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Effect of crustose lichen (*Ochrolecia frigida*) on soil CO_2 efflux in a sphagnum moss community over western Alaska tundra

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Abstract

Soil CO_2 efflux-measurements represent an important component for estimating an annual carbon budget in response to changes in increasing air temperature, degradation of permafrost, and snow-covered extents in the Subarctic and Arctic. However, it is not widely known what is the effect of curstose lichen (*Ochrolecia frigida*) infected sphagnum moss on soil CO_2 emission, despite the significant ecological function of sphagnum, and how lichen gradually causes the withering to death of intact sphagnum moss. Here, continuous soil CO_2 efflux measurements by a forced diffusion (FD) chamber were investigated for intact and crustose lichen sphagnum moss covering over a tundra ecosystem of western Alaska during the growing seasons of 2015 and 2016. We found that CO_2 efflux in crustose lichen during the growing season of 2016 was 14 % higher than in healthy sphagnum moss community, suggesting that temperature and soil moisture are invaluable drivers for stimulating soil CO_2 efflux, regardless of the restraining functions of soil moisture over emitting soil carbon. Soil moisture does not influence soil CO_2 emission in crustose lichen, reflecting a limit of ecological and thermal functions relative to intact sphagnum moss. During the growing season of 2015, there is no significant difference between soil CO_2 effluxes in intact and crustose lichen sphagnum moss patches, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). Considering annual soil CO_2 effluxes simulated by temperature, as well as monitoring of snow depth by time-lapsed camera, average snow-covered and snow-free CO_2 contributions to annual carbon budgets correspond to 28.4 % and 71.6 % in intact sphagnum moss cover, and 25.0 % and 75.0 % in a crustose lichen sphagnum moss colony, respectively. Therefore our findings demonstrate that soil CO_2 emissions in the crustose lichen-infected sphagnum moss community would be steadily stimulated by a widespread outbreak of airborne plants over intact sphagnum moss, and by a rapid degradation of permafrost in response to drastic changes in climate and environment in the Subarctic and Arctic.

1 Introduction

Soil carbon dioxide (CO_2) efflux, produced through the decomposition of soil organic carbon and roots, signifies the second largest terrestrial carbon source on both time and space scales (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Bond-Lamberty and Thomson, 2010). This efflux is susceptible to increasing air temperature (ACIA, 2004; AMAP, 2011), the degradation of permafrost (Schuur et al., 2009; Jensen et al., 2014; Lawrence et al., 2015; Natali et al., 2015), changing snow cover extent (AMAP, 2011), and the expansion of the shrub community (Sturm et al., 2005; Bhatt et al., 2013). All of this suggests an alteration of the terrestrial carbon cycle in response to drastic changes in climate and environment in the Arctic (ACIA, 2004; AMAP, 2011). These changes affect the high-latitude terrestrial carbon cycle and budget, via changes in vegetation productivity (Euskirchen et al., 2006; Barr et al., 2007; Bhatt et al., 2013), decomposition of soil organic matter (Piao et al., 2008; Wu et al., 2012), and the degradation of permafrost (Schuur et al., 2009; Jensen et al., 2014; Lawrence et al., 2015; Natali et al., 2015). Of the changes documented in the Arctic, an increase in temperature is most important, as it drives positive feedbacks on regional and pan-Arctic scales (Chapin et al., 2000; ACIA, 2004). Soil carbon dynamics in tundra and boreal forest ecosystems represent strong temperature sensitivity, a factor characterized by Q_{10} value, which describes an increase in respiratory rate with a given 10 °C temperature change (Xu and Qi, 2001; Davidson and Janssens, 2006; Bond-Lamberty and Thomson, 2010; Mahecha et al., 2010; Kim et al., 2013; 2014a; 2014b; 2016; Kim, 2014). Bond-Lamberty and Thomson (2010) estimated a global soil respiration rate of 98 ± 12 GtC ($1 GtC = 10^{15}$ gC), indicating an increase of 0.1 GtC year^{-1} over two decades. This rate of increase suggests a CO_2 emission response factor of 1.5 compared to air temperature, which is consistent with enhanced soil CO_2 emission response to a warming global climate.

Sphagnum moss (*Sphagnum* spp.) is widely distributed over the permafrost regions of the Subarctic and Arctic, and the thermal insulative capacity and preservation of permafrost is strongly influenced by the water content of the moss layer (Yoshikawa et al., 2004). Living sphagnum mosses have impressive water holding potential, with a number of species able to hold

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twenty or more times as much water as their dry weight (Turetsky et al., 2010). Sphagnum moss habitats store large amounts of carbon, which helps reduce global warming (Fraser and Keddy, 2005). Nevertheless, crustose lichen (*Ochrolecia frigida*) infects the living sphagnum moss community through airborne spread and finally causing the withering to death of healthy sphagnum moss. Lichen is a composite organism that arises from algae, with cyanobacteria living among filaments of multiple fungi species in a mutualistic relationship (Vitt et al., 1988; Hasselbach and Neitlich, 1998; Spribille et al., 2016). Lichens may have tiny, leafless branches (fruticose), a flat leaf-like structure (foliose), flakes that lie on the surface like a peeling plant (crustose), a powder-like appearance (leprose), or other growth forms (Hasselbach and Neitlich, 1998; USDA, 2006). Lichens do not have roots that absorb water and nutrients as plants do, but like plants, they produce their own nutrition by photosynthesis in foliose and fruticose forms (Hahn et al., 1993; Otto et al., 1996; Hasselbach and Neitlich, 1998; Inoue et al., 2014). Most lichens produce abundant sexual structures and appear to disperse only by sexual spores (Murtagh et al., 2000). The crustose lichens *Graphisscripta parella* and *Ochrolecia frigida* reproduce sexually by self-fertilization (i.e., they are homothallic). This breeding system enables successful reproduction in harsh environments (Murtagh et al., 2000). However, it is not well known what is the influence of crustose lichen-infected sphagnum moss cover, which is commonly distributed on several moss species and peats in the high Arctic (Gary Laursen; personal communication). The crustose lichen *O. frigida* is a sorediate Arctic lichen that grows on plant materials, displays pink ascoma discs (Hasselbach and Neitlich, 1998), and shows high adaptation for light reflectance (Hahn et al., 1993; Otto et al., 1996). Thus, if crustose lichens invade over sphagnum moss cover, the moss could wither and die, losing its preservation of permafrost. Here we investigated the difference in soil carbon emission from healthy and crustose lichen-infected sphagnum communities in a tundra ecosystem during the growing season.

Temperature and soil moisture are the most significant parameters for governing soil CO_2 efflux across the tundra and boreal forest ecosystems of the Subarctic and Arctic (Lloyd and Taylor, 1994; Davidson et al., 1998; Davidson and Janssens, 2006; Rayment and Jarvis, 2000; Oberbauer et al., 2007; Kim et al., 2007; 2013; 2014a; 2014b; 2016; Jansen et al., 2014; Kim, 2014;

Euskirchen et al., 2017); further, these environmental parameters must be efficiently validated for terrestrial ecosystem process-based models (e.g., Land Surface Models), for the assessment of carbon balance and budgets on regional and global scales. Consistent exertions are needed to evaluate these environmental parameters modulating soil CO_2 efflux in the sphagnum moss community of the tundra ecosystem during the growing season. Euskirchen et al. (2017) found that increases in air temperature and soil temperature at soil depths may have triggered a new trajectory of CO_2 release from 2008 to 2015, which would be a significant feedback toward further warming if it is representative of large areas of the Arctic.

The purposes of this study are to 1) determine the environmental drivers resolving soil CO_2 emissions in intact and crustose lichen-infected sphagnum moss regimes of the tundra ecosystem in western Alaska; 2) estimate soil CO_2 emission in sphagnum moss communities by continuous forced diffusion (FD) chamber system during the growing seasons of 2015 and 2016; and 3) assess the contributions from seasonally snow-covered- and snow-free-period carbon toward the simulated annual carbon budget, based on in-situ temperature and snow depth.

2 Materials and Methods

2.1 Sampling Descriptions and Methods

The crustose lichen (*Ochrolecia frigida*) strongly adheres to a substrate such as sphagnum moss, making separation from the substrate impossible without destruction. Generally, crustose lichens that cling to soil, rock, and tree bark can be found in a wide range of areas. In this study, we found several crustose lichen colonies on sphagnum moss in the tundra ecosystem of western Alaska (Supplementary Figure S1). Crustose lichen eventually causes a withering to death of sphagnum moss that has preserved discontinuous permafrost from degradation, due to protection from water evaporation (Yoshikawa et al., 2004).

