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Seasonality alters drivers of soil enzyme activity in subalpine grassland soil undergoing climate change

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ABSTRACT

In mountain ecosystems with marked seasonality, climate change can affect various processes in soils, potentially modifying long-term key soil services *via* change in soil organic carbon (C) storage. Based on a four-year soil transplantation experiment in Swiss subalpine grasslands, we investigated how imposed climate warming and reduced precipitation modified the drivers of soil carbon enzyme potential activities across winter and summer seasons. Specifically, we used structural equation models (SEMs) to identify biotic (microbial community structure, abundance and activity) and abiotic (quantity and quality of organic matter resources) drivers of soil C-enzymes (hydrolase and oxidase) in two seasons under two different climate scenarios. We found contrasting impacts of the climate manipulation on the drivers of C-enzymes between winter and summer. In winter, no direct effect of climate manipulation (reduced rainfall and warming) on enzyme activity was observed. Yet, climate indirectly down-regulated enzyme activity through a decrease in the availability of water extractable organic carbon (WEOC) labile resources. During summer, reduced soil moisture –induced by the climate manipulation– directly reduced soil microbial biomass, which led to a decrease in C-enzyme activity. In general, across both seasons, neither microbial community structure, nor organic matter quality were strong determinants of enzymatic activity. In particular organic matter recalcitrance (aromaticity) was not found as a general driver of either hydrolase or oxidase C-enzyme potential activities, though we did observe higher C-enzyme activities led to an increase of particulate organic matter recalcitrance in the summer season. Overall, our results highlight the seasonality of climate change effects on soil organic matter enzymatic decomposition, providing a comprehensive picture of seasonal potential cause and effect relationships governing C mineralization in subalpine grasslands.

1. Introduction

Soils store vast amounts of carbon (C) as soil organic matter (SOM), which equals, if not exceeds, the collective C stock in the atmosphere and vegetation (IPCC, 2013). Soil microbial communities play a key role in SOM decomposition processes, annually releasing ca. 60 GtC as respired CO_2 into the atmosphere (IPCC, 2013; Lal, 2008), or roughly double the anthropogenic greenhouse gas contribution. To decompose SOM, soil microorganisms release soil extracellular enzymes, which break down SOM through hydrolytic or oxidative processes (Burns et al., 2013; Sinsabaugh, 2010). This enzymatic depolymerisation process is a crucial step as it has been hypothesized to be the rate-limiting step in SOM decomposition processes, thus controlling C storage in soil (Bengtson and Bengtsson, 2007; Conant et al., 2011). In a warmer world, kinetic theory predicts enzyme activities to increase (Davidson and Janssen, 2006). In soil, however, enzyme activity rates are thought

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to be primarily determined by the frequency of substrate-enzyme interactions (Conant et al., 2011). The probability for enzymes to interact with substrates is controlled by a combination of biological, physical and chemical drivers (Dungait et al., 2012) which correspond mainly to (i) the quantity and turnover of the enzyme pool produced by microbial communities, (ii) the chemistry and availability/protection of OM substrates and (iii) the soil moisture and temperature conditions that define the physical conditions in which enzymes operate. However, it is difficult to understand the effects of climate change on all of these factors combined. Explicit consideration of both direct and indirect impacts of climate change on soil microorganisms and organic matter protection are required to understand complex interactions and feedbacks (Bardgett et al., 2008; Schmidt et al., 2011).

Mountain ecosystems cover 12.3% of all terrestrial land area and store large amounts of soil organic carbon as decomposition processes are limited by cold temperatures (Körner et al., 2011; Houghton, 2007; Wohlfahrt et al., 2008). These regions are currently experiencing strong climatic changes with alterations in temperatures, precipitation and seasonal intensity and duration (Gobiet et al., 2014). Moreover mountain areas offer an opportunity to test the impact of climate change as elevation gradients represent natural climate change experiments ideally suited to predicting future climate scenarios (Körner, 2007).

Future climate change scenarios for the European Alps predict an increase in mean annual temperature (MAT), together with a decrease in snow cover in winter and an increase in the frequency of extreme events such as drought and heat waves in summer (C2SM. 2011; IPCC. 2013). Such changes have already been reported to strongly alter the drivers of soil potential enzyme activities (Henry. 2013). Climate change, particularly warming and drought, is expected to affect the dynamics of soil microbial communities, organic substrate availability and therefore enzyme decomposition kinetics (Allison and Vitousek, 2005; Conant et al., 2011; Davidson and Janssens, 2006). Although we largely understand the impact of climate on microbial communities and OM substrate availability, a key knowledge gap remains to understand how changing ecological conditions affect interactions between microbial communities and substrate availability in driving C-degrading enzyme activities. This needs addressing urgently in order to build a framework to predict the future capacity of soils to act as a C sink (Sinsabaugh, 2010).

