



Ecoenzymatic stoichiometry and microbial nutrient limitation in rhizosphere soil in the arid area of the northern Loess Plateau, China

Yongxing Cui^{a,b}, Linchuan Fang^{a,*}, Xiaobin Guo^c, Xia Wang^{a,b}, Yanjiang Zhang^d, Pengfei Li^{a,b}, Xingchang Zhang^{a,**}

^a State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences, Ministry of Water Resources, Yangling, 712100, PR China

^b University of Chinese Academy of Sciences, Beijing, 100000, PR China

^c Agricultural Production and Research, Department of Fisheries, Forestry, and Agrifoods, Government of Newfoundland and Labrador, Canada

^d College of Resource and Environment, Northwest A & F University, Yangling, 712100, PR China

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ABSTRACT

Arid ecosystems are characterized as having stressful conditions of low energy and nutrient availability for soil microorganisms and vegetation. The rhizosphere serves as the one of most active microorganism habitats, however, the general understanding of the ecoenzymatic stoichiometry (exoenzymes) and microbial nutrient acquisition in rhizosphere soil is limited. Here, we investigated the vegetation communities and determined the soil physicochemical properties, microbial biomass, and enzymatic activities in rhizosphere under different vegetation and soil types in the arid area of the northern Loess Plateau. Type II standard major axis (SMA) regression analysis showed that the plants played a more important role than soil properties in determining ecoenzymatic stoichiometry. Linear regression analysis displayed a microbial stoichiometric homeostasis (community-level) in rhizosphere. The Threshold Elemental Ratio (TER) revealed that the microbial nutrient metabolisms of rhizosphere were co-limited by N and P in the *A. ordosica* and *A. cristatum* communities of loess, and *A. cristatum* communities of feldspathic sandstone weathered soil. Binding spatial ordination analysis (RDA and CCA) demonstrated that soil physical properties (e.g., soil moisture, silt and clay contents) have more contribution to ecoenzymatic stoichiometry than the other investigated soil parameters, whereas soil nutrients (e.g., total organic carbon, nitrogen, and phosphorus) predominantly controlled microbial nutrient ratios. Therefore, the ecoenzymatic stoichiometry in rhizosphere is greatly regulated by plants and soil physical properties. The microbial N and P are co-limited under Gramineae plant in loess and feldspathic sandstone weathered soil regions. Meanwhile, the microbial nutrient limitation is mainly affected by soil nutrient supply. These findings could be crucial for illuminating rhizosphere microbial metabolism and revealing the nutrient cycling of root-soil interface under arid and oligotrophic ecosystems.

1. Introduction

The Loess Plateau is one of the most eroded regions in China and has some of the most vulnerable ecological systems in the world (Li et al., 2011). The northern region of Loess Plateau is a prairie desert transition zone (Wen et al., 2007) and is a typical dryland (Noymeir, 2003; Pointing and Belnap, 2012). Estimates of carbon storage for dryland regions indicate that they possess 36% of the total carbon storage worldwide (Campbell et al., 2008). The main vegetation types in the Loess Plateau are desert grasslands, which represent an important pool (8%) of global carbon (C) reservoirs. In desert grasslands, the major

inputs of soil organic matter (SOM) are derived from underground biomass (root systems), rather than aerial biomass. The underground biomass also provides the principal source of soil nitrogen and phosphorus to the aerial biomass (Sims, 1978). Therefore, soil nutrient turnover and its availability in rhizosphere soils are critical for plant survival and ecosystem stabilization in ecological critical zones.

Nutrient turnover is mainly driven by microorganisms through SOM decomposition, but arid ecosystems are usually characterized by low energy and nutrient availability for soil microorganisms (Schimel et al., 2007). Due to the low water availability of these regions, the decomposition efficiency is slower than that of humid regions (Burke et al.,

* Corresponding author.

** Corresponding author.

E-mail addresses: fli629@hotmail.com (L. Fang), zhangxc@ms.iswc.ac.cn (X. Zhang).

