higher and had a larger variance than that of the other sites. In contrast, Site 4 had the lowest soil surface temperatures and variances. The gravimetric soil water content, measured several times in late July to early August in 1995 and 1996, ranged from 6–19% at Site 1, 18–21% at Site 2, 68–92% at Site 3, and 100–170% at Site 4.

SOIL SAMPLING

Soil samples for biomass measurements were collected from each site with 6 subsamples on 2 August 1995. Soil samples for respiration measurement were collected at adjacent sampling points with 6 subsamples on 30 July 1996. At Site 1 and Site 2, soil from the 0–3-cm layer was sampled with a soil corer (9 cm diameter, 3 cm depth). At Sites 3 and 4, soil from the surface down to 3 cm below the vegetation was taken by cutting 10 × 10–cm blocks of the organic soil material with a knife. Within 1 h after the sampling, soil samples were transported to the laboratory in Ny-Ålesund. Immediately upon arrival, plant roots and stones in the soil subsamples were removed by handpicking, and then each subsample was prepared for measurement of biomass and respiration as described below.

BIOMASS MEASUREMENT

The microbial biomass was measured by the substrate-induced respiration procedure (Anderson and Domsch, 1978; Cheng and Virginia, 1993). Approximately 30 g of soil from each subsample from each site was placed in a petri dish ($\phi = 7$ cm); then 1% glucose solution (about 4.4 mg C g^{-1} soil d.w.) was added to the soil sample to bring the soil water content to near its holding capacity. Five hours after glucose addition, the substrate-induced respiration was measured at 22°C using a soil respiration measuring method with a continuous open-airflow system (Bekku et al., 1997) and an infrared gas analyzer (LI-6250, LI-COR, Lincoln, NE, U.S.A.). The microbial biomass C was calculated using the equation y (μg $C_{biomass}$ g^{-1} soil d.w.) = 40.4 x + 0.37, where x is the substrate-induced respiration (μl CO_2 h^{-1} g^{-1} soil d.w.) (Anderson and Domsch, 1978; Cheng and Virginia, 1993). Following the measurement, soil samples were oven-dried at 105°C for 3 d and weighed. A more detailed description is given by Bekku et al. (1999).

RESPIRATION MEASUREMENT

After the 6 subsamples from the respective sites were mixed and homogenized, approximately 30 g of soil was placed in a petri dish ($\varphi = 7$ cm). Three replicates for each site were incubated at 8 ± 2°C for 10 d. This temperature condition was similar to the mean soil temperature in the field during the growing season. The gravimetric water content of the soil was kept with the addition of distilled water at approximately 18%, 25%, 90%, and 170% for Sites 1, 2, 3, and 4, respectively, which were equivalent to 65%, 53%, 73%, and 76% of the water-holding capacity of the soil from each respective site.

The soil microbial respiration rate was measured using an open-airflow gas exchange system with an infrared gas analyzer (LI-6252, LI-COR, Lincoln, NE, U.S.A.) (Bekku et al., 1997) 10 d after the start of the incubation. The petri dish with the soil sample was placed in a cylindrical chamber ($\varphi = 9$ cm, h = 3.5 cm) in a water bath to control the soil temperature, and ambient air containing 347–350 ppmv CO_2 was pumped through the chamber at the rate of 0.5l min^{-1}. The soil temperature in the chamber was monitored with a copper-constantan thermocouple. The temperature dependence of the respiration rate was determined by changing the temperature from 2°C to 20°C at 3–4° intervals. It took about 1–2 h to attain a constant respiration rate at each temperature. The absence of hysteresis of respiration rates in response to the temperature change was confirmed by additional measurements conducted under a reverse temperature regime in some samples. Following the measurement, soil samples were oven-dried at 105°C for 3 d and weighed. The soil total carbon and nitrogen contents were measured using a CHN/O elemental analyzer (Perkin Elmer 2400II, CN, U.S.A.).

The substrate-specific respiration rate (microbial respiration rate per gram soil carbon) were calculated by dividing the microbial respiration rate at 8°C by the carbon content in the soil sample. The temperature coefficient (Q_{10}) of the respiration rate was calculated from exponential regression equations between the measurement temperature and the respiration rate in Fig. 1:

$$R = \alpha e^{\beta T} \quad (1)$$

$$\text{Ln } R = \beta T + \ln \alpha \quad (2)$$

$$Q_{10} = e^{10\beta} \quad (3)$$

where R is the microbial respiration rate (μg CO_2 g^{-1} soil h^{-1}), T is the soil temperature (°C), and α and β are regression coefficients.

