



Defoliation intensity and elevated precipitation effects on microbiome and interactome depend on site type in northern mixed-grass prairie

Bin Ma^{a,b}, Yanjiang Cai^{c,*}, Edward W. Bork^d, Scott X. Chang^{b,c,**}

^a Institute of Soil and Water Resources and Environmental Science, College of Environmental and Resource Sciences, Zhejiang University, Hangzhou, China

^b Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, Alberta T6G 2E3, Canada

^c State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Hangzhou 311300, China

^d Department of Agricultural, Food and Nutritional Science, University of Alberta, 410 Agriculture/Forestry Centre, Edmonton, Alberta T6G 2P5, Canada

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ABSTRACT

Soil microorganisms play critical roles in maintaining ecological functions of the northern mixed-grass prairie. While defoliation regimes and elevated precipitation affect plant community composition and primary productivity in these grasslands, their effects on soil microbiome and interactome have not been studied. We examined the response of soil microbiome and interactome to long-term (2010–2015) treatments of varying defoliation regimes (low vs. high intensity and low vs. high frequency) and two precipitation conditions (ambient vs. elevated) on two contrasting sites (a dry vs. a mesic site) in a northern mixed-grass prairie. High intensity defoliation reduced alpha-diversity and altered the beta-diversity of soil microbial communities in the mesic site but not in the dry site, while elevated precipitation reduced alpha-diversity and altered the beta-diversity of soil microbial communities in both sites. Defoliation and precipitation did not show interaction effects on overall alpha- and beta-diversity, but did combine to influence the interactome network. High intensity defoliation promoted the oligotrophic genera *Spartobacteria* (Verrucomicrobia), *Pseudonocardia* (Actinobacteria), and *Conexibacter* (Actinobacteria), while elevated precipitation promoted the copiotrophic genera *Nitrososphaera* (Thaumarchaeota), *Andersenella* (Proteobacteria), *Sphingomonas* (Proteobacteria), and *Acidobacteria Gp16* (Acidobacteria). High intensity defoliation increased the number of linkages for Alphaproteobacteria and Acidobacteria, and decreased the number of linkages for Gemmatimonadetes and Spartobacteria in the interactome networks. However, elevated precipitation increased the number of linkages for Actinobacteria and Gemmatimonadetes and decreased the number of linkages for Spartobacteria and Acidobacteria. Our results show that defoliation intensity and elevated precipitation affected the microbiome and associated interactome network within soils of the northern mixed-grass prairie by affecting different functional taxonomic groups, indicating distinct scenarios for defoliation and precipitation in affecting soil microbial communities.

1. Introduction

The northern mixed-grass prairie, covering much of Alberta and Saskatchewan in Canada, and the northern Great Plains of the United States, occupy more than 10 M ha (Ricketts, 1999). Soil microorganisms play critical roles in maintaining ecological functions of the northern mixed-grass prairie, including forage production, carbon (C) sequestration, and biodiversity conservation (Hewins et al., 2015). Due to its arid nature, fertilization is uncommon in this region, with soil microorganisms regulating the biogeochemical cycles to supply nutrients required for plant growth (Macdonald et al., 2004). Soil microorganisms can affect plant community diversity in grassland by mediating the

negative feedback on plant growth caused by the accumulation of pathogens (Fitzsimons and Miller, 2010). Soil microbial activities also determine the decomposition and the associated cycling of soil organic C (Hewins et al., 2016; Li et al., 2017). Detailed knowledge on the microbial community in the northern mixed-grass prairie is required for better understanding their ecological functions in the face of ongoing land-use and global change.

Grazing and hay harvesting are widely practiced land-use approaches in the northern mixed-grass prairie (Deutsch et al., 2010). Repeated defoliation at different frequencies and intensities during the growing season has been found to alter both plant composition (Broadbent et al., 2016) and primary productivity (Bork et al., 2017) of

* Corresponding author. State Key Laboratory of Subtropical Silviculture, Zhejiang A & F University, Hangzhou 311300, China.

** Corresponding author. Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, Alberta T6G 2E3, Canada.

E-mail addresses: yjcai@zafu.edu.cn (Y. Cai), scott.chang@ualberta.ca (S.X. Chang).

northern mixed-grass vegetation. Defoliation could considerably impact the soil microbial community by altering the amount and composition of litter and root exudates, which are essential for the growth of soil microorganisms (Macdonald et al., 2006). Defoliation may also influence the soil microbial community by reducing the demand for water and nutrients by vegetation (Deutsch et al., 2010). While varied defoliation intensity and frequency are known to change plant composition and diversity (Broadbent et al., 2016), the effect of these disturbances on soil microbial community composition remain unexplored.

Climate models predict that precipitation in the northern mixed-grass prairie will increase by 36% from 2020 to 2080 (Jiang et al., 2017). Altered precipitation could profoundly impact terrestrial ecosystems at various scales, from the individual organism and associated population, to the community and landscape levels, and consequently have the potential to alter the C biogeochemical balance in semi-arid ecosystems (Poulter et al., 2014). Altered precipitation can affect the soil microbiome directly by changing soil water availability (Zhao et al., 2016), and indirectly by changing plant growth and biomass production (Broadbent et al., 2016), as well as vegetation composition (Bork et al., 2017). Soil microbial activities represented by extracellular enzymes were reduced by 4 years of water addition in a northern mixed-grass prairie site (Hewins et al., 2016). Although previous studies have addressed the effect of defoliation on soil microbial communities under water stress (Williamson and Wardle, 2007), soil microbial responses to defoliation are unknown if water stress is relieved by the predicted precipitation increases (Jiang et al., 2017).

