

Ecoenzymatic stoichiometry at the extremes: How microbes cope in an ultra-oligotrophic desert soil



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ABSTRACT

Arid ecosystems are characterized by stressful conditions of low energy and nutrient availability for soil microorganisms. It has been observed that the ecoenzymes needed for the transformation of organic compounds into assimilable products show similar scaling relationships in different habitats (logarithmic C:N:P scaling ratios ~1:1:1). In this study in Cuatro Ciénegas Basin (CCB) in the Chihuahuan desert of México, we report among the lowest ecoenzymatic activities yet quantified in soil. Nevertheless, activities for both organic N and organic P acquisition enzymes scale with C acquisition with a slope of ~1.0, indicating that the soil microbial communities of this ultra-oligotrophic desert ecosystem follow the global ecoenzymatic stoichiometry patterns. CCB soil microbial communities were co-limited by C and either by N or P but this co-limitation played out differently in different parts of the CCB as indicated by microbial ecoenzymatic shift to allocate more resources to acquire and immobilize the scarcer nutrient. By extending ecoenzymatic analyses to these ultra-oligotrophic soils, our findings support the broad utility of the approach in illuminating how microbes acquire limiting resources in arid ecosystems.

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1. Introduction

Drylands (defined as sites with <500 mm mean annual precipitation; Noy-Meir, 1973) cover more than one-third of the Earth's continental surface and thus constitute the most extensive terrestrial biome on the planet (Pointing and Belnap, 2012). Estimates of carbon storage for dryland regions indicate that they contribute 36% of the total carbon storage worldwide (Campbell et al., 2008). A high proportion of these dryland areas is covered by grasslands, which represent an important pool (8%) of global carbon (C) reservoirs (IPCC, 2001). In desert grasslands, the main inputs of soil organic matter (SOM) are from underground biomass rather than from aerial biomass (Sims and Singh, 1978); the former also represents the principal source of soil nitrogen (N) and phosphorus (P).

Due to the low water availability of desert ecosystems, SOM decomposition is slower than in more humid settings (i.e. tropical

or temperate forest ecosystems; Burke et al., 1998). Thus, arid ecosystems are usually characterized by stressful conditions of low energy and nutrient availability for soil microorganisms (Schimel et al., 2007) and N and P availability often limit primary productivity as well as microbial activity (López-Lozano et al., 2012).

Additionally, in soils derived from geologic substrata with low apatite content (as is the case for the soil in our study), both organic P and occluded P are the dominant forms in the soil (Walker and Syers, 1976; Perroni et al., 2014a) but these are relatively unavailable to plants. Therefore, P availability in these soils depends on mineralization of organic P fractions by soil microorganisms (Walker and Syers, 1976; Cross and Schlesinger, 2001), making microbial P limitation especially relevant for soil carbon processing in desert regions.

Most soil organic compounds are transformed or metabolized by microbes (Bradford et al., 2013), mainly by heterotrophic microorganisms that produce extracellular enzymes (ecoenzymes) that cleave organic molecules to allow C, N, and P assimilation (Waring et al., 2014). Ecoenzyme biosynthesis responds to environmental signals such as low nutrient availability to meet microbial nutrient demands; additionally, ecoenzymes can also enter the soil after cell lysis (Rilling et al., 2007; Sinsabaugh et al., 2009).

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After the recognition that coenzymes are major drivers of C and nutrient cycling in terrestrial, freshwater, and marine ecosystems, several coenzymes have been identified as useful indicators of nutrient deficiency and microbial nutrient demand (Burns, 1982; Nannipieri, 1994; Olander and Vitousek, 2000; Schimel and Weintraub, 2003; Renella et al., 2006; Sinsabaugh et al., 2009; Sinsabaugh and Follstad, 2012; Sinsabaugh et al., 2012; Waring et al., 2014). These enzymes are: β -1,4-glucosidase (BG) and cellobiohydrolase (CBH) as indicators of energy (C) demand; β -1,4-N-acetylglucosaminidase (NAG) and leucine aminopeptidase (LAP) as indicators of N demand; and acid or alkaline phosphatase (AP), as indicator of P demand (Schimel and Weintraub, 2003). These enzymes catalyze terminal reactions that produce assimilable molecules containing C, N, and P from high molecular weight organic compounds (Sinsabaugh et al., 2009).

Soil microorganisms acclimate to stress by reassigning key resources (i.e. energy, C, N, and P) to acquisition mechanisms rather than growth (Schimel et al., 2007). While it has also been reported that the ratios of C:N:P in microbial biomass are relatively constrained across ecosystems relative to variability in environmental nutrient availability (Cleveland and Liptzin, 2007), these ratios in the soil microbial biomass could nevertheless indicate how allocation shifts alter nutrient demand. For example, higher biomass C:N ratios likely reflect a greater overall investment in C-rich structural cellular material (Paul and Clark, 1996) while lower N:P ratios may reflect the higher allocation to P-rich ribosomes (Elser et al., 2003). Because coenzymatic activities reflect the microbial cell's response to meet its metabolic nutrient demands in response to environmental nutrient availability, ratios of commonly measured coenzymatic activities can be used to assess how the microbial community invests in energy relative to multiple nutrient acquisition under *in situ* conditions as it copes with resource limitation.

