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CO_2 efflux from the biological soil crusts of the High Arctic in a later stage of primary succession after deglaciation, Ny-Ålesund, Svalbard, Norway

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ABSTRACT

The CO_2 efflux from representative tundra ecosystems in the high Arctic should be monitored in order to evaluate the potential future sensitivity of the carbon cycle to climate change. However, studies on the soil CO_2 efflux from them are still limited, especially deglaciated area due to the Arctic warming. The ecosystem in Ny-Ålesund, Svalbard, Norway (~79°N) has gradually undergone substantial alterations due to deglaciation induced by climate change, where biological soil crusts (BSCs, mainly consisting of cyanobacteria, algae, lichen, and bryophytes, etc. on the soil surface) are widely formed in the glacier foreland and further developed especially in the later stages of primary succession. In this study, soil CO_2 efflux from partly or totally covered with black-colored BSCs (BSCs-B) was measured from 2007 to 2009 using portable dynamic chamber system. The objectives of this study were (i) to quantify the CO_2 efflux from the soil, (ii) to examine the controlling factors which affect the temporal and spatial variation of soil CO_2 efflux, (iii) to examine the contribution of BSCs-B to soil CO_2 efflux, and (iv) to estimate the relationship between soil CO_2 efflux and microbial activity to evaluate its role on the surface carbon budget at deglaciated area. It was found that the emission of soil CO_2 from BSCs-B was consistent through the long-term in situ measurement in the high arctic tundra. Soil CO_2 efflux ranged from 0.3 to 0.7 $\mu mol\, m^{-2}\, s^{-1}$ with means of 0.56 ($\pm$0.07) $\mu mol\, m^{-2}\, s^{-1}$ in 2007, 0.54 ($\pm$0.13) $\mu mol\, m^{-2}\, s^{-1}$ in 2008, and 0.51 ($\pm$0.09) $\mu mol\, m^{-2}\, s^{-1}$ in 2009. The soil temperature (Ts) explained 50–70% of the temporal variation of the soil CO_2 efflux when temperature ranged from 6 to 12 °C, whereas Ts is not controlling factor for spatial variation of soil CO_2 efflux considering the low coefficient of variation (CV). In the meanwhile, soil water content (SWC) was not a main controlling factor for temporal variation of soil CO_2 efflux. Even though CV of SWC was not low, spatial variation of SWC could not explain that of soil CO_2 efflux. The soil CO_2 efflux was spatially affected by BSCs-B coverage, amount of pebble, and the nearby vegetation distribution. All enzyme activities exhibited significantly higher values in BSCs-B than in mineral soil of BSCs ($p < 0.01$). The activities of enzymes in BSCs-B generally exhibited positive correlations with the soil CO_2 efflux except for humic substances ($R^2 = 0.52$). It can be concluded that the magnitude of the soil CO_2 efflux from BSCs-B is comparable to those from moss and vascular plants in the surface carbon budget.

1. Introduction

The carbon cycle of the Arctic has the potential to influence the climate system through feedback pathways involving responses in the regional terrestrial and marine ecosystems (McGuire et al., 2009). Accordingly, accurate prediction of the carbon cycle of the Arctic is necessary for better prediction of the future climate

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change. However, it is difficult to evaluate whether the Arctic is a long-term source or sink for atmospheric CO_2 due to the constraints of measurements on CO_2 emission and uptake by ecosystems, and the high degree of their spatial and temporal variability in the Arctic (ACIA, 2004). In addition, estimates of the sensitivity of the carbon cycle of the Arctic during the remainder of the 21st century have a high rate of uncertainty (McGuire et al., 2009).

The topography and ecosystem in the high Arctic area have been changed due to the retreat of glaciers in response to climate warming. As glaciers retreat, soil surfaces emerge and expose new terrestrial environments to potential colonization by microorganisms and higher plants (Breen and Lévesque, 2006). Pioneering organisms such as cyanobacteria, green algae, lichen, mosses, fungi, and heterotrophic bacteria are the first organisms to colonize the exposed soil surface. Over time an organic layer less than 0.01 m thick, known as a biological soil crusts (BSCs), can be created by those organisms in the early stage of primary succession (Belnap and Lange, 2001).

The formation of the BSCs has progressed in the glacier foreland in Ny-Ålesund, Svalbard archipelago, Norway in the high Arctic (~79°N). The BSCs mainly consists of the organic residue from dead lichen and moss, few lichen, and cyanobacteria. Through the mechanism of succession, vascular plants (e.g., *Salix polaris* Wahlenb.) and moss (e.g., *Sanionia uncinata* (Hedw.) Loeske) become dominant around the BSCs far away from the glacier. The BSCs change or develop into dominant vegetation types in a later stage of primary succession after deglaciation. In Ny-Ålesund, moss covers the largest area, followed by the BSCs with black color (BSCs-B). One of the conspicuous characteristics of the BSCs is the development of BSCs-B which is soil surface communities consisting of black-colored organic residue and algae, cyanobacteria, and lichen on the BSCs-B (Yoshitake et al., 2007).

Major processes in the carbon cycle in the ecosystem in Ny-Ålesund are photosynthesis and respiration of moss, vascular plants, BSCs, and so on and decomposition of organic matter by microbes in the soil. A wealth of carbon cycle related research on the ecosystem has been performed since the early 1990s. Previous studies were focused on measurements and modeling of the carbon budget or carbon cycle at the ecosystem level (Lloyd, 2001; Nakatsubo et al., 2005; Uchida et al., 2002; Uchida et al., 2010; Yoshitake et al., 2010), measurements of CO_2 flux from soil, vascular plants, and moss and their controlling factors at the process level, and manipulation experiments (Bekku et al., 2003, 2004a,b; Boddy et al., 2008; Nakatsubo et al., 1998; Yoshitake et al., 2007). These studies were much more processed in the laboratory by sampling. However, studies on the role of BSCs-B in the high Arctic are limited based on in situ measurements on long-term basis with consideration of its inter-annual variations of CO_2 emission magnitude (Nakatsubo et al., 1998; Yoshitake et al., 2007).

BSCs-B may be a significant carbon pool at the net ecosystem exchange of CO_2 due to its abundant organic carbon and its large occupying area. In addition, because of its darker and rougher surface, it can not only induce a low albedo but also can increase the ambient soil temperature (Gold, 1998), which would likely to strengthen the soil CO_2 emission. Recently, Ny-Ålesund has experienced an increase in temperature. Maturilli et al. (2013) showed a temperature increase of +1.35 K per decade from 1993 to 2011. In addition, it is expected to witness a substantial warming with increases of 4–6 °C in temperature and 5% precipitation by 2100 (AICA, 2005; Førland et al., 2011). Therefore, an evaluation of the carbon cycle in this location including BSCs-B may provide insight into the possible evolution of the carbon cycle in the Arctic. Hypothesis is the soil CO_2 efflux enhanced by the BSCs-B significantly contributes to ecosystem respiration.

