



Responses of soil microbial functional genes to global changes are indirectly influenced by aboveground plant biomass variation



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ABSTRACT

Global nitrogen (N) deposition and precipitation change are two important factors influencing the diversity and function of terrestrial ecosystems. While considerable efforts have been devoted to investigate the responses of aboveground plant communities to altered precipitation regimes and N enrichment, the variations of belowground soil microbial communities are not well understood, particularly at the functional gene structure level. Based on a 9-year field experiment established in a typical steppe in Inner Mongolia, China, we examined the impacts of projected N deposition and precipitation increment on soil microbial functional gene composition, and assessed the soil/plant factors associated with the observed impacts. The overall functional gene composition significantly shifted in response to precipitation increment, N deposition and their combinations (all ADONIS $P < 0.05$), and such changes were primarily correlated with soil pH, microbial biomass, and microbial respiration. Water supply increased the abundances of both carbon (C) and N cycling genes, suggesting that the projected precipitation increment could accelerate nutrient cycling in this semi-arid region. N effects were mainly observed on the genes involved in vanillin/lignin degradations, implying that the recalcitrant C would not accumulate in soil under future scenarios of higher N deposition. Structural equation modeling (SEM) analysis revealed that soil dissolved organic carbon (DOC) was a key factor directly determining the abundance of C degradation and N cycling genes, and aboveground plant biomass indirectly influenced gene abundance through enhancing DOC. The present work provides important insights on the microbial functional feedbacks to projected global change in this semi-arid grassland ecosystem, and the mechanisms governing C and N cycles at the regional scale.

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1. Introduction

The diversity and function of terrestrial ecosystems are greatly influenced by anthropogenic disturbance and global climate change worldwide. Increased atmospheric nitrogen (N) deposition, caused by fossil fuel combustion and application of N fertilizers, is

an important aspect of anthropogenic global change (Galloway et al., 2008; Schlesinger, 2009; Canfield et al., 2010). In addition, precipitation regimes are predicted to change at both global and regional scales (IPCC, 2013). Predicting ecosystem responses to global change is a fundamental issue in ecology. It has been well documented that the aboveground plant community is sensitive to precipitation change (Cleland et al., 2013; Eskelinen and Harrison, 2015) and N deposition (Stevens et al., 2004; Clark and Tilman, 2008), particularly in arid and semi-arid grassland ecosystems, where water and N are generally considered to be limiting resources (Harpole et al., 2007; Yang et al., 2011; Xu et al., 2012b). A growing body of evidence suggests that higher precipitation increases plant species richness (Bai et al., 2008; Xu et al., 2015b),

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whereas N fertilization is reported as the main driver of the loss of species richness (Gough et al., 2000; Stevens et al., 2004; Yang et al., 2011). Plant primary productivity and litter quality are generally enhanced by both precipitation increment (Harpole et al., 2007; Bai et al., 2008; Wu et al., 2011; Allison et al., 2013) and N inputs (Suding et al., 2005; LeBauer and Treseder, 2008; Phoenix et al., 2012; Xu et al., 2015b) in N-limited arid and semi-arid terrestrial ecosystems.

Although considerable effort has been devoted to investigating aboveground plant communities in response to precipitation change and N deposition in the past decade, the impacts of projected global change on belowground microbial communities and soil carbon (C) and N cycling processes they mediate are not well understood. By sequencing taxonomic gene markers (e.g., 16S rRNA), a number of recent studies indicated that N addition (Campbell et al., 2010; Ramirez et al., 2010; Zhang et al., 2014a) and precipitation changes (Clark et al., 2009; Evans et al., 2014; Barnard et al., 2015) could alter the diversity and composition of soil microbial communities. In general, increases in N input would increase the relative abundance of copiotrophic taxa (those taxa that have higher N demands and adept at catabolizing more labile C pools), such as Proteobacteria; and reduce that of oligotrophic taxa (those taxa that are adept at catabolizing more recalcitrant C pools), typically represented by Acidobacteria (Fierer et al., 2007). As a consequent, N enrichment is proposed to result in a shift towards labile C decomposition (Fierer et al., 2007; Ramirez et al., 2010). The responses of microbial communities to precipitation regimes are inconsistent, though it was generally hypothesized that increased precipitation would increase soil nutrients level, and subsequently the relative abundance of copiotrophic taxa. In a shortgrass steppe ecosystem, it was reported that Actinobacteria tended to be less abundant under drought (Evans et al., 2014). However, an experiment conducted in a California annual grassland showed that the relative abundance of Acidobacteria increased, and that of Actinobacteria decreased, with wet-up treatment (Barnard et al., 2015). The ecological categories of Actinobacteria are not very clear, and previous publications documented the mixed results, with their relative abundance increasing (Ramirez et al., 2010, 2012; Zeng et al., 2016), or remaining unchanged (Fierer et al., 2007; Zhang et al., 2014a; Li et al., 2016) in response to nutrients addition. Another field experiment demonstrated that the larger, but less frequent, rainfall events enhanced the relative abundance of Verrucomicrobia and Alphaproteobacteria (Evans and Wallenstein, 2012). Verrucomicrobia typically showed an oligotrophic tendency (Ramirez et al., 2012), however, the irresponsiveness of this phylum to elevated nutrients level has also been documented (Li et al., 2016). Although increasing information on the effects of N deposition and precipitation regimes on microbial taxonomic genes has been collected, the responses of soil microbial functional gene diversity and composition to global change, and their potential linkages to soil processes, still remain unclear. Soil microbial communities play important roles in litter decomposition and are key drivers of nutrient cycling in terrestrial ecosystems. Evaluating the effects of global change on soil microbial functional genes is critical for predicting functional feedbacks to the climate system (Zhou et al., 2012; Xue et al., 2016) and deepening our understanding of C and N cycles at a regional scale.

