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Spring drying and intensified summer rainfall affected soil microbial community composition but not enzyme activity in a subtropical forest

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ABSTRACT

The predicted changes in the seasonal precipitation pattern could influence the soil microbial communities composition and function. However, the responses of soil microbes to seasonal changes in precipitation are poorly understood, especially in subtropical forests with distinct dry–wet seasons. A manipulation experiment lasted for two years to determine the effects of reduced rainfall in spring and increased rainfall in summer (the wet season) on the composition and function of soil microbial community in a subtropical forest. We excluded 67% of throughfall during spring and then added the equivalent amount of water back to the exclusion plots in intense rainfall events during summer. Throughfall exclusion reduced the soil water content (SWC) by 4.8–6.5%, and water addition increased the SWC by 12.5% but without statistical significance. However, wet-season water addition significantly decreased the ratio of fungal to bacterial phospholipid fatty acids by 12.7% in a relatively dry year (2014). Amplicon sequencing indicated that water addition increased the rare bacterial phylum *Gemmatimonadetes*, which accounted for 0.59–0.73% of the total OTUs in the soil. Water addition also increased *Basidiomycota* and decreased *Ascomycota*; these two phyla accounted for 71–86% of the total fungal OTUs in the soil. Soil enzyme activities were unaffected by reduced rainfall in spring and increased rainfall in summer, expect that β-1,4-glucosidase activity which was positively related to SWC. Our results suggest that bacteria are more responsive than fungi to reduced rainfall in the spring, while fungi are more responsive than bacteria to increased rainfall in the summer. To clarify how microbial functions change in response to changes in precipitation, future research should assess the expression of functional genes.

1. Introduction

Climate models project that most regions of the world will experience changes in the precipitation pattern (Seneviratne et al., 2012). An altered precipitation pattern (amount, timing, and intensity of rainfall) will influence soil moisture, and is therefore likely to affect soil nutrient cycles and microbial activity (Alvarez-Clare and Mack, 2011; Schlesinger et al., 2016). This is because soil water availability is a dominant controller of microbial community composition and function (Castro et al., 2010; Landesman and Dighton, 2010; Malik et al., 2016; Ren et al., 2017), and because soil microorganisms regulate many crucial ecosystem processes such as litter decomposition, biogeochemical cycle, and plant growth (Bardgett et al., 2008; Carney and Matson, 2005; Wardle et al., 2004). It follows that documenting microbial responses to the potential precipitation changes will help us to understand the potential effects of precipitation on biogeochemical cycles.

Decreased rainfall may alter the microbial communities composition and functioning by restricting substrate diffusion and by increasing the physiological stress experienced by microbes (Schimel et al., 2007). Because of differences in their physiologies, microbial taxa may respond differently to a reduction in precipitation. Drought-tolerant microbial groups may withstand decreased precipitation. Relative to other kinds of microbes, for instance, fungi that form hyphae are less affected

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by substrate limitation, and Gram-positive (G^+) bacteria with strong cell walls are less sensitive to osmotic pressure (Landesman and Dighton, 2010). Fungi have higher carbon (C) growth efficiencies than bacteria and are thus able to retain much of the C in soil (Strickland and Rousk, 2010). Consequently, changes in soil water content may influence the composition and function of microbial communities, and may potentially affect C and nutrient cycling (Malik et al., 2016; Ren et al., 2017; Sardans and Peñuelas, 2005).

In contrast to decreased precipitation, increased rainfall may stimulate microbial activities by increasing the diffusion of substrates to microbes and by alleviating water stress. Increased rainfall, however, may also enhance anoxic conditions and nutrient leaching, and thus inhibit microbial activities in humid ecosystems (Bouskill et al., 2013). Alternatively, ecosystems with high rainfall or high seasonality in precipitation regimes will be less affected by precipitation change than other ecosystems, because the magnitude of soil moisture change may be insufficient to affect microbial growth (Ren et al., 2017). In some moist or seasonal xeric ecosystems, for example, an altered precipitation pattern may fail to significantly change the soil microbial community composition and function (Landesman and Dighton, 2010). Therefore, the degree to which microbial composition and functions change in response to precipitation change are contingent on the magnitude of the precipitation change and on the local historical climate (Bouskill et al., 2013).

Few experiments involving the manipulation of precipitation have been conducted in humid ecosystems (Beier et al., 2012), and most have focused on the effects of drought (Bouskill et al., 2016). Subtropical forests which are characterized with dry-wet season are projected to experience deficient rainfall in the spring which is prior to the summer monsoons in East Asia (Xin et al., 2006; Zhou et al., 2011). Subtropical forests are important for the terrestrial carbon cycle because, among other forests in Asia or elsewhere at the same latitude, they have the highest net ecosystem production (Yu et al., 2014). A recent study of subtropical forests found that precipitation change could alter soil respiration and soil microbial biomass, but the effects on bacteria, fungi, microbial phyla, and microbial enzyme activities were not assessed (Jiang et al., 2013).