The objectives of this study were (i) to quantify the CO_2 efflux from the soil, (ii) to examine the controlling factors which affect the temporal and spatial variation of soil CO_2 efflux, (iii) to estimate the relationship between the soil CO_2 efflux and microbial activity, and (iv) to examine the contribution of BSCs-B to soil CO_2 efflux. The soil CO_2 efflux was measured using an in situ chamber system

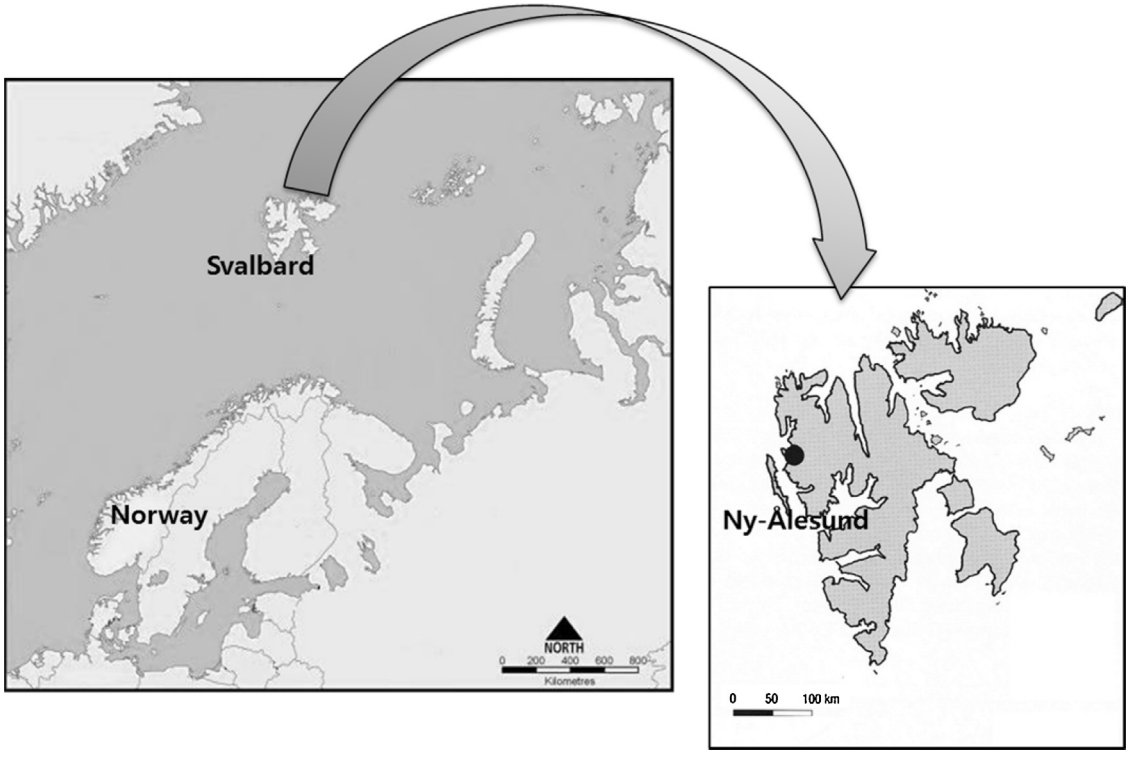

Fig. 1. Study site in Ny-Ålesund, Svalbard, Norway.

with physical and biological variables during summer from 2007 to 2009.

2. Materials and methods

2.1. The study site

The study site is located in a tundra ecosystem at Ny-Ålesund (78°55′24″N, 11°55 15″E), Svalbard archipelago, Norway (Fig. 1). Ny-Ålesund is situated on the south side of the deep and sheltered Kongs Fjord on the west coast of Spitsbergen, the largest island of Svalbard archipelago. The annual mean air temperature and precipitation are—4.2 °C and 393 mm yr^{-1}, respectively and mean of air temperature and precipitation in July are 5.7 °C and 35 mm $month^{-1}$, respectively from 2000 to 2009 (http://retro.met.no). Snow-free period is roughly from June to August and the remainder is snow-covered season (e.g., Maturilli et al., 2013)

The measurement plot (30 m × 30 m) for CO_2 efflux is located at a tundra ecosystem ~70 m away from the southeast of the Korean Dasan station, Ny-Ålesund. The dominant vegetation comprises mosses (e.g., *S. uncinata* (Müll. Hal) Ochyra & Hedenäs and *Wanstorfia sarmentosa* (Wahlenb.) Hedenäs), covering roughly 50% of the study area, and vascular plants (e.g., *Silene acaulis* (L.) Jacq. and *S. polaris* Walhenb) covering 15% of the study area.

The site is characterized by BSCs-B, which covers around 35% of the study area to a depth of 0.005–0.01 m between these plants. There are a few lichens (e.g., *Ochrolechia frigida* (Sw.) Lynge and *Cladonia borealis* S. Stenroos, etc.) on the BSCs-B, a little pebbles and small amounts of wild animal excrement (e.g., reindeer, fox, and goose). The soil texture under the BSCs is sandy loam. The land surface is flat, but some areas show heterogeneous inclination.

2.2. Environmental conditions and measurements

The coverage of BSCs-B, pebbles, lichen on the BSCs-B, and moss inner collars, distribution of vegetation around collars, and micro topography of surface were examined at the 20 locations (referred to here as locations Nos. 1–20) (Table 1). The 20 locations were assorted considering dominant amount among BSCs-B (B; Nos 1, 3, 5, 7, 8, 9, 11, 12, 13, 14, 15, and 16), pebbles (P; Nos 2, 4, 6, and 10), and moss (M; Nos 17, 18, 19, and 20) inner collar. Chemical and physical soil properties (e.g., total organic carbon, total nitrogen, and bulk density etc.) are examined for BSCs-B and mineral soil of BSCs near several locations of soil CO_2 efflux.

Soil CO_2 efflux and moss CO_2 efflux were measured at the 20 locations using a opaque closed-dynamic chamber system (LI-6400 with LI-6000-9 soil chamber, LI-COR, Inc., Lincoln, NE USA) (Table 1). PVC collars (0.106 m in diameter and 0.08 m in height) were set up on every location at a depth of 0.01–0.02 m to minimize disturbance of the soil surface against repeated measurements (Fig. 2). Measurement locations for soil CO_2 efflux were determined at the 16 points of intersection of grid in the 30 m × 30 m plot. The moss CO_2 efflux was measured at the dominant area of moss nearby the soil CO_2 efflux measurement for comparison (Fig. 3). The locations of moss CO_2 efflux, Nos. 17, 18, 19, and 20, corresponded with the locations of soil CO_2 efflux, Nos. 2, 9, 12, and 16, respectively. Soil CO_2 efflux and moss CO_2 efflux were measured on average 14 times per season from the end of June to early August of 2007–2009. The CO_2 efflux was measured twice per location for 10 min between 9am and 5pm every other day. Detailed information on the field operation and calibration of the closed dynamic chamber system was described in Chae et al. (2003).

The soil temperature (Ts) at a depth of 0.1 m and the volumetric soil water content (SWC) in a 0 –0.1 m layer were measured along with the CO_2 efflux measurements, using a portable soil temperature probe (LI-6000-09TC, LI-COR, Inc. Lincoln, NE USA) and a portable volumetric soil water content sensor (Hydro Sense, Campbell Scientific Australia Pty., Ltd., QLD, Australia), respectively.

Diurnal variation measurements of soil CO_2 efflux were conducted to examine the response under simultaneously changing Ts and SWC at five locations (Nos. 1, 5, 8, 13, and 15) at intervals of four hours on July 17th (DOY 199) and 18th (DOY 200), 2008.

The BSCs-B and mineral soil under BSCs-B for the chemical and physical analyses were collected by using can cores on July 31st (DOY 213), 2007 at six points nearby locations 1, 2, 6, 9, 12, and 15. The six sample locations were determined to consider the various magnitude of soil CO_2 efflux together with their spatial distribution

Table 1
Coverage of biological soil crusts with black color (BSCs-B), pebble, lichen, and moss inner collar, distribution of vegetation around collar, and micro topography of surface (—; flat, ∧; slope up (3–5°), ∧∧; slope up (6–8°), ∨; slope down (3–5°), and ∨∨; slope down (6–8°)) for 20 locations Nos (main character of each location; B (BSCs-B), P (pebbles), and M (moss)) of CO_2 efflux.

