Soil Biology and Biochemistry 116 (2018) 388–398

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Plant diversity is coupled with beta not alpha diversity of soil fungal communities following N enrichment in a semi-arid grassland

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ARTICLE INFO

Keywords:
Above- and below-ground interactions
N enrichment
Plant diversity
Semi-arid grassland
Soil fungal diversity

ABSTRACT

Soil fungi and plants are tightly linked in pathogenic, commensal, and mutualistic ways. These interactions play a critical role in terrestrial ecosystem decomposition, nutrient cycling, and maintenance of plant productivity and diversity. A comprehensive understanding whether this fundamental plant-fungi relationship persists in ecosystems with increased N input is, however, still lacking. In this study, we investigated the relationships between plant and soil fungal diversity in a 6-year multi-level nitrogen addition experiment in a semi-arid grassland in northern China, using Illumina Miseq sequencing of the ITS1 barcode region for fungal identification. We hypothesized that N-induced changes in plant communities would be positively associated with those in soil fungal communities, and that the corresponding changes in both communities can be explained by the direct functional associations between plant and soil fungal communities and their shared environmental drivers. Our results showed that N-induced changes in plant alpha diversity, i.e., Shannon diversity, showed no significant relationship with those in soil fungal alpha diversity. The lack in significance of the relationship was primarily due to their contrasting correlates with N-induced soil physicochemical variables (i.e., soil available P (AP), inorganic N (NH_4^+_N and NO_3^-_N) and organic C content), and weakened plant-fungi functional associations. In contrast to the lack of relationship between plant and soil alpha diversity, we did find a significant positive relationship between plant and fungal beta diversity (compositional dissimilarity between plots) under N enrichment. Our results reveal that the same soil physicochemical variables, including soil AP, inorganic N, moisture, pH, and associated extractable cations, correlated with compositional changes in plant and fungi following N enrichment. The strong coupling of plant and fungal beta diversity could largely be driven by their consistent responses to these shared edaphic factors. As such, our results suggest that information on N-induced changes in plant diversity can be used to predict beta, but not alpha diversity of soil fungal communities in semi-arid grassland ecosystems.

1. Introduction

Since the start of the twentieth century, anthropogenic activities associated with agricultural fertilization, fossil combustion, and dust productions have greatly increased the biogeochemical cycles of nitrogen (N) around the globe (Galloway et al., 2004). The global N deposition is expected to continue to increase in the coming decades, and the average N deposition rate is estimated to double or triple over the next century (Lamarque et al., 2005). In grassland ecosystems, many studies have focused on plant community responses to N deposition, and have demonstrated consistent loss of grassland plant diversity, with corresponding increases in plant productivity and shifts in community composition (Clark et al., 2007; Cleland and Harpole, 2010). The responses to N enrichment of the belowground microbial community, and fungi in particular, however, remains poorly understood. Soil fungi nevertheless have important effects on terrestrial decomposition, nutrient cycling, and plant diversity (van der Heijden et al., 2008; Voriskova and Baldrian, 2013). Soil fungi interact with plant communities in commensal, pathogenic, and mutualistic ways, and as such are commonly thought to be strongly coupled with plant communities (van der Heijden et al., 2008; Dodds and Rathjen, 2010). A thorough understanding of whether these tight plant-fungi linkages still persist under scenarios of increased N deposition is, however, still lacking.

There is increasing recognition that aboveground plants and

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http://dx.doi.org/10.1016/j.soilbio.2017.10.039
Received 5 June 2017; Received in revised form 16 September 2017; Accepted 31 October 2017

belowground microbes of ecosystems are tightly associated through a variety of both indirect and direct pathways that operate across different levels of ecological organizations (Wardle et al., 2004). Plant communities with a higher diversity are expected to promote a higher diversity in soil microbes by increasing the diversity of physical microhabitats, micro-climatic conditions, and food resources, and because of the higher diversity of plant hosts for pathogenic and symbiotic microbes (Wardle, 2006; Eisenhauer et al., 2010; Millard and Singh, 2010). Similarly, a higher microbe diversity is believed to maintain or promote plant diversity through the increase in the diversity of soil available nutrients, and the regulation of competitive interactions among plants (van der Heijden et al., 2008). As a consequence of these indirect and direct aboveground-belowground functional linkages, plant community diversity is widely believed to be a suitable predictor of belowground microbial diversity (Kardol and Wardle, 2010; Hiiesalu et al., 2014). Next to the theoretical support for aboveground-belowground associations, empirical evidence for the positive relationship between both alpha and beta plant and microbial diversity has recently been increasing, with experiments at local to regional scales (Gao et al., 2013; Milcu et al., 2013; Hiiesalu et al., 2014; Chen et al., 2017; Yang et al., 2017). On a global scale, however, no significant association between plant and fungal alpha diversity was observed due to the predominant role of large-scale coarse environmental heterogeneity in structuring plant and fungal communities (Prober et al., 2015). Compared to other microbial groups, evidence particularly indicates stronger aboveground-belowground relationships for fungal communities because fungi are thought to be more directly dependent on plant C compounds, and fungal pathogens or mycorrhizal fungi are tightly linked to plants through parasitic or symbiotic connections (Millard and Singh, 2010; Gao et al., 2013).