All statistical analysis was conducted using StatView (SAS Institute Inc., 1998). The microbial biomass, microbial respiration rate

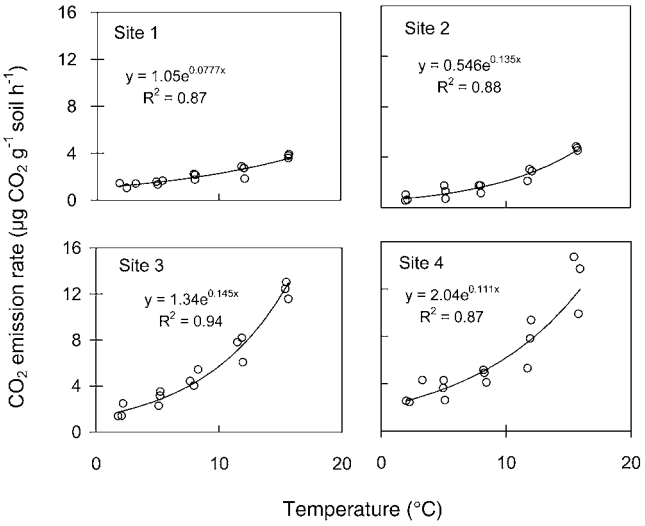

FIGURE 1. Relationships between the soil temperature and microbial respiration rate. The data are plotted together for three soil replicates in the respective study site.

at 8°C, and substrate-specific respiration rate were analyzed by one-way ANOVA plus a post hoc test (Fisher's PLSD) among the 4 sites. For the analysis of Q_{10} values, Eq. 1 was log-transformed as Eq. 2; then we conducted an analysis of covariance (ANCOVA) on the values of log R among the 4 study sites.

Results and Discussion

SOIL MICROBIAL BIOMASS AND RESPIRATION RATE

The mean microbial biomass in a 0–3-cm soil layer increased with successional age (Table 2). At Site 1, where the soil is low in carbon and nitrogen (Table 1), the microbial biomass was extremely small (55μg $C_{biomass}$ g^{-1} soil d.w.). With the progress of vegetational succession, the microbial biomass increased gradually (Table 2) with corresponding increases in soil carbon and nitrogen (Table 1). At Site 4, the soil microbial biomass was more than 10-fold higher than that in Site 1 (724μg $C_{biomass}$ g^{-1} soil d.w.).

The microbial respiration rate in soil samples at all sites increased exponentially with the temperature (Fig. 1). We had expected that the microbial respiration rates at a given temperature would increase continuously with successional age, as seen in microbial biomass; however, they increased as a step change (Table 2). For example, the microbial respiration rate at 8°C, a temperature close to the mean soil temperature in the growing season, was 0.48 and 0.43 (μg C g^{-1} soil d.w. h^{-1}) at Sites 1 and 2 and 1.26 and 1.29 (μg C g^{-1} soil d.w. h^{-1}) at Sites 3 and 4, respectively.

On the other hand, the respiration rates per gram of soil carbon, i.e., the substrate-specific respiration, apparently decreased with successional age (Table 2): those data were significantly different between Sites 1 and 2 and between Sites 2 and 4 (Fisher's PLSD, $P < 0.05$). Similar phenomena have been indicated in previous studies: Šantrůčková and Straškraba (1991) demonstrated a steep negative hyperbolic relationship between the biomass-specific respiration rate and the microbial biomass in a secondary succession. Insam and Haselwandter (1989) indicated a decrease in the metabolic quotient (biomass-specific respiration rate) with the progress of a primary succession on a glacier forefront in Austria and ascribed it to a shift in the soil microflora from "r" strategists to slower-growing "K" strategists. Ohtonen et al. (1999) reported that microbial respiration increased, while specific activities (biomass-specific respiration and carbon use efficiency of soil microbial community) decreased over the successional gradient on a glacier forefront in the state of Washington, U.S.A. They also indicated that the decreases in specific activities resulted from an alternation in the microbial community from one that is bacterial-dominated to one that is fungal-dominated with primary succession (Ohtonen et al., 1999).