Location No.		Inner collar				Around collar	
		BSCs-B (%)	Pebble (%)	Lichen (%)	Moss (%)	Vegetation and pebble	Micro topography
1	(B)	>95	<5	50		Few moss and vascular plant	—
2	(P)	0–10	40	<5		Few vascular plant dominant pebble	∧
3	(B)	>95	<5	50		Few vascular plant and moss	∨∨
4	(P)	0–5	30	0		Dominant pebble	—
5	(B)	>95	<5	50		Abundant vascular plant and moss	—
6	(P)	20–50 (thin)	50–80	10		Few vascular plant /abundant pebble	∧∧
7	(B)	100	0	30		Abundant vascular plant and few moss	∨
8	(B)	100	0	50		Dominant moss	∧
9	(B)	95–100	0–5	10		Few moss/abundant pebble	∧
10	(P)	0–5	80–90	0		Few vascular plant/dominant pebble	∨
11	(B)	50–80 (thin)	0	50		Few vascular plant and abundant moss/abundant pebble	∨∨
12	(B)	70–90	10-30	50		Few moss/few pebble	—
13	(B)	90–100	0–10	50		Dominant vascular plant and moss/few pebble	—
14	(B)	80–90 (thin)	10–20	50		Few moss/abundant pebble	∧
15	(B)	80–100	0	30		Abundant vascular plant and moss/abundant pebble	∨
16	(B)	70–90	10–30	20		Few moss and pebble	∧
17	(M)	–	–	–	100	Dominant moss	∧
18	(M)	–	–	–	100	Dominant moss	∧
19	(M)	–	–	–	100	Dominant moss	—
20	(M)	–	–	–	100	Dominant moss	∧

Fig. 2. Photo shots of soil CO_2 efflux measurements of biological soil crust with black color, Nos. 7 (a), 6 (b), and 10 (c), and a photo shot of moss CO_2 efflux, No. 19 (d) in PVC collar (10.6 cm in diameter and 8 cm in height).

within the plot: average (e.g., Nos. 1, 2, 9, and 12), maximum (No. 15), and minimum (No. 6) for soil CO_2 efflux. Soil texture was measured by a pipette method, and total organic carbon (Walkley-Black method), total nitrogen (Micro Kjeldahl method), pH (w/v = 1:5), and total phosphorus and potassium (ICP-ES) were analyzed from the black organic and mineral soil.

To investigate the relationship between soil CO_2 efflux and the microbial activity, additional soil samples were collected separately from the BSCs-B and mineral soil in a 0–0.1 m layer. The soil samples were also collected nearby locations Nos. 2, 6, 9, and 15 on June 30th (DOY 182), 2008 and nearby location Nos. 1, 5, 6, 12, and 13 on July 28th (DOY 210), 2008. However, microbial activity at the three locations (Nos. 1, 5, 13) could not be completely analyzed for all extracellular enzymes due to a shortage in the amount of the sample. The soil samples were stored under low temperature (around 10 °C) using an icebox for two-day shipping to analyze microbial activity in Korea. The average Ts and SWC were 10.2 (±2.0) °C and 10.1 (±0.6) °C and 21(±5)% and 15 (±4)% for each sampling date, respectively.

The extracellular enzyme activities of ß-glucosidase (C), *N*-acetylglucosaminidase (N), phosphatase (P), and Arylsulfatase (S) were determined in order to assess the general microbial activity in the soil samples. These enzymes are involved in carbon, nitrogen, phosphorus, and sulfur mineralization. Methylumbelliferyl compounds were used as a model substrate (Freeman et al., 1995). Briefly, 5 mL of MUF-glucopyranoside (400 μM), MUF-*N*-acetyl-glucosamine (400 μM), MUF-phosphate (800 μM), or MUF-sulfate (400 μM) was added to one gram of soil or BSCs-B and incubated at 10 °C for 60 min. The reaction was terminated by centrifuging samples, and fluorescence in the supernatant was determined using a fluorometer (FLUOstar OPTIMA).

2.3. Statistics analysis

In order to investigate the dependency of soil CO_2 efflux on Ts or SWC, equations for the exponential function of Ts (Eq. (1); Lloyd and Taylor, 1994) and the parabolic function (not shown) of SWC (Mielnick and Dugas, 2000) were used. The coefficients a and b were derived from non-linear least-square fittings ($a > 0$ and $b > 0$).

$$\text{Soil}CO_2\text{efflux} \approx ae^{bTs} \quad (1)$$

The differences in the magnitude of soil CO_2 efflux among three years and among the 16 locations for each year were tested by using one-way ANOVA and were verified by using post hoc Tukey's HSD test and homogeneity of variance. The differences in Ts and SWC were also tested by same methods.

3. Results

3.1. Soil properties

Total organic carbon amounts of the BSCs-B and the mineral soil layer were 45 (±27)% and 16 (±8)%, respectively. Carbon to nitrogen ratio (C/N) of BSCs-B and mineral soil ranged from 3.3 to 45.4 and 2.3 to 13.9, respectively. The range of the C/N ratio of BSCs-B is considerable, resulting from that in No. 15 with much higher carbon content and lower nitrogen content. The pH of both layers were almost same (5.5), the water content of the BSCs-B was twice as much than that of the mineral soil layer, and the average bulk density of the mineral soil was 0.77 (±0.18) g cm^{-3} (Table 2).

3.2. Temporal changes in soil CO_2 efflux and controlling environmental factors

Fig. 3 shows the temporal variation of the averaged soil CO_2 efflux, Ts, and SWC for 16 locations and precipitation in July from 2007 to 2009. The soil CO_2 efflux ranged from 0.3 to 0.7 μmol m^{-2} s^{-1} with means of 0.56 (±0.07) μmol m^{-2} s^{-1} in 2007, 0.54 (±0.13) μmol m^{-2} s^{-1} in 2008, and 0.51 (±0.09) μmol m^{-2} s^{-1} in 2009. The soil CO_2 efflux showed no significant differences in magnitude among the three years ($p > 0.05$). Consequently, soil CO_2

