European Journal of Soil Biology 80 (2017) 69–76

Contents lists available at ScienceDirect

European Journal of Soil Biology

journal homepage: http://www.elsevier.com/locate/ejsobi

Determinants of soil extracellular enzyme activity in a karst region, southwest China

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ARTICLE INFO

Article history:
Received 23 January 2017
Received in revised form
14 March 2017
Accepted 3 May 2017
Available online 8 May 2017

Handling editor: Y. Kuzyakov

Keywords:
Extracellular enzyme activity
Soil
Karst
Land use
Spatial variables
Variation partitioning

ABSTRACT

Soil extracellular enzymes are crucial in biogeochemical cycling and ecosystem functioning. Most previous studies addressed the determinants of soil extracellular enzyme activity (EEA) in small-scale regions with acid soils, yet uncertainty exists in large-scale regions with alkaline soils. In this study, the activities of 7 soil extracellular enzymes related to carbon, nitrogen and phosphorus cycling were assayed in a regional-scale karst area, southwest China. Soil samples were collected from secondary forest, shrubland, grassland and cropland underlain by either dolomite or limestone. The enzyme activity profiles were significantly different between dolomite and limestone or among the four land use types according to multi-response permutation procedure analysis. Variation partitioning indicated that soil properties, spatial variables and land use together explained 43% of EEA variation. Soil properties explained the largest proportion of EEA variation (36.5%). The variation explained by spatial variables and land use was mostly shared with soil properties, resulting in small unique fractions explained by these two factors (5.5%), especially spatial variables (2.2%). Among the soil properties, soil moisture, contents of silt and total nitrogen were the most important variables responsible for EEA variation. Our results suggest that regional EEA variation can be well explained by soil properties in the karst regions.

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1. Introduction

Soil extracellular enzymes control the rate-limiting step of soil organic matter (SOM) decomposition and nutrient cycling [1] by depolymerizing polymeric macromolecules into low molecular weight and dissolved organic compounds, which are the immediate energy and other nutrient substrates for microbial communities [1,2]. The patterns and determinants of extracellular enzyme activities (EEAs) can provide useful information about soil functioning and its responses to human disturbances (e.g., land use change) or environmental changes [3,4].

Over the past decades, many studies have been conducted to investigate the levels and spatiotemporal variation of EEAs at small scales. According to these studies, EEAs are sensitive to a few environmental variables [5]. Soil organic carbon (SOC), total nitrogen (N), pH and soil moisture were identified as the major soil physicochemical variables affecting soil hydrolytic enzyme activity [6–9]. The effectiveness of these variables in regulating EEAs was found to vary with ecosystems. For example, SOC and soil total N was important in affecting EEAs in both forest and grassland soils, while pH was effective only in forest soils, and Ca content were only effective in grassland soils [7]. The effects of these variables were also found to vary with enzyme types. For example, soil moisture was positively related to β-glucosidase and cellobiohyrolase during the growing season and β-N-acetylglucosaminidase during the dry season [8]. However, whether the influencing factors identified at small scales can explain EEA variation at regional scales is still an open question. For example, pH was identified as a major factor according to a review paper which synthesized data from 40 ecosystems [6], but a study conducted in a tropical watershed of 45067 ha showed no significant correlation between pH and all five studied hydrolytic enzymes [3]. The inconsistent results indicate that the factors regulating EEA variation may be ecosystem specific or enzyme specific or the mechanisms underlying EEA variation are

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http://dx.doi.org/10.1016/j.ejsobi.2017.05.001
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poorly understood.

Considering the key role of soil enzymes in SOM decomposition and nutrient turnover, knowledge of large-scale EEA patterns and their determinants is necessary for understanding the biochemical controls of soil C storage [6]. Nevertheless, few studies on EEA patterns have been conducted at regional scales [3,7–12]. The relevant studies identified soil physicochemical variables influencing EEA variation [7–9], or explored the linkages between microbial community compositions and EEAs [10–13], or determined the influences of both land use and soil properties on EEAs [3,4]. Only few studies reported the effects of land use, spatial variables and soil physiochemical variables together on the variation of EEAs [14]. More importantly, the relative contributions of land use, spatial variables and soil physiochemical variables to EEA variation have never been investigated to our knowledge.

To fill this gap, we conducted a study in a calcareous karst region, southwest China. Soil sampling was conducted at a regional scale, and soil samples collected from four land use types, i.e., secondary forest, shrubland, grassland and cropland underlain by two lithology types, i.e., dolomite and limestone, which are typical in the karst region. The major objectives of this study were to (i) evaluate how soil enzyme activity profiles differed between the two lithology types or among the four land use types. Enzyme activity profiles were used to describe an overall characteristic of all studied enzyme activities [9,12]; (ii) determine the relative importance of land use, spatial variables and soil physiochemical variables in determining variation of EEAs at the regional scale; (iii) identify the major soil physiochemical properties that influence regional EEA variation at the regional scale. Because relevant researches are fewer in alkaline soils comparing to those in acid soils, our study will provide important knowledge for understanding the controlling factors of the variation of enzyme activity in calcareous regions.

