Soil Biology & Biochemistry 112 (2017) 1–13

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Altitudinal, seasonal and interannual shifts in microbial communities and chemical composition of soil organic matter in Alpine forest soils

José A. Siles [a], Tomas Cajthaml [b, c], Alena Filipová [b, c], Stefano Minerbi [d], Rosa Margesin [a, *]

[a] Institute of Microbiology, University of Innsbruck, Technikerstrasse 25, A-6020 Innsbruck, Austria
[b] Institute of Microbiology, Academy of Sciences of the Czech Republic, v.v.i., Vídeňská 1083, CZ-142 20 Prague 4, Czech Republic
[c] Institute for Environmental Studies, Faculty of Science, Charles University in Prague, Benatska 2, CZ-128 01 Prague 2, Czech Republic
[d] Division Forestry, Autonomous Province of Bozen/Bolzano, Brennerstrasse 6, I-39100 Bozen/Bolzano, Italy

A R T I C L E I N F O

Article history:
Received 16 November 2016
Received in revised form
13 April 2017
Accepted 19 April 2017
Available online 27 April 2017

Keywords:
Elevational (altitudinal) gradient
Forest
Microbial community
PLFA
Pyrolysis
Soil organic matter (SOM) composition

A B S T R A C T

The study of soil microbial communities and chemical properties of soil organic matter (SOM) over altitudinal mountain gradients have been regarded as especially useful to better predict and help mitigate the effects of climate change. However, there is a lack of surveys considering altitudinal, seasonal and interannual variations at the same time. Here, we investigated four forest sites, along an altitude gradient (545–2000 m a.s.l.), in spring and autumn during two consecutive years (2014 and 2015) regarding i) soil temperature and physicochemical properties; ii) SOM chemical composition using pyrolysis; iii) soil microbial activity (basal respiration, potential enzyme activities, community level physiological profiles (CLPP)); iv) archaeal, bacterial and fungal abundance (qPCR, phospholipid fatty acid (PLFA) analysis, numbers of culturable heterotrophic bacteria); and v) microbial community structure (PLFA analysis). Sites at high altitudes (alpine, subalpine) showed lower mean, maximum and minimum soil temperatures respect to those at lower altitudes (montane, submontane) and were characterized by increased levels of SOM and nutrients, higher archaeal, bacterial and fungal abundance as well as higher microbial activities. Soils at the sites at higher altitudes presented a higher humification degree of SOM, as demonstrated by an enhanced content of aromatic compounds and fatty acids. The seasonal effect determined a rise in the content of SOM, some soil nutrients, basal respiration and microbial abundance in autumn respect to spring over the altitudinal gradient as well as a change in the structure of microbial community and SOM molecular composition. Interannuality had a significant effect on the relative abundance of various chemical groups of SOM compounds and on the ratios of microbial groups, and produced an increase in microbial abundance in the second study year, as a consequence of the increased soil maximum temperatures recorded in this year. CLPP showed to be site-specific with limited seasonal and interannual variations. Altitudinal, seasonal and interannual changes in chemical composition of SOM were explained by variations in PLFA-based microbial community structure as well as in the abundance of bacteria and fungi, which, in turn, were affected by climatic conditions.

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1. Introduction

Forest ecosystems play a crucial role in terrestrial carbon (C) cycling since they store large quantities of C in several pools (vegetation, litter and soil) and exchange large amounts of C with the atmosphere through photosynthesis and respiration. Among the different organic C reservoirs in forests, soil is the main one, accumulating C as soil organic matter (SOM). In fact, SOM has been recognized as the largest terrestrial pool of C, with a greater C content than the sum of atmospheric C and terrestrial vegetation C (Flato et al., 2013). Changes in the organic C pool stored in SOM are driven by changes in the balance between atmospheric CO_2 uptake by plant primary production and soil CO_2 effluxes from root respiration and microbial decomposition processes (Dieleman et al., 2013). Since the annual effluxes of CO_2 from soils to the atmosphere may be 8–10 times the amount derived from fossil fuel combustion (Lal, 2008), a change in this balance may have a significant impact on atmospheric CO_2 levels and result therefore in a positive feedback to global warming (Heimann and Reichstein,

* Corresponding author.
E-mail address: Rosa.Margesin@uibk.ac.at (R. Margesin).

http://dx.doi.org/10.1016/j.soilbio.2017.04.014
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2008; Gutiérrez-Girón et al., 2015).