This study therefore aims to determine the effect of climate change on multiple interactive drivers of C-enzyme activities in winter and summer seasons in a subalpine grassland. We sought to perform an integrative analyses on previously published datasets from an altitudinal transplant experiment (moving soil turves to a lower altitude) with detailed data on soil microbial activity, abundance and structure; as well as SOM organic matter resources availability and chemistry (Puissant et al., 2015, 2017) collected after four years of imposed climate change. Structural equation modelling (SEM) based on path analysis have been used to evaluate how climate change influenced the interactions between microbes and SOM protection that driven C-enzyme potential activities. The climate change manipulation led to a discontinuous and thinner snow cover in winter and a warmer and drier climate in summer seasons. The effect of the climate change manipulation on the drivers of C- enzymes potential activities were evaluated separately in winter and the summer seasons to specifically examine different seasonal drivers. Our specific objectives were to (i) evaluate how the climate change manipulation affected C-degrading enzyme potential activities (hydrolase and oxidase) due to direct effects on microbial communities as well as effects on SOM resource availability and chemistry; and (ii) to determine whether the effects were consistent across seasons (winter vs summer).

2. Materials and methods

2.1. Study site and experimental manipulations

The experiment was located in the Swiss Jura mountain range and consisted of a high-to-low elevation soil translocation. Our highest site (1350m a.s.l, Combe des Amburnex, N 46°54′, E 6°23′) acted as the donor site. Its long-term mean annual temperature is +4.5 °C and mean annual rainfall is 1750 mm, which includes over 450 mm of snow. Combe des Amburnex is a species rich grassland and the soil type is Cambisol (IUSS Working Group WRB, 2007) on Jurassic limestone with an organic carbon content of 77 g kg^{-1} in average (Puissant, 2015).

We performed a four-year climate manipulation experiment which simulated a year-round intensive climate change scenario, expected regionally within the 21st century (A2 scenario, Meehl et al. 2007) aiming an average of 4 °C (MAT, +4 °C) temperature increase and 40% decrease in precipitation (MAP, −40%) (Gavazov et al., 2013). From the donor site (Combe des Amburnex), ten monotliths of undisturbed soil (30 cm depth) and its vegetation were placed in rectangular PVC boxes (60 × 80 and 35 cm in height), further referred to as mesocosms. Five mesocosm were placed back in their home site, i.e. at the same altitude (control, 1350 m a.s.l.), whilst the remaining five mesocosms were brought to a lower-altitudinal site (570 m a.s.l., Arboretum d'Aubonne, N46°51′, E6°37′) to simulate the envisaged climate scenario. All mesocosms were placed in pre-dug pits.

In the winter and summer season of the fourth year of the transplantation experiment, five intact soil cores (5 cm diameter × 10 cm length), i.e. one core per replicate mesocosm, were taken, placed in a cool box, and transported to the lab before analysis.

2.2. Soil microclimate

Soil temperature within the topsoil horizon were recorded every minute in each mesocosm, using Em50 data-loggers (Decagon Devices, Inc., USA) coupled to ECH2O EC-TM probes inserted at 3 cm depth. The gravimetric soil water content was measured by drying soil at 105 °C for 48 h according to norm NF ISO 16586 (2003). Winter sampling (February 20th, 2013) corresponded to the maximum snow cover at the control high elevation site, whereas at the low elevation site (570 m a.s.l.), the snow cover had melted completely several times during the winter, resulting in strong mid-winter soil temperature fluctuations. The daily average soil temperature at 3 cm depth within the mesocosms was 0.6 and 1.2 °C and the gravimetric soil moisture content 50% and 43% at the high and low elevation sites, respectively (Puissant et al., 2015). Summer sampling (September 2nd, 2013) corresponded to a dry period at the end of summer with an average soil temperature at 3 cm depth of 13.2 and 18.4 °C and gravimetric soil moisture of 33% and 21% at the high and low elevation sites, respectively. Overall, our climate manipulation increased the mean annual soil temperature by 4 °C (November 2012 to October 2013).

2.3. Soil analysis

For all chemical soil analyses, samples were dried at 40 °C as indicated in norm NF ISO 11464 (2006). In order to identify the effect of climate change on the drivers of potential C-enzymes activities with a structural equation modelling (SEM) approach, we used published data on the effect of the climate manipulation on (i) soil microbial activity, abundance and structure (Puissant et al., 2015) and on (ii) SOM organic matter resources availability and chemistry (Puissant et al., 2017). Data used to perform SEMs are summarized in Table 1. Details on each method perfomed to obtain all the variables used for SEM models can be found in Supplementary material.