2. Material and methods

2.1. Study region

The study region (23°40′ N – 25°25′ N, 107°35′ E – 108°30′ E) was located in the northwest of Guangxi Zhuang Autonomous Region, southwest China. The sampling area covered about 9000 km^2. Mean annual air temperature in this region is 19.6–21.6 °C, with the lowest monthly mean in January (10.1–12.2 °C) and the highest in July (28.0–28.6 °C). Mean annual precipitation ranges from 1389 to 1750 mm with a distinct seasonal pattern. The period from April to September is wet season and that from October to March is dry season. The region is characterized by a typical karst landscape with gentle valleys flanked by steep hills. The lithology in the karst areas is limestone, dolomite and their mixtures. The soil is calcareous lithosols (limestone soil) over both limestone and dolomite.

2.2. Soil sampling

Soil sampling was conducted from the end of April to early June 2015. In total, 124 sites were selected. The number of sites for each lithology type, land use type, and slope position was presented in Table 1. Briefly, the selected sampling sites covered two lithology types, i.e., limestone and dolomite. In each lithology, four land use types, including secondary forest, shrubland, grassland and cropland, were selected. Considering that the karst region is characterized by gentle valleys flanked by steep hills, the sampling sites were distributed over three slope positions, i.e. valley, foot slope, and back slop. The slope was typically 15° to 20°. For most of the sampling sites, obvious organic layer was absent, so samples from the organic layer were not collected. Since soil depth was much heterogeneous and only shallow soil layers could be found in most of the sampling sites, mineral soil to a depth of 15 cm were collected after the removal of organic layer (if available) in order to make comparison among sampling sites. Ten to fifteen soil cores (5 cm in diameter) were collected for each site and mixed to a composite sample. Additional soil cores were collected to determine bulk density (BD). Roots and stones were picked out using forceps and soils were passed through a 2-mm mesh sieve on site. The sieved soil samples were divided into portions for further processes. The samples for analyses of EEAs were kept on ice in the field and were stored under 4 °C in the laboratory. Subsamples were dried at 105 °C to determine gravimetric water content (GWC). The records for each location include geographic coordinates, elevation, lithology, land use types and slope position. Soil properties are presented in Table 2.

Table 1
Number of the sampling sites for each lithology type, land use type, and slope position.

Slope/Lithology	land use type				
	Cropland	Grassland	Shrubland	Forest	Total
Valley					
Dolomite	4	6	6	6	22
Limestone	5	4	6	5	20
Foot slope					
Dolomite	4	6	5	6	21
Limestone	5	3	6	5	19
Back slope					
Dolomite	4	6	6	6	22
Limestone	5	4	6	5	20
Total	27	29	35	33	124

2.3. Assay of soil extracellular enzyme activities

Seven soil enzymes involved in C, N and phosphorus (P) cycling were assayed using substrates presented in Table 3 with published microplate protocols [15,16]. Enzyme assays were conducted within one month following field sampling. Soil suspensions were prepared by homogenizing 1 g of fresh soil in 125 ml of buffer, which was 50 mM sodium bicarbonate (pH 8.0) for alkaline phosphatase assay and 50 mM sodium acetate (pH 5.0) for the other EEA assays according to Sinsabaugh et al. (2008) [6]. All the assays except peroxidase were fluorimetric using black polystyrene 96-well microplates. The 96 wells were assigned into sample assay, soil control, quench standard, reference standard, negative control and blank wells. First, 200 µl of buffer was added into the blank, reference standard, and negative control wells. Next, 50 µl of buffer was added into the blank and sample control wells. Then, 20 µl of blended soil slurry was added into the quench standard, soil control, and sample assay wells; 50 µl of 10 M MUB solution was added into the reference standard and quench standard wells. Lastly, 50 µl of a 200-µM MUB-linked substrate was added into negative control and sample assay wells. There were eight replicate wells for each kind of the assigned wells per soil sample. The microplates were incubated in the dark at 25 °C for up to 4 h depending on the assay. At the end of the incubation, a 10 µl aliquot of 1.0 M NaOH was added to each well to stop the reaction. Fluorescence was determined using a microplate fluorometer (Infinite 200 Pro, Tecan, Switzerland) at 365 nm excitation and 450 nm emission. Enzyme activities were presented in units of nmol h^{-1} g^{-1} and calculated by the following equations:

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