The semiarid temperate grassland in northern China is of a typical vegetation type in the Eurasian continent, covering 78% of the grasslands area in China (Kang et al., 2007). These grasslands support diverse species of plants and are of great importance to ecosystem services, functions, and socio-economics of the region. It has been predicted that the summer precipitation in Northern China will increase by 50% (Sun and Ding, 2010) and the atmospheric N deposition in this area is also expected to increase in the

coming decades (Bai et al., 2008, 2010). To predict the ecosystem response to the projected global change, a field experiment manipulating water and multi-level N addition was established in 2005 in a natural steppe in Duolun, Inner Mongolia, China (Xu et al., 2010). After 9 years of treatment, our previous results showed that the plant communities are sensitive to N enrichment and increased precipitation in terms of species richness, community composition and stability (Xu et al., 2010, 2012a, b; 2014, 2015a, b). We recently analyzed the response of soil bacterial diversity and community composition to the increased precipitation and N deposition by sequencing of 16S rRNA gene amplicons, and found that the N enrichment induced co-variation between bacterial and plant communities, and increased precipitation dampened the N effects (Li et al., 2016). However, microbial functional feedback to global change has been rarely studied and requires more direct observed evidence. The specific aims of this study were to examine the impacts of long-term N amendments and precipitation increment on soil microbial functional genes, and to determine what mechanisms might be responsible for the observed responses.

We hypothesized that the abundance of functional genes involved in C and N cycling would be stimulated by precipitation increment and N enrichment in this semi-arid grassland ecosystem, directly associated with increased water availability and nutrient resources. We also expected that the increase in plant productivity induced by water supply (Bai et al., 2008) and N deposition (Gough et al., 2000) would indirectly stimulate C degradation genes through enhancing plant C inputs to the soil. In particular, because increased precipitation and N amendments can reduce the C:N ratio and improve the chemical quality of the litter inputs (Lü et al., 2012; Allison et al., 2013), we further predicted that the abundance of labile C degradation genes will respond more strongly to projected global change, whereas the genes involved in recalcitrant C degradation will show weaker responses. We tested these hypotheses using the newest generation of the functional gene array GeoChip (version 5.0_60K) to detect microbial functional gene abundance and composition in soil samples treated with 9-year N fertilization and water addition.

2. Materials and methods

2.1. Site description and experimental design

The study sites were located at the Restoration Ecological Research Station (E 116°17'20", N 42°2'29"), Duolun, Inner Mongolia, Northern China. Mean annual precipitation (MAP) is ~380 mm, with >80% of the precipitation occurring between June and September. Mean annual temperature is 2.1 °C, with mean monthly temperature ranging from -17.5 °C in January to 18.9 °C in July. The soil is classified as Calcis-orthic Aridisol according to the US Soil Taxonomy classification. Soil texture of the experimental site is sandy loam with 62.75% sand, 20.30% silt, and 16.95% clay (Chen et al., 2009). The experiment was established in a natural steppe ecosystem that has been fenced since 2000 to prevent grazing by large vertebrate herbivores (Xu et al., 2010).

A field experiment with a constant increase in precipitation and N supply was established in 2005 to examine the potential effects of N deposition and changes in precipitation regime on ecological processes. A split-plot experimental design was employed, which involves two levels of precipitation (ambient or added) applied at the plot scale and four levels of N (0, 5, 10, 15 g N m⁻² yr⁻¹) applied to subplots within precipitation treatments. The estimated mean nitrogen deposition rate in northern China is about 8.3 g N m⁻² year⁻¹ (He et al., 2007). Consequently, the total amounts of N inputs varied from approximately 8.3 to 23.3 g N m⁻² year⁻¹, simulating the continuous increasing of N deposition in this region. Each

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