In the last few years, it has been highlighted that the analysis of SOM chemical properties helps to understand SOM vulnerability and predict the response of climate (Xu et al., 2009). The characteristics of SOM can have significant impacts on its turnover dynamics, which could considerably change the magnitude, the temporal pattern and even the direction of ecosystem response to alterations related to climate change (e.g., increasing CO_2 levels, N deposition, increasing soil temperature or changes in vegetation composition) (Xu et al., 2009; Djukic et al., 2010b). The chemical SOM composition is dependent on the decomposition process, whose main drivers are substrate type and quality (tree species, nutrient availability, decay stage and fragment size), composition, abundance and activity of the decomposer community (microorganisms and fauna) and environmental parameters (soil mineralogy and texture, soil structure and moisture regime, soil nutrient availability, soil pH and temperature) (Russell et al., 2015; Magnússon et al., 2016). Altitudinal gradients have been recognized as useful "natural experiments" for the studies assessing the SOM chemical composition since they are characterized by dramatic changes in climate and biotic characteristics that occur over short distances. In addition, the altitudinally-defined vegetation belts on mountain slopes are counterparts to the latitudinally-controlled climatic zones (Körner, 2007; Zhang et al., 2013). In the last few years, several studies have addressed SOM composition in various altitudinal gradients (e.g., Chen and Chiu, 2003; Dalmolin et al., 2006; Djukic et al., 2010b; Dymov et al., 2015; Wang et al., 2016) using nuclear magnetic resonance (NMR) or Fourier transform infrared spectroscopy (FTIR). Most of these studies mainly detected increasing O-alkyl C and decreasing alkyl C contents in SOM with an increase in altitude, which seems to be related to a lower SOM humification rate at higher altitudes, while the relatively higher temperature at lower altitudes seems to enhance decomposition. However, there are also studies that show no clear patterns of SOM composition over altitudinal gradients and state that the specific environmental conditions and vegetation at each site control SOM characteristics (Djukic et al., 2010b; Balaria et al., 2014).

Soil microorganisms mediate 85–90% of SOM transformation (Wolters, 2000) via processes such as decomposition, polymerization and immobilization through the production of enzymes (Ng et al., 2014). Many studies have investigated changes in diversity (Fierer et al., 2010; Shen et al., 2014; França et al., 2016; Siles and Margesin, 2016), community structure (Margesin et al., 2009; Xu et al., 2015), abundance (Djukic et al., 2010a; Wang et al., 2014) and enzyme activities (Margesin et al., 2014; Siles et al., 2016) of forest soil microbial communities along a variety of altitudinal gradients. However, the number of works studying altogether SOM composition and characteristics of soil microbial communities along the same altitudinal gradient, and elucidating the links between them, is scarce. Cusack et al. (2011), studying two tropical forests differing in altitude, concluded that differences in chemical SOM composition between the two forests were driven by site-specific changes in microbial community characteristics and enzyme activities. On the other hand, Xu et al. (2014) found, over an altitudinal gradient on the Tibetan Plateau, a positive correlation between O-alkyl C compounds of SOM and microbial biomass (bacteria and fungi), but a negative correlation between alkyl-C contents of SOM and fungal biomass as well as the fungal/bacterial ratio, evidencing the predominant role of the fungal community during SOM transformation.

All the aforementioned studies on SOM composition and/or its relations with microbial communities over forest altitudinal gradients did not consider the effect of season. However, seasonality, alternating climatic conditions, takes a decisive control on tree physiology, photosynthesis and discharge of new SOM into soil (Rasche et al., 2011). Likewise, the importance of season on vegetation is greatly affected by the type of vegetation, whose composition is highly variable over altitudinal gradients. Deciduous forests are characterized by photosynthetic activity of trees during the vegetative period and a short period of litterfall in autumn, when fresh litter with easily available nutrients accumulates on the forest floor. In contrast, coniferous forests are characterized by a longer vegetative period and the enrichment of soil with more recalcitrant litter compared to that of deciduous vegetation (Voříšková et al., 2014; Žifčáková et al., 2016). Soil microbial communities may be affected by seasonal vegetation changes, but also by other factors, such as temperature and moisture, which are directly influenced by season (Siles et al., 2016). Likewise, the interannual seasonal variability in temperature and precipitation can also play an important role in plant growth and soil microbial community structure in forests (Burke, 2015). Therefore, interannual and seasonal changes are important for the direct and indirect modelling of factors that influence SOM chemical properties and soil microbial communities. Integrative studies on altitudinal gradients should consider interannual and seasonal effects of environmental changes on SOM chemical composition and properties of soil microbial communities, and should elucidate the links between these parameters. Such studies are extremely useful to improve simulation models and mitigation strategies for climate change.

Here, we studied an altitudinal gradient consisting in four forest sites (including submontane, montane, subalpine and alpine vegetation) situated in the Italian Alps, to evaluate the effects of year (interannuality), season and altitude (site) on: i) soil temperature and physicochemical properties; ii) SOM chemical composition using pyrolysis with in situ methylation using tetramethylammonium hydroxide followed by gas-chromatography mass-spectrometry (TMAH-Py-GC-MS); iii) microbial activity (basal respiration, potential enzyme activities, community level physiological profiles (CLPP)), abundance (qPCR, phospholipid fatty acid (PLFA) analysis, numbers of culturable heterotrophic bacteria) and community structure (PLFA analysis) of forest soil communities. Finally, we aimed to discover the main drivers of changes in SOM chemical composition by investigating the significant links between SOM molecular structure and soil environmental and physicochemical properties as well as features of microbial communities. We hypothesized that SOM composition is influenced by microbial activity, abundance and community structure, which in turn are influenced by environmental (climatic) factors.

2. Materials and methods

2.1. Study sites

Four sites (M, K, R, and S) were selected across an altitudinal gradient from 545 to 2000 m above sea level (a.s.l.) and represented a climosequence, including submontane, montane, subalpine, and alpine vegetation zones. The study sites are located in South Tyrol (Italy), and represent widely distributed and forestally significant forest types in this part of the Italian Alps. All sites were SW-exposed and contained the same bedrock. A detailed description of each site has been reported (França et al., 2016; Siles et al., 2016). The main characteristics of the studied sites are summarized in Table 1.

2.2. Soil sampling

Eight sampling spots distributed uniformly over each site

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