According to Sinsabaugh et al. (2009), coenzyme activity involves an intersection of Ecological Stoichiometry Theory (EST) with the Metabolic Theory of Ecology (MTE), offering promise to improve our understanding of energy and nutrient controls on microbial community metabolism (Sinsabaugh et al., 2012). This intersection can be understood via the Threshold Elemental Ratio (TER), that defines the element ratio 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, 2002; Frost et al., 2006). Additionally, under EST, organisms can be characterized with respect to their strength of stoichiometric homeostasis, e.g. the degree to which their biomass elemental composition shifts in response to the elemental composition of its diet or environmental resource supplies (Sterner and Elser, 2002). When the stoichiometric composition of the organism does not vary with changes in resource stoichiometry, the organism is considered strictly homeostatic. The growth of such strictly homeostatic organisms is strongly regulated by the most limiting nutrient and such an organism would be expected to respond with shifts in coenzymes that contribute to this homeostasis. In contrast, when the stoichiometry of the organism changes proportionately with the stoichiometry of the resource, the organisms are characterized as weakly or non-homeostatic; such adjustments may dampen the immediate impacts of nutrient limitation on growth but require a capacity for extensive storage (Sterner and Elser, 2002).

Our main objective in this study was to calculate the soil coenzymatic stoichiometry and determine its relation with soil energy (organic carbon) and nutrient availability for the soil microbe community in an extremely oligotrophic desert ecosystem with very low soil organic matter content. For that, we measured soil organic nutrients, nutrients within the microbial biomass, soil

coenzyme activities, and we estimated microbial homeostasis at the community level in two energy-contrasting soils within the Cuatro Ciénegas Basin, México. We sought to quantify soil and microbial C:N:P ratios together with coenzymatic activity to determine the roles of energy and nutrient limitation in affecting microbial metabolism under these stressful conditions. Our hypothesis is that under lower soil C availability, the microorganisms invest more energy in nutrient acquisition rather than on increasing their biomass, by producing more coenzymes associated with the scarcer nutrient. This mechanism allows the microbial soil community to maintain nutrient homeostasis in soils with constrained energy availability. Our data shed light on the factors controlling carbon and soil nutrient cycling within and across desert ecosystems and extend the range of our current understanding of coenzymatic coupling in soil ecosystems.

2. Methods

2.1. Site description and soil sampling

This study was carried out in a grassland soil in the central region of the Chihuahuan Desert in the Cuatro Ciénegas basin (26°50'N and 102°8'W) in Coahuila, Mexico (740 m a. s.l). The climate is hot and arid; in spite of an average annual temperature of 21 °C, temperatures as high as 45 °C have been reported, mainly in July, as well as temperatures below 0 °C in January (SMN, CONAGUA, 2013). The mean annual precipitation is 253 mm but this is highly variable among years (Fig. 1). The majority of rainfall occurs mainly in summer. In the western side of the basin, Jurassic-era gypsum is the dominant parent material while in the eastern side Jurassic-era sandstones dominate (McKee et al., 1990). According to the world reference base for soil resources (WRB), the dominant soils are *Gypsisols* and *Calcisols* for the western and eastern sides, respectively. In both parts of the basin the grass *Sporobolus airoides* (Torr.) is the dominant plant species (Perroni et al., 2014b).

A sampling site was selected in each side of the basin: Churince (CH), in the western side; 26° 50.561'N; –102° 08.099'W; and Rancho Pozas Azules reserve (PA) in the eastern side; 26° 49.635'N; –102° 01.470'W. Total aboveground biomass was 493 ± 61 and 323 ± 9 g m⁻²; meanwhile total belowground biomass was 751 ± 170 and 289 ± 23 g m⁻² for the western and the eastern sides, respectively (Tapia-Torres et al., 2015; Montiel-González unpublished data). Additionally, total C, N and P concentrations were 13.4 ± 1.8 mg g⁻¹; 0.9 ± 0.2 mg g⁻¹; 0.09 ± 0.01 mg g⁻¹, for the western side; and 5.9 ± 0.7 mg g⁻¹; 0.6 ± 0.07 mg g⁻¹;

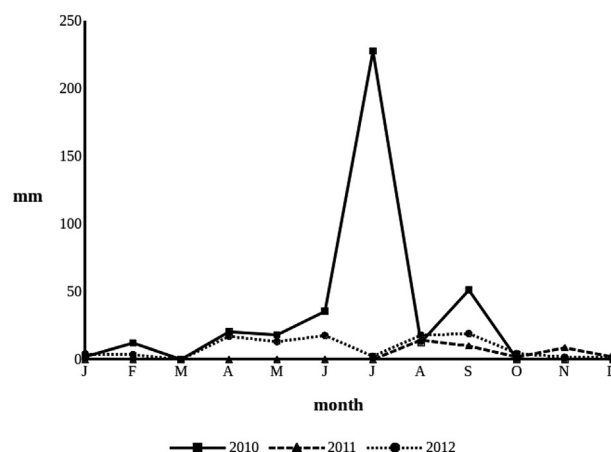


Fig. 1. Monthly rainfall for 2010, 2011 and 2012 year at Cuatro Ciénegas Basin.

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