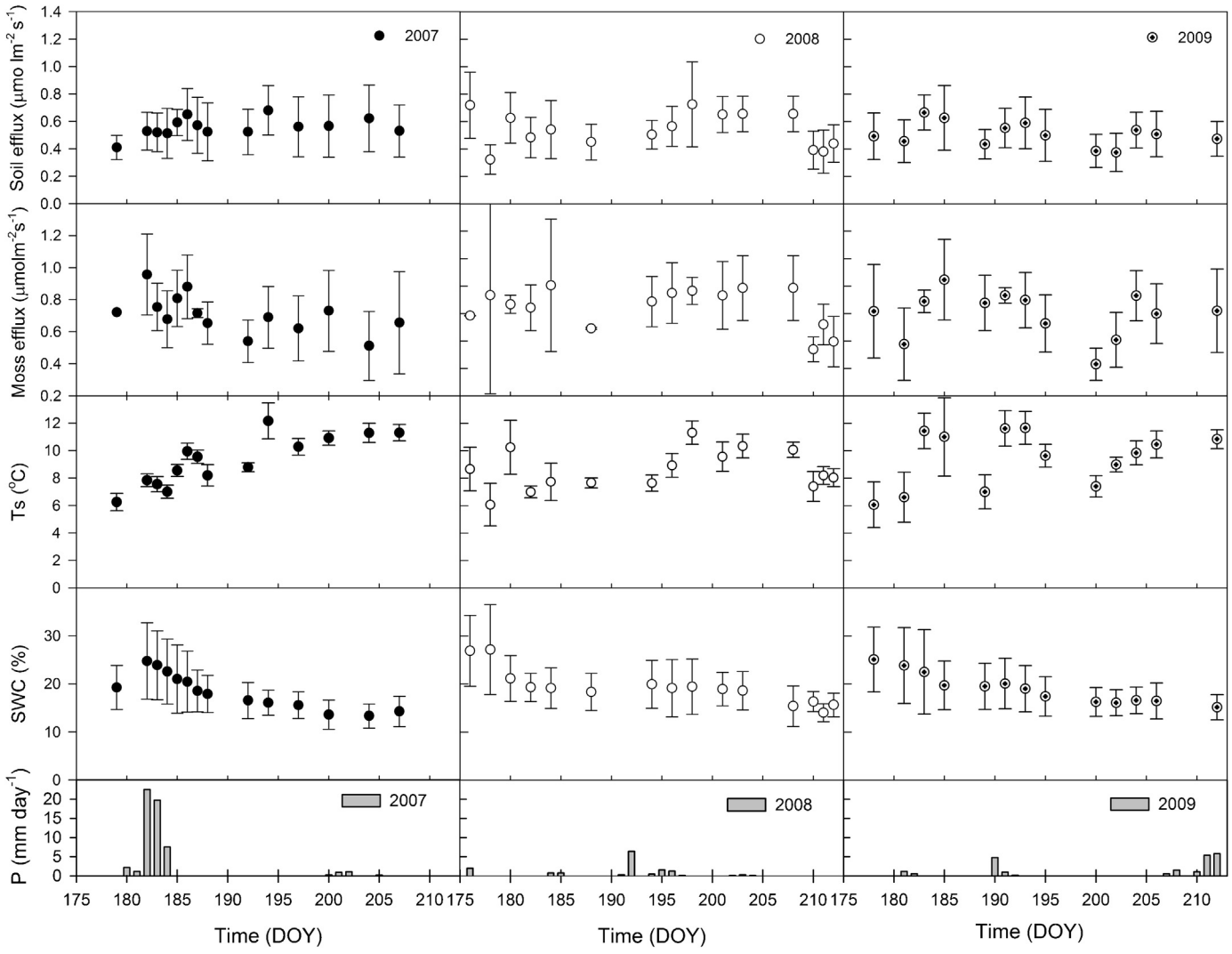

Fig. 3. Temporal variation of the soil CO_2 efflux, moss CO_2 efflux, soil temperature (Ts) at 5 cm depth, soil water content (SWC) in a 0-0.1 m layer, and precipitation during summer from 2007 to 2009.

Table 2
Soil properties of the biological soil crusts with black color (BC) and mineral soil (MS) of biological soil crusts for the near several locations of soil CO_2 efflux (TOC; total organic carbon, T-N; Total nitrogen, C/N; carbon to nitrogen ratio, T-P; total phosphorus, K; potassium, BWC_g/SWC_g; gravimetric BSC-B water content and soil water content, BD; bulk density, ST; soil texture, SL; sandy loam, SCL; sandy clay loam, N/A; not available).

Location No.		TOC ($g C kg^{-1}$)	T-N ($g C kg^{-1}$)	C/N	T-P ($mg kg^{-1}$)	K ($mg kg^{-1}$)	pH	BWC_g/SWC_g (%)	BD ($g cm^{-3}$)	ST
1	BC	14	4.2	3.3	468	97	5.2	34.2	–	-
	MS	16	1.8	8.9	506	16	5.4	11.9	0.89	SL
2	BC	N/A	N/A	N/A	N/A	N/A	N/A	N/A	–	-
	MS	11	4.8	2.3	727	29	5.5	16.4	0.73	SCL
6	BC	41	7.3	5.6	464	315	5.6	19	–	-
	MS	15	1.6	9.3	578	16	6	13.5	0.53	SCL
9	BC	34	4.1	8.3	507	147	5.4	23.5	–	-
	MS	32	2.3	14	651	19	4.8	17.1	0.75	SCL
12	BC	87	N/A	N/A	606	N/A	5.4	33.1	–	-
	MS	12	1.8	6.7	742	15	5.5	10	0.66	SL
15	BC	50	1.1	45.5	620	60	5.9	20.8	–	–
		MS	9	1.6	5.6	422	1	5.9	10.4	1.04
Mean (STD)	BC	45 (±27)	4 (±3)	11.3 (±10.6)	533 (±75)	155 (±113)	5.5 (±0.3)	26.1 (±7.1)		
	MS	16 (±8)	2 (±1)	8.0 (±7.0)	605 (±126)	16 (±9)	5.5 (±0.4)	13.2 (±3.0)	0.77 (±0.18)	

was consistently emitted through the long-term in situ measurement.

The averaged Ts ranged from 6 to 12 °C with means of 9.3 (±1.8) °C, 8.6 (±1.5) °C, and 9.4 (±2.0) °C for 2007, 2008, and 2009. The SWC ranged from 13 to 27% with means of 18 (±4)%, 19 (±4)%, and 19 (±3)% for 2007, 2008, and 2009. Ts and SWC also showed no significant differences in magnitudes for three years ($p > 0.05$) as soil CO_2 efflux.

Temporal pattern of the soil CO_2 efflux roughly followed that of Ts, but not that of SWC. The soil CO_2 efflux for three years correlated significantly with Ts: 2007 ($R^2 = 0.57$), 2008 ($R^2 = 0.68$), and 2009 ($R^2 = 0.48$). In the meanwhile, there was no relationship between SWC and soil CO_2 efflux for parabolic function ($R^2 = 0.11$). The Q_{10} (increase in reaction rate per 10 °C) were 1.7 (2007), 3.7 (2008), and 1.9 (2009) for each year by least-squares regression based on van't Hoff equation. This range is similar to results of previous research on the growing season in areas nearby this site (Bekku et al., 2003; Elberling, 2007). Precipitation was above normal in 2007 (52 mm month^{-1}), but below normal in 2008 (12 mm month^{-1}) and 2009 (21 mm month^{-1}) in July based on the last 10-year mean.

Diurnal variation of soil CO_2 efflux was measured at five locations (closed circles in Fig. 4). The locations with well developed (fully covered and thick) BSCs-B and expected warm weather conditions were especially chosen to focus on the response of BSCs-B with Ts. Fortuitously, the days chosen for diurnal measurement e were the warmest days of that year. The relationship between mean soil CO_2 efflux and Ts based on the diurnal variation measurement was significant ($R^2 = 0.63$; line (a) in Fig. 4). The minimum (0.53 (±0.09) μmol m^{-2} s^{-1}) and maximum (0.81 (±0.07) μmol m^{-2} s^{-1}) values of soil CO_2 efflux were found at approximately 3 am and 3 pm LST, respectively. Ts increased from 8 to 12 °C and the SWC decreased from 19 to 15%. This relationship was compared with that between averaged soil CO_2 efflux and Ts obtained over July of 2008 from the corresponding locations of diurnal variation (open circles in Fig. 4), when Ts and SWC varied from 6 to 12 °C and from 15 to 20%, respectively. The relationship obtained over July was also significant ($R^2 = 0.61$; line (b) in Fig. 4). This means general relationship between soil CO_2 efflux and Ts on the developed BSCs-B with a SWC range from 15 to 20%, and the Ts explained over 60% of the variation of soil CO_2 efflux.