1998), thus soil nutrient availability often limits both primary productivity and microbial growth (Bünemann et al., 2012; Xu et al., 2015). For example, soil phosphorus derived from plant residues can easily form an insoluble substance with calcium and magnesium. Thus, organic and occluded P become the dominant forms in the soil (Cross and Schlesinger, 2001). The decomposition of soil organic compounds can provide energy to microorganisms, making microbial nutrient acquisition especially relevant to soil carbon processing in dryland regions, which renders the transformation and metabolism of microorganisms in the soil crucial for the improvement of nutrient availability.

The transformation of SOM is mainly conducted by the coenzymes of heterotrophic microorganisms that cleave organic molecules to allow the assimilation of C, N, and P (Waring et al., 2014). Coenzyme biosynthesis responds to environmental signals such as nutrient availability, but they can also be released into the soil via microbial cell lysis. Several coenzymes have been identified as useful indicators of nutrient deficiency and microbial nutrient demand, since they are major drivers of C and nutrient turnover in different ecosystems. β -1,4-glucosidase (BG), β -1,4-N-acetylglucosaminidase (NAG), and acid or alkaline phosphatase (AP) can serve as indicators of energy (C) demand, N demand, and P demand, respectively (Schimel and Weintraub, 2003), since they catalyze terminal reactions that produce assimilable molecules containing C, N, and P from high weight molecular organic compounds (Sinsabaugh et al., 2009).

The rhizosphere soil is the most active microorganism habitat with very high coenzymatic activities (Gartner et al., 2012). The cycling of nutrients between the soil, microbes, and plants of the rhizosphere is mediated by enzymes that are produced to depolymerize organic substrates (Sterner and Elser, 2002b; Bell et al., 2013). Studies have shown that coenzymes are not only produced by soil microorganisms, but also by plant root cells (Dakora and Phillips, 2002; Sinsabaugh, 2010). Nutrient cycles such as organic matter decomposition and N mineralization can be altered by the presence of plant roots (Cheng et al., 2003). Roots also affect the activity and composition of soil microbial communities through altering soil physical properties during plant growth (Bird et al., 2011). Therefore, understanding the coenzymatic stoichiometry and the pattern of nutrient turnover involving microbes in rhizosphere soil is vitally important to achieve a better picture of soil nutrients cycling and availability in the ecological critical zone.

Soil microorganisms acclimate to stress by reassigning key resources to nutrient acquisition mechanisms, rather than growth (Schimel et al., 2007). While it has also been reported that the ratio of C:N:P in microbial biomass is relatively conserved across ecosystems compared to the ratio in the soil, the microbial biomass ratio could indicate how allocation shifts alter nutrient demand (Cleveland and Liptzin, 2007). According to Sinsabaugh et al. (2009), coenzyme activities are involved in an intersection of Ecological Stoichiometry Theory (EST) with the Metabolic Theory of Ecology (MTE), the combination of which can improve our understanding of energy and nutrient controls on microbial metabolism (Sinsabaugh et al., 2012). This intersection can be

illuminated via the Threshold Elemental Ratio (TER), which defines the element ratios at which growth shifts between nutrient limitation (represented by N and P, at high C:N or C:P) and energy (represented by C, lower C:N or C:P) (Sterner and Elser, 2002a). Additionally, under EST, organisms can be characterized with respect to the strength of their stoichiometric homeostasis. When the stoichiometric composition of the organism does not vary with changes in resource stoichiometry, it is considered to be strictly homeostatic (Sterner and Elser, 2002a). Therefore, the application of those methods and models can assist to identify microbial metabolic limitation in the ecological critical zone.

In the present research, we hypothesized that: (1) rhizosphere coenzymatic stoichiometry is greatly affected by plant species because of the different root systems and their correspondingly physiological processes; and (2) microbial nutrient acquisition in rhizosphere is limited by N or/and P rather than by C due to the nutrients (N or/and P) competition between roots and microbes. Specially, factors shaping the coenzymatic stoichiometry and microbial nutrient limitation in rhizosphere were also investigated. Therefore, we studied the coenzymatic stoichiometry related to C, N, and P cycling, identified microbial nutrient limitation in the rhizosphere soil in the arid area of the northern Loess Plateau, China.