Our research site is located within a tundra ecosystem of dominant caribou lichen (*Cladonia mitis, Cladonia crispata, and Cladonia stellaris*), sphagnum moss (*Sphagnum magellanicum, Sphagnum angustifolium, and Sphagnum fuscum*) and tussock tundra (*Eriophorum vaginatum*) communities. Understory lichen, sphagnum moss, and tussock tundra occupied fractions of 27, 53, and 20 % of the site, respectively. Using a forced diffusion (FD) chamber system method (Kim et al., 2016), soil CO_2 efflux was continuously measured at intact and crustose lichen-infected sphagnum communities (64°51'42.8"N; 163°42'39.1"W; 42 a.s.l.m.) underlain by discontinuous permafrost in the tundra ecosystem of Council in western Alaska, during the growing seasons of 2015 and 2016.

The annual average air temperature and precipitation were -3.2 °C and 394 mm, respectively, at the Nome airport from 1907 to 2016. Air temperature ranged from 24.2 °C in June to -33.1 °C in January in 2015, and from 22.4 °C in May to -27.1 °C in December in 2016 at Council. Annual precipitation in 2015 and 2016 were 401 and 632 mm, respectively, including winter snowfall (Western Regional Climate Center). During the growing season (June to September), average ambient temperature and summed precipitation were 9.5 ± 4.9 °C and 272 mm in 2015 (Kim et al., 2016), and 12.1 ± 3.8 °C and 597 mm in 2016, respectively. The precipitation in August to September corresponds to 67 and 66 % of the entire growing seasons for 2015 and 2016, respectively. Growing season temperature and precipitation for the past century was 8.4 ± 2.5 °C and 215.4 mm, indicating cooler and much drier conditions. In other words, the growing periods in 2015 and 2016 represent much hotter and wetter conditions than during the rest of the past century. Our research site can be only be approached from early June to early October, as the access road to Skookum Pass is kept closed during the snow-covered period by the Alaska Department of Transportation.

Soil temperature was measured at 2 and 5-cm depths below the surface within intact and crustose lichen-infected sphagnum moss colonies using two loggers with five sensors in 2015 and 2016 (logger: U12-006; sensor: TMC-HD, Onsetcomp, USA). Ambient temperature at 2.0 m above the surface was also monitored at the site. Soil moisture at 2 and 5-cm depths below the surface of each sphagnum colony was also measured with two loggers and four probes (logger: H21-002; probe: SMD-M005, Onsetcomp, USA) in parallel with soil temperature (Figure 2), showing the same period as observations of soil CO_2 efflux-measurement. Snow depth was monitored using time-lapse camera at a six-hour interval from September 22, 2015 to June 13, 2016 (Supplementary Figure S2).

2.2 Forced Diffusion (FD) CO_2 Efflux Chamber

The FD CO_2 efflux chamber (Eosense, Canada) is a yearlong continuous soil CO_2 efflux-measuring system similar to a dynamic chamber, as described in Kim et al. (2016) in detail. The FD structure consists of a single high-accuracy CO_2 sensor, an internal data-logger, two valves, and a small diaphragm pump that operates only for short duration to bring a target air sample to the sensor (Risk et al., 2011). The CO_2 sensor can determine a wide range efflux of 0 to 20 μmol m^{-2} s^{-1} at a measuring interval from 5 to 1440 min, under the ambient temperature of -20 to 50 °C. The sensor is operated by a 12-volt power supply system including a cold-proofed external battery (105-A AGM PVX-1040, USA), a 140-W solar panel (KD140GX-LFBS, Kyocera Solar Inc., Japan), and a solar power charge converter (Morningstar S20 SunSaver, USA). As shown in Supplementary Figure S1-a, we chose two target areas of intact and crustose lichen-infected sphagnum communities, representing a relatively smooth and flat surface for mounting the FD chamber on a previously installed soil collar (7.5-cm inside diameter; 9.0-cm outside diameter; 10-cm height). The chamber was fixed with an attached mounting ring and four legs. Two FD chambers were monitored from June 25, 2015 at the intact and crustose sphagnum microsites. However, we could not determine the winter season CO_2 efflux during the observation periods of 2015 and 2016 due to the heavy snow-covered solar panel by unexpected winter storms. We confirmed heavy snowfall in early December of over 1.0 m using time-lapse camera data.

As shown in Figure 1, we performed a test in sampling time between 10-min (with 30-min average) and 30-min intervals at the intact sphagnum community from June 25 to July 23, 2015. Soil CO_2 efflux at mean 30-min with 10-min intervals and at 30-min intervals was 0.91 ± 0.21 μmol m^2 s^{-1} and 0.90 ± 0.20 μmol m^2 s^{-1}, respectively, suggesting that there was no significant difference, based on a one-way ANOVA at the 95 % confidence level ($p < 0.001$). As a result, we set the 30-min sampling interval during the observation periods of 2015 and 2016, in order to maintain low power consumption.

2.3 Simulated Soil CO_2 Efflux

We estimated the temperature sensitivity of soil CO_2 efflux collected by FD chamber by plotting the exponential relationship between air temperature and soil temperature at depths of 2 and 5 cm, in intact and crustose lichen-infected sphagnum moss colonies, by using the following equation:

$$CO_2\ efflux = \beta_0 \times e^{\beta 1 \times T}, \qquad (1)$$

where CO_2 *efflux* is the *measured daily soil* CO_2 *efflux* (μmol m^{-2} s^{-1}), T is temperature (°C), and β_0 and β_1 are constants. This exponential relationship is commonly used to represent soil carbon flux as a function of temperature (Davidson et al., 1998; Xu and Qi, 2001; Davidson and Janssens, 2006; Rayment and Jarvis, 2000; Kim et al., 2014a, 2014b, 2016). Q_{10} temperature coefficient values were calculated as in Davidson and Janssens (2006) and Kim et al. (2016):

$$Q_{10} = e^{\beta 1 \times 10}, \qquad (2)$$

Q_{10} here is a measure of the change in reaction rate at intervals of 10 °C and is based on Van't Hoff's empirical rule that a rate increase of 2 to 3 times occurs for every 10 °C rise in temperature (Lloyd and Taylor, 1994).

A reference value for $R_{10} = \beta_0 \times e^{\beta 1 \times 10}$ (i.e., soil CO_2 efflux normalized to air temperature of 10 °C), where β_0 and β_1 are constants from equation (1), based on monthly calculations. Using the calculated values for Q_{10} and R_{10}, soil CO_2 efflux was simulated on the basis of the measured air temperature. Simulated monthly soil CO_2 efflux values R_i (μmol m^{-2} s^{-1}) (as in Qi et al. (2002); Curiel Yuste et al. (2004, 2005); Edwards et al. (2006); Gaumont-Guay et al. (2006, 2008); Begeron et al. (2007); Kim et al. (2014, 2016); and Makita (2017)), were calculated as:

$$R_i = R_{10} \times Q_{10}^{[(T-10)/10]}. \qquad (3)$$

The parameters of the nonrectangular hyperbola function were determined daily, using a seven-day moving window and the least-squares method. Soil CO_2 efflux (SR) was estimated using the following two models (Ueyama et al., 2014):

$$CO_2\ efflux = R_0 \times Q_{10}^{(Ta/10)}\ , \qquad (4)$$

$$CO_2\ efflux\ = R_{ref} \times [\frac{E_0}{R_{gas}}\left(\frac{1}{T_k + T_{ref} - T_0} - \frac{1}{T_k + T_a - T_0}\right)], \qquad (5)$$

where T_a is air temperature at 0.5 m, R_o represents soil CO_2 efflux at 0 °C, and Q_{10} is the temperature sensitivity coefficient of soil CO_2 efflux. R_{ref} is the soil CO_2 efflux at T_{ref}, E_0 is the activation energy, and R_{gas} is the ideal gas constant. T_k, T_0, and T_{ref} are 273.15 K, 227.13 K, and 283.15 K, respectively (Lloyd and Taylor, 1994). We used the conventional Q_{10} model to estimate soil CO_2 efflux, but used the Lloyd and Taylor model equation (6) for uncertainty estimates, as Q_{10} exhibited clear seasonal variations, whereas E_0 showed no discernable seasonal variation.

3 Results and Discussion

3.1 Temporal Variations in Environmental Parameters

Ambient air temperature at 2.0 m above the surface ranged from -33 °C to 24 °C for 2015, and from -27 °C to 22 °C for 2016. Average air temperature was 10.7 and 11.6 °C during the growing seasons (June to September) of 2015 and 2016, respectively, which was much higher than the 8.7 °C annual average air temperature during the growing seasons of 1960 and 2016. Figure 2 shows temporal variations in soil temperature and soil moisture at 2-cm (Figure 2a) and 5-cm (Figure 2b) depths during the observation periods of 2015 and 2016. Soil temperature at 2-cm depth was greater than at 5-cm depth during the growing seasons, indicating a significant difference at intact sphagnum moss but no significant difference for the crustose sphagnum moss community, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). Soil temperature at 2 cm for the intact sphagnum regime was higher than at the crustose colony, representing a significant difference (95 % confidence level; $p < 0.05$); on the other hand, soil temperature at 5 cm for intact sphagnum was lower than the crustose community, though not significantly different (95 % confidence level; $p < 0.05$), as shown in Table 1.