TABLE 2

Microbial biomass and respiratory properties in soil at depth of 0–3 cm at respective successional stages. Values followed by the same letter within each column are not significantly different ($P > 0.05$)

	Microbial biomass (μg $C_{biomass}$ g^{-1} soil d.w.)*	Microbial respiration rate at 8°C (μg C g^{-1} soil d.w. h^{-1})**	Substrate-specific respiration rate (μg C mg soil C^{-1} h^{-1})**	Q_{10} value***
Site 1	55 (29)[a]	0.48 (0.05)[a]	0.034 (0.008)[a]	2.2 (1.8–2.7)[a]
Site 2	201 (38)[b]	0.43 (0.04)[a]	0.020 (0.005)[b]	3.9 (2.7–5.6)[b]
Site 3	221 (122)[b]	1.26 (0.14)[b]	0.014 (0.001)[bc]	4.3 (3.3–5.1)[b]
Site 4	724 (474)[c]	1.29 (0.08)[b]	0.006 (0.0007)[c]	3.0 (2.3–3.9)[b]

* Values indicate means of six replicates with SD in parentheses.

** Values indicate means of three replicates with SD in parentheses.

*** Values in parentheses indicate a 95% confident interval.

While we do not have quantitative data for microbial flora, the decrease in the substrate-specific respiration with successional age in the present study might also reflect a change in the microbial flora with primary succession. In particular, a drastic change might occur in microbial properties between Sites 1 and 2. Site 1 differs significantly from the older sites (Sites 2 and 3) in microbial biomass, substrate-specific respiration, and Q_{10}, as described below, while those in the older sites are quite similar (Table 2) despite the enormous differences in vegetation and soil development between Sites 2 and 3 (Table 1). These results would indicate the rapid development of microbiological properties as compared with vegetational succession along this chronosequence. It is also likely that the dominant carbon source for microbes would change with a succession from an algal-derived carbon to a more recalcitrant litter of vascular plants and mosses. Ley et al. (2001) showed that the microbial biomass of salicylate mineralizers that can mineralize lignin and polyphenols was larger in vegetated soils than in barren soils in a high-altitude talus slope in the Colorado Rocky Mountains. Thus, in the present study, the microbial flora might shift from a bacterial-dominated community to a fungal-dominated one, corresponding to the change in substrate quality through succession, and this could be a cause of the decrease in the substrate-specific respiration with succession. In addition, the accumulation of the humic materials that are not available for microbial respiration may contribute to the smaller values in the substrate-specific respiration in older sites (Sites 3 and 4). This is supported by the fact that the soil C/N ratio declines to an equilibrium value of 17 in the older sites (Table 1).

The temperature dependence of microbial respiration, expressed as Q_{10}, was 2.2, 3.9, 4.1, and 3.0 at Sites 1, 2, 3, and 4, respectively (Table 2). The Q_{10} value was not significantly different among Sites 2, 3, and 4, though the one in Site 1 was significantly lower than those in other sites (ANCOVA, $P < 0.05$). The Q_{10} values, except for that in Site 1, were higher than those in temperate ecosystems reported in previous studies (median value 2.4; Raich and Schlesinger, 1992) but were within the range of those reported in a previous study on arctic soils (3.5–4; Heal et al., 1981). There seems to be a general tendency toward higher-Q_{10} values in colder ecosystems or at lower temperatures (Ross and Cairns, 1978; Lloyd and Taylor, 1994; Kirschbaum, 1995). Though the mechanisms for this phenomenon have not been clarified, it has been suggested that temperature increases in northern ecosystems would have greater impacts on decomposition rates because of high Q_{10} in soil respiration (Billings et al., 1983;