Growing evidence is amounting that human-induced N enrichment strongly impacts the diversity and structure of both plant and soil fungal communities in grassland ecosystems (Treseder, 2004; Egerton-Warburton et al., 2007; Cleland and Harpole, 2010; Leff et al., 2015). A key understanding lies in whether and how N-induced aboveground plant changes correspond to those in belowground fungal community changes. If the aboveground-belowground linkages persist under N enrichment, information on plant communities and their responses to N enrichment can be used to predict belowground fungal communities and their responses to these global change factors (van der Heijden et al., 1998; De Deyn and Van der Putten, 2005). Although changes in plants and soil fungi following N enrichment are thought to be interrelated (O'Connor et al., 2002), the empirical support so far shows rather mixed results.

Some studies have shown that the diversity and composition of soil fungal communities shifts in response to N addition, and they related these shifts to changes in plant community (Leff et al., 2015; Chen et al., 2016a). Others have found that N enrichment weakens plant-fungi linkages because the effects of N-induced plant community changes on soil fungi are outweighed by the effects of N-induced changes in the soil physicochemical environment (Wei et al., 2013; Chen et al., 2015a). Some recent large-scale studies have shown that plant and soil fungal communities are shaped by the same environmental drivers, leading to coupled plant and fungal richness (Tedersoo et al., 2014) and community composition variations (Prober et al., 2015). The results of these studies hence suggest that whether or not plants and soil fungi have consistent responses to N enrichment, depends not only on their functional associations, but also on the N-induced shifts in soil physicochemical environments. Direct and systematic tests of the relationship between the diversity of plant and soil fungal communities in response to N enrichment have, however, rarely been carried out.

To assess and compare the changes in plant and soil fungal communities in response to N enrichment, we tested the relationship between plant and soil fungal diversity (both alpha and beta diversity) in a 6-year N addition experiment in a typical semi-arid steppe of northern China. Elevated N decreases plant diversity, alters the dominance and structure of the community, and modifies the soil physicochemical environment (Clark et al., 2007; Cleland and Harpole, 2010; Chen et al., 2015a). As such, we hypothesized that under N enrichment conditions: (1) the reduced plant richness would be associated with a reduced soil fungal species richness (i.e., plant alpha diversity predicts alpha diversity of the soil fungal community); (2) the altered plant community composition would be positively associated with the altered soil fungal community composition (i.e., plant beta diversity predicts beta diversity of the soil fungal community); and (3) the corresponding changes in both communities can be explained by the direct functional associations between plant and soil fungal communities and their shared environmental drivers.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted at the National Grassland Ecosystem Research Station (41°44′N, 115°40′E, 1475 m a.s.l.), which is located in a semi-arid grassland in Guyuan County, Hebei Province, China. The semi-arid continental monsoon climate is characterized by a wet summer but dry winter and spring. The mean annual precipitation (1980–2011) is 401 mm, with most precipitation occurring in the growing season (May–September). The mean annual air temperature is 1.4 °C, with the mean monthly temperature ranging from −18.6 °C in January to 21.1 °C in July. The annual ambient N deposition rate in northern China is about 2.5 g N m^{-2} yr^{-1} (Jia et al., 2014). However, in some regions, it may exceed 15.7 g N m^{-2} yr^{-1} (He et al., 2010).

The study site has a calcic-orthic Aridisol soil (according to the ISSS Working Group RB, 1998), with a loamy-sand texture. The plant community in the study area is dominated by a perennial grass, *Leymus chinensis*, and two perennial forbs, *Artemisia scoparia* and *Saussurea amara*, which together account for about 80% of the total biomass in the site.

The nitrogen addition experiment used in this study has already been described in detail by Chen et al. (2016b). As such, we only provide a summary in this paper. In 2011, an area with fairly uniform vegetation and soil characteristics was selected and fenced. Within this area, 36 plots with a size of 5 × 5 m and a 1-m-wide buffer zone were laid out in a randomized complete block design with six replicate blocks. Six levels of N addition treatments (0, 1.0, 4.5, 9.2, 15.8, and 25.2 g N m^{-2} yr^{-1}) were randomly assigned to each of the six blocks. N was added to the experimental plots three times a year from 2011 to 2016 in the form of granular urea (N, 46%). The three application periods (mid-June, mid-July, and mid-August) were selected to coincide with the periods of maximum precipitation during the growing season. We set the nitrogen addition levels to both realistic (e.g., 1.0 g N m^{-2} yr^{-1}–15.8 g N m^{-2} yr^{-1} fall within the range of realistic local N deposition rates) and unrealistic doses (25.2 g N m^{-2} yr^{-1}), in order to gain insight into the plant and soil fungal communities responses and their relationships under both current and potential future scenarios of N deposition.

2.2. Plant and soil sampling

In 2016, at peak aboveground biomass (mid-August), plant species richness (number of plant species) was recorded using a single 1 × 1 m quadrat located at the center of each plot. Additionally, all plants were harvested from two randomly placed 0.5 × 0.5 m quadrats that did not overlap with the 1 × 1 m quadrat and were at least 0.5 m away from the plot's edge. Plant species were classified into five functional groups (perennial forbs, annual/biennial forbs, perennial grasses, perennial legumes, and other graminoids). Plant community composition (dry weight proportion) was calculated after the harvested plant samples were oven-dried at 65 °C for 48 h. We used both the observed plant species richness and Shannon diversity index to represent plant alpha