From the strong linear relationship between air temperature and soil temperature, air temperature accounts for 82 % and 76 % of variability in soil temperature at 2- and 5-cm depths during the growing seasons of 2015 and 2016, respectively. Ambient temperature was a useful proxy for soil temperature. The air temperature of 13.0 ± 1.9 °C in August of 2016 was much greater than 10.1 ± 2.7 °C in August of 2015, resulting in the significant difference in soil temperature at 2- and 5-cm depths in August between 2015 and 2016, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). This may have prompted the difference in soil CO_2 emission between the Augusts of 2015 and 2016, as temperature is a key driver in regulating soil CO_2 production and emission to the atmosphere (Xu and Qi, 2001; Davidson and Janssens, 2006; Kim et al., 2014b; 2016).

Peaks in soil moisture during the soil thawing of early May were found at 2- and 5-cm depths in 2015 and 2016 (Figure 2), suggesting the response from soil moisture at 2- and 5-cm depths for intact sphagnum is much more sensitive to soil thawing than at crustose regime. This may reflect the difference in moisture holding capacity between live and shriveled sphagnum. During the observation periods of 2015 and 2016, soil moisture at 2- and 5-cm depths in intact sphagnum moss cover was explicitly higher than in crustose sphagnum moss patch, indicating a significant difference, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). Soil moisture at 2-cm depth was lower than 5-cm depth at the intact sphagnum moss colony, showing a significant difference based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). However, at the crutose lichen-infected sphagnum moss regime, soil moisture at 2-cm depth was similar to those at 5-cm depth, representing no significant difference based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). This reflects the lower, analogous soil moisture between 2- and 5-cm depths of crustose moss relative to intact sphagnum moss, proving that the forfeiture of essentially physiological and ecological functions occurs by the airborne infection of crustose lichen (*O. frigida*) on healthy sphagnum moss.

Soil moisture was sensitive to rainfall events during the growing seasons of 2015 and 2016. Soil thawing timing can detect a sudden rise of soil moisture at 2- and 5-cm depths in intact and crustose sphagnum moss communities in early spring of 2015 and 2016 (Figure 2b), in parallel to a sharp jump of soil temperature at 2-cm depth at both sphagnum moss regimes (Figure 2a). We computed thawing rates between 2- and 5-cm depths when soil moisture was over 0.20 m^3 m^{-3}, representing thawing rates in the early spring of 2015 and 2016 of 0.75 and 0.27 cm day^{-1} at intact sphagnum moss. On the other hand, thawing rates at crustose sphagnum moss between the two depths are nearly 0 cm day^{-1}. This demonstrates the crustose lichen-infected sphagnum moss loses the soil moisture holding capacity by causing the withering and death of intact sphagnum moss. However, the mean thawing rate of 0.438 cm day^{-1} is comparable with those in this study during the growing seasons of 2011 to 2014 obtained at neighboring sites (Kim et al., 2016). When soil temperature drops to below zero during the late growing season of 2015, soil moisture falls sharply at 2-cm depth in intact (0.24 to 0.16 m^3 m^{-3}) and crustose (0.22 to 0.05 m^3 m^{-3}; Figure 2a), respectively. Ironically, soil moisture at 2-cm depth in crustose sphagnum moss has maintained higher levels than in intact sphagnum moss since August of 2016; on the other hand, soil moisture at 5-cm depth in crustose sphagnum moss since the late growing season of 2016 is lower than the intact sphagnum moss community. The latter demonstrates natural phenomena as shown in 2015 (Figure 2a and 2b).

These changes in daily snow accumulation and ablation are documented by time-lapse camera at six-hour intervals from September 22, 2015 to June 13, 2016, as shown in Supplemental Figure S2. Snow-covered day and snow-disappearance day are November 3, 2015 and May 6, 2016, respectively, based on the criteria that 1) lingering snowpack cover exceeds fifteen consecutive days upon the snow-covered day, and 2) less than half of the surface is covered by snowpack according to the naked eye upon the snow-disappearance day.

3.2 Seasonal Variations in Soil CO_2 Emissions

Soil CO_2 efflux-measurement was initiated on intact and crustose lichen-infected sphagnum moss communities beginning June 25, 2015. CO_2 emissions and air temperature were measured with the FD chamber system at both sphagnum moss regimes from June 25 to November 9, 2015, and from June 18 to September 28, 2016, respectively (Figure 3). Unfortunately, we could not determine the winter season soil CO_2 emission, due to shutoff of the solar panel power supply by unexpected deeper snowfall in the early winter of 2015. Average growing season soil CO_2

effluxes at intact and crustose sphagnum moss regimes were 0.39 ± 0.18 and 0.38 ± 0.22 μmol m^{-2} s^{-1} for 2015, and 0.38 ± 0.21 and 0.42 ± 0.27 μmol m^{-2} s^{-1} for 2016, respectively (Table 1). The difference in soil CO_2 effluxes between intact and crustose for the first efflux-measuring year (2015) was not significant, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). However, the difference between the regimes for the second year (2016) was significant (95 % confidence level, $p < 0.05$), indicating the average ratio of crustose to intact soil CO_2 effluxes was 1.70 ± 1.27 (Table 1), a distinct increment of 70 % compared to intact soil CO_2 emissions during the growing season of 2016. Responses from soil CO_2 efflux at intact sphagnum moss to crustose sphagnum moss showed positively linear relationships ($Intact\ CO_2 = 0.98 \times Crustose\ CO_2 - 0.01$; $R^2 = 0.73$ *for 2015*; $Intact\ CO_2 = 0.51 \times Crustose\ CO_2 + 0.24$; $R^2 = 0.17$ *for 2016*), as shown in Figure 4. This implies that higher soil CO_2 efflux during the growing season of 2016 is associated with enhanced decomposition of organic matter at crustose lichen-infected sphagnum moss under a hotter and drier soil environment (Figure 2), relative to the intact sphagnum moss community.

There is little data on CO_2 efflux-measurements from crustose lichen-infected sphagnum moss, which may indicate a lack of attention toward the ecological and climate impacts upon crustose lichen in Arctic terrestrial ecosystems. On the other hand, biological soil crusts (BSCs), which are the first organisms to colonize the exposed soil surface, inhabit an organic layer less than 0.01 m thick in the early stage of primary succession after glaciers retreated (Belnap and Lange, 2003). Also, BSCs consist of the organic residues from lichen, moss, and cyanobacteria through the successional stages after deglaciation. Nakatsubo et al. (1998), Yoshitake et al. (2007), and Chae et al. (2016) measured soil microbial respiration on the BSCs with black color (BSCs-B), including soil surface communities consisting of blackish organic residues in Ny-Ålesund, Svalbard, Norway, ranging from 0.21 to 0.35 μmol m^{-2} s^{-1}. These values are similar to the results obtained in this study; however, previous results were determined by the manual chambers when they infrequently visited the sites in summer (Savage and Davidson, 2005). Depending on the observation schedule and field sites, the low-data approach can suffice for seasonal totals, but may lead to critical episodic and process-driven events being missed or misinterpreted. Parkin and Kaspar (2003) offered a detailed study on the effect of measuring frequency, demonstrating that using a scheduled daily measurement for CO_2 efflux-estimates can result in a deviation of up to 30 % from the daily average. The net impact this bias has on estimated effluxes depends on the daily emission range, meaning that the estimation error will change with environmental and seasonal trends (Savage and Davidson, 2005; Kim et al., 2016).

3.3 Sensitivity of Soil CO_2 Emissions to Temperature and Soil Moisture

Responses in soil CO_2 efflux observed at intact and crustose lichen-infected sphagnum moss communities to temperature in air and soil at 2- and 5-cm depths during the observation periods of 2015 and 2016 are shown in Figure 5. Soil CO_2 efflux follows the normal exponential relationship to temperature as in the equation (1). In terms of month-based Q_{10} value as listed in Table 2, the values in June and July of 2015 are much lower than other months, due to nearly fixed soil CO_2 effluxes at intact and crustose sphagnum moss communities relative to changes in temperature (Figure 3). Furthermore, the highest Q_{10} values in September of 2016 at intact sphagnum moss are 10.8, 17.3, and 48.6 for the temperature in air and soil 2- and 5-cm depths, respectively. The greatest Q_{10} values in August of 2016 at crustose sphagnum moss were 3.32, 15.9, and 16.3 for the temperature in air and soil 2- and 5-cm depths, respectively. This suggests a seasonal dependence of soil CO_2 efflux on temperature for two sphagnum moss patches. Average temperature in air and soil at 2- and 5-cm depths elucidates over 60 % of variability in soil CO_2 effluxes at intact and crustose sphagnum moss for 2015; however, the sensitivity of soil CO_2 effluxes to temperature for 2016 was much lower than for 2015.

