



Warming and increased precipitation enhance phenol oxidase activity in soil while warming induces drought stress in vegetation of an Arctic ecosystem

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ABSTRACT

Global climate change models predict that surface temperature and precipitation will increase in the Polar Regions. Arctic tundra soils contain a large amount of carbon, which may be vulnerable to decomposition under potential climate change. However, mechanistic understanding of the decomposition process and the consequent changes remains lacking. In the present study, we conducted a manipulation experiment at an arctic soil system in Cambridge Bay, Canada, where temperature and precipitation were increased artificially by installing open top chambers and adding distilled water during growing seasons. After one and half year of environmental manipulation, we investigated extracellular enzyme activities, which are related to decomposition, and analyzed stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in soils and plants, which are related to water and nitrogen availability. Hydrolase (β -D-glucosidase, cellobiase, N-acetyl-glucosidase and aminopeptidase) activity did not differ significantly under different treatments. However, phenol-oxidase showed higher activity under warming combined with increased precipitation than under other treatments. Stable isotope ratio ($\delta^{13}\text{C}$) in plants revealed that drought stress in vegetation was induced under warming. We concluded that in the long term, climate change may amplify the feedback of soil to climate change in arctic tundra soil.

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1. Introduction

Arctic soil is an important ecosystem that contains a huge amount of carbon stock because of the low rate of decomposition in cold temperatures. The magnitude of this carbon stock is quite uncertain but is currently estimated at 1672 Pg of organic carbon (Tarnocai et al., 2009). This organic carbon stored in the Tundra is thought to be vulnerable to climate change, and the emission of even a small fraction of this carbon stock may significantly increase the atmospheric greenhouse gas (GHG) concentration. Moreover, global climate change models predict the highest increase in temperature and slight increase in precipitation in the Arctic region (IPCC, 2007). These phenomena can lead to substantial changes in carbon balance and climate change feedback in the system.

Microorganisms produce enzymes that are directly involved in organic matter decomposition. Extracellular enzymes produced by microbial organisms decompose polymerized or macromolecular substrates into small molecules to absorb substrates into the cell. Phenol oxidase is particularly important because it is responsible for recalcitrant carbon mineralization, which is often the rate-limiting step in organic matter

mineralization (Freeman et al., 2001, 2004). Because recalcitrant phenolic compounds can inhibit the activity of hydrolases, phenol oxidase activation can augment overall extracellular enzyme activity. Previous studies have shown that warming and precipitation change may lead to destabilization of old organic carbon, but little is known about the effect on enzyme process (Davidson and Janssens, 2006; Kim et al., 2012; Kwon et al., 2013).

Factors influencing enzyme activity include temperature, moisture, redox potential, pH, salinity, substrate availability, biomass, adsorption by clay minerals, and humus (Freeman et al., 1998; Gianfreda et al., 1996; Kang et al., 2009; Vo and Kang, 2012). Some of the factors are related to enzyme producer propagation and some are related to the reaction rate of discharged enzymes (Burns, 1982). In Arctic or boreal/alpine regions, climate changing factors including temperature increase, CO_2 elevation, and nitrogen enrichment have been considered as factors influencing enzyme activity. Moorhead and Linkins (1997) reported that elevated CO_2 levels alter enzymic characteristics of root surface, suggesting that arctic plants respond to elevated CO_2 by increasing nutrient acquisition activity. An investigation of seasonal variation in enzyme activity found that it showed low sensitivity to temperature in summer and suggested that N-limitation is a reason for this (Wallenstein et al., 2009). Koch et al. (2007) suggested that temperature sensitivity of enzyme activity is higher in winter. Sistla and Schimel (2013) reported

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that warming treatment amplified the seasonal cycle of extracellular enzyme activity. Wang et al. (2010) found that nitrogen fertilization did not influence enzyme activity.

The indirect effects of warming constitute another important issue. In addition to the direct effects of higher temperature, warming may cause drought stress in microorganisms and plants via accelerated evapotranspiration. Allison and Treseder (2008) raised soil temperature, which resulted in soil moisture decline. In this study, warming and drying suppressed microbial activity including enzyme activity, and bacterial and fungal abundance. This suppression can be assessed by using stable isotope signatures of plant materials. Heavy carbon isotope (^{13}C) is depleted to greater extents in plant product when the stomata are wide open owing to sufficient moisture supply during photosynthesis. Therefore, natural abundance of ^{13}C is a good indicator of moisture availability or drought stress in plants (Stewart et al., 1995; Warren et al., 2001).

In spite of the importance of having a mechanistic understanding of the decomposition process and the resulting changes in arctic soil under global climate change, our understanding remains lacking. The aim of this study is to reveal the effects of warming and precipitation change on 1) microbial enzyme activity in soils and 2) stable isotopic signature of plant in an arctic ecosystem by employing open-top chamber methods.

2. Material and methods

2.1. Study site

Our study site is in Cambridge Bay, Nunavut, Canada. Cambridge Bay is included in the Arctic Circle, and the study site is located at 69°07'48" N and 105°03'36" W. The minimum daily mean temperature observed in January is $-33\text{ }^{\circ}\text{C}$, and the daily mean temperature rises above zero from June to August. The average precipitation between 1971 and 2000 was 140 mm per year. The vegetation consists of mosses, lichens, herbs and shrubs of height less than 10 cm. *Dryas integrifolia* and *Carex* spp. dominate the vegetation.

