



Divergent responses of soil microbial communities to water and nitrogen addition in a temperate desert



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ABSTRACT

Increasing precipitation and N deposition are reported in northern China. However, their impacts on soil microorganisms are still unclear. We aimed to elucidate how increasing precipitation and N deposition alone and in combination would affect soil microorganisms in interplant soils and beneath shrubs of *Haloxylon ammodendron*. A 30% increase in precipitation and 5 gN m⁻² yr⁻¹ addition were applied to simulate precipitation increasing and N deposition in a temperate desert steppe across 2011–2013. Increasing precipitation significantly increased microbial biomass carbon (MBC) and respiration (MR), as well as bacterial and fungal PLFAs. N addition slightly increased MBC, MR, as well as total, bacterial, and fungal PLFAs in interplant, while decreasing all of them beneath shrubs. N addition consistently increased microbial biomass nitrogen (MBN) at both microsites, but only decreased the ratio of MBC to MBN beneath shrubs. Both water and N addition had no impacts on the ratio of fungal to bacterial PLFAs (F:B), suggesting no impacts of water or N addition on microbial community composition. Microbial biomass, respiration, bacterial and fungal PLFAs were positively related to soil water content across treatments, suggesting that the increasing MR under increasing precipitation was mainly contributed by increasing microbial biomass rather than altering microbial community composition. In addition, the interaction of precipitation and N addition on microorganisms is discrepant between interplant and beneath shrubs, with significant effects beneath shrubs and no impacts in interplant. Our results support the hypothesis that water and N are co-limiting factors in desert ecosystems, but the effects are habitat-specific in deserts.

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1. Introduction

Soil microbial communities are an important component of terrestrial ecosystems, and are key to depicting ecosystem processes and understanding ecosystem responses to global climate change (Liang et al., 2011; Lucas et al., 2007; Stroud et al., 2007). A wide array of studies has demonstrated that soil microbial communities are very sensitive to the variation of abiotic and biotic cues, including plant community composition and productivity (Abbott et al., 2011; Lambers et al., 2009), soil pH (Pietri and Brookes, 2009), soil water availability (Zhang et al., 2013) and temperature (Zhou et al., 2013). The response magnitude and direction of microbial communities to climate change cues differ from plants (Balsler et al., 2010). Moreover, the responses of soil microbial communities in these studies are not consistent (Balsler et al., 2010). Using microbial community structure assay methodologies, including PLFAs and molecular methods, we can discern the variation of soil microbial communities in response to climate and improve the recognition of below-ground biogeochemical cycles.

Precipitation is predicted to increase in arid regions of the central Asia (IPCC, 2007). In deserts, increases of the annual precipitation and larger rainfall pulses can alter biochemical cycling (Austin et al., 2004), trigger microbial growth (Zhang et al., 2013) and even change soil microbial community composition (Fierer et al., 2003; Gutknecht et al., 2012; Hawkes et al., 2011). For example, increased precipitation is reported to increase the availability of respiratory substrates (Zhou et al., 2013), which can change the responses of microbial C utilization and stimulate microbial growth and physiological activities (Williams and Rice, 2007; Zhou et al., 2013). Meanwhile, increased precipitation may also change microbial community composition because the microorganism responds differently to altered precipitation (Fierer et al., 2003; Freckman, 1986; Hawkes et al., 2011; Sommers et al., 1980; Williams and Rice, 2007). However, the change of microbial community growth in responses to environmental cues is not always accompanied by the changed microbial community composition. Some studies have reported that increased precipitation can only increase microbial biomass and activity, but exert no impacts on microbial community composition in arid and semiarid ecosystems (Cruz-Martínez et al., 2009; Gutknecht et al., 2012; Lamb et al., 2011; Zhang et al., 2013). Overall, a comprehensive study, including microbial biomass, activity

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and community composition, is needed to understand mechanisms underlying microbial responses to changes in precipitation.

Besides precipitation, due to increased anthropogenic activities and excessive application of fertilizer, N deposition in northern China increased from $1.3 \text{ gN m}^{-2} \text{ yr}^{-1}$ in 1980 to $3.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ in 2012. Similarly, in northwestern China, N deposition has reached a rate of $2.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ (Liu et al., 2013). N deposition in drylands has become an important potential factor affecting ecosystem processes (Liu et al., 2011; Zhou et al., 2012). Increased N availability can consistently increase respiratory substrates for microbes through stimulating plant growth (LeBauer and Treseder, 2008; Lu et al., 2011). However, increased substrate availability does not always lead to increased soil microbial biomass under N addition (Treseder, 2008), since over N loading can decrease soil pH and increase Al^{3+} content in soil, which can produce toxicity to soil microbes (Vitousek et al., 1997). Thus, contrasting microbial responses to N enrichment have been observed among studies (Liu et al., 2010; Nilsson and Wallander, 2003; Treseder, 2008; Waldrop and Zak, 2006). For instance, Nemergut et al. (2008) showed that the relative proportion of fungi was decreased while bacteria increased after 18 years of N fertilization in an alpine tundra. Similarly, de Vries et al. (2006) showed that fungi were decreased while the bacteria were not affected under N addition in a pasture in the Netherlands. These studies suggest that N addition leads to uncertain changes in microbial community composition (Gallo et al., 2004; Nilsson et al., 2007; Siguenza et al., 2006). In addition, although studies on the effects of increased precipitation and N alone have been widely conducted, empirical studies on microbial responses to the concurrent increase in precipitation and N are scarce in arid lands where water and N are two predominant limiting factors (Kieft et al., 1998; Peterjohn and Schlesinger, 1991).