During the observation periods of 2015 and 2016, soil temperature at 2- and 5-cm depths is strongly dependent on seasonal variations in air temperature. Temperature is a most significant driver in modulating soil CO_2 emission in terrestrial ecosystems (Davidson et al., 1998; Xu and Qi, 2001; Davidson and Janssens, 2006; Rayment and Jarvis, 2000; Bond-Lamberty and Thomson, 2010; Kim et al., 2014a, 2014b, 2016). On the other hand, soil moisture is an important parameter in constraining CO_2 emissions in the intact sphagnum moss community, tundra ecosystems of west Alaska during the growing seasons of 2011 and 2012 (Kim et al., 2014b), and other terrestrial ecosystems (Davidson and Janssens, 2006; Davidson et al., 1998; Oberbauer et al., 2007; Jansen et al., 2014). Although there was heavy rain for August and

September of 2016 (393.5 mm) compared to 2015 (181.5 mm), observed soil CO_2 effluxes at intact and crustose sphagnum moss communities were not lower than 2015. This may be due to a loss of water-retaining capacity at the crustose lichen-infected sphagnum moss regime, with higher soil CO_2 effluxes than the intact sphagnum moss in the latter half of the 2016 growing season. Moreover, we found that soil moisture content at 5-cm depth in intact sphagnum moss is much greater than in the crustose sphagnum moss colony since August of 2016, as shown in Figure 2b. Therefore, while soil moisture acts as a well-known key role in restraining soil CO_2 emissions in the intact sphagnum moss community, soil moisture in crustose sphagnum moss is not prompted to emit soil carbon to the atmosphere (Table 1).

The correlation coefficients (R^2) for temperature in air and soil at intact and crustose sphagnum moss of 2015 were higher than 2016. We found distinct difference in the response from soil CO_2 efflux to air and soil temperature at 2- and 5-cm depths. Q_{10} values at intact and crustose sphagnum moss during 2015 and 2016 can be estimated by equation (2). Q_{10} value increases with soil depth, indicating that the extent of soil temperature at deeper soil depth appears much narrower than at shallower depth (Mikan et al., 2004; Pavelka et al., 2007; Kim et al., 2014; Kim et al., 2016).

During the growing seasons of 2015 and 2016, Figure 6 shows seven-day moving Q_{10} values, calculated for each of research plots using equation (6). Using average two-growing-season Q_{10} values ± standard deviation for air temperature, soil temperature at 2- and 5-cm depths are 2.37 ± 0.68, 2.25 ± 0.72, and 2.16 ± 0.58 at intact, and 2.31 ± 0.65, 2.44 ± 0.63, and 2.59 ± 0.77 at crustose sphagnum moss, respectively. Furthermore, Q_{10} values at crustose sphagnum moss are wildly more fluctuant than Q_{10} values at intact sphagnum moss in late growing seasons of 2015 and 2016.

3.4 Estimation of Simulated Soil CO_2 Efflux

Based on Q_{10} and R_{10} relationships (equation 2 ~~and 3~~), simulated daily soil CO_2 effluxes at intact and crustose sphagnum moss communities were estimated using equation (3) and *in-situ* temperature in air and soil at 2- and 5-cm depths from June 25, 2015 to September 28, 2016, with temporal variation in air temperature (Figure 7). Temporal variations in simulated soil CO_2 effluxes are synchronized with seasonal variation of ambient temperature, reflecting that soil temperature at 2- and 5-cm depths accounted for 92 and 82 % of the variability in air temperature at intact sphagnum, and 88 and 82 % of the variability in air temperature at the crustose sphagnum moss colony for 2015, respectively. For 2016, soil temperature at 2- and 5-cm depths elucidated 90 and 76 % of the variability in air temperature at intact sphagnum, and 81 and 80 % of the variability in air temperature at crustose sphagnum moss community, respectively. Air temperature is an important key in stimulating soil temperature in terrestrial ecosystems (Kim et al., 2014a, 2016). The relationships between observed and simulated daily soil CO_2 effluxes were positively linear during the two growing seasons of 2015 and 2016, as shown in Figure 8. This suggests that the observed soil CO_2 effluxes account for 64, 70, and 72 % of the variability in daily soil CO_2 effluxes simulated by temperature in air and soil at 2- and 5-cm depths at intact sphagnum moss cover, and the observed soil CO_2 effluxes explain 48, 63, and 60 % of the variability in simulated daily soil CO_2 effluxes by three temperatures at the crustose sphagnum moss colony, respectively. During the two growing seasons of 2015 and 2016, the difference between observed and simulated soil CO_2 effluxes by temperature in air and soil 2- and 5-cm depths at two sphagnum moss colonies were significantly different, based on a one-way ANOVA at the 95 % confidence level ($p < 0.05$). However, the difference between observed and simulated soil CO_2 effluxes from air temperature at intact sphagnum moss cover for 2016 is not explicitly significant difference ($p < 0.05$).

Average simulated monthly soil CO_2 efflux was also computed and is listed in Table 3, showing the seasonal pattern and including the low rate of CO_2 emission that can be expected overwinter during snow-covered period (186 days), as described in section 3.1 and shown in Supplemental Figure S2. Although non-growing season soil CO_2 efflux by FD chamber was not measured in this study, determining the annual carbon budget using simulated daily soil CO_2 efflux for three temperatures with time-lapse camera data, we can establish seasonal budgets during snow-covered and snow-free periods. Simulated soil CO_2 effluxes in intact sphagnum moss are 13.7, 22.0, and 22.5 gC m^{-2} $period^{-1}$ for temperature in air and soil at 2- and 5-cm depths during the snow-covered period, corresponding to 20.0, 30.5, and 34.8 % of annual simulated carbon

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emissions, respectively. The winter-simulated soil CO_2 effluxes in crustose lichen-infected sphagnum moss are 10.4, 16.8, and 17.1 gC m^{-2} period^{-1} for three temperatures, corresponding to 16.2, 28.4, and 30.4 % of annual simulated carbon emission, respectively. On the other hand, during the snow-free period, average simulated soil CO_2 effluxes in intact sphagnum moss are 57.1, 50.2, and 41.9 gC m^{-2} period^{-1} for temperature in air and soil 2- and 5-cm depths, corresponding to 80.0, 69.5, and 65.2 % of annual carbon emissions, respectively. Further, the simulated soil CO_2 effluxes in crustose lichen-infected sphagnum moss are 55.7, 43.8, and 40.5 gC m^{-2} period^{-1} for three temperatures, corresponding to 83.8, 71.6, and 69.6 % of annual simulated carbon emission, respectively.

On the whole, 28.4 % and 25.0 % of annual simulated soil CO_2 effluxes in intact and crustose sphagnum moss patches (respectively) were likely emitted through the snowpack to the atmosphere during the non-growing season with the remainder during the growing season. Many previous studies on winter soil CO_2 efflux-measurement have represented similar aspects, and winter contributions to soil CO_2 emission have generally elucidated 10 to 30 % of annual carbon budgets for tundra (Oechel et al., 1997; Fahnestock et al., 1998; Björkman et al., 2010; Kim et al., 2013; 2016), alpine and subalpine forests (Brooks et al., 1996; Mast et al., 1998; Monson et al., 2006), and boreal forests (Winston et al., 1997; Kim et al., 2007; 2013; Kim, 2014).

Kim et al. (2014b) found the deviation between the manual chamber and continuous measurement by FD chamber methods as high as 47 %. This may be due to differences in measuring method and frequency under sunny sky (manual) compared to year-long and continuous (FD). The additional measuring frequency possible with FD could cause some re-evaluation of interpreted annual carbon budgets at representative spots, and would aid in applying terrestrial ecosystem models (e.g., land surface models (LSMs)) to high time-resolution data. Therefore, continuous monitoring of soil CO_2 efflux-measurement using FD chambers initiates new fields of opportunity and understandings. As drastic climate warming enhances permafrost degradation in the Subarctic and Arctic, we will reckon with large stocks of ancient soil carbon that will become available for microbial activation (Schuur et al., 2009; Tarnocai et al., 2009; Grosse et al., 2011), as well as other ecological and biogeochemical significance

(Walter et al., 2008; Schuur et al., 2009; Zona et al., 2009; Sachs et al., 2010; Lawrence et al., 2015; Natali et al., 2015) across the landscape. Therefore, yearlong soil CO_2 efflux using FD chamber systems will be required to pursue concurrent changes in carbon storage response to a microbial outbreak in the Arctic-wide distributed extents of the sphagnum moss regime (Whalen and Reeburgh, 1998).

