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# Seasonal influence of climate manipulation on microbial community structure and function in mountain soils

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## ABSTRACT

Microbial communities drive soil organic matter (SOM) decomposition through the production of a variety of extracellular enzymes. Climate change impact on soil microbial communities and soil enzymatic activities can therefore strongly affect SOM turnover, and thereby determine the fate of ecosystems and their role as carbon sinks or sources.

To simulate projected impacts of climate change on Swiss Jura subalpine grassland soils, an altitudinal soil transplantation experiment was set up in October 2009. On the fourth year of this experiment, we measured microbial biomass (MB), microbial community structure (MCS), and soil extracellular enzymatic activities (EEA) of nine hydrolytic and oxidative extracellular enzymes in the transplanted soils on a seasonal basis.

We found a strong sampling date effect and a smaller but significant effect of the climate manipulation (soil transplantation) on EEA. Overall EEA was higher in winter and spring but enzymes linked to N and P cycles showed higher potential activities in autumn, suggesting that other factors than soil microclimate controlled their pool size, such as substrate availability. The climate warming manipulation decreased EEA in most cases, with oxidative enzymes more concerned than hydrolytic enzymes. In contrast to EEA, soil MB was more affected by the climate manipulation than by the seasons. Transplanting soils to lower altitudes caused a significant decrease in soil MB, but did not affect soil MCS. Conversely, a clear shift in soil MCS was observed between winter and summer. Mass-specific soil EEA (EEA normalized by MB) showed a systematic seasonal trend, with a higher ratio in winter than in summer, suggesting that the seasonal shift in MCS is accompanied by a change in their activities. Surprisingly, we observed a significant decrease in soil organic carbon (SOC) concentration after four years of soil transplantation, as compared to the control site, which could not be linked to any microbial data.

We conclude that medium term (four years) warming and decreased precipitation strongly affected MB and EEA but not MCS in subalpine grassland soils, and that those shifts cannot be readily linked to the dynamics of soil carbon concentration under climate change.

## 1. Introduction

The persistence of the large amount of organic carbon stored in mountain grassland soils strongly depends on the expected modification of the rate of microbial decomposition of soil organic matter (SOM) under a changing climate (Sjögersten et al., 2011;

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Saenger et al., 2013). Climate control on the rate of SOM decomposition can be evaluated by considering soils as a “black box”, and monitoring soil C outputs such as soil respiration under various climatic conditions (Bahn et al., 2008; Bond-Lamberty and Thomson, 2010). However, the emergence of a new generation of models of soil organic C (SOC) dynamics, integrating some principles of microbial ecology (biomass, community structure and metabolic activities of microorganisms), aims for a better understanding of the climate dependency of microbial mechanisms involved in SOM decomposition (Lawrence et al., 2009; Allison et al., 2010; McGuire and Treseder, 2010; Wang et al., 2013).

Soil microbial communities affect SOM decomposition by a variety of extracellular enzymes (EEs), exudated to the soil matrix; each EE being specific to a certain chemical bond. Soil EEs depolymerize SOM through several types of chemical reactions, such as hydrolysis (hydrolytic EEs) or oxidation (oxidative EEs), the latter having received relatively little attention in soil research (Sinsabaugh, 2010). Even though the regulation of SOM turnover by soil microorganisms has recently been questioned (Kemmitt et al., 2008; Bradford, 2013), SOM enzymatic depolymerization has been hypothesized to be the rate-limiting step in SOM decomposition (Bengtson and Bengtsson, 2007; Conant et al., 2011). This key soil process is tightly linked to soil microclimate (temperature and moisture), and also to EE pool size, which is mediated by the complex strategies of soil microbial communities (Allison and Treseder, 2008; Burns et al., 2013; Steinweg et al., 2013).

