Review Paper

Responses of soil total microbial biomass and community compositions to rainfall reductions

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ARTICLE INFO

ABSTRACT

Rainfall reductions influence ecosystem processes through impacts on the microbial community. However, the response of soil microbial community and their interactions with ecosystem processes remain unclear. In this study, we conducted a meta-analysis to synthesize the response of soil total microbial biomass and community composition to experimental rainfall reductions and the implications for soil carbon dynamics. The results showed that rainfall reductions significantly decreased soil total microbial biomass and bacterial abundance, but no significant effects on fungal abundance were observed. While, within bacterial and fungal groups, rainfall reductions only significantly influenced the relative abundance of *Proteobacteria, Gemmatimonadetes,* and *Chloroflexi*, but did not affect *Gram-positive bacteria (GP)*, *Gram-negative bacteria (GN)*, *Actinomycetes, Arbuscular mycorrhizal fungi,* and other sequenced bacterial phyla. These contrasting responses suggested that rainfall reductions had major effects on total microbial biomass but minor effects on community compositions. Further analysis showed that the direction and magnitude of total microbial biomass responses were mainly explained by the size of rainfall reductions rather than the duration. Particularly, higher decreases in total microbial biomass were observed in sites where more rainfall was excluded. Reductions in total microbial biomass were larger in forests with higher aridity index (AI) than in grass/shrublands with lower AI, and stronger reductions in microbial biomass were observed at higher mean annual precipitation (MAP)/sites with higher AI. Moreover, both soil organic carbon (SOC) and soil respiration (SR) significantly declined under reduced rainfall experiments and had positive relationships with changes in total microbial biomass, especially in humid lands (AI ≥ 0.65). The microbial responses to aridity levels indicated that soil carbon in humid lands may be highly susceptible to future drought scenarios. This meta-analysis highlighted the importance of considering the size of rainfall reductions and aridity levels when modeling and projecting soil carbon dynamics.

1. Introduction

Global warming has intensified the hydrological cycle, leading to changes of precipitation regimes at global scales (Park et al., 2016; Zhou et al., 2016a). The magnitudes of precipitation change could potentially cause alterations of the carbon cycle in terrestrial ecosystems, and such ecosystem responses are largely dependent on the belowground microbial community (Bardgett et al., 2008; Beier et al., 2012). Thus, identifying the microbial community responses to changing precipitation can greatly improve the projection ability of C-climate feedback under future global climate change (Beier et al., 2012; Davidson and Janssens, 2006). In recent years, a multitude of precipitation manipulation studies have reported microbial community responses in specific ecosystems (Beier et al., 2012; Nielsen and Ball, 2015; Rousk et al., 2013; Serna-Chavez et al., 2013). However, findings have been diverse and substantial uncertainty still surrounds when describing broad patterns of microbial community to rainfall reductions across a larger scale (Shen et al., 2015; Xi and Bloor, 2016). Since this involves the complex interactions that occur between soil microbes and other biotic and abiotic factors, thus microbial feedbacks on terrestrial

carbon dynamics are difficult to predict (Davidson and Janssens, 2006; Singh et al., 2010). To improve the prediction of the terrestrial carbon cycle-global warming feedback, a broad-scale synthesis of soil microbial response to rainfall reductions is urgently needed.

In response to rainfall reductions, soil microbial biomass and community compositions have different response directions (Manzoni et al., 2012). For instance, rainfall reductions make soil microbial biomass change through direct (e.g., reduction in soil water) and indirect effects (e.g., modification of plant net primary productivity). Specifically, limited soil water availability, caused by large-size rainfall reductions, decreases solute mobility and constrains the substrate supply to the decomposers (Ilstedt et al., 2000; Manzoni et al., 2014). In this way, rainfall reductions could directly inhibit microbial growths (Bardgett et al., 2008; Manzoni et al., 2012). In addition, the reductions in aboveground net primary production (ANPP) due to decreased rainfall can cause a decline in microbial biomass because of reductions in carbon and nitrogen from detritus entering the soil (Austin and Vitousek, 2000; Schrama and Bardgett, 2016). In contrast, several microbial species such as *Gram-positive bacteria, Actinobacteria*, and *Arbuscular mycorrhizal fungi* are tolerant to water stress due to their ability to explore the soil for water (Manzoni et al., 2012; Riah-Anglet et al., 2015; Zeglin et al., 2013), and obtain available nutrients through a thick and interlinked peptidoglycan cell wall (Bardgett et al., 2008; Lennon et al., 2012; Manzoni et al., 2012). Therefore, this leads to the hypothesis that rainfall reductions might have contrasting effects on soil microbial biomass and community compositions.