4 Conclusions

Soil CO_2 efflux measurement is an important component for estimating annual carbon budgets in response to changes in increasing ambient temperature, thawing permafrost, and snow-covered extent in the Subarctic and Arctic. Here, continuous monitoring of soil CO_2 efflux using a forced diffusion (FD) chamber system was performed at intact and crustose lichen (*Ochrolecia frigida*)-infected sphagnum moss communities of tundra ecosystem in western Alaska during the growing seasons of 2015 and 2016. Temperature was a key driver in governing soil CO_2 efflux at two sphagnum moss patches during the observation periods of 2015 and 2016. Furthermore, ambient temperature elucidates over 80 % of the variability in soil temperature at 2- and 5-cm depths during those two growing seasons. At the crustose sphagnum moss community, the differences in soil temperature and soil moisture at 2- and 5-cm depths are not explicit, suggesting the loss of ecological and thermal functions. Thus, soil moisture plays a significant role in retraining soil CO_2 emission in healthy sphagnum moss carpets (Davidson et al., 1998; Davidson and Janssens, 2006; Oberbauer et al., 2007; Jansen et al., 2014; Kim et al., 2014b). Further, soil moisture in withered sphagnum moss patches is not so much as a limiter as a stimulator for soil carbon emission. Responses from soil CO_2 efflux at intact sphagnum moss to crustose sphagnum moss patches show positive linear relationships, indicating that soil CO_2 efflux at crustose sphagnum moss explains 73 % and 17 % of variability in soil CO_2 efflux at the intact sphagnum moss colony for 2015 and 2016, respectively. This implies that high soil CO_2 efflux during the growing season of 2016 resulted from enhanced decay of soil organic matter at crustose lichen-infected sphagnum moss under the hot and moist soil environment relative to the intact sphagnum moss community. This finding thus demonstrates the shriveled sphagnum moss colony is an atmospheric CO_2 source reservoir, and that the degradation of permafrost will be stimulated by the widespread outbreak of airborne crustose lichen on the healthy sphagnum moss community response to rapid climate change in the Subarctic and Arctic.

Simulated daily soil CO_2 effluxes at intact and crustose lichen-infected sphagnum moss communities were estimated using *in-situ* temperature in air and soil at 2- and 5-cm depths from June 25, 2015 to September 28, 2016, with temporal variation in air temperature, which can discriminate between seasonally snow-covered and snow-free soil carbon emissions. Time-lapse camera data provides us beneficial information for the snow-covered period of 185 days and the snow-free period. Average winter soil CO_2 effluxes at intact and crustose sphagnum moss communities are 19.4 and 15.3 gC m^{-2} $period^{-1}$, respectively, corresponding to 28.4 and 20.0 % of annual simulated carbon emission, with the remainder during the snow-free period. These values are equivalent to 10 to 30 % of the annual carbon budget observed in various tundra ecosystems. At the crustose lichen-infected sphagnum moss colony, daily soil CO_2 effluxes simulated by temperature will be underestimated due to lack of consideration of additional contributions from soil CO_2 efflux regardless of the effect of soil moisture. However, at the intact sphagnum moss regime, simulated daily soil CO_2 effluxes will be relatively overestimated owing to no regard of constrained soil CO_2 efflux by the influence of soil moisture. However, as conducted by Risk et al. (2011), the monitoring of soil CO_2 efflux must also show representative points during the snow-covered and snow-free periods, along with the monitoring of environmental parameters within the sites.

In conclusion, these findings imply that soil CO_2 emission at a crustose lichen-infected sphagnum moss community will be gradually enhanced by the wide spread of aerial plants on flawless sphagnum moss patches, the subsequently increased decay of soil organic matter, and the rapid degradation of permafrost, in response to recent and drastic changes in climate and environment in the Subarctic and Arctic.

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Figure Legends

Figure 1. The linear relationship of soil CO_2 efflux measured by forced diffused (FD) chamber system between each ten-min (with thirty-min average) and thirty-min interval at intact sphagnum community from June 25 to July 23, 2015. This suggests there is no significant difference, based on a one-way ANOVA at the 95 % confidence level ($p < 0.001$). The dashed line denotes a 1:1 line.

Figure 2. Temporal variations in soil temperature (solid line) and soil moisture (dotted) at a) 2-cm depth and b) 5-cm depth at intact and crustose sphagnum moss regimes during the observation periods of 2015 and 2016.

Figure 3. Temporal variations in mean daily soil CO_2 effluxes with standard deviation (95 % confidence level) and ambient temperature at intact and crustose sphagnum moss colonies during the observation periods of 2015 and 2016.

Figure 4. Responses from soil CO_2 effluxes at intact to crustose sphagnum moss during a) 2015 (circles) and b) 2016 (squares). The thin dotted line indicates a 1:1 line. Correlation curves for 2015 and 2016 are shown by solid and dotted lines, respectively.

Figure 5. Responses from mean daily soil CO_2 effluxes to air temperature (pluses), soil temperature at 2 cm (triangles), and 5 cm (grey circles) below the surface at a) intact and b) crustose for 2015, and c) intact and d) crustose for 2016. Correlation curves for air temperature and soil temperature at 2- and 5-cm depths are shown by solid, dashed, and dotted lines, respectively.

Figure 6. Temporal variations in Q_{10} values using equation (6) for air temperature (solid line), soil temperature at 2 cm (dotted), and 5 cm (grey) below the surface at a) intact and b) crustose for 2015, and c) intact and d) crustose for 2016. Q_{10} values observed at crustose sphagnum moss for September of 2015 and 2016 show much wider fluctuation than at intact sphagnum moss.

Figure 7. Temporal variations in soil CO_2 efflux simulated by equation (3) and air temperature at

a) intact and b) crustose sphagnum moss from June 25, 2015 to September 30, 2016. Shaded columns represent the observation periods of 2015 and 2016.

Figure 8. Relationship between mean daily observed soil CO_2 effluxes (OSR_{intact} and $OSR_{crustose}$) and simulated soil CO_2 efflux (SSR) based on air temperature (AT), soil temperature at 2- (ST2) and 5-cm (ST5) depths at 1) intact and 2) crustose sphagnum moss. Thin dotted lines indicate a 1:1 line. In Figure a), $OSR_{intact} = 1.02\ SSR_{AT} + 0.05$ ($R^2 = 0.64$) (solid line), $OSR_{intact} = 1.34\ SSR_{ST2} + 0.01$ ($R^2 = 0.70$) (dashed line), and $OSR_{intact} = 2.24\ SSR_{ST5} - 0.12$ ($R^2 = 0.72$) (dotted line), and in Figure b), $OSR_{crustose} = 0.95\ SSR_{AT} + 0.06$ ($R^2 = 0.48$) (solid line), $OSR_{crustose} = 1.48\ SSR_{ST2} + 0.01$ ($R^2 = 0.63$) (dashed line), and $OSR_{crustose} = 1.74\ SSR_{ST5} - 0.04$ ($R^2 = 0.60$) (dotted line), respectively.

Table 1. Monthly mean (standard deviation) in CO_2 efflux, ratio of crustose to intact efflux (C/I), and soil temperature and soil moisture at 2 and 5 cm depths in intact and crustose sphagnum moss communities during the growing seasons of 2015 and 2016

Year	Month	CO_2 efflux (μmol m^{-2} s^{-1})		C/I Ratio	Soil temperature (°C)				Soil moisture (m^3 m^{-3})			
		Intact	Crustose		Intact		Crustose		Intact		Crustose	
					2 cm	5 cm	2 cm	5 cm	2 cm	5 cm	2 cm	5 cm
2015	June*	0.45 (0.09)	0.42 (0.11)	0.93	10.5 (2.13)	7.53 (1.18)	9.94 (1.51)	8.93 (1.18)	0.22 (0.11)	0.21 (0.02)	0.20 (0.02)	0.24 (0.03)
	July	0.53 (01.0)	0.51 (0.15)	0.97	13.0 (2.21)	9.59 (1.62)	12.4 (1.93)	11.3 (1.71)	0.23 (0.01)	0.23 (0.02)	0.21 (0.01)	0.23 (0.02)
	August	0.42 (0.16)	0.41 (0.22)	0.95	9.27 (1.50)	7.24 (0.98)	8.79 (1.33)	8.26 (1.04)	0.25 (0.02)	0.24 (0.03)	0.23 (0.02)	0.25 (0.04)
	September	0.21 (0.13)	0.19 (0.16)	0.86	2.68 (3.32)	2.24 (2.39)	2.28 (3.29)	2.35 (2.83)	0.26 (0.03)	0.28 (0.04)	0.22 (0.05)	0.25 (0.04)
	Growing season #	0.39 (0.18)	0.38 (0.22)	0.93	8.49 (4.94)	6.47 (3.54)	8.02 (4.86)	7.45 (4.24)	0.24 (0.03)	0.24 (0.03)	0.22 (0.03)	0.24 (0.03)
2016	June**	0.27 (0.07)	0.47 (0.22)	2.01	12.5 (1.72)	9.19 (1.24)	11.9 (1.14)	10.6 (1.09)	0.23 (0.01)	0.20 (0.01)	0.23 (0.02)	0.21 (0.03)
	July	0.45 (0.17)	0.52 (0.21)	1.36	12.8 (1.88)	10.1 (1.34)	12.1 (1.65)	11.3 (1.37)	0.22 (0.03)	0.21 (0.04)	0.22 (0.03)	0.20 (0.02)
	August	0.50 (0.22)	0.51 (0.33)	1.13	11.3 (1.52)	8.91 (1.11)	11.0 (2.09)	10.3 (1.73)	0.26 (0.02)	0.30 (0.02)	0.29 (0.04)	0.25 (0.05)
	September**	0.21 (0.15)	0.23 (0.15)	1.99	4.34 (2.79)	3.73 (2.05)	3.93 (2.78)	3.98 (2.41)	0.26 (0.01)	0.31 (0.04)	0.29 (0.03)	0.25 (0.03)
	Growing season #	0.38 (0.21)	0.43 (0.27)	1.70	10.0 (4.06)	7.87 (2.98)	9.53 (4.04)	8.91 (3.52)	0.24 (0.03)	0.26 (0.06)	0.26 (0.04)	0.23 (0.03)

