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Resource limitation of soil microbes in karst ecosystems

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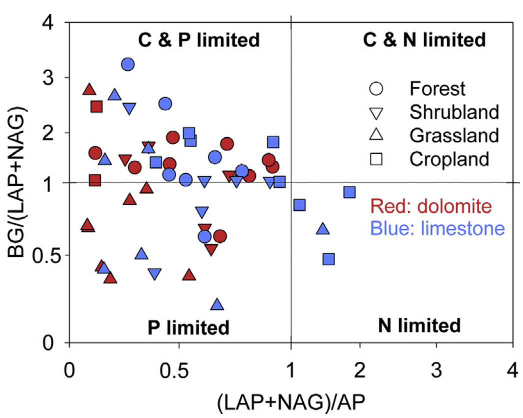
HIGHLIGHTS

- Soil microbial resource limitation was investigated in karst ecosystems.
- Soil microbes were limited by carbon and phosphorus, rather than by nitrogen.
- Lithology controls the pattern of microbial P limitation along the succession.

GRAPHICAL ABSTRACT



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ABSTRACT

Knowledge about resource limitation to soil microbes is crucial for understanding ecosystem functions and processes, and for predicting ecosystem responses to global changes as well. Karst ecosystems are widespread in the world, and play a key role in regulating the global climate, however, the patterns of and mechanisms underlying microbial resource limitation in karst ecosystems remain poorly known. Here we investigated the microbial resource limitation in a karst region, by selecting four main land-use types, i.e. cropland, grassland, shrubland and secondary forest, in areas underlain by two lithology types, i.e. dolomite and limestone, in southwest China. Ecoenzymatic stoichiometry was used as an indicator of microbial resource limitation. Overall, soil microbes in karst ecosystems were more limited by carbon and phosphorus, rather than by nitrogen. Further analyses revealed that the patterns of carbon and phosphorus limitation were different among land-use or lithology types. Microbial carbon limitation was greatest in cropland and forest but lowest in grassland, and was greater under dolomite than under limestone. Microbial phosphorus limitation decreased from secondary forest to cropland under dolomite areas, but showed no difference among ecosystem types under limestone areas, indicating that lithology controls the pattern of microbial phosphorus limitation along the post-agriculture succession. Our study describes a general pattern of microbial resource limitation in karst ecosystems, and we suggest that lithology may provide a new mechanism for explaining the variations of microbial resource limitation along the post-agriculture succession in different regions.

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1. Introduction

Karst ecosystems are widespread in the world, accounting for about 15% of the world's land area (Sweeting, 1995). These ecosystems are developed underlain by carbonate rock (e.g., limestone or dolomite), and thus soil in karst ecosystem has special properties (Chen et al., 2018). Recent studies suggest that karst soil is a huge carbon (C) pool due to its large area and high C concentration (Ahmed et al., 2012; Li et al., 2017; Wen et al., 2016). In particular, most soil C in karst regions concentrate upon soil surface where microbes are more active (Ahmed et al., 2012), meaning that soil C may be more sensitive to global environment changes, such as increased atmospheric CO_2 and nitrogen (N) deposition. Therefore, any small change in karst soil C pool may have great influence on the global climate.

Soil microorganisms play a key role in soil C cycle by controlling the decomposition of soil organic matter (Blagodatskaya and Kuzyakov, 2013). However, microbial processes largely depend on microbial biomass and activity, which in turn are often limited by the availability of resources such as C, N and phosphorus (P). This is referred to as microbial resource limitation (Ekblad and Nordgren, 2002; Hill et al., 2014), or substrate limitation (Edr and Wood, 2001). Most early studies suggested that soil microbes are commonly limited by available C, but recent studies proposed that N and P are also the important limiting nutrients for microbial growth (Schimel and Weintraub, 2003). Due to the important role that soil microorganisms play in ecosystem processes, knowing which resource limits the growth and activity of soil microorganisms is crucial for understanding the function of the ecosystem, and is helpful to predict the ecosystem responses to global changes. Nevertheless, previous studies have mainly focused on the resource limitation of aboveground plants, and the resource limitation of soil microorganisms has long been neglected (Edr and Wood, 2001; Sistla et al., 2012). Thus, to date, the patterns of and mechanisms underlying microbial resource limitation in karst ecosystems are still poorly understood.

The patterns of microbial resource limitation are controlled by many factors. Land use change, including agricultural abandonment, has been documented to change the resource availability for microbial growth, and thus leads to the variations in microbial resource limitation (Fanin et al., 2016). Available researches have revealed various patterns of microbial resource limitation along the post-agriculture succession. For example, in a high arctic glacier foreland, Yoshitake et al. (2007) found that microbes were limited by both C and N in the early stage of succession; thereafter, N limitation was mitigated. Aikio et al. (2000) reported increasing N limitation of soil microbes during the succession in a post-glacial land uplift island in Finland. In the other secondary successions, P limitation was found to be more evident with the development of the ecosystem (Liu et al., 2012; Scheu, 1990). While it has been suggested that factors such as soil properties (Castle et al., 2017) and soil types (Fanin et al., 2016) may explain these differential patterns of microbial resource limitation following the succession, many uncertainties still exist.