The microbial interactome, defined as the collective interactions taking place among all community members, provides opportunities for understanding community composition and function (Lima-Mendez et al., 2015), and corresponding ecological functions in grasslands (Shi et al., 2016). Members of microbial communities may influence each other antagonistically by competing for resources, producing inhibitory chemicals, or cooperating synergistically through syntrophy and symbiosis (Faust and Raes, 2012). Competitive exclusion of large clades under certain conditions may underlie the ecological similarity of co-occurring soil bacteria (Goberna et al., 2014) and syntrophic inter-specific cooperation is prevalent in biofilm formation (Ren et al., 2015). Network-based analytic approaches provide promise for exploring microbial interactions within complex environments ranging from gastrointestinal tracts (Freilich et al., 2010) and bioreactors (Nobu et al., 2015), to soils (Barberán et al., 2012; Ma et al., 2016) and oceans (Lima-Mendez et al., 2015). The analysis on network complexity provides a new perspective on microbial community assemblage and adds to our understanding of microbial community ecology (Shi et al., 2016). However, to the best of our knowledge, the impact of defoliation and elevated precipitation on the soil microbial interactome in grasslands has not been studied.

To better understand how the northern mixed-grass prairie ecosystem responds to variable defoliation regimes under elevated precipitation during the growing season, a long-term manipulative field experiment was initiated in 2010 (Broadbent et al., 2016). From this field experiment and other studies in the region, defoliation and soil moisture have been found to influence plant growth and productivity (Bork et al., 2017; Deutsch et al., 2010), plant community composition and diversity (Broadbent et al., 2016), and soil N₂O emission (Cai et al., 2016), as well as extracellular enzyme activities (Hewins et al., 2016). Given the close association between soil factors, microbiomes and corresponding plant community composition and activities previously detected, we hypothesized that defoliation and elevated precipitation will change soil factors, microbiomes, and the resulting interactome within these northern mixed-grass prairie ecosystems.

2. Materials and methods

2.1. Site description

The study was conducted at two contrasting sites, including a dry site and a mesic site, both situated in the Brooks Plain of the Dry Mixed-grass Prairie Natural Subregion in Alberta, Canada. Sites were located within the Mattheis Research Ranch managed by the University of Alberta. Mean annual precipitation and daily temperature from 1961 to 2016 were 330.5 mm and 4.1 °C, respectively, and the growing season (days above 5 °C) was approximately 185 days long (<http://agriculture.alberta.ca>). Sites were chosen based on internal uniformity of topography (both sites were level) and an initial late-seral plant community composition. The dry site (50.707° N, 111.874° W) had a Rego Brown Chernozemic soil (pH = 6.7, EC = 27 μs cm⁻¹, soil organic C = 1.1%, total soil nitrogen (N) = 0.1% in the top 15 cm), and was dominated by *Hesperostipa comata*, *Bouteloua gracilis* and *Pascopyrum smithii* (Broadbent et al., 2016). The mesic site (50.893° N, 111.874° W) had a Gleyed Eluviated Brown Chernozemic soil (pH = 6.3, EC = 37 μs cm⁻¹, soil organic C = 2.3%, total soil N = 0.2% in the top 15 cm), with abundant *Pascopyrum smithii*, and less abundant *Hesperostipa comata* and *Koeleria macrantha* (Broadbent et al., 2016). The mesic site was located in a low-lying area, and therefore benefited from periodic runoff from surrounding uplands during heavy rainfall events. The soil at the mesic site had a finer texture (sandy loam) as compared to the dry site (loamy sand).

2.2. Experimental design

Watering and defoliation treatments were applied in a fully randomized 2 × 4 factorial design, with six replicates at each site, for 6 consecutive growing seasons from 2010 through 2015. Treatments were applied to 1 × 1 m plots, which were separated by at least a 0.5 m buffer zone. Precipitation or watering treatments included no water addition (ambient precipitation) and watering to augment rainfall and maintain 150 mm of monthly precipitation from early June to late August each year (elevated precipitation). This roughly doubled the average June precipitation, the month with the highest rainfall, and was used to ensure that soil moisture availability did not constrain plant growth. Water was obtained from a freshwater wetland near the Mattheis Ranch headquarters, and was tested for salinity and nutrient content, both of which were low. Watering occurred at approximately 10 d intervals.

Defoliation treatments were low intensity at high frequency (LIHF), high intensity at low frequency (HILF), and high intensity at high frequency (HIHF) throughout the growing season, with an additional defoliation treatment deferred until the end of the growing season (referred to as the control, CK) (Broadbent et al., 2016). Plots in the HIHF and HILF treatments were clipped to 2 cm height every three and six weeks, respectively, from late May through to the end of August each year (2010–2015), and ensured extensive removal of leaf area. In contrast, LIHF plots were clipped to a more conservative 5 cm height every three-weeks during the early- and mid-growing season; this height was used to prevent shorter statured species (e.g., *Bouteloua gracilis*) from escaping defoliation. All plots, including the CK plots, were clipped to 2 cm height in late August, after the growing season and coincident with the onset of dormancy. This was done to maintain consistency with ongoing land use (cattle grazing) in the region. While end of year defoliation represented an intense defoliation event, our treatments facilitated testing of the additive impact of early- and mid-growing season defoliation at different intensities and frequencies on the microbiome.

2.3. Soil sampling and characterization

For this study, four of the six replicates of each treatment were

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