* The peridof 2015 is June 25 to 30.

** The period of 2016 is June 18 to 30 and September 1 to 28.

The growing season denotes June to September of 2015 and 2016.

Table 2. Q_{10} values and correlaton coefficients in the exponential equation for soil CO_2 efflux response to temperature in intact and crustose sphagnum moss communities of tundra , western Alaska during the observeration periods of 2015 and 2016, for which is the the equation is CO_2 efflux = β_0 x $\exp^{(\beta 1 x T)}$, based on a one-way ANOVA at the 95% confidence level

Year	Month	Depth	Intact		Crutose	
Year		(cm)	Q_{10}	R^2	Q_{10}	R^2
2015*	June+July	Air 50	1.15	0.05	0.90	0.01
		2	1.25	0.07	1.34	0.03
		5	1.44	0.10	1.28	0.02
	August	Air 50	3.51	0.53	6.34	0.37
		2	3.53	0.49	7.99	0.47
		5	5.89	0.47	9.38	0.38
	September	Air 50	2.18	0.50	2.29	0.23
		2	3.90	0.44	4.80	0.30
		5	6.12	0.41	5.46	0.26
	Oct + Nov	Air 50	1.18	0.01	3.48	0.38
		2	1.47	0.03	6.01	0.44
		5	1.43	0.01	11.40	0.33
	Mean	Air 50	2.42	0.61	3.10	0.59
		2	2.82	0.65	3.87	0.64
		5	4.29	0.65	4.53	0.60
2016**	June+July	Air 50	1.27	0.02	0.83	0.11
		2	2.00	0.08	2.01	0.03
		5	3.79	0.17	1.42	0.01
	August	Air 50	3.16	0.12	3.32	0.07
		2	5.92	0.17	15.90	0.42
		5	5.34	0.08	16.30	0.30
	September	Air 50	10.80	0.56	1.55	0.05
		2	17.30	0.47	2.23	0.09
		5	48.60	0.47	2.03	0.05
	Mean	Air 50	3.88	0.45	2.05	0.16
		2	4.46	0.45	3.30	0.43
		5	7.88	0.46	3.59	0.40

* The measuring period of 2015 is from June 25 to November 9.

** The period of 2016 is from June 18 to September 28.

Table 3. Observed and simulated CO_2 efflux based on temperature in intact and crustose sphagnum moss communities during 2015 and 2016

Date	CO_2 efflux (μmol m^{-2} s^{-1})							
	Observed	Simulated			Observed	Simulated		
(mm-yy)	Intact	Air	2 cm	5 cm	Crustose	Air	2 cm	5 cm
Jul-15	0.53 (0.10)	0.46 (0.11)	0.40 (0.07)	0.29 (0.04)	0.51 (0.15)	0.47 (0.13)	0.37 (0.13)	0.33 (0.05)
Aug-15	0.42 (0.16)	0.31 (0.07)	0.29 (0.06)	0.24 (0.04)	0.41 (0.22)	0.30 (0.08)	0.26 (0.06)	0.24 (0.05)
Sep-15	0.21 (0.13)	0.18 (0.08)	0.16 (0.06)	0.15 (0.04)	0.19 (0.16)	0.16 (0.08)	0.14 (0.05)	0.14 (0.05)
Oct-15	0.14 (0.08)	0.13 (0.05)	0.12 (0.04)	0.13 (0.02)	0.14 (0.12)	0.11 (0.05)	0.10 (0.03)	0.10 (0.02)
Nov-15	0.17 (0.06)	0.08 (0.04)	0.12 (0.01)	0.12 (0.01)	0.09 (0.04)	0.06 (0.04)	0.09 (0.01)	0.09 (0.01)
Dec-15	N.D.	0.04 (0.03)	0.11 (0.01)	0.11 (0.01)	N.D.	0.03 (0.02)	0.09 (0.01)	0.09 (0.01)
2015**	0.39 (0.19)	0.32 (0.15)	0.28 (0.11)	0.23 (0.07)	0.37 (0.20)	0.31 (0.16)	0.26 (0.11)	0.24 (0.09)
Jan-16	N.D.#	0.06 (0.03)	0.11 (0.01)	0.12 (0.01)	N.D.	0.05 (0.02)	0.09 (0.01)	0.09 (0.01)
Feb-16	N.D.	0.06 (0.01)	0.11 (0.01)	0.12 (0.01)	N.D.	0.05 (0.02)	0.09 (0.01)	0.09 (0.01)
Mar-16	N.D.	0.04 (0.02)	0.11 (0.01)	0.11 (0.01)	N.D.	0.03 (0.02)	0.08 (0.01)	0.08 (0.01)
Apr-16	N.D.	0.12 (0.03)	0.12 (0.01)	0.12 (0.01)	N.D.	0.10 (003)	0.10 (0.01)	0.10 (0.01)
May-16	N.D.	0.29 (0.19)	0.23 (0.09)	0.16 (0.05)	N.D.	0.28 (0.22)	0.18 (0.08)	0.15 (0.06)
Jun-16	0.27 (0.07)*	0.40 (0.12)	0.34 (0.07)	0.25 (0.04)	0.47 (0.22)*	0.40 (0.14)	0.29 (0.08)	0.26 (0.06)
Jul-16	0.45 (0.17)	0.45 (0.12)	0.39 (0.06)	0.30 (0.04)	0.52 (0.21)	0.46 (0.14)	0.36 (0.06)	0.33 (0.04)
Aug-16	0.50 (0.22)	0.40 (0.07)	0.34 (0.05)	0.27 (0.03)	0.51 (0.33)	0.39 (0.08)	0.32 (0.07)	0.30 (0.05)
Sep-16	0.21 (0.15)	0.22 (0.08)	0.19 (0.05)	0.17 (0.03)	0.24 (0.15)	0.20 (0.09)	0.16 (0.05)	0.16 (0.04)
2016**	0.40 (0.22)	0.36 (0.13)	0.31 (0.10)	0.25 (0.06)	0.43 (0.28)	0.36 (0.15)	0.28 (0.10)	0.27 (0.09)

* The observed value is June 18 to 30, 2015.
** denote growing season (July to September) of 2015 and 2016.
\# indicates not determined.

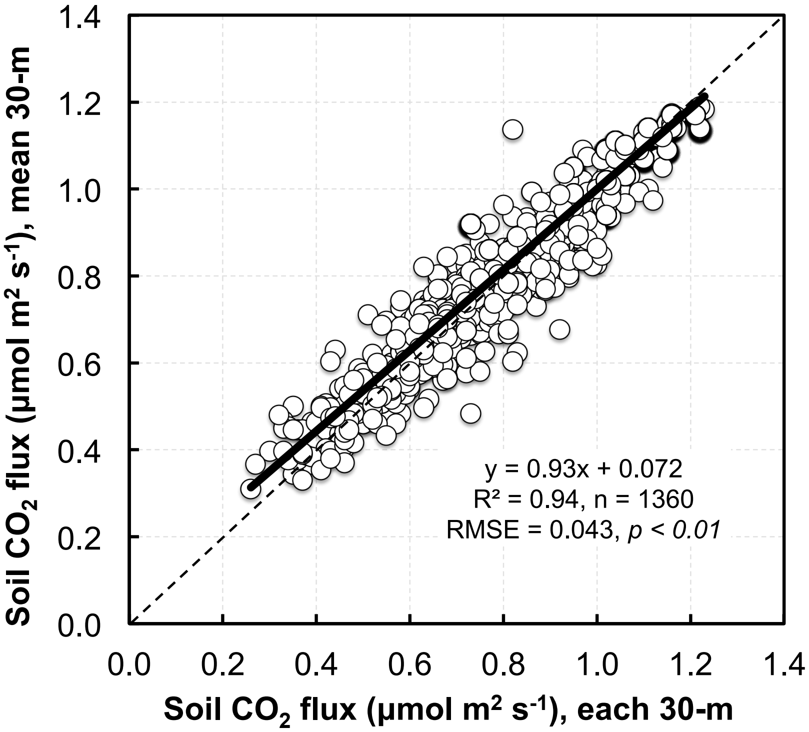

Figure 1. The linear relationship of soil CO_2 efflux measured by forced diffused (FD) chamber system between each ten-min (with thirty-min average) and thirty-min interval at intact sphagnum community from June 25 to July 23, 2015. This suggests there is no significant difference, based on a one-way ANOVA at the 95 % confidence level ($p < 0.001$). The dashed line denotes a 1:1 line.

