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Vegetation-soil system controls soil mechanisms for nitrogen transformations in an oligotrophic Mexican desert



Yunuen Tapia-Torres^a, Nguyen E. López-Lozano^{b, c}, Valeria Souza^c, Felipe García-Oliva^{a, *}

^a Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Mexico

^b División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica (IPICyT), San Luis Potosí, S.L.P., Mexico

^c Instituto de Ecología, Departamento de Ecología Evolutiva, Universidad Nacional Autónoma de México, CU, AP 70-275, Coyoacán 04510, México DF,

Mexico

A R T I C L E I N F O

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ABSTRACT

Vegetation communities with high soil carbon (C) inputs, e.g. grassland ecosystems, promote N protection via microbial communities in the soil whereas communities with low soil C inputs, e.g. desert scrub ecosystems, promote nitrification and are therefore susceptible to N loss. This study examines this relationship more closely by assessing the effects of two vegetation-soil systems on soil N transformation, in a grassland-desert scrub in Cuatro Ciénegas Basin, Mexico. Metrics used in our study include: the belowground biomass of C, N and phosphorus (P) in both vegetation types; the availability of C, N and P in the soil; and the potential transformation of these nutrients by the microbial community which was characterized by 16S rRNA clone libraries. We found: (1) a higher NH_4^+ and microbial N concentration in the grassland soil than in the desert scrub soil, and (2) a different bacterial soil communities between both vegetation-soil systems. These findings suggest an interrelationship between nutrients in the belowground biomass, soil nutrient dynamics, and the soil bacterial community whereby grasslands promote a closed system that conserves N, whereas desert scrub vegetation exhibits an open system that sheds N.

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1. Introduction

Drylands constitute the most extensive terrestrial biome on the planet, covering more than one-third of Earth's continental surface (Pointing and Belnap, 2012). Grasslands and desert scrub are the predominant vegetation types in drylands (Epstein et al., 2002), and are known to influence patterns of soil carbon (C) and nitrogen (N) distribution within the soil (West and Klemmedson, 1978). Grasses allocate more of their biomass to their roots and the majority of this root biomass is concentrated in the top 0.5 m of the soil. By contrast, desert scrub plants allocate less of their total biomass below ground (Goodale and Davidson, 2002). The two vegetation types found in these ecosystems correspond with varying quantities of organic C (OC) and N inputs to the soil.

Nutrient dynamics in desert ecosystems is also closely linked to seasonal variation in air temperature and moisture (Burke, 1989). As a result, organic matter (OM) decomposition, microbial

* Corresponding author. E-mail address: fgarcia@cieco.unam.mx (F. García-Oliva). immobilization and N mineralization are largely confined to the growing season, when the moisture and temperature of the desert are amenable to microbial activity (O'Brien, 1978). After this initial summer boom, however, microbial activity typically decreases as the rate of soil-nutrient transformations slows down and sources of C in the soil diminish (Montaño et al., 2007; Schimel and Weintraub, 2003).

Although the soil is an important reservoir of OC, only a low concentration is readily available to microorganisms (Daniel, 2005). Indeed, the available form of C, termed dissolved organic carbon (DOC), typically accounts for only 0.05–4% of soil organic carbon (SOC) and varies in concentration according to soil and vegetation types (Haynes, 2005). Once a microbe has taken up the organic molecules, the availability of inorganic molecules within the ecosystem is entirely determined by the metabolism of the microbiota (Schimel and Schaeffer, 2012). For example, C availability promotes N immobilization by heterotrophic microorganisms, decreasing the N budget in the soil and thereby reducing N availability for plants and microbes (Chapin et al., 2002; Montaño et al., 2007). The enzymes involved in N transformation include hydrolases, oxidases, deaminases and lyases, all of which are



produced by plants, animals and microorganisms (Jones et al., 2004). These enzymes act intra-cellularly, decomposing the organic nitrogen (ON) until only the N in excess of microbial demand is released to the soil as ammonium (NH⁺₄). This is understood to be a closed system because all N is entirely conserved through the activities of biota in the ecosystem. Similar observations have been made in studies of desert soils (López-Lozano et al., 2012), as well as in other ecosystems (tropical deciduous forest; Montaño et al., 2007).

By contrast, when the availability of DOC is low, autotrophic pathways, such as nitrification, are favored, and nitrate (NO_3^-) accumulates (Vitousek, 2002). Finally, NO_3^- is released to the atmosphere by denitrification or leached from the soil. These autotrophic strategies are associated with an open system, where N can be lost from the ecosystem. In this way, C availability affects both soil N transformation and soil bacteria composition by favoring the activities of taxa adapted to grow on resources supplied by soil organic matter (SOM) inputs (Thomson et al., 2010).

López-Lozano et al. (2012) conducted a study on two sites with different humidity in the gypsum rich Cuatro Ciénegas basin (CCB), a Mexican desert oasis ecosystem. They found that the site with higher DOC concentration also exhibited higher quantities of NH[‡], microbial C (Cmic) and N concentration. As expected, a higher bacterial taxonomic diversity at this site was associated with denser vegetation and more water availability. This humid and richer site had a closed N cycle with greater N immobilization. However, in the dry site with poor plant coverage and lower DOC, nitrification dominated over N microbial immobilization which resulted in N losses. This last study was the first to characterize the soil microbial community and its relationship to nutrient dynamics in CCB.