Only few studies have assessed the effect of *in situ* climate change (using e.g. overhead infrared heaters, open top chambers, soil altitudinal transplantation) on potential soil extracellular enzyme activities (EEA), and most of them focused on the growing season only (Burns et al., 2013). Climate change could lead to contradictory effects on microbial decomposition with decreased enzyme production (synthesis and secretion), increased enzyme-catalysed reactions, and modified enzyme stability in soils (Burns et al., 2013). Altered precipitation generally has a greater impact on soil EEA than temperature change, which is often not significant (Henry, 2013). Seasonal climate effects are generally known to be stronger on soil EEA than experimental climate manipulations (see Weedon et al., 2011 for a review), suggesting other drivers like plant nutrient demand and/or substrate quality and availability for soil EEA (German et al., 2011). On the other hand, climate warming affects also seasonal development, typically in mountain regions with a shortening of the snow period, which affects soil processes (Robroek et al., 2012). However, seasonal changes in soil EEA are not unidirectional, and depend on the studied enzyme and ecosystem type (Löffler et al., 2008; Baldrian et al., 2013; Steinweg et al., 2013). As such, it appears difficult to predict modifications in the rate of SOM enzymatic depolymerisation under projected climate change (Davidson and Janssens, 2006; Burns et al., 2013). Moreover, there is a lack of knowledge on the effect of climate change on the relationships between soil microbial biomass (MB), microbial community structure (MCS) and EEA, which impedes building a predictive framework (Sinsabaugh, 2010). Apart from generally observed seasonal shift in MCS and MB (Bardgett et al., 1999; Lipson and Schmidt, 2004; Waldrop and Firestone, 2006; Pascault et al., 2010), climate manipulations (mostly long term warming, i.e. >10 years) also impact on MCS (Rinnan et al., 2007; Budge et al., 2011). The link between MB and soil EEA is not clear, with a majority of studies showing no correlation as evidenced by climate induced modifications of mass-specific EEA (i.e. EEA per mg MB C; Waldrop and Firestone, 2006; Schindlbacher et al., 2011; Steinweg et al., 2013), while some enzyme-based models explicitly hypothesize that EEA is tightly linked to MB (e.g. Wang et al., 2013).

In this study, we used an altitudinal transplantation experiment of grassland turfs in mesocosm boxes to investigate the climate impact (both the seasonal influence and the climate-manipulation effect on the fourth year of experimentation) on microbial decomposition in subalpine grasslands of the Swiss Jura. The transplantation experiment simulated two realistic climate change scenarios, with increased air temperatures ranging between 2 °C and 4 °C and decreased precipitation ranging between 20% and 40%. These changes reflect current predictions of climate change for the 21st century in temperate mountain regions (Frei et al., 2006; Meehl et al., 2007; C2SM, 2011). Previous results from the same experimental plots have already shown (i) a significant decrease in soil respiration (Gavazov, 2013; Mills et al., 2014), and (ii) a significant increase in soil dissolved organic carbon (DOC) concentration in soil solution collected by zero tension lysimeters (Gavazov, 2013) under both climate change scenarios, and (iii) a significant decrease in aboveground biomass production under the most intensive climate change scenario (+4 °C and 40% decrease in precipitation; Gavazov et al., 2014).

Here, we investigated three key elements related to microbial decomposition: soil microbial abundance/biomass, soil microbial C, N and P enzymatic activities and soil microbial community structure across seasons. Our main objectives were to assess (i) the seasonal dynamics of various enzyme pool sizes in mountain grassland soils, and their relationships with microbial abundance and community structure; (ii) the medium term (four years) impact of two climate change scenarios on soil microbial abundance, community structure and activities across seasons, and their links with SOC concentration in mountain grassland soils.

## 2. Materials and methods

### 2.1. Design of the altitudinal soil transplantation experiment

The experimental design of this study was based on a mesocosm turf transplantation carried out in 2009 (Gavazov et al., 2013, 2014), and focused on the response of subalpine grasslands in the Swiss Jura mountains to two intensities of climate change. This manipulation successfully simulated year-round moderate and intensive climate change scenarios expected regionally in the 21st century (A1B and A2 scenarios, respectively; Frei et al., 2006; Meehl et al., 2007). Briefly, 15 mesocosms, made of rectangular PVC boxes (60 × 80 and 35 cm in height), containing monoliths of undisturbed soil (30 cm depth), and their intact herbaceous vegetation typical of open grasslands (consisting mainly of graminoids with few forbs; Gavazov et al., 2014) were taken from a subalpine pasture located at 1350 m a.s.l. (Combe des Amburnex, N46°54′, E6°23′). The soil type is Cambisol (IUSS Working Group WRB., 2007), and the parent material is Jurassic limestone. The 15 mesocosms were then transplanted (5 per site) in common gardens at the site of origin (control: 1350 m a.s.l.) and two lower-altitudinal sites: 1010 m a.s.l. (Saint-George, N46°52′, E6°26′) and 570 m a.s.l. (Arboretum d'Aubonne, N46°51′, E6°37′). Climate conditions in the Swiss Jura are typical for an oceanic mountain climate, with significant amount of precipitation and large annual temperature variation. At the highest site (control; 1350 m a.s.l.), the mean annual temperature is +4.5 °C and the mean annual rainfall is 1750 mm, including over 450 mm of snow. The soil transplantation simulates a climate warming with an average 2 °C and 4 °C temperature increase and 20% and 40% decrease in precipitation at the intermediate site and the lowest site, respectively (see Gavazov et al., 2013 for a more detailed description of climate data).