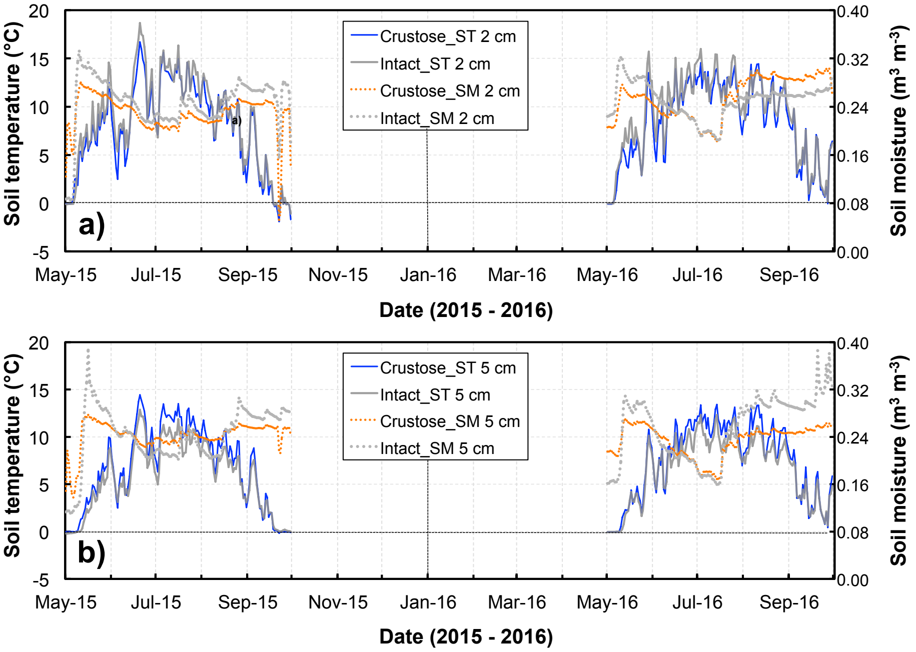

Figure 2. Temporal variations in soil temperature (solid line) and soil moisture (dotted) at a) 2-cm depth and b) 5-cm depth at intact and crustose sphagnum moss regimes during the observation periods of 2015 and 2016.

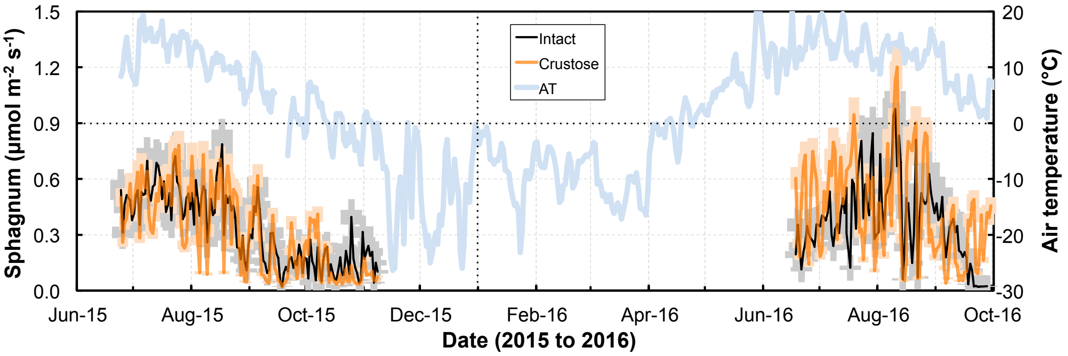

Figure 3. Temporal variations in mean daily soil CO_2 effluxes with standard deviation (95 % confidence level) and ambient temperature at intact and crustose sphagnum moss colonies during the observation periods of 2015 and 2016.

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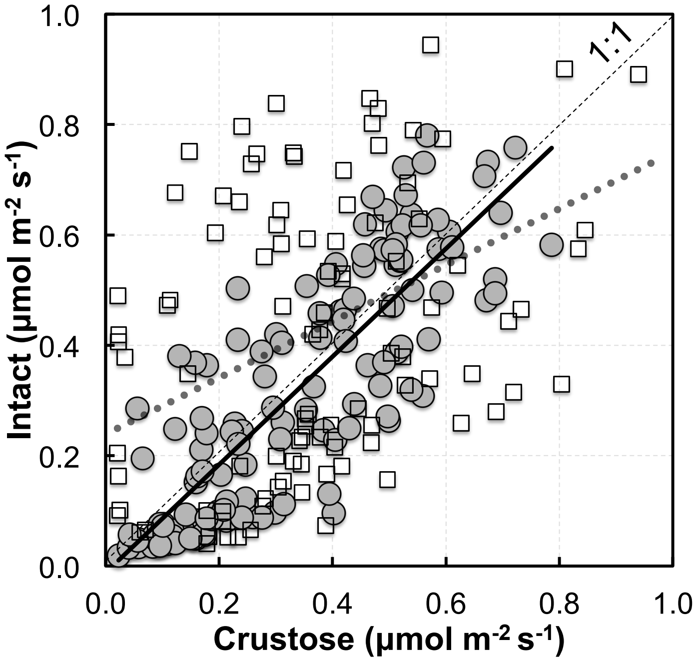


Figure 4. Responses from soil CO_2 effluxes at intact to crustose sphagnum moss during a) 2015 (circles) and b) 2016 (squares). The thin dotted line indicates a 1:1 line. Correlation curves for 2015 and 2016 are shown by solid and dotted lines, respectively.

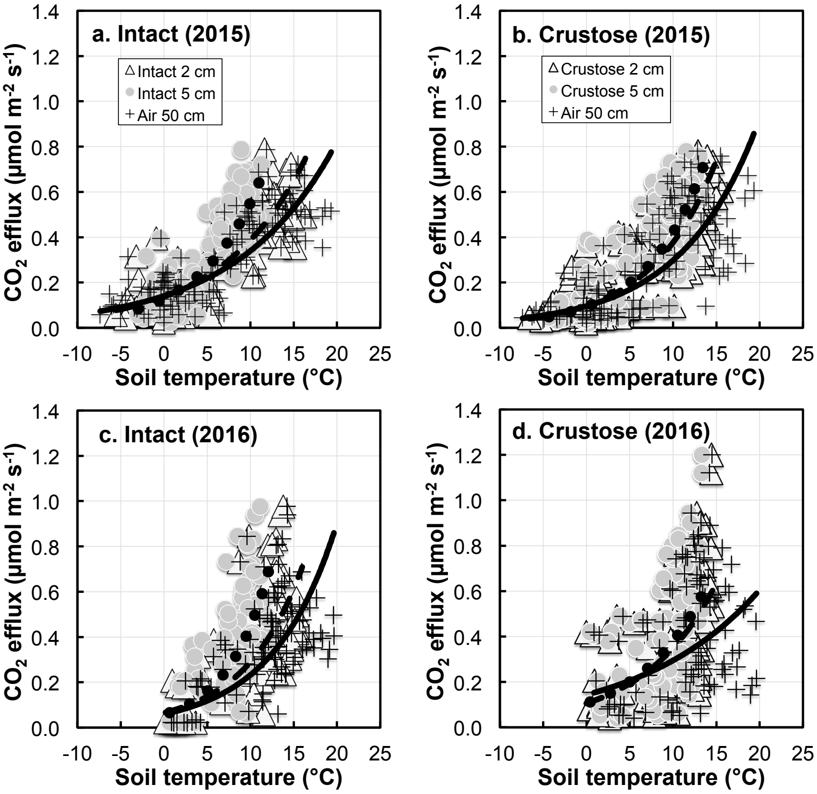


Figure 5. Responses from mean daily soil CO_2 effluxes to air temperature (pluses), soil temperature at 2 cm (triangles), and 5 cm (grey circles) below the surface at a) intact and b) crustose for 2015, and c) intact and d) crustose for 2016. Correlation curves for air temperature and soil temperature at 2- and 5-cm depths are shown by solid, dashed, and dotted lines, respectively.