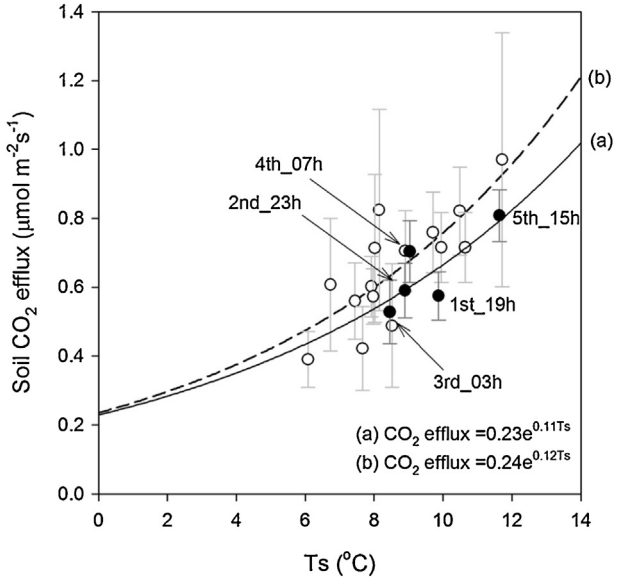

Fig. 4. Relationship between soil CO_2 efflux and soil temperature (Ts) for an interval of four hours on July 17th (DOY 199) and 18th (DOY 200) 2008 (location Nos. 1, 5, 8, 13, and 15) (a) and relationship between averaged soil CO_2 efflux and Ts at same locations in 2008 (b). The regression lines are: (a) solid line $y = 0.2292e^{0.10661066x}$ ($R^2 = 0.63$), (b) dashed line $y = 0.2351e^{0.11701170x}$ ($R^2 = 0.61$).

3.3. Spatial changes in soil CO_2 efflux and controlling factors

Fig. 5 shows averaged soil CO_2 efflux, Ts, and SWC values from each location for study periods. The soil CO_2 efflux ranged from 0.3 to 0.9 μmol m^{-2} s^{-1} and the mean was 0.55 (±0.14) μmol m^{-2} s^{-1}. The soil CO_2 efflux among the 16 locations showed significant differences in magnitudes ($p < 0.05$). In order of magnitude, the magnitudes of the soil CO_2 efflux at location Nos. 8, 15, 13, and 5 were above average, whereas those of Nos. 6, 14, 3, 12, and 11 were below average (Fig. 5). The SWC among the 16 locations showed significant differences in magnitudes ($p < 0.05$), and the Ts showed no significant differences (Fig. 5).

Overall, the above average soil CO_2 efflux values occurred in fully covered BSCs-B with dominating or abundant vegetation around them and with very small amount of pebbles inner collars, whereas the average and below average soil CO_2 efflux were relatively partly covered or thin and cracked BSCs-B with little vegetation outside of collars and abundant pebbles according to Table 1 and Fig. 5. The soil CO_2 efflux for the 16 locations showed significantly positive (or negative) linear correlation for amount of vegetation (or pebbles) ($p < 0.05$) (Fig. 6c and b); on the other hand linear relationship between soil CO_2 efflux and the coverage of BSCs-B was not significant (Fig 6a). However, when the soil CO_2 efflux of three locations (i.e., Nos. 2, 4, and 10) for none or very few BSCs-B were excluded, the soil CO_2 efflux showed significant linear correlation for the coverage of BSCs-B ($p < 0.05$; Fig 6a). Even though coverage of BSCs-B was below 20% of the area inner collar, unexpectedly, the magnitudes of soil CO_2 efflux at these locations were on an average. The coverage of the BSCs-B inner collar showed a positive relationship with distributions of the vegetation around the collar ($p < 0.05$; Fig 6d).

The coefficient of variation (CV) of the 16 locations was investigated to evaluate the spatial variation of soil CO_2 efflux, Ts, and SWC. The CV values of soil CO_2 efflux for each period were 27%, 23%, and 21% for 2007, 2008, 2009, and also those for Ts and SWC varied from 5 to 7% and from 17 to 19%, respectively (Fig. 5).

3.4. Comparison of soil CO_2 efflux to moss CO_2 efflux

The temporal variation of the moss CO_2 efflux for four locations was measured in July from 2007 to 2009. The moss CO_2 efflux ranged from 0.2 to 1.0 μmol m^{-2} s^{-1} with means of 0.71 (±0.18) μmol m^{-2} s^{-1}, 0.66 (±0.26) μmol m^{-2} s^{-1}, and 0.59 (±0.24) μmol m^{-2} s^{-1} for 2007, 2008, and 2009, respectively (Fig. 3). The moss CO_2 efflux also showed no significant differences in magnitude during the three years ($p > 0.05$).

Comparing the magnitudes of soil CO_2 efflux with that of the moss for the four locations, the moss CO_2 efflux showed significantly higher values than soil CO_2 efflux ($p < 0.05$; Table 3). The moss CO_2 efflux consisting of microbial respiration and dark respiration was 15 to 20% higher than soil CO_2 efflux. The magnitudes of Ts and SWC for soil and moss were compared for the corresponding locations, respectively (Table 3). Ts and SWC for soil and moss showed no significant differences in magnitude during 2007 and 2008 ($p > 0.05$).

3.5. Microbial activity

The magnitudes of the extracellular enzyme activities of C, N, S, and P were used as a surrogate for the microbial activity in BSCs-B and in mineral soil. Particularly, ß-glucosdiase activity is related to cellulose decomposition and hence may represent a direct process