2.2. Climate change manipulation

A climate change model (Bell et al., 2003) predicts that mean air temperature will rise by $2.8\text{ }^{\circ}\text{C}$ and precipitation will increase by 15.6 mm (0.52 mm per week) during growing season (April to October) in 2040–2069 compared to that in 1971–2000 in Cambridge Bay. Considering this prediction, we conducted a manipulation experiment to investigate the impact of climate change on SOM (soil organic matter) decomposition that is relevant to GHG emission. A radiator or heating wire can raise the temperature by as much as predicted, but they may disturb or dry the soil system; therefore, we used an open-top chamber, which allows for air circulation, to increase air temperature. Moreover, we realized the precipitation increase of 0.5 mm per week.

We considered four types of treatments for climate change manipulation: no treatment (control), increased precipitation, warming, and warming with increased precipitation. In the warming plot, a hexagonal, lucent open-top chamber made of polycarbonate having a diameter of 2 m was installed, and in the increased precipitation plot, 2 L of distilled water was added to soil in a square plot ($2 \times 2\text{ m}$) every week. In the warming with increased precipitation plot, the soil in the installed open-top chamber was watered. The increased precipitation plot received additional precipitation of 4 mm per year compared with control plot which received average 147 mm of total precipitation in 2012–2013. We set five blocks (plot groups) with relatively uniform active layer depths in each block and conducted four kinds of treatments in each of the five blocks. The manipulation experiment was conducted from mid-July to early October in 2012 and from late June to early October in 2013. Monitored air temperature in the warming plot increased by $1\text{--}2\text{ }^{\circ}\text{C}$, but no change in soil moisture content was detected in the increased precipitation plot because soil moisture content varied largely

with locations. Given that 2 mm and 4 mm of weekly water addition were undetectable in a previous study (Sullivan et al., 2008), and that the precipitation in July and August ranged 14–56 mm per month, 0.5 mm per week of water addition might be too low to detect.

2.3. Soil and plant sampling

2.3.1. Soil

Soil from two depth layers (D1: 0–5 cm, D2: 5–10 cm) were collected from three points in a plot and combined to represent a sample for each plot. The first sampling was conducted shortly before the start of manipulation in July 2012. The second sampling was conducted in the middle of the second year's manipulation period (August 2013).

2.3.2. Plant leaves

Warming and precipitation addition can change plant biomass and coverage as observed by Wahren et al. (2005). We did not measure the biomass per se, but surveyed surface coverage of plant in July

Table 1

Soil properties at depths of 0–5 cm (D1) and 5–10 cm (D2) before manipulation (2012) and after manipulation (2013).

Water content (%)				
	2012		2013	
	D1 ^a	D2 ^b	D1 ^a	D2 ^b
No treatment	54.6(6.1)	42.1(7.9)	55.0(3.8)	34.2(8.7)
Precipitation	60.8(1.9)	49.4(5.5)	54.1(3.9)	40.9(7.7)
Warming	60.0(6.0)	45.8(5.9)	51.8(6.7)	41.4(5.0)
W + P	60.7(4.0)	51.2(8.0)	52.7(5.5)	39.6(6.8)
Organic matter (%)				
	2012		2013	
	D1 ^a	D2 ^b	D1	D2
No treatment	51.9(9.0)	34.4(8.9)	54.4(6.0)	32.3(13.6)
Precipitation	58.8(5.5)	43.9(6.6)	52.8(7.9)	49.2(22.3)
Warming	60.4(9.2)	38.5(5.6)	52.5(11.4)	35.9(8.2)
W + P	58.5(7.7)	49.0(7.6)	53.1(8.3)	33.1(6.1)
DOC (mg g ⁻¹ soil)				
	2012		2013	
	D1 ^a	D2 ^b	D1 ^a	D2 ^b
No treatment	0.18(0.03)	0.10(0.02)	0.20(0.03)	0.11(0.03)
Precipitation	0.23(0.01)	0.13(0.02)	0.22(0.03)	0.14(0.03)
Warming	0.22(0.03)	0.14(0.02)	0.22(0.05)	0.12(0.02)
W + P	0.24(0.02)	0.13(0.03)	0.20(0.03)	0.11(0.02)
SUVA ₂₅₄ (m ⁻¹ mg ⁻¹ L)				
	2012		2013	
	D1	D2	D1 ^a	D2 ^b
No treatment	5.0(0.2)	4.0(0.2)	3.1(0.2)	2.3(0.3)
Precipitation	4.7(0.3)	4.4(0.4)	3.0(0.3)	2.3(0.1)
Warming	4.7(0.3)	4.2(0.3)	3.0(0.1)	2.8(0.2)
W + P	4.6(0.1)	5.2(0.4)	3.1(0.2)	2.6(0.2)
A254/A365				
	2012		2013	
	D1 ^a	D2 ^b	D1 ^a	D2 ^b
No treatment	6.6(0.1)	11.4(0.9)	5.7(0.2)	6.5(0.1)
Precipitation	7.1(0.2)	11.3(2.0)	5.3(0.4)	6.5(0.1)
Warming	7.0(0.4)	10.3(1.0)	5.8(0.2)	6.1(0.2)
W + P	7.7(0.7)	9.8(1.0)	5.8(0.2)	6.5(0.1)

Letters (a and b) denote the significant difference between depths ($P < 0.05$).
(): standard error.

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