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Natural grassland as the optimal pattern of vegetation restoration in arid and semi-arid regions: Evidence from nutrient limitation of soil microbes

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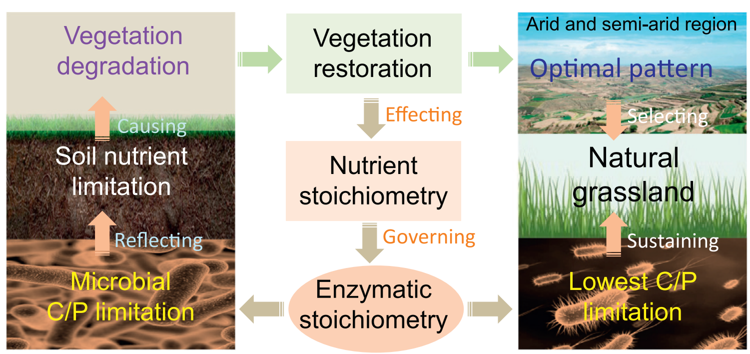
HIGHLIGHTS

- Microbial metabolisms were co-limited by C and P in arid and semi-arid regions
- Vegetation restoration affected the characteristics of soil microbial metabolism
- Microbial C and P limitations were the lowest in the natural grassland
- Microbial metabolic limitations depend on the balance of nutrient stoichiometry

GRAPHICAL ABSTRACT



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ABSTRACT

Soil microbial metabolism is vital for nutrient cycling and aboveground ecosystem stability. A general understanding of microbial metabolism and nutrient limitation under human disturbance in arid and semi-arid regions, which are the largest and most fragile oligotrophic ecosystems globally, however, is still limited. We quantified and compared the characteristics of nutrient limitation of soil microbes under natural/artificial grassland and shrubland, an ecological forest, an economic forest, and sloped cropland in typical arid and semi-arid ecosystems on the Loess Plateau, China. Vegetation restoration significantly affected the activities of extracellular enzymes and ecoenzymatic stoichiometry mainly by affecting soil nutrients and nutrient stoichiometry. A vector analysis of enzyme activity indicated that microbial communities were co-limited by carbon (C) and phosphorus (P) in all types of vegetation restoration. Linear regression indicated that microbial C and P limitations were significantly correlated with the stoichiometry of soil nutrient, suggesting that the balance of nutrient stoichiometry is an important factor maintaining microbial metabolism and elemental homeostasis. C and P limitations in the microbial communities were the lowest in the natural grassland. This implies that both vegetation and microbial communities under the restoration pattern of natural grassland were more stable under environmental stress, so the restoration of natural grassland should be recommended as the preferred option for ecosystem restoration in these arid and semi-arid regions.

1. Introduction

Land degradation has become more intense around the world under climate change, especially in arid and semi-arid regions due to

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anthropogenic activities and poor land management (Lal, 2001). Approximately 1.5 billion people are directly affected by land degradation (Godfray et al., 2010). Land degradation not only induces the deterioration of ecological functions and land productivity by soil erosion, desertification, and salinization, but also threatens socio-economic and cultural development at regional and global scales (Zhang et al., 2011; Liu and Shao, 2015). Ecological restructuring and vegetation restoration have recently been carried out globally for preventing land degradation and mitigating climate change (Deng et al., 2014).

Ecological restructuring and vegetation restoration have brought large ecological benefits. Vegetation restoration can prevent soil erosion (Zhang et al., 2011; Deng et al., 2012), increase the sequestration of soil carbon (Lal, 2002; Deng et al., 2014), improve soil nutrient status (Cao et al., 2008; Wang et al., 2011) and improve microbial properties (Fu et al., 2009; Zhang et al., 2016). Ecological restructuring and vegetation restoration in arid and semi-arid regions, however, are confronted with serious challenges due to the constraints of various environmental factors. Soil water, one of the most limiting factors in arid and semi-arid regions, is the key factor affecting vegetation survival and ecosystem stability in arid and semi-arid ecosystems (Wang et al., 2008). For example, continuous water consumption by vegetation leads to a deficiency of soil water and the emergence of dried soil layers, which can cause the degeneration of vegetation communities on the Loess Plateau in China (Wang et al., 2011; Liu and Shao, 2015). Nutrient contents and plant-microbe interactions also play key roles in plant growth and ecosystem stability (Bloom et al., 1985; Fowler, 1986; Forde and Lorenzo, 2001), a deficiency of soil water is not the sole cause of vegetation degradation. The roles of nutrients regulated by microorganisms in vegetation degradation in arid and semi-arid ecosystem have nevertheless rarely been studied.

Microorganisms provide plants with available nutrients but also compete nutrients with roots for nutrients when deficient (Inselsbacher et al., 2010; Sinsabaugh and Shah, 2011). Nutrient availability is generally low in arid and semi-arid regions such as the Loess Plateau because of the low primary productivity, high nutrient immobilization by calcium and magnesium, and high nutrient loss by soil erosion (Feng et al., 2013). The low nutrient availability may thus also be an important factor limiting plant growth. Soil water deficiency can also limit the transport and availability of soil nutrients, which would intensify the competition for nutrients between plants and microbes in micro-environments (Ouyang et al., 2016). A deficiency of available nutrients may greatly aggravate vegetation degeneration in arid and semi-arid regions due to the strong competition for nutrients between plants and microbes. The characteristics of microbial metabolic limitations are therefore important indicators for determining the relationship between vegetation degeneration and soil nutrient limitation in arid and oligotrophic ecosystems.