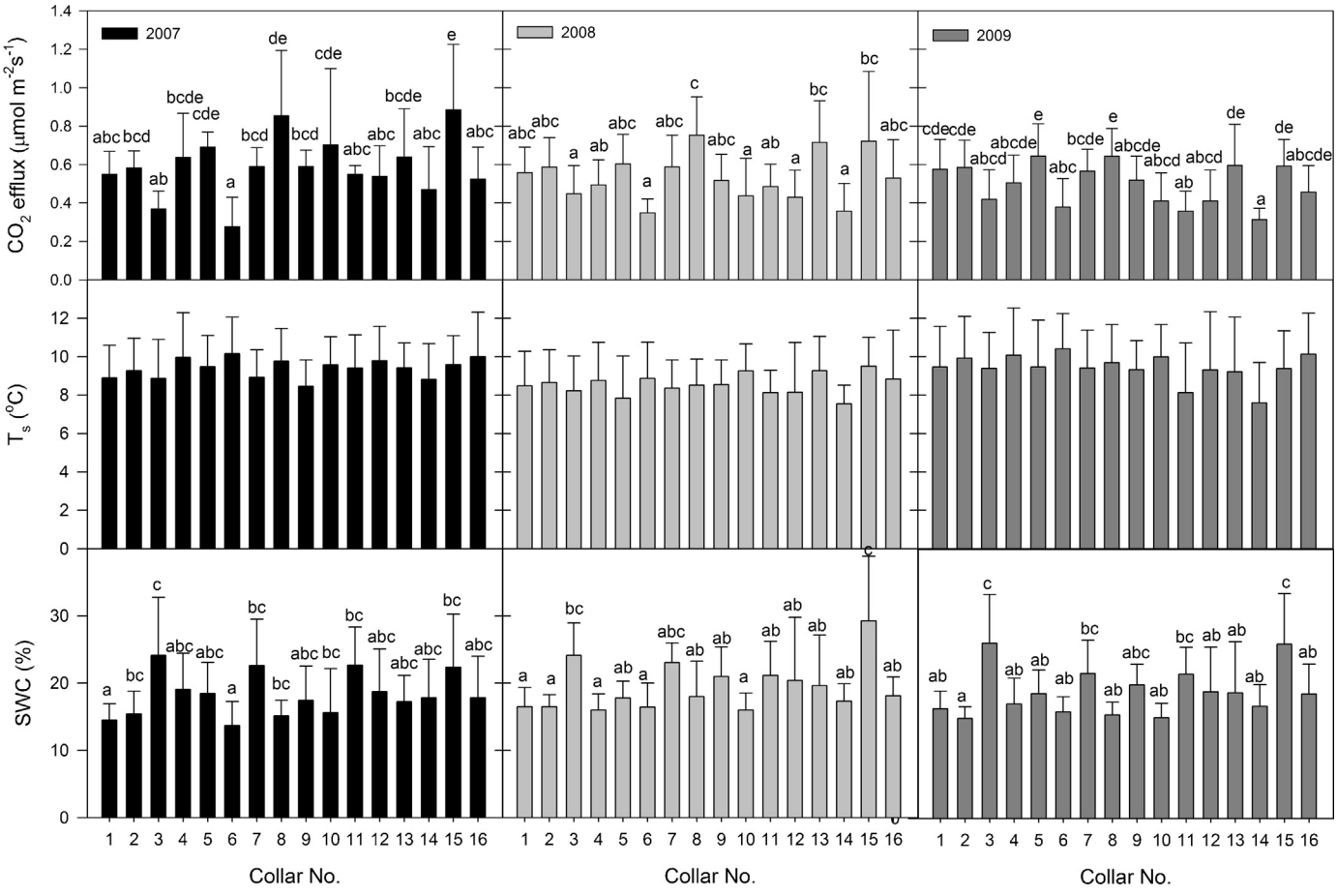

Fig. 5. Variation of soil CO_2 efflux, soil temperature (Ts) and soil water content (SWC) for 16 locations during summer from 2007 to 2009. Bars with different letters are significantly different (Tukey's HSD test, $p < 0.05$).

rate of organic carbon degradation. Additionally, *N*-acetylglucosamindase, phosphatase, and arylsulfatase are responsible for mineralization of organic N, P and S respectively. All enzyme activities exhibited significantly higher values in BSCs-B than in mineral soil ($p < 0.01$; Table 4).

The relationships between enzyme activities in the BSCs-B and the soil CO_2 efflux were not significant. However, if the outlier (No. 15) of BSCs-B is removed, the relationship between all enzyme activities in the BSCs-B and CO_2 efflux was significant (C; $R^2 = 0.52$, N; $R^2 = 0.32$, P; $R^2 = 0.75$, S; $R^2 = 0.44$) (Fig. 7). The condition of BSCs-B in No. 15 is qualitatively different from the condition of the other locations.

4. Discussion

For the three measurement periods, in 2007, 2008, and 2009, the average soil CO_2 efflux ranged from 0.51 to 0.56 μmol m^{-2} s^{-1}. The measured soil CO_2 efflux values were summarized in Appendix A with previous studies in situ obtained using the chamber method in high Arctic ecosystems in Svalbard during summer (Bekku et al., 2004a; Björkman et al., 2010; Dziadowiec, 1983; Nakastubo et al., 1998; Sendstad, 1981). The reported in situ measured soil CO_2 efflux ranged from 0.0 to 0.6 μmol m^{-2} s^{-1}. According to Nakatsubo et al. (1998), the soil CO_2 efflux from the bare soil showed a value between 0 and 0.2 μmol m^{-2} s^{-1} during the first stage of biological soil crust formation. As the crust started to form and vegetation was abundant, the soil CO_2 efflux became higher based on other results than that of bare soil. The magnitudes of soil CO_2 efflux from this study were compared with those from reported in the literatures for sites with similar vegetation (sites 3–3 and 4–2 of Nakatsubo et al., 1998 and site 3 of Bekku et al., 2004a), and it was found that soil CO_2 efflux obtained in this work was similar to or higher than those of the sites documented in the literature (see Appendix A).

The measured soil CO_2 efflux was used to understand the contribution of soil CO_2 efflux to ecosystem respiration (Re) which is sum of respiration from leaf, stem, root and organic matter. The Re was roughly estimated with each component of Re from previous studies which are (i) dark respiration (Rd) of moss, roughly 0.32 μmol m^{-2} s^{-1} at 5.7 °C (i.e., *S. uncinata*) from Uchida et al. (2002), (ii) Rd of vascular plants, 0.85 μmol m^{-2} s^{-1} from Nakastubo et al. (1998) and the equation for *S. polaris* ($Rd = 0.44246\, e^{0.10011T}$ from Muraoka et al. (2002) neglecting the influence by other vascular plants due to small coverage, (iii) root respiration by mixed community of bryophytes and vascular plants, 0.21 μmol m^{-2} s^{-1} (i.e., arithmetic average of 0.33 μmol m^{-2} s^{-1}, 0.36 μmol m^{-2} s^{-1}, 0.11 μmol m^{-2} s^{-1}, and 0.05 μmol m^{-2} s^{-1}) from Nakastubo et al. (1998). Estimates of each component of Re, soil CO_2 efflux, Rd of moss, Rd of vascular plants and Rr of vascular plants were 0.56 of this study, 0.32, 0.85 and 0.21 μmol m^{-2} s^{-1}, respectively.

Considering the spatial coverage (BSCs; 35%, moss; 50%, vascular plants; 15%) of each component within the study site to estimate Re, soil CO_2 efflux, dark respiration of moss, and the dark respiration and root respiration of vascular plants were 38, 31, and 31% of Re. While moss and vascular plants uptake atmospheric CO_2 by photosynthesis and emit CO_2 to the atmosphere by respiration, BSCs mostly emit CO_2 to the atmosphere via