We previously found that soil fungi were more sensitive than bacteria to a reduction in dry-season throughfall in a subtropical forest soil (Zhao et al., 2017). Our understanding of microbial responses to changes in precipitation in subtropical forests remains incomplete, however, because both reduced precipitation in spring (spring drying) and increased precipitation in summer are predicted for the subtropics (Xin et al., 2006; Zhou et al., 2011). In this study, we mimicked this precipitation pattern by reducing water input in the spring and increasing water input in the summer, such that annual precipitation amount remained constant. This design enabled us to focus on the outcomes of altered rainfall regimes rather than on changes in annual rainfall amounts (Knapp et al., 2008). We used phospholipid fatty acid (PLFA) analysis and amplicon sequencing to determine the soil microbial community composition, and we also measured enzyme activities to assess microbial functioning. Our first hypothesis was that a reduction in spring rainfall would increase the relative abundance of drought-tolerant microbial groups (such as G^+ bacteria) and suppress enzyme activities. Our second hypothesis was that an increase in summer rainfall would have limited impacts on microbial community composition and enzyme activities because the background precipitation is often high during summer in subtropical East Asia; as a result, an input of additional water would not represent a substantial change.

2. Materials and methods

2.1. Study site and experimental design

We set up an experiment at the Heshan National Field Research Station of Forest Ecosystem (112°50′ E, 22°34′ N) in southern China, which has a subtropical humid monsoon climate. The mean air temperature is ca. 21 °C. The mean annual precipitation is 1800 mm. About 80% of the rainfall occurs in the hot-wet season (April to September) and 20% in the cool-dry season (October to March). The vegetation type is evergreen broadleaved forest, which is dominated by *Schima superba* and *Michelia macclurei*. The soils are classified as Ultisols according to the USDA's soil taxonomy (Soil Survey Staff, 2010).

The experiment included four control plots (hereafter AC plots) and four precipitation-changed plots with a drying spring to simulate the extended dry season (hereafter ED plots). In each ED plot, precipitation was manipulated with clear shelters that covered 67% of the total plot area and 25 automated sprinklers (Fig. S1). The details of this precipitation-control equipment were described in our previous study (Zhao et al., 2017). In ED plots, we excluded 67% of throughfall during spring (April to May) and then added the excluded water back in large events (ca. 55 mm/day) twice per month during the summer (June–-September). The total amount of additional rainfall during the summer was equal to the total amount of excluded rainfall during the spring. The additional rainfall in the summer was water that was pumped from a nearby pond and applied with sprinklers. The nutrient content was lower in the pond water than in the throughfall, and the pH was similar (Zhao et al., 2017). The AC plots received the natural rainfall. The annual precipitation was 2100 mm in 2013 and 1576 mm in 2014.

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The experimental treatments were applied for two hydrological years: 2013 (October 1st, 2012 to September 30 th, 2013) and 2014 (October 1st, 2013 to September 30th, 2014). The details of the soil sampling and storage conditions were described in our previous study (Zhao et al., 2017). In brief, soil samples (4.5-cm diameter × 10-cm depth) were collected in both AC and EC plots January (the dry season), May (spring wet season) with throughfall exclusion, and September (summer wet season) with water addition. The soil samples (48 in total; 2 treatments × 4 replicate plots/treatment × 3 sampling months/year × 2 years) were analysed for soil chemical properties, microbial biomass, and PLFAs, but only the samples collected in 2014 (24 in total) were analysed for enzyme activity and microbial sequences.

2.2. Soil physicochemical properties

Soil water content (SWC) was assessed by oven-drying 10 g fresh soil samples at 105 °C for 24 h. The pH of soil was measured in an air-dried soil/water (1/2.5, v/v) suspension. The determination of total organic C (TOC) was based on the $K_2Cr_2O_7$ titration method. Dissolved organic C (DOC) was extracted in 0.5 M K_2SO_4 and determined with a TOC auto-analyzer (Shimadzu Corp., Kyoto, Japan). Total nitrogen (N) and total phosphorus (P) were determined by the indophenol blue colorimetric method and the molybdenum antimony blue colorimetric method, respectively. The contents of exchangeable NH_4^+-N and NO_3^--N were determined by the indophenol blue colorimetric method and the cadmium reduction method, respectively. Soil microbial biomass (MBC and MBN) were determined by the chloroform fumigation extraction method (Vance et al., 1987).

2.3. PLFA analysis

The extraction and analysis of PLFAs were based on the method modified from Frostegård and Bååth (1996). Microbial lipids were extracted from a mixture of freeze-dried soil (8 g) and chloroform/methanol/phosphate (1/2/0.8 in volume) buffer. The lipid fraction was separated from neutral lipids and glycol-lipids in solid phase extraction tubes. After trans-esterified and methylated, the lipid fraction mixed with 19:0 internal standard were analyzed by gas chromatography–mass spectrometry (Agilent Technologies, CA, USA). The FAME profiles were identified using the Sherlock™ fatty acid ID system (MIDI, Inc., DE, USA).