Microorganisms acquire soil nutrients by secreting extracellular enzymes to degrade complex organic compounds. The secretion of extracellular enzymes is also the rate-limiting step for microorganic metabolism (Jones et al., 2009). Extracellular enzymatic activities (EEA) can thus be used to identify the relationships between microbial metabolism and nutrient cycling (Sinsabaugh et al., 2008; Burns et al., 2013; Duan et al., 2018). Ecoenzymatic stoichiometry is an indicator of the ability of microorganisms to use nutrients, which can be used to assess the flow of energy in an ecological system (Jones et al., 2009; Sinsabaugh et al., 2008, 2009) and to estimate the balance between microbial nutrient demand and soil nutrient supply (Sterner and Elser, 2002; Sinsabaugh et al., 2009). For example, ecoenzymatic stoichiometry analysis has been used to identify phosphorus (P) limitation in tropical forest eocsystems (Waring et al., 2014) and nitrogen (N) and P co-limitation in arid and oligotrophic ecosystems (Tapia-Torres et al., 2015). Studying ecoenzymatic stoichiometry for identifying microbial metabolic limitations in anthropogenic arid and semi-arid ecosystems is thus crucial.

To illustrate the microbial metabolic limitations through ecoenzymatic stoichiometry, Sinsabaugh et al. (2008) developed a method to visualize the relative C, N and P controls on soil microbial communities by plotting ratios of enzymatic activities associated with C, N and P acquisition. Moorhead et al. (2016) proposed using the 'length' and 'angle' of vectors in plots of proportional C:N *vs.* C:P activities of enzyme to quantify the relative investments in C *vs.* nutrient acquisition (vector length) or P *vs.* N acquisition (vector angle). Translating these ratios into vector lengths and directions (angles) indicated the simultaneous, relative resource demands of the microbial community independent of variations in total enzyme activity and provided clear metrics of relative C limitation (length) and relative P *vs.* N limitation (angles) (Moorhead et al., 2016). Fanin et al. (2016), for example, used vector analysis of ecoenzyme activities to determine that the overall N requirement of microbial communities increased relative to P during litter decomposition, but that the C requirement increased more rapidly than either N or P in most of ecosystems. The application of this method can help to identify microbial metabolic limitation, which may provide key evidence of plant death during vegetation restoration.

Vegetation degradation is particularly serious on the Loess Plateau (Lal, 2002; Wu et al., 2003). The 'Grain-for-Green' programme, one of the world's most ambitious conservation set-aside programmes, was launched in China in 1999 (Feng et al., 2013; Deng et al., 2017). Much of the reconstructed vegetation on the Loess Plateau has died and aged, as in many other places in recent years (Chen et al., 2007; Zhao et al., 2014). The Loess Plateau, as a typical area with degraded vegetation, therefore provides an opportunity to identify the factors that play important roles in limiting survival of vegetation in arid and semi-arid regions and to determine the best patterns of vegetation restoration.

Considering the water-limited and oligotrophic environmental conditions in arid and semi-arid regions, we hypothesized that: (1) soil microbial communities would suffer from strongly nutrient limitation because soil water limits nutrient availability and microbial activity, (2) microbial nutrient limitations would vary greatly under different patterns of vegetation restoration due to the distinct plant-microbe feedbacks and strategies of nutrient acquisition, and (3) microbial nutrient limitations would be strongly correlated with the stoichiometries of soil nutrients and the activities of extracellular enzymes due to the elemental stoichiometric balance of microbial biomass. We therefore investigated the characteristics of extracellular enzymes involved in C, N, and P cycling, and identified microbial nutrient limitation in various patterns of vegetation restoration on the central Loess Plateau (a typical fragile ecosystem). This study provides fundamental information and novel ideas for assessing vegetation degradation in arid and semi-arid systems.

2. Materials and methods

2.1. Study site and sampling

The study site was in the Zhifanggou Watershed, Shaanxi Province, China (36°46′N, 109°16′E, Fig. 1). The watershed contains the typical types of vegetation in this hilly-and-gully region of the Loess Plateau. There has a semi-arid climate, with a mean annual temperature of 8.8 °C and a mean annual precipitation of 510 mm, most of which falls from July to September. The soil is mainly composed of a Huangmian soil (Calcaric Cambisol, FAO classification), developed on wind-deposited loessial parental material and characterized by yellow particles, absence of bedding, silty texture, looseness, macroporosity, and wetness-induced collapsibility. The study area is subjected to both wind and water erosion.

Soil and water conservation, integrated management, and vegetation restoration have been carried out in this area since the mid-1980s as a pilot project (Ping and Liu, 2009). The conversion has caused a significant change in vegetation type. The region currently consists of grassland, shrubland, forest, and sloped cropland. It has also been used to monitor vegetation restoration as a field experimental site of the