Nutrient dynamics is direct function of microbial diversity in the soil. For example, in a wide sampling of soils in North America, Fierer et al. (2007) found a negative correlation between Acid-obacteria abundance and C mineralization rates, whereas the abundances of β -Proteobacteria and Bacteroidetes positively correlated with C mineralization rates. No such correlation was observed, however, with other groups like α -Proteobacteria, Firmicutes, and Actinobacteria. However, in the desert soil of CCB, Lopez-Lozano et al. (2013) found a positive correlation between the anaerobic photosynthetic Cloroflexi and TM6 with total organic C (TOC) availability. This suggests that in this site soil microbes also fix C, having a key role in soil productivity.

The main objective of this study was to examine the effects of a vegetation-soil system on potential soil N transformation and availability in a grassland-desert scrub in the Cuatro Ciénegas basin during two contrasting seasons. Our hypothesis was that mineralization and immobilization processes are more important in the grassland ecosystem and thus that N is more protected in a closed cycle. This contrasts with the desert scrub ecosystem where nitrification could be the most important process in N transformation, given the scarcity of OM inputs to the soil. Additionally, we expected a higher microbial immobilization and mineralization in the warmer and moist season (summer) than in the cold and dry season (winter).

To test the hypothesis, we measured the C, N and P concentration in the root biomass of the two vegetation-soil systems. We also quantified soil C, N and P availability and determined the potential transformation of these nutrients by the microbial community, which was characterized by 16S rRNA clone libraries. We observed different potential N transformation in each site along with contrasting microbiota. As expected, we found these microbial transformations were higher during the summer season than in the winter season.

2. Materials and methods

2.1. Site description and soil-vegetation sampling

This study was carried out in the Cuatro Ciénegas basin (26°50'N and 102°8′W) located at 740 m above sea level. in the Chihuahuan desert. Mexico. The climate is hot and arid, with an annual precipitation of 252 mm, which occurs mainly in summer and occasionally in winter. The average annual temperature is 21 °C, with July as the hottest (28 $^{\circ}$ C) and January as the coldest month (15 $^{\circ}$ C; Cuatro Ciénegas weather station). According to the world reference base for soil resources (WRB, 2007), the dominant soils are gypsisols and leptosols, as opposed to Jurassic gypsum and limestone (McKee et al., 1990). The main vegetation types are grassland dominated by Sporobolus airoides (Poaceae) and Allenrolfea occidentalis (Amaranthaceae); and desert scrub dominated by Jatropha *dioica* (Euphorbiaceae) and *Larrea tridentata* (Zygophyllaceae) (Perroni et al., 2014). Each vegetation type is growing over different bedrock and consequently defines the two vegetation-soil systems studied: grassland over gypsisol and desert scrub over leptosol. The grassland site was located in the valley bottom on gypsum without the influence of lime-stone from Sierra de San Marcos. In contrast, this lime-stone influence the desert scrub soils, which was located on the foot slope of this ridge. There are five plant species in the grassland and 21 species in the desert scrub, with only one species present in both habitats (Prosopis laevigata; Perroni et al., 2014).

A sampling site was selected for each vegetation-soil system. These two sites are separated by 3.5 km. In August 2007 (summer sampling) and February 2008 (winter sampling), a 100 by 50 m plot was demarcated at each sampling site. The plots were divided into 10 transects, separated from each other by a distance of 10 m. A sampling subplot of 2×2 m (4 m²) was selected randomly on each transect; 15 cm deep soil samples were taken from five locations (one central point and four corners) within each sampling subplot, and then were mixed to form one composite sample. In total, 10 composite samples were taken at each site during each sampling date. Afterwards, each sampling subplot was divided into four parts for sampling aboveground vegetation. In two of these four parts, all aboveground biomass was collected and stored in black plastic bags before laboratory analyses of total carbon (TC) and total nitrogen (TN). Five root samples were collected in each of the 10 transects per plot and stored in the same way, and the same analyses were performed. The vegetation sampling was conducted only in one season (August 2007). Soil for biogeochemical analysis was stored in black plastic bags and refrigerated at 4 °C for laboratory analyses. As a way of characterizing the bacterial community at each site, 100 g samples were taken from each subplot and used to prepare one composite sample from each site and each sampling season. The resulting four samples were immediately stored in liquid nitrogen until DNA extraction.

2.2. Biogeochemical analyses

Soil pH was measured in deionized water (1:2 w: v) with a digital pH meter (Corning). A subsample (100 g) was oven-dried at 75 °C to constant weight for soil moisture determination using the gravimetric method. All C forms analyzed were determined with a Total Carbon Analyzer (UIC Mod. CM5012; Chicago, E.U.A), while N and P forms determined by colorimetrical analyses using a Bran-Luebbe Auto Analyzer III (Norderstedt, Germany).

Before the analyses of total nutrient forms, soil samples were dried and then ground with a pestle and mortar. Total carbon and inorganic carbon were determined by combustion and coulometric detection (Huffman, 1977). TOC was calculated as the difference between total C (TC) and inorganic C (IC). For total N (TN) and TP

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