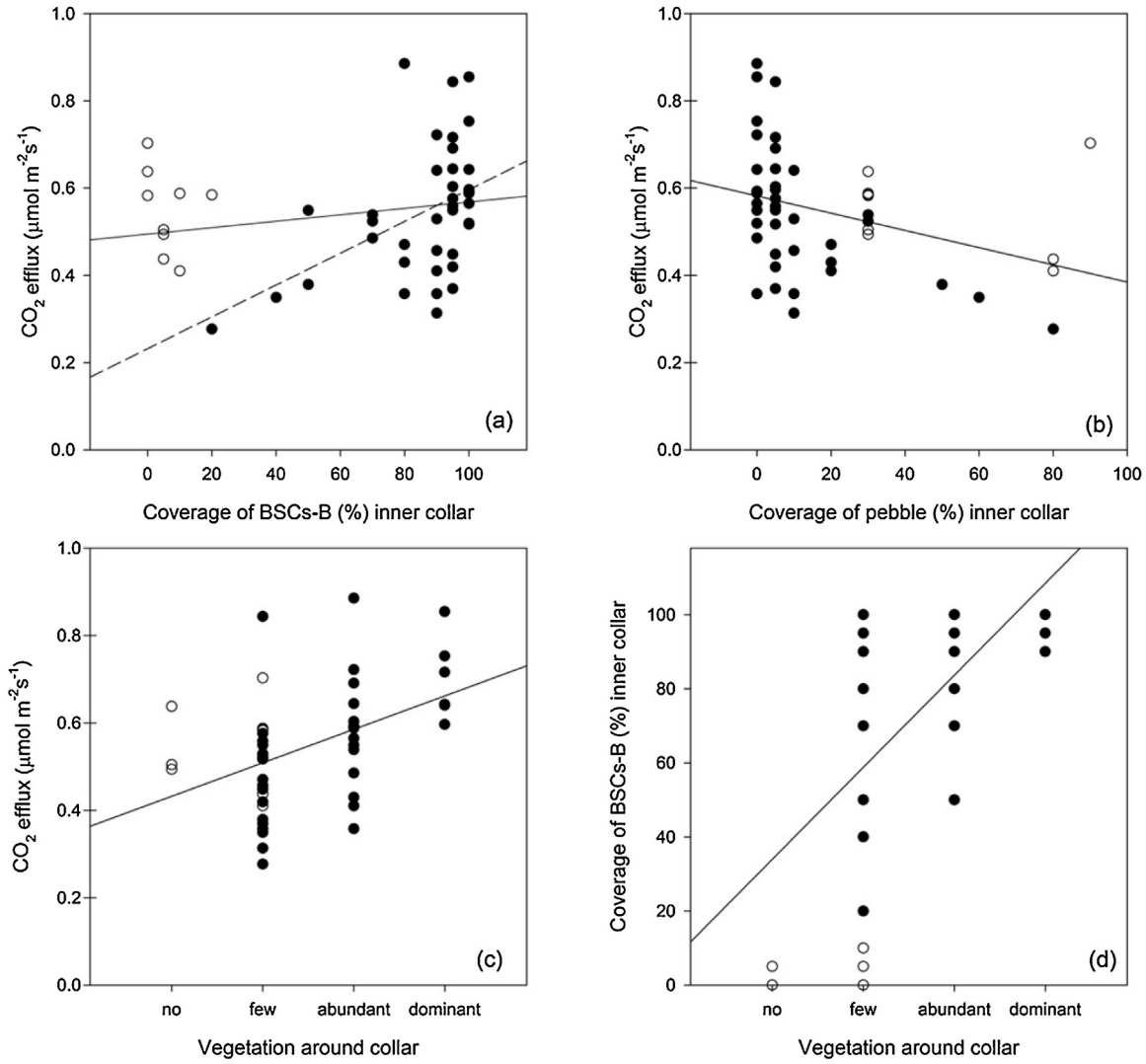

Fig. 6. Relationship between soil CO_2 efflux and coverage of the biological soil crusts with black color (BSCs-B) (a), pebble inner collar (b), and distribution of vegetation around the collar (c) and relationship between coverage of the BSCs-B and distribution of vegetation around the collar (d). Solid line (—) is fitting line with whole data and dashed line (—) is fitting line with whole data except Nos. 2, 4 and 10 (open circle, o).

Table 3
Soil CO_2 efflux, moss CO_2 efflux, soil temperature (Ts (soil), Ts (moss)) and soil water content (SWC (soil), SWC (moss)) for each four couple location (Nos. 2 and 17, 9 and 18, 12 and 19, and 16 and 20).

Parameters	Soil CO_2 efflux/Moss CO_2 efflux ($\mu mol\, m^{-2}\, s^{-1}$)	Ts (soil)/Ts (moss) (°C)	SWC (soil)/SWC (moss) (%)
2007	0.62 (±0.14)/0.71 (±0.18), $p < 0.05$	9.4 (±1.8)/9.1 (±1.6), $p > 0.05$	17 (±5)/19 (±6), $p > 0.05$
2008	0.57 (±0.17)/0.66 (±0.26), $p < 0.05$	8.3 (±2.0)/8.1 (±1.7), $p > 0.05$	19 (±5)/20 (±5), $p > 0.05$
2009	0.49 (±0.14)/0.59(±0.24), $p < 0.05$	9.7 (±2.3)/8.5 (±2.2), $p < 0.05$	18 (±4)/20 (±6), $p < 0.05$

Table 4
Comparison of enzyme activities between biological soil crusts with black color (BC) and mineral soil (MS) collected at 30th June (location Nos. 2, 6, 9, and 15) and 28th July, 2008 (location Nos. 6 and 12). All enzyme activities are significantly different at $p < 0.01$ (mean ± S.E., $n = 6$).

Enzyme activity ($nmol\, g^{-1}{}_{dw}\, min^{-1}$)	ß-glucosidase	*N*-acetylglucosamindase	Phosphatase	Arylsulfatase
June 30th BC	20.1 (±3.6)	23.9(±3.7)	30.6 (±6.5)	6.0 (±2.6)
MS	5.2 (±1.4)	8.5 (±1.7)	6.8 (±1.2)	1.0 (±0.4)
July 28th BC	23.1 (±2.8)	25.4(±3.9)	30.3 (±2.9)	6.1 (±2.8)
MS	7.7 (±3.4)	10.8 (±2.6)	9.9 (±4.1)	2.1 (±1.6)