TABLE 3

Soil microbial biomass and respiration rates from several ecosystems

Ecosystem	Location	Soil microbial respiration (μg C g^{-1} soil h^{-1})	Temp.[a] (°C)	Biomass (μg $C_{biomass}$ g^{-1} soil)	Method[b]	Soil carbon content (%)	Author
High Arctic primary succession	Svalbard (79°N, 12°E)	0.43–1.29	8	55–724	SIR	1.4–22	Present study
High Arctic tundra	Greenland (76°N, 68°W)	n.d.[e]	—	150–930	FE	(0.93–3.83)[d]	Jones et al. (2000)
Low Arctic tundra	Alaska (68°N, 149°W)	n.d.[e]	—	2300–13,000	SIR & FE	11.5–43.1	Cheng and Verginia (1993)
Low Arctic tundra	Alaska (68°N, 148°W)	2.3–5.0	9	n.d.[e]	—	19.9–43.0	Nedelhoffer et al. (1992)
Alpine primary succession	Austria (47°N, 11°E)	0.16–4.5	22	42–2250	SIR	0.19–7.08	Insam and Haselwandter (1989)
Alpine primary succession	Washington (48°N, 120°W)	0.03–0.16	n.a.[f]	11–42	SIR	(0.23–0.57)[d]	Ohtonen et al. (1999)
High altitude talus slopes	Colorado (40°N, 105°W)	n.d.[e]	—	0.028–207	SIGR	0.5–14	Ley et al. (2001)
Boreal forest	Saskatchewan, Canada	25–50	10	400–17,000	FE	39.8–41.4	Uchida et al. (1998)
Permanent pasture	North Wyke, England	0.9–2.6	23	1000–1700	FE	5.66–6.59	Lovell et al. (1995)[c]
Secondary succession	Southern Bohemia	1.0 ± 0.66	25	420 ± 220	FI	1.2–4.8	Šantrůčková and Straškraba (1991)
Cultivated land	Germany (51°N, 11°E)	n.d.[e]	22	200–900	SIR	0.1–8.3	Insam and Domsch (1988)
Tropical forest, savanna cropland	India (24–26°N, 82–85°E)	n.d.[e]	—	210–460	FE	0.5–3.0	Singh and Singh (1995)

[a] Temperature at which soil microbial respiration was measured.

[b] Method for measuring microbial biomass: SIR = substrate-induced respiration method; SIGR = substrate-introduced growth response method; FE = fumigation extraction method; FI = fumigation incubation method.

[c] The values were calculated based on Tables 3 and 4 in Lovell et al. (1995).

[d] The values in parentheses indicate percentages of soil organic matter.

[e] n.d. = not described.

[f] n.a. = not available.

Nadelhoffer et al., 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995). However, it would be premature to conclude that the Q_{10} of soil respiration is higher in arctic regions or lower-temperature environments than in warmer ecosystems. There were some exceptions in the present study ($Q_{10} = 2.2$ in Site 1) and in previous studies. Nadelhoffer et al. (1991) showed that the Q_{10} was smaller than or equal to 1 at low temperatures (3–9°C) and 3 at higher temperatures (9–15°C) in tundra soils. Lipson et al. (2002) reported that the Q_{10} value for soil microbial respiration over a range of 0–22°C was larger in summer soil ($Q_{10} = 3.6$) than in winter soil ($Q_{10} = 2.3$) in alpine dry-meadow soils. Furthermore, specific respiration and its temperature dependence have been found to differ substantially among several fungal species isolated from arctic soil (Heal et al., 1981). Flanagan and Bunnell (1980) showed that the temperature dependence of respiration varied among fungal and bacterial species in tundra soil reflecting soil depth (habitat temperature) and substrate quality. While a relatively extensive database exists on the temperature dependence of soil respiration, very few of these data are from arctic ecosystems. In order to realistically predict the responses of the decomposition rate to the climate change, more effort is needed to capture the variability in the Q_{10} value in arctic areas and to clarify the factors affecting the variation.

COMPARISON WITH OTHER ECOSYSTEMS

Table 3 summarizes the soil microbial biomass and microbial respiration rates in high- and low-arctic ecosystems and in the warmer ecosystems reported by other researchers. In a comparison of arctic areas, the microbial biomass in the present study was as high as that in Greenland (Jones et al., 2000) but smaller than that in Alaska (Cheng and Virginia, 1993). The microbial biomass and soil microbial respiration in the present study were comparable (Insam and Haselwandter, 1989) or larger (Ohtonen et al., 1999) than those in an alpine successional series in lower latitudes. In a comparison with temperate or tropical ecosystems, the microbial biomass in the present study was comparable with those in cultivated land (Insam and Domsch, 1988) or even larger than those in secondary successional series (Šantrůčková and Straškraba, 1991), tropical forests, and croplands (Singh and Singh, 1995). As a whole, the microbial biomass tends to be higher in soils that have higher soil carbon or organic matter content regardless of whether the ecosystems are warmer or colder. Generally, the microbial biomass and soil respiration rate per unit area are lower in arctic ecosystems than they are in warmer ecosystems (Heal et al., 1981; Raich and Schlesinger, 1992); however, this is partly because of the thin active layer in arctic soils. If they are compared on a unit-per-gram soil basis instead of by area, the microbial biomass and respiration rate measured at 8–9°C in both the high and low arctic were comparable or even larger than those measured at 22–25°C in temperate and tropical ecosystems (Table 3). These data suggest that soil microbial flora are well adapted to their cold and severe environments and that the potential for decomposition of soil organic matter may not be less in arctic ecosystems than in warmer ecosystems.