Furthermore, climatic regimes may potentially influence the patterns of ecosystem processes response to rainfall reductions as well (Beier et al., 2012; Nielsen and Ball, 2015). For instance, Wilcox et al. (2017) showed that the sensitivities of ANPP and belowground net primary production (BNPP) to drought were similar in magnitude but responded differently under xeric and mesic climatic regimes. A synthesis of 91 reduced rainfall experiments also indicated that soil respiration, especially heterotrophic respiration, tended to be more responsive to decreased precipitation in more humid lands (Liu et al., 2016). A commentary from Luo et al. (2017) highlighted the importance of altered precipitation for belowground processes to ANPP. Previous studies also found that microbial processes responded differently to changes in NPP and soil carbon dynamics under precipitation variability in different climatic regimes (Beier et al., 2012; Landesman and Dighton, 2010; Nielsen and Ball, 2015). Therefore, under this framework, another critical knowledge gap is emerging that whether various climatic regimes would yield different changes in microbial biomass, and this lack of understanding presents a further challenge for predicating soil carbon dynamics under future climate scenarios.

To address these gaps, we synthesized results from 114 cases studies that reported total microbial biomass and/or community compositions responses to rainfall reductions or drought experiments, while recording soil organic carbon and soil respiration. Aridity index alteration in these case studies ranged from 0.136 to 2.111. We used meta-analysis methods with this data set to test the following three hypotheses: (1) rainfall reductions had major effects on soil total microbial biomass but minor effects on microbial community compositions; (2) differential responses of total microbial biomass to rainfall reductions depended on the size of rainfall reductions and climatic conditions (mean annual precipitation and aridity index); and (3) microbial response to rainfall reductions would determine the soil carbon dynamics in different climatic regimes. Therefore, the objectives of this study were to: (1) understand how total microbial biomass and microbial compositions respond to rainfall reductions on a large scale; (2) investigate the relationships between the response of total microbial biomass and climatic regimes; and (3) discuss the potential implications for belowground carbon dynamics.

2. Methods

2.1. Source of data and specific criteria

We searched journal articles published before January 2017 using the Web of Science (http://apps.webofknowledge.com/), Google Scholar (http://scholar.google.com/), and China National Knowledge Infrastructure (http://www.cnki.net/). Articles were selected based on the following criteria: (1) only field experiments were included; (2) experimental sites must include both control and rainfall reduction treatments; (3) means, standard deviations (SDs), and numbers of replicates were reported. If standard errors (SE) were reported, the SDs were transformed based on the following equation:

$$SD = SE \times \sqrt{n}$$

where n is the number of replicates; (4) reduced rainfall protocols (size and duration) and vegetation types had to be clearly described or accessible from the cited articles, study duration was at least one growing season; (5) if more than one field manipulation experiment was reported in the same article but for various vegetation types (e.g., forest, shrub and grassland), in which each case study was independent; (6) if microbial biomass or compositions were measured multiple times within a given study, we only chose the latest sampling date; (7) if the results were reported for different soil layers, we only included the uppermost soil layer (Garcia-Palacios et al., 2015); (8) no other forcing factors (like nutrient addition, warming, etc.).

2.2. Reduced rainfall experiments and microbial measurements

The keywords and phrases used for identifying reduced rainfall experiments were "climate change" OR "drought" OR "decrease precipitation" OR "precipitation decrease" OR "decrease rain" OR "rain decrease" OR "exclu precipitation" OR "precipitation exclu" OR "exclu rain" OR "rain exclu" OR "reduc precipitation" OR "precipitation reduc" OR "reduc rain" OR "rain reduc" OR "rain roof".

In current meta-analysis, authors used four methods to assess the microbial biomass and community compositions. First, total microbial biomass was determined by chloroform fumigation (CF) (Vance et al., 1987), or phospholipid fatty acids (PLFA) (Zelles, 1997); if the case study used both two methods, we chose the first one (CF) to reflect the total microbial biomass (Treseder, 2008). Second, microbial composition was determined by PLFA and quantitative polymerase chain reaction analysis (qPCR) (Smith et al., 2006). Through using these two methods, we recorded the abundances of bacteria, *Gram positive bacteria (GP), Gram negative bacteria (GN), fungi, Arbuscular mycorrhizal fungi (AMF), Actinomycetes (ACT)*, and the ratios of fungi to bacteria (F: B) and *Gram positive bacteria* to *Gram negative bacteria* (GP: GN). Moreover, we also used the community sequencing approach (particularly RNA) to record bacterial phyla (i.e., *Proteobacteria, Acidobacteria, Actinobacteria, Chloroflexi, Nitrospirae, Gemmatimonadetes, Verrucomicrobia, Bacteroidetes,* and *Planctomycetes*) and fungal dominant phyla (i.e., *Ascomycota, Basidiomycota, Zygomycota*). However, the data regarding the fungal phyla were relatively sparse and could not be used for further analysis.

A total of 114 reduced rainfall experiments were selected from 45 articles that measured total microbial biomass and/or community compositions (Fig. S1, Text S1). Among these experiments, rainfall reductions ranged in magnitude from 5 to 100% relative to control plots. Reductions in rainfall of 0–33% were considered small (Small-reduced rainfall), reductions of 34–66% were considered medium (Medium-reduced rainfall), and reductions of 67–100% were considered large (Large-reduced rainfall). When analyzing the relationships with total microbial biomass, all manipulation levels were pooled together. Sites that experienced reductions in precipitation for ≤2 years indicated short-reduced rainfall, 2–6 years of reductions indicated medium-reduced rainfall, and reductions greater than 6 years indicated long-