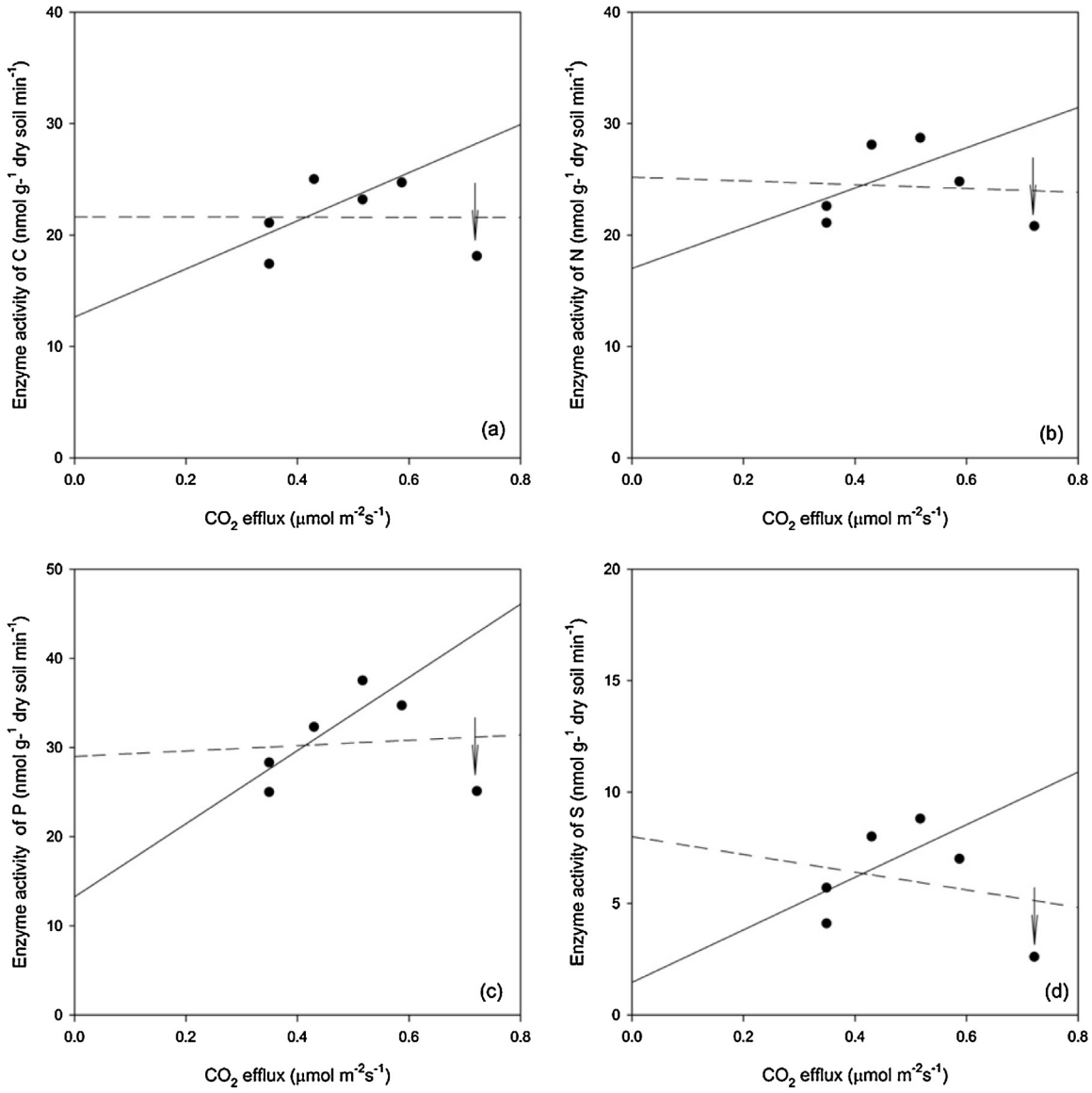

Fig. 7. Relationship between soil CO_2 efflux and microbial activities of biological soil crusts with black color using extracellular enzyme activities of ß-glucoidase (C) (a), *N*-acetylglucosaminidase (N) (b), phosphatase (P) (c), and Arylsulfatase (S) (d). Arrow(↓) in each figure is the outlier (No. 15). Dashed line (—) is fitting line with whole data and solid line (—) is fitting line with data excluded No. 15.

decomposition of organic matter. Given its abundance, BSCs-B should therefore be a major carbon pool in the exchange of CO_2 at the site.

Soil water content was not a main controlling factor for temporal variation of soil CO_2 efflux. SWC inconsistently showed a positive or negative relationship with soil CO_2 efflux at some location, but it could not be correlated with that. This can be due to the relatively well-drained soil condition due to thawing in the high Arctic. This is in accordance with the findings of Elberling (2007) and Strebel et al. (2010), who reported seasonal trends of relationship between soil CO_2 efflux with SWC at Svalbard using same instruments. In the meanwhile, even though CV of SWC was not low, spatial variation of SWC could not explain that of soil CO_2 efflux.

Coverage and thickness of the BSCs-B inner collar showed a positive relationship with the distribution of vegetation around the collar. Consequently, the magnitude of soil CO_2 efflux was influenced by the successional stage of BSCs-B and the distribution of vegetation because BSCs-B with abundant organic carbon supports microbial respiration. However, relationship between soil CO_2 efflux and the coverage of BSCs-B was not significant due to parts of soil CO_2 efflux which are irrelevant to effect of BSCs-B coverage or have another main controlling factor. On the other hand, the soil CO_2 efflux showed significant linear correlation for the coverage of BSCs-B without them. The environmental conditions of these locations are entirely different from the other locations because BSCs-B on the BSCs with pebbles has been gradually developing over the three year period. Therefore, BSCs-B and the other parts of BSCs need to be measured separately to explain the mechanism for emission of soil carbon.

The enzyme activities reported in the present study were much lower than those reported from other Arctic tundra soils (Wallenstein et al., 2009), but this appeared to be related to differences in methods (e.g., buffer addition and enzyme extraction). The overall results indicated that microbial activities were generally higher in the BSCs-B than in the mineral soil at the study site. This is in accordance with the findings of Wallenstein et al. (2009), who reported higher enzyme activities in organic layers than in the mineral soils of shrubs.

The BSCs-B appeared to be more active in decomposition and material cycling compared with carbon poor mineral soil. We originally anticipated a positive correlation between CO_2 flux and enzyme activities, but did not observe a significant correlation due to extremely low activities at the location No. 15. It is not clear why such discrepancy appeared, but we speculate that inhibitory compounds such as humic substances or phenolics may be abundant at the location No. 15. This may provide carbon sources but inhibit extracellular enzyme activities by absorbing in to the active sites of enzymes (Freeman et al., 2001). However, the enzymes activities in BSCs-B exhibited significant correlation with soil CO_2 efflux without No. 15. It seems that enzyme activities measured in BSCs-B can serve as a good surrogate for CO_2 emission in an Arctic tundra system. Gold (1998) reported that the reduced albedo of BSCs-B surfaces leads to higher surface temperatures (8–12 °C) and soil temperatures (4–5 °C) at 0.05 m depth than in non-crusted areas in sunny conditions which may result in more CO_2 emission. This suggests that more attention should be paid to the role of BSCs-B to better understanding of the carbon cycle in the high Arctic when considering the large area they occupies.

5. Conclusion

In this study, we found that soil CO_2 from biological soil crusts with black color was consistently emitted through the long-term in situ measurement in high arctic tundra. Although the estimates of contribution of soil CO_2 efflux to ecosystem respiration was rough, we concluded that its magnitude was significant compared to those from moss and vascular plants in the surface carbon budget. Soil temperature was main controlling factor of the temporal variation of soil CO_2 efflux. Even though spatial variation of soil water content was not small, soil water content could not explain that of soil CO_2 efflux. In addition, we focused on the role of biological soil crusts with black color for soil CO_2 efflux. The coverage and quality of biological soil crusts with black color affected the spatial variation of soil CO_2 efflux. The activity of enzymes in biological soil crusts with black color exhibited generally significant positive correlations with the soil CO_2 efflux except for humic substances. We suggest that soil CO_2 efflux from biological soil crusts with black color must be considered due to an important carbon source in the exchange of CO_2 when carbon cycle is estimated in high arctic tundra under changing climate.

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Appendix A.

Table A1

Table A1
Measured soil CO_2 efflux in situ using chamber method in high Arctic, Svalbard.

Site (season or month)	Soil CO_2 efflu ($\mu mol\ m^{-2}\ s^{-1}$)	Vegetation type	Reference
Spitsbergan, Norway (summer)	0.25 ~ 0.61	Tundra (lichens)	Sendstad, 1981
Spitsbergan, Norway (summer)	0.20 ~ 0.36	Tundra	Dziadowiec, 1983
Ny-Ålesund, Norway (July to August)		Tundra	Nakatsubo et al., 1998
	Site 1: 0.00 ~ 0.20	(bare soil)	
	Site 2: 0.05 ~ 0.26	(bare soil)	
	Site 3–1: 0.08	(bare soil)	
	Site 3–2: 0.25 ~ 0.35	(crust of cyanobacteria and lichens)	
	Site 3–3: 0.51 ~ 0.61	(bryophytes and plants)	
	Site 4–1: 0.21 ~ 0.30	(crust of cyanobacteria and lichens)	
	Site 4–2: 0.24	(bryophytes and plants)	
Ny-Ålesund, (79°N, 12°E) Norway (July to August)		Tundra	Bekku et al., 2004a
	Site 1: 0.04	(little plants; front of glacier toe)	
	Site 2: 0.28	(few vegetation patches; moraine)	
	Site 3: 0.40	(bryophytes and vascular plants; moraine)	
	Site RB: 0.02	(no organic soil and plants; riverbed)	
Adventdalen (78° 10′N, 16° 04E) Svalvard (Summer)		Tundra	Björkman et al., 2010
	Site 1–1: 0.26 (±0.04)		
	Site 1–2: 0.29 (±0.03)		
	Site 2–1: 0.34 (±0.05)		
	Site2–2: 0.42 (±0.09)		
Ny-Ålesund, (78° 55′N, 11° 56E) Norway (July; 3yrs)		Tundra (bryophytes, few vascular plants, and black crusts)	Present study
	0.56 (±0.07, 2007)		
	0.54 (±0.13, 2008)		
	0.51 (±0.09, 2009)		

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