'Resource islands' due to the discontinuous distribution of perennials is common in many arid and semiarid regions (Barth and Klemmedson, 1978; Jackson and Caldwell, 1993). The patchy distribution of resources generates contrasting habitats for microbes, with high substrates and nutrients for microbes usually beneath shrubs (Reynolds et al., 1999). Meanwhile, due to the leaching from the shrub stem-flow, soil pH is lower beneath shrubs than interplant (Li et al., 2011; Wang et al., 2011). In addition, field observation found that moss usually inhabits beneath perennials while lichen and cyanobacteria distribute in the interplant soil (Su et al., 2013), suggesting that the soil microbial composition also differs between beneath shrubs and in interplant. Therefore, it is expected that soil microbial biomass, activity and structure in interplant and beneath perennials may respond differently to increasing precipitation and N deposition. More importantly, due to the different coupling patterns of water and nutrient between beneath shrubs and interplant, soil microbial activities may be co-limited by water and nutrient in interplant, while singularly limited by water beneath shrubs. Thus, the effects of combined addition of water and N may differ between two microsites.

Northern China is predicted to experience increasing precipitation through 2030 (Liu et al., 2010) and the current N deposition rate is $2.5 \text{ gN m}^{-2} \text{ yr}^{-1}$ (Liu et al., 2013). Here, we simulated a 30% increase in annual precipitation and $5 \text{ gN m}^{-2} \text{ yr}^{-1}$ deposition in the Gurbantunggut Desert, northwestern China, to explore the responses of microbial biomass, activity and community composition to water and N addition, alone and in combination. Here, we aimed to test the four hypotheses. First, we hypothesized that increased precipitation would increase microbial biomass and respiration and shift microbial community composition, since increased precipitation can increase substrate availability to microbes, and bacteria are more sensitive to improved soil environmental conditions; second, because of the contrasting respiratory substrates in soils between beneath shrubs and in interplant, N addition effects on microbial biomass, activity and community composition would differ between microsites; third, the synchronous water addition with natural precipitation inputs in our study would exert significant inter-annual effects on the interactive effects of water and N addition on

soil microbial communities. Finally, the microbial responses to the combined addition of water and N would be dependent on resource islands.

2. Materials and methods

2.1. Study site description and experiment design

The experiments were conducted in the vicinity of the southeastern Gurbantunggut Desert ($44^{\circ}17'N$, $87^{\circ}56'E$, 475 m a.s.l.), Xinjiang, northwestern China. This region has a continental arid, temperate climate, with a hot, dry summer and cold winter. The annual mean temperature is 6.6°C and the annual mean precipitation is 160 mm; in which 70% to 80% fall in April–September. The pan evaporation is 2000 mm. Soils are desert solonetz at 0–100 cm, with aeolian sandy soil at the top. The shrubs of *Tamarix ramosissima*, *Haloxylon ammodendron* and *Haloxylon persicum* are accompanied with some perennials and annuals take a nearly 30–40% of vegetative coverage in early spring and summer. Biological soil crust also provides a stable soil surface cover. The interplant soil is covered by cyanobacterial-lichen crusts, which are composed of *Microcoleus vaginatus*, *Microcoleus paludosus*, *Anabaena azotica*, *Porphyrosiphon martensianus*, *Collema tenax*, *Psora decipiens*, *Xanthoparmelia desertorum* and *Diploschistes muscorum*. The soil beneath shrubs is covered by moss crusts, which are mainly comprised of *Syntrichia caninervis*, *Bryum argenteum*, and *Tortula muralis*. Surface soil properties (0–5 cm) differ profoundly between interplant and beneath shrubs of *H. ammodendron* (Table S1). Although cyanobacterial-lichen crusts have the N-fixation ability, this is limited in soil wet period. Soil organic carbon, total N and total phosphorus are significantly higher beneath *H. ammodendron*, due to the nutrient accumulation effects of stem flow, litter accumulation and decomposition and root growth. Soil pH and electronic conductivity (EC) were also higher beneath *H. ammodendron*. Soil bulk density was lower beneath *H. ammodendron*.

Two treatments were combined in the present study: water and N addition. The combination of the two treatments resulted in four experimental groups: water addition (W), N addition (N), water plus N addition (WN), and control (C). Water addition treatments followed each precipitation event, producing a synchronous water addition with normal precipitation. In each water and water plus N addition plots, the extra 30% precipitation was collected using a rainfall collection pan. The pans were constructed from galvanized iron sheets, and the total area of pans in each plot was equal to 30% area of the plot. Each pan was erected at a slight angle, and precipitation received by pans was collected in a bucket which was buried in soil. Precipitation treatment was carried out throughout the whole experimental duration (from April 2011 to November 2013), and immediately after each rainfall event, the collected precipitation was evenly sprayed onto the plots during the early morning or late afternoon to prevent excessive evaporation. In the N and WN treatment plots, a total of 5 gN m^{-2} was added each year, NH_4NO_3 was diluted in 15-L water (equal to 0.15 mm rainfall) and evenly sprayed. The same amount of distilled water was added in the C and W treatment plots. The experiment used a completely randomized block design. There were six blocks and each block had four plots. The four treatments were randomly arranged into plots in each block, and totally, each treatment had six replications. Each plot was $10 \times 10 \text{ m}$, with 10 m wide buffer zone between adjacent plots. All experimental design and instrument arrangements were conducted in 2010, and before the application of treatment, vegetation and soil nutrient characteristics (soil organic matter, soil total nitrogen, soil total phosphorus, soil potassium and inorganic nitrogen) all showed no statistically significant difference between treatments using block as a covariance in ANCOVA analysis.

2.2. Soil sampling and measurements

Five soil cores (5 cm diameter, 5 cm depth) were used to collect soil samples on August 10th in 2011, 2012 and 2013. According to the field

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