Although arctic ecosystems may have potential decomposition rates comparable to those of temperate ecosystems, the actual decomposition rates are low because of the thinness of the active soil layer. If future global warming increases the habitat temperature and the depth of the soil active layer, the soil respiration would increase according to a relatively high Q_{10} (Billings et al., 1983; Nadelhoffer et al., 1992; Oechel and Vourlitis, 1994). However, as shown in the present study, there may be some variation in the temperature dependence of soil respiration even in the same climatic conditions. Furthermore, there are some possibilities of change in the Q_{10} value as a result of acclimatization to warming (Luo et al., 2001; Bekku et al., 2003), probably due to change in species composition (Flanagan and Bunnell, 1980), substrate limitation (Nadelhoffer et al., 1992; Holland et al., 1995; Luo et al., 2001), and other factors. Further studies are needed to elucidate the existence and mechanisms of temporal and spatial variability in temperature dependence of soil respiration.

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References Cited

Anderson, J. P. E., and Domsch, K. H., 1978: A physiological method for the quantitative measurement of microbial biomass in soil. *Soil Biology and Biochemistry,* 10: 215–221.

Bekku, Y., Koizumi, H., Oikawa, T., and Iwaki, H., 1997: Evaluation of four methods for measuring soil respiration. *Applied Soil Ecology,* 5: 247–254.

Bekku, Y., Kume, A., Nakatsubo, T., Masuzawa, T., Kanda, H., and Koizumi, H., 1999: Microbial biomass in relation to arctic deglaciated moraines. *Polar Bioscience,* 12: 47–53.

Bekku, Y. S., Nakatsubo, T., Kume, A., Adachi, M., and Koizumi, H., 2003: Effect of warming on the temperature dependence of soil respiration rate in arctic, temperate and tropical soils. *Applied Soil Ecology,* 22: 205–210.

Bekku, Y. S., Kume, A., Masuzawa, T., Kanda, H., Nakatsubo, T., and Koizumi, H., 2004: Soil respiration in a high arctic glacier foreland in Ny-Ålesund, Svalbard. *Polar Bioscience* 17: 36–46.

Billings, W. D., Luken, J. O., Mortensen, D. A., and Peterson, K. M., 1983: Increasing atmospheric carbon dioxide: possible effects on arctic tundra. *Oecologia,* 58: 286–289.

Bunnell, F. L., Miller, O. K., Flanagan, P. W., and Benoit, R. E., 1980: The microflora: composition, biomass, and environmental relations. *In* Brown, J., Miller, P. C., Tieszen, L. L., and Bunnell, F. L. (eds.), *An Arctic Ecosystem: The Coastal Tundra at Barrow*, *Alaska*. Pennsylvania: Hutchinson and Ross, 255–290.

Cheng, W., and Virginia, R. A., 1993: Measurement of microbial biomass in arctic tundra soils using fumigation-extraction and substrate-induced respiration procedures. *Soil Biology and Biochemistry,* 25: 135–141.

Flanagan, P.W., and Bunnell, F. L., 1980: Microflora activities and decomposition. *In* Brown, J., Miller, P. C., Tieszen, L. L., and Bunnell, F. L. (eds.), *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*. Pennsylvania: Hutchinson and Ross, 291–334.

Heal, O. W., Flanagan, P. W., French, D. D., and Maclean, S. F., 1981: Decomposition and accumulation of organic matter. *In* Bliss, L. C., Heal, O. W., and Moore, J. J. (eds.), *Tundra Ecosystems: A Comparative Analysis*. London: Cambridge University Press, 587–633.

Holland, E. A., Townsend, A. R., and Viousek, P. M., 1995: Variability in temperature regulation of CO_2 fluxes and N mineralization from five Hawaiian soils: implications for a changing climate. *Global Change Biology,* 1: 115–123.

Insam, H., and Domsch, K. H., 1988: Relationship between soil organic carbon and microbial biomass on chronosequences of reclamation sites. *Microbial Ecology,* 15: 177–188.

Insam, H., and Haselwandter, K., 1989: Metabolic quotient of the soil microflora in relation to plant succession. *Oecologia,* 79: 174–178.