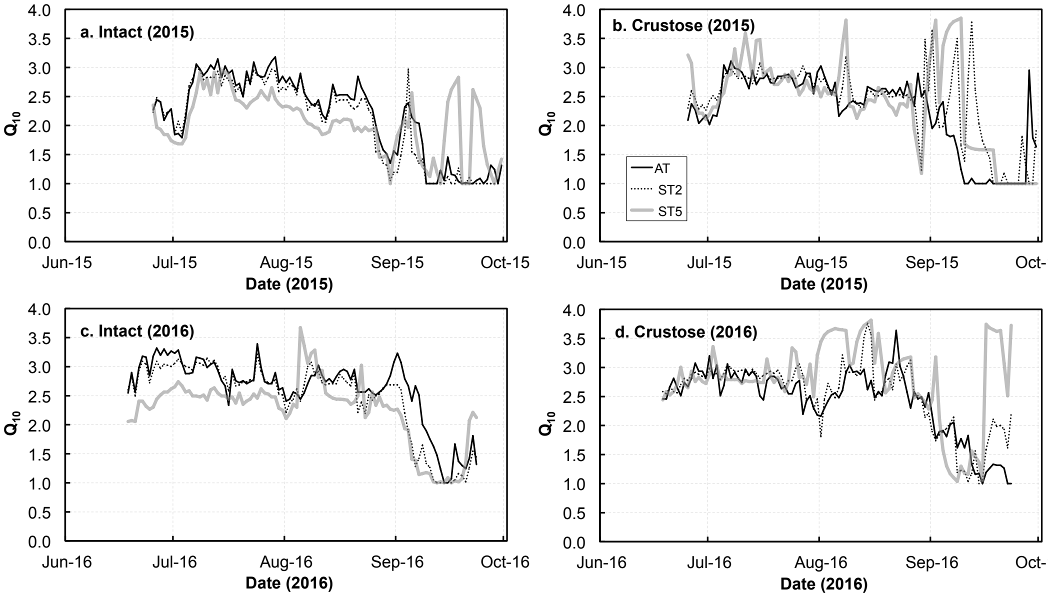
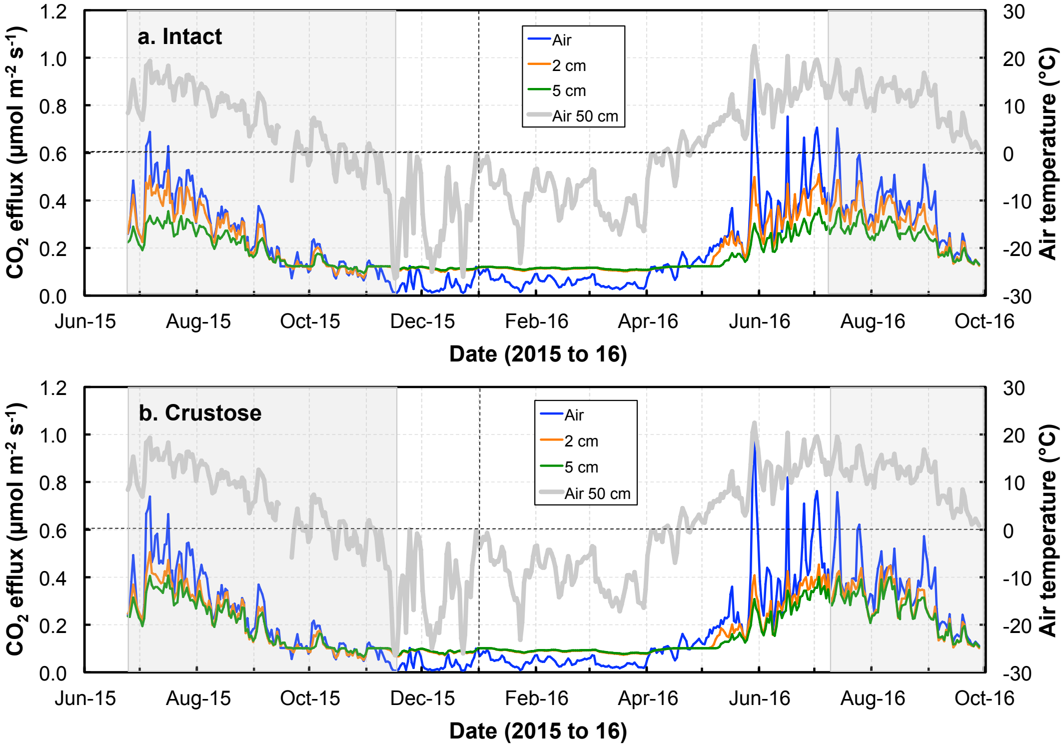


Figure 6. Temporal variations in Q_{10} values using equation (6) for air temperature (solid line), soil temperature at 2 cm (dotted), and 5 cm (grey) below the surface at a) intact and b) crustose for 2015, and c) intact and d) crustose for 2016. Q_{10} values observed at crustose sphagnum moss for September of 2015 and 2016 show much wider fluctuation than at intact sphagnum moss.



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2 **Figure 7**. Temporal variations in soil CO_2 efflux simulated by equation (3) and air temperature at
3 a) intact and b) crustose sphagnum moss from June 25, 2015 to September 30, 2016. Shaded
4 columns represent the observation periods of 2015 and 2016.

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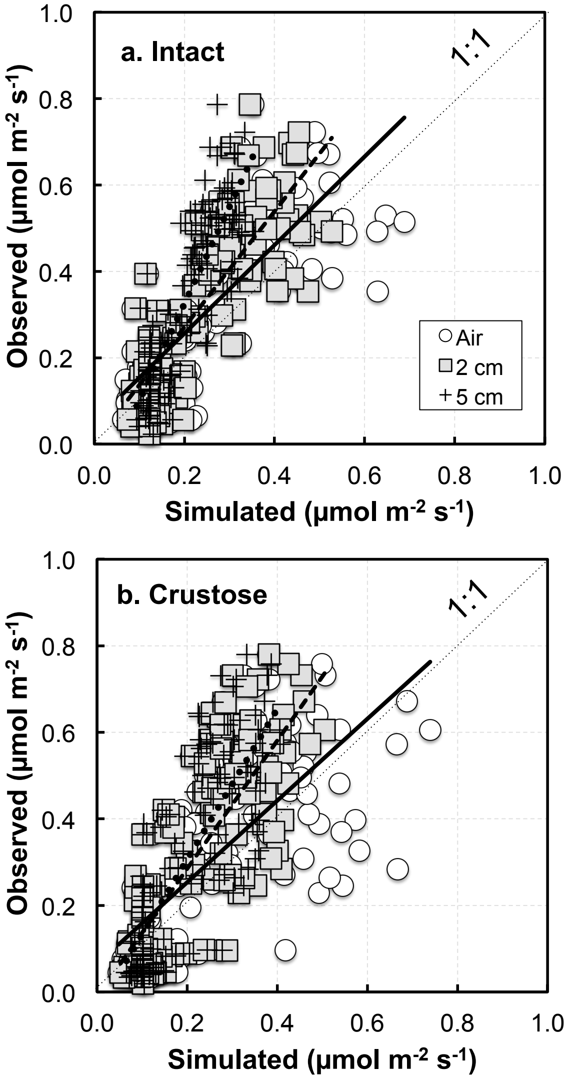

Figure 8. Relationship between mean daily observed soil CO_2 effluxes (OSR_{intact} and $OSR_{crustose}$) and simulated soil CO_2 efflux (SSR) based on air temperature (AT), soil temperature at 2- (ST2) and 5-cm (ST5) depths at 1) intact and 2) crustose sphagnum moss. Thin dotted lines indicate a 1:1 line. In Figure a), $OSR_{intact} = 1.02\ SSR_{AT} + 0.05$ ($R^2 = 0.64$) (solid line), $OSR_{intact} = 1.34\ SSR_{ST2} + 0.01$ ($R^2 = 0.70$) (dashed line), and $OSR_{intact} = 2.24\ SSR_{ST5} - 0.12$ ($R^2 = 0.72$) (dotted line), and in Figure b), $OSR_{crustose} = 0.95\ SSR_{AT} + 0.06$ ($R^2 = 0.48$) (solid line),

$OSR_{crustose} = 1.48\ SSR_{ST2} + 0.01$ ($R^2 = 0.63$) (dashed line), and $OSR_{crustose} = 1.74\ SSR_{ST5} - 0.04$ ($R^2 = 0.60$) (dotted line), respectively.