2. Materials and methods

2.1. Study site and sampling

This research was carried out in natural grassland and shrubland ecosystems. The sites were located in Zhun Geer county of the northern region of the Loess Plateau (latitude 40° 10' to 39° 35' N and longitude 110° 35' to 111° 23' E), China (Fig. S1). The mean annual temperature of this region is 6.7 °C, with a mean minimum temperature in January of -7.6 °C and a mean maximum temperature in August of 36.5 °C. It has arid and semi-arid climate zones and the mean annual precipitation is 390 mm, with over 60% falling between July and September. The dominant plant communities in the three sections are *Artemisia ordosica*, *Agropyron cristatum*, and *Pinu tabuliformis*.

Three soil types were selected as the field experiment areas (Fig. S1), which are aeolian sandy soil on the northern side, loess on the eastern side, and feldspathic sandstone weathered soil on the western side (Calcaric Cambisol, FAO classification). There were three sampling sites from each experiment area that include the *Artemisia ordosica*, *Agropyron cristatum*, and *Pinus tabuliformis* plant communities. The descriptions of each sampling site were shown in Table 1. Three 100 m × 100 m plots were established at each sampling site in August 2016. Five 1 m × 1 m (grass community) and 5 m × 5 m (shrub community) quadrats were randomly established in each plot for measuring the characteristics of the vegetation. Plant coverage, aboveground biomass, and maximum/mean height were separately measured for each species in each quadrat. The Shannon index of plant community (H_{plant}) was calculated (Tscherko et al., 2004) and the number of species was used to estimate the richness (S_{plant}).

Table 1
The geographical features of the sampling sites.

Soil type	Abbreviation	Vegetation type	Slope aspect	Slope gradient	Altitude (m)	Main species
Aeolian sandy soil	AS	<i>A. ordosica</i>	E10°N	20°	1291	<i>A. ordosica</i> ; <i>L. davurica</i> ; <i>S. viridis</i> ; <i>P. sphondyliodes</i> ; <i>A. melilotooides</i> Pall
		<i>A. cristatum</i>	E20°N	18°	1229	<i>A. cristatum</i> ; <i>E. humifusa</i> ; <i>A. scoparia</i> ; <i>H. altaicus</i> ; <i>S. viridis</i>
		<i>P. tabuliformis</i>	W17°N	15°	1239	<i>P. tabuliformis</i> ; <i>C. chinensis</i> ; <i>A. scoparia</i> ; <i>S. nigrum</i>
Loess	LO	<i>A. ordosica</i>	E15°N	25°	1298	<i>A. ordosica</i> ; <i>S. grandis</i> ; <i>V. amoena</i> ; <i>C. endivia</i> ; <i>C. florida</i>
		<i>A. cristatum</i>	E18°N	28°	1230	<i>A. cristatum</i> ; <i>M. suavacolen</i> ; <i>P. sphondyliodes</i> ; <i>A. melilotooides</i> Pall; <i>H. altaicus</i>
		<i>P. tabuliformis</i>	W15°N	20°	1269	<i>P. tabuliformis</i> ; <i>C. chinensis</i> ; <i>S. grandis</i> ; <i>L. davurica</i> ;
Feldspathic sandstone weathered soil	FS	<i>A. ordosica</i>	E35°N	10°	1243	<i>A. ordosica</i> ; <i>L. davurica</i> ; <i>H. fruticosum</i> ; <i>P. sativa</i> ;
		<i>A. cristatum</i>	W25°N	26°	1345	<i>A. cristatum</i> ; <i>L. davurica</i> ; <i>A. frigida</i> ; <i>B. pilosa</i>
		<i>P. tabuliformis</i>	E15°N	15°	1251	<i>P. tabuliformis</i> ; <i>S. grandis</i> ; <i>A. vestita</i> ; <i>M. sativa</i> ; <i>A. scoparia</i>

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