Jones, M. H., Fahnestock, J. T., Stahl, P. D., and Welker, J. M., 2000: A note on summer CO_2 flux, soil organic matter, and microbial biomass from different high-arctic ecosystem types in Northwestern Greenland. *Arctic, Antarctic, and Alpine Research,* 32: 104–106.

Kirschbaum, M. U. F., 1995: The temperature dependence of soil organic matter decomposition and effect of global warming on soil organic C storage. *Soil Biology and Biochemistry,* 27: 753–760.

Ley, R. E., Lipson, D. A., and Schmidt, S. K., 2001: Microbial biomass levels in barren and vegetated high altitude talus soils. *Soil Science Society of America Journal,* 65: 111–117.

Lipson, D. A., Schadt, C. W., and Schmidt, S. K., 2002: Changes in soil microbial community structure and function in an alpine dry meadow following spring snow melt. *Microbial Ecology,* 43: 307–314.

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

Lovell, R. D., Jarvis, S. C., and Bardgett, R. D., 1995: Soil microbial biomass and activity in long-term grassland: effects of management changes. *Soil Biology and Biochemistry,* 27: 969–975.

Luo, Y., Wan, S, Hui, D, and Wallace, L. L., 2001: Acclimatization of soil respiration to warming in a tall grass prairie. *Nature,* 413: 622–625.

Lynch, J. M., 1984: Interactions between biological processes, cultivation and soil structure. *Plant and Soil,* 76: 307–318.

Minami, Y., Kanda, H., and Masuzawa, T., 1996: The relationship between distribution of bryophytes and soil conditions on deglaciated arctic terrain in Ny-Ålesund. *Proceedings NIPR Symposium on Polar Biology,* 9: 307–312.

Muraoka, H., Uchida, M., Mishio, M., Nakatsubo, T., Kanda, H., and Koizumi, H., 2002: Leaf photosynthetic characteristics and net primary production of the polar willow (*Salix polaris*) in a high arctic polar semi-desert, Ny-Ålesund, Svalbard. *Canadian Journal of Botany,* 80: 1193–1202.

Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Laundre, J. A., 1991: Effects of temperature and substrate quality on element minelalization in six arctic soils. *Ecology,* 72: 242–453.

Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., and Linkins, A. E., 1992: Microbial processes and plant nutrient availability in arctic soils. *In* Chapin, F. S., III., Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds), *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. San Diego, CA: Academic Press, 281–300.

Nakatsubo, T., Bekku, Y., Kume, A., and Koizumi, H., 1998: Respiration of belowground parts of vascular plants: its contribution to total soil respiration on a successional glacier foreland in Ny-Ålesund, Svalbard. *Polar Research,* 17: 53–39.

Oechel, W. C., and Billings, W. D., 1992: Effects of global change on the carbon balance of arctic plants and ecosystems. *In* Chapin, F. S., III., Jeffries, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. San Diego, CA: Academic Press, 139–168.

Oechel, W. C., and Vourlitis, G. L., 1994: The effects of climate change on land-atmosphere feedbacks in arctic tundra regions. *TREE,* 9: 324–329.

Ohtonen, R., Frize, H., Pennanen, T., Jumpponen, A., and Trappe, J., 1999: Ecosystem properties and microbial community changes in primary succession on a glacier forefront. *Oecologia,* 119: 239–246.

Raich, J. W., and Schlesinger, W. H., 1992: The global carbon dioxide flux in soil respiration and its relationships to vegetation and climate. *Tellus,* 44B: 81–99.

Ross, D. J., and Cairns, A., 1978: Influence of temperature on biochemical processes in some soils from tussock grasslands. *New Zealand Journal of Science,* 21: 13–25.

Šantrůčková, H., and Straškraba, M., 1991: On the relationship between specific respiration activity and microbial biomass in soils. *Soil Biology and Biochemistry,* 23: 525–532.

Singh, S., and Singh, J. S., 1995: Microbial biomass associated with water-stable aggregates in forest, savanna and cropland soils of a seasonally dry tropical region, India. *Soil Biology and Biochemistry,* 27: 1027–1033.

Uchida, M., Nakatsubo, T., Horikoshi, T., and Nakane, K., 1998: Contribution of microorganisms to the carbon dynamics in black spruce (*Picea mariana*) forest soil in Canada. *Ecological Research,* 13: 17–26.

Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H., 2002: Net photosynthesis, respiration, and production of the moss *Sanionia uncinata* on a glacier foreland in the high arctic, Ny-Alesund, Svalbard. *Arctic, Antarctic, and Alpine Research,* 34: 287–292.

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