



Controls on microbially regulated soil organic carbon decomposition at the regional scale



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ARTICLE INFO

Keywords:

Soil respiration
Q₁₀
Enzyme activity
Landscape scale
Regional scale

ABSTRACT

Even small changes in microbial decomposition rates of soil organic carbon (SOC) at the regional scale have the potential to modify land-atmospheric feedbacks at the global scale. Limited understanding of the regulation of microbial driven processes has led to major uncertainty in global SOC estimates. Therefore, to better understand the large scale processes controlling SOC dynamics, we examined the influence of SOC quantity, quality, and soil physical and biochemical properties on soil basal respiration and of the temperature sensitivities (Q₁₀) of soil respiration and enzymes (β-glucosidase and xylanase) at two scales: landscape (two individual areas, each approximately 27 km²) and regional (pooled data of both areas). Soil samples (0–30 cm soil depth) originated from 41 agricultural sites distributed over two areas in southwest Germany differing in climatic and geological conditions. We used a two-step data analysis procedure; variable selection through random Forest regression, followed by shortlisting of significant explanatory variables using linear mixed-effect models. Microbial biomass regulated soil basal respiration at both scales, whereas soil C:N ratio played an important role only at the regional scale based on mixed-effect models. Soil texture significantly explained temperature sensitivity (Q₁₀) of soil respiration at both scales. Different SOC quality fractions characterized by midDRIFTS played a minor role, whereas extractable organic C related negatively to the respiration Q₁₀. Soil properties controlling soil enzymes (Q₁₀) were scale-specific. We found pH to be the main factor affecting β-glucosidase Q₁₀ at the landscape scale. We argue that scale-specificity of variables may depend on homogeneity of study areas and should be considered when exploring SOC dynamics. Our study identified direct and indirect controlling factors affecting soil basal respiration and its temperature sensitivity, providing vital information for SOC dynamics at large scales.

1. Introduction

Soil respiration, a primary pathway of soil organic carbon (SOC) loss, plays a significant role in the global C cycle (Chen et al., 2015; Jiang et al., 2015). Globally, 50–90 Pg CO₂-C per year are emitted from soils into the atmosphere and it has been suggested that ongoing global warming will increase this flux (Del Grosso et al., 2005; Bond-Lamberty and Thomson, 2010; Subke and Bahn, 2010). Recent studies have estimated global SOC stocks of 510–3040 Pg C, a six-fold variation using different models (Todd-Brown et al., 2013), resulting in uncertainty about the response of soil C to changing climate. This demonstrates the need for a better mechanistic understanding of SOC decomposition at large scales (Todd-Brown et al., 2013; Hararuk et al., 2015).

SOC dynamics are controlled by factors like climate, landscape position and biotic properties as well as their complex interactions (Burke et al., 1989; Luo et al., 2017). For example in regions with similar mineralogy, clay content is usually highly related to SOC stabilization (Burke et al., 1989). Doetterl et al. (2013) demonstrated, however, that understanding spatially variable SOC stocks requires the consideration of multiple environmental processes. Therefore, landscapes differing in the above mentioned soil forming factors might show specific controls of climatic and soil physiochemical and biotic properties on SOC dynamics that demand investigation. Although soil respiration is the primary process by which C is released from the soil, little information about its regulation at the regional scale is available. In the few studies which have focused on the main factors influencing

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soil respiration, the use of a broad range of explanatory variables such as SOC, soil bulk density and texture, total nitrogen (TN), pH, and C:N ratio have thus far not provided a clear picture at landscape and regional scales (Friedel et al., 2006; Chen et al., 2010; He et al., 2015).

Soil temperature plays an important role in SOC dynamics with usually negative association to SOC density, observed even at large scales (Wang et al., 2014). Since microbial processes largely control the decomposition and stabilization of SOC, the temperature sensitivity of microbial respiration is likely to have a strong influence on the response of SOC content to global warming (Meier et al., 2010; Wieder et al., 2015). On the regional scale, temperature sensitivity of SOC decomposition may be controlled by site specific soil properties such as substrate quality and quantity, as well as other physiochemical soil properties including pH, soil moisture, diffusion limitation, and soil texture (Davidson and Janssens, 2006; Lützwow and Kögel-Knabner, 2009; Suseela et al., 2012; Yu et al., 2015). Stabilization of available substrate by physical and chemical processes, e.g. isolation within soil aggregates and adsorption onto mineral surfaces, along with its spatial distribution, may also restrict a SOC decomposition response to temperature (Davidson and Janssens, 2006; Poll et al., 2006; Kemmitt et al., 2008; Lützwow and Kögel-Knabner, 2009). Chemical recalcitrance of SOC is also one of the major constraints on the temperature response of decomposition, although contradictory results have been reported (Fang et al., 2005; Knorr et al., 2005; Conen et al., 2006; Fierer et al., 2006; Benbi et al., 2014; Xu et al., 2014). Characterizing SOC quality is, therefore, a promising tool for explaining regional variation in the temperature response of soil respiration.

The quality of SOC has been characterized by a variety of techniques (Lützwow et al., 2007). Diffuse Reflectance Fourier Transform mid-infrared Spectroscopy (midDRIFTS) is a high throughput method that has been successfully applied to characterize SOC fractions (Demyan et al., 2013; Kunlanit et al., 2014) making this technique useful for studies at large scales with many samples. Many studies have shown mid-infrared spectral changes both in applied residues and bulk soil during incubation (e.g. Spaccini et al., 2001; Calderón et al., 2011; Kunlanit et al., 2014). Studies have also shown differing functional group contributions between light and heavy soil organic matter fractions (Demyan et al., 2012). However, as with other analytical methods, midDRIFTS might have its limits such as overlapping peaks resulting from more than one vibrational functional group and the fact that the spectrum is a result of vibrations of both mineral and organic components (e.g. Demyan et al., 2012).