Lithology is an important factor that influences soil development since it regulates many of the processes at the Earth surface, including the fluxes of matter to soils (Hartmann and Moosdorf, 2012). Previous studies have documented that lithology influenced soil properties and microbial community structures (D'Amico et al., 2015; Reith et al., 2012). Due to its influence on soil properties and microbial communities, it is reasonable to hypothesize that lithology also has an effect on microbial resource limitation. However, to our knowledge, no studies have been conducted to assess this effect, and whether or not lithology is a mechanism that controls the direction and magnitude of microbial resource limitation following post-agriculture succession has also not been investigated.

Little research on microbial resource limitation in the past may be partly attributed to a lack of suitable methods. Traditional methods for quantifying microbial resource limitation are measuring the effects of substrate addition on microbial biomass or respiration as a proxy for microbial resource limitation (Stotzky and Norman, 1961). However, these methods are time-consuming and relatively difficult to implement. Recently, ecoenzymatic stoichiometry has been suggested as a useful indicator of the relative resource limitation of microbial assemblages since extracellular enzyme activity reflects the cell's response to whether the available environmental resources can meet its metabolic demands (Sinsabaugh et al., 2009). The four extracellular enzymes most commonly assayed are β-D-glucosidase (BG), L-leucine aminopeptidase (LAP), β-*N*-acetylglucosaminidase (NAG), and acid/alkaline phosphatase (AP), and they are assumed to be proxy indicators of overall C, N, and P acquisition (Sinsabaugh, 1994). Based on this hypothesis, Sinsabaugh et al. (2008) suggested that the relative ratios of BG/AP and BG/(NAG + LAP) can reflect the relative demands in acquiring C vs. P and C vs. N, respectively. Moorhead et al. (2016) proposed that the vector length and angle of ecoenzymatic stoichiometry, that are calculated by the proportional activity of C/N/P acquiring enzymes, can reflect relative C vs. nutrient limitation and relative P vs. N limitation of soil microbes. Compared to the method that involves substrate addition, ecoenzymatic stoichiometry is more cost-effective (Hill et al., 2014). Using ecoenzymatic stoichiometry, many studies have reported microbial resource limitation in different regions or ecosystems (Hill et al., 2014; Sinsabaugh and Follstad Shah, 2011; Tapia-Torres et al., 2015), but no study was conducted to assess the microbial resource limitation in karst regions at a large scale.

In this study, using ecoenzymatic stoichiometry as indicators of microbial resource limitation, a regional-scale investigation of microbial resource limitation was conducted in southwest China, where has the one of the largest karst areas in the world, covering about 0.51 million km^2 (Jiang et al., 2014). In a previous study, we have studied microbial resource limitation in a single karst forest (Chen et al., 2018). In the current study, we aimed to investigate the regional-scale patterns of microbial resource limitation in different land-use types and under typical karst lithology types, i.e. dolomite and limestone. Four land-use types, i.e. cropland, grassland, shrubland, and secondary forest, were selected, and they were used to represent different succession stages, which is a space-for-time substitution approach (Li et al., 2017). Previous work by Zhang et al. (2015) on nutrient limitation of plant growth have found that grassland and secondary forest in karst regions are limited by N and P, respectively, but shrubland is constrained by N and P together. Thus, we hypothesized that the N and P limitation of soil microbes may follow a similar pattern with plants (Hypothesis I). However, plants are rarely C-limited while C limitation in microbes is common (Schimel and Weintraub, 2003). Previous studies have shown that microbial C limitation will be more evident as an ecosystem develops (Yoshitake et al., 2016; Yoshitake et al., 2007), thus we hypothesized that a similar pattern for microbial C limitation will occur along the post-agriculture succession within the study regions (Hypothesis II). In addition, it has been found that limestone have higher SOC, total N, and total P than dolomite (Li et al., 2017; Wen et al., 2017). Higher resource content may reduce the potential in resource limitation, we therefore hypothesized that microbial C, N, and P limitation will be more evident in dolomite than in limestone (Hypothesis III). Finally, we expected that there exist interaction effects of land use and lithology on microbial resource limitation (Hypothesis IV), which could provide an explanation for the inconsistent results regarding microbial resource limitation along the succession in the previous studies.

2. Materials and methods

2.1. Study region

This study was conducted in the northwest of Guangxi Zhuang Autonomous Region, southwest China (23°40′ N–25°25′ N, 107°35′ E–108°30′ E) (Chen et al., 2016). This region has a typical subtropical monsoon climate. Mean annual air temperature ranges from 17.8 to 21.1 °C, with the lowest monthly mean in January (7.8–11.2 °C) and the highest