Microbially produced enzymes mediate the rate-limiting step of SOC depolymerization (Kandeler et al., 2006; Min et al., 2014) and a considerable proportion of heterotrophic respiration is controlled by the enzyme activities (Dungait et al., 2012; Ali et al., 2015). To improve our understanding of the temperature sensitivity of soil respiration, it is therefore important to investigate the factors controlling the temperature response of enzyme activities. High temperatures accelerate microbial decomposition of SOC by increasing activities of soil enzymes (Wallenstein et al., 2011), while quantity of organic matter may control or mask the temperature effect on enzyme activities. For example, German et al. (2011) found as much as a 50% decrease in starch mineralization when its relative contribution was below ca. 10% of the total SOC due to a reduction in starch-degrading enzymes. Trasar-Cepeda et al. (2007) found increasing activation energies in soils with increasing amounts of SOC; however, this effect was enzyme dependent. Also changes in microbial community composition may lead to a different spectrum of enzymes and isoenzymes which in turn might have different responses to temperature, thus affecting the observed enzyme temperature sensitivities from C substrates (Davidson and Janssens, 2006; Ali et al., 2015).

In the present study, we sampled soils from two landscapes differing in climatic and edaphic conditions and investigated the data at two scales: landscape scale (representing the two individual areas; the Kraichgau and the Swabian Alb, each around 27 km²) and regional

scale (representing pooled data of both areas, situated approximately 95 km apart from each other). The objective was to investigate the specificity of the factors explaining SOC decomposition dynamics to landscapes differing in their climatic, physiochemical, and biotic properties. We hypothesized that the quality of SOC, as characterized by midDRIFTS, would be a primary factor in explaining basal respiration and its temperature sensitivity due to its respective lability and relevance for microbially-mediated decomposition (soil respiration and enzyme activities). We related landscape/regional variation in basal soil respiration, its short-term temperature sensitivity, and the temperature responses of two soil enzymes degrading SOC of varying complexities (β -glucosidase and xylanase), to a set of biotic, physical and chemical soil properties.

2. Materials and methods

2.1. Study areas and soil sampling

The two areas of the present study are located in southwest Germany and are part of the integrated research project “Agricultural Landscapes under Global Climate Change – Processes and Feedbacks on Regional Scale” (<http://klimawandel.uni-hohenheim.de/>) of the German Research Foundation (DFG). The first area lies in the central Swabian Alb (500–850 m a.s.l.) characterized by extensively used grass- and croplands with a cool and humid climate (mean annual temperature of 7.0 °C, precipitation 800–1000 mm). Soils in this area developed mainly from Jurassic limestone into shallow and stony Leptosols (WRB, 2007). The second is the Kraichgau area (100–400 m a.s.l.), which is largely covered with loess and is a fertile and intensively cropped hilly area. Soils in the Kraichgau developed mainly into Regosols and Luvisols (WRB, 2007). In comparison to the Swabian Alb, the Kraichgau is characterized by a warmer and drier climate (mean annual temperature of 9.3 °C, precipitation 720–830 mm). Average total nitrogen fertilization (between 2010 and 2012) was 227 kg N ha⁻¹ in the Kraichgau (170–274 kg N ha⁻¹) and 216 kg N ha⁻¹ in the Swabian Alb (180–244 kg N ha⁻¹). In 2009, soil moisture networks within 27 km² domains were installed on agricultural fields in each landscape and consisted of 20 sites in the Swabian Alb and 21 in the Kraichgau (Fig. S1). At each site, soil temperature, moisture and precipitation data are continuously recorded. Soil type at each individual site belongs to the main soil types of that landscape. Common crops grown in both landscapes included Rapeseed (*Brassica napus*), Mustard (*Sinapis arvensis*), Barley (*Hordeum vulgare*), Spelt (*Triticum spelta*), Wheat (*Triticum aestivum*) and Pea (*Pisum sativum*), whereas the Swabian Alb had in addition to above mentioned crops also Maize (*Zea mays*), Oats (*Avena*) and different species of clover (*Trifolium*). For a detailed description of the moisture networks, we refer to Poltoradnev et al. (2015). Soil samples from these 41 soil moisture network sites were collected between 17 April and 9 May, 2013. Four soil cores (\varnothing 2.5 cm) to 30 cm depth were taken from each site, and mixed thoroughly to get one composite sample per site. Samples were kept in cooling boxes, transferred to the laboratory, sieved through a < 2 mm sieve and stored at –24 °C until further analysis. Studies have shown no considerable effects of freezing soils to –20 ± 2 °C on soil properties like microbial biomass and basal soil respiration (Stenberg et al., 1998).

2.2. SOC characterization

SOC was characterized by Diffuse Reflectance Fourier Transform mid-Infrared Spectroscopy (midDRIFTS). With this technique, organic and inorganic functional groups are characterized by the reflectance of their characteristic bending and stretching vibrations in the mid-infrared range. Soil samples were ball milled and dried overnight at 32 °C before measurement. Soil spectra were scanned on a Tensor-27 Fourier transform spectrometer (Bruker Optik GmbH, Ettlingen, Germany) equipped with a liquid N cooled mid-band mercury-cadmium-telluride

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