



Long-term fire management history affects N-fertilization sensitivity, but not seasonality, of grassland soil microbial communities



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ARTICLE INFO

Keywords:

Tallgrass prairie
Nitrogen
Fire
Bacteria
Archaea
Copiotroph

ABSTRACT

Nitrogen (N) availability is a driver of soil microbial diversity and function, and is affected by prescribed burning (N removal through volatilization) and fertilization (N addition). Because soil microbes control critical feedbacks to ecosystem function, it is important to understand the dynamics and responses of microbial populations under conditions of contrasting N availability. This study took place at a long-term field manipulation in which native tallgrass prairie was annually burned or not burned, and annually fertilized or not fertilized, in a factorial design, since 1986. Composite surface soil samples (0–15 cm) were collected monthly between November 2014 and December 2015 from replicate plots to evaluate event-based (post-fire, post-fertilization), seasonal, and long-term responses of soil microbial communities to management and environmental changes. Bacterial 16S rRNA gene and fungal ITS population sizes were estimated using qPCR, and bacterial community composition (BCC) was measured using Illumina MiSeq sequencing of 16S rRNA genes. We expected seasonal and event-based change in all parameters, and that total microbial population sizes and diversity would be lower in soils with higher N availability, due to greater competitive dominance of nitrophilic or copiotrophic taxa. Bacterial and fungal population sizes varied significantly by sampling month, in that bacterial populations were approximately $10\times$ greater in summer (June–August), but did not change in response to management events or long-term treatments. In contrast, very few individual taxonomic groups displayed seasonal or event-based responses, and there was no significant whole-community turnover on weekly or monthly time-scales; instead, BCC was strongly impacted by both the long-term fire and fertilization treatments. Specifically, there were increases and decreases in putatively "copiotrophic" and "oligotrophic" prokaryotic Phyla in response to long-term N fertilization, which were significantly stronger and more predictable in soils following long-term fire suppression. These results reveal that while long-term grassland management changes BCC beyond the detected range of seasonal variability, total bacterial populations change coherently month-to-month, potentially due to significant plant inputs of labile carbon during the growing season. Furthermore, because prescribed burning reduces soil N availability, the interactive responses to fire suppression plus fertilization suggest that higher background levels of soil N availability may increase the magnitude of soil microbial sensitivity to N fertilization.

1. Introduction

As multiple global environmental factors continue to change, it is essential to understand how soil biota respond to environmental variability, particularly in threatened ecosystems such as the tallgrass prairie (Seastedt et al., 2008). Tallgrass prairie ecosystems compose < 5% of their original range due to conversions to agriculture, urbanization, and woody encroachment (Hoekstra et al., 2005). Ecologists and land managers recognize the need to manage the remaining tallgrass prairie to ensure habitat conservation for species that rely on this ecosystem, as well as for the maintenance of regionally and globally

important ecosystem functions. Soil microbes mediate valuable grassland functions, including decomposition, soil fertility, and carbon storage, and understanding the environmental controls over microbial communities will help inform future land management decisions that maintain these critical ecosystem services (Torsvik and Ovreas, 2002; Van Der Heijden et al., 2008; van der Putten et al., 2013).

Microbes are often sensitive to environmental change due to their relatively short generation time, small size, and large surface area to volume ratio (Schmidt et al., 2007; Shade et al., 2013) and within the heterogeneous soil habitat, soil microbial communities are taxonomically and functionally diverse. Therefore, environmental drivers

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of changes in soil microbial dynamics have the potential to occur on multiple time scales with differential effects on specific populations with different niche preferences (Bardgett et al., 2005; Fierer et al., 2010). It is well-known that tallgrass prairie ecosystems have undergone considerable long-term changes due to anthropogenic activities such as fire suppression, which has led to woody encroachment (Ratajczak et al., 2014) and accumulations of soil organic carbon (C) and nitrogen (N) (Dooley and Treseder, 2012; Turner et al., 1997), and increases in biologically available soil N from atmospheric deposition, caused primarily by increased use of fossil fuels and N fertilizers (Farrer et al., 2013; Galloway et al., 2004). However, less is known about whether microbial turnover on shorter time scales is reflective of cumulative long-term ecosystem change. An understanding of the typical range of microbial cell and community composition variability in the short term is needed to provide context to understand the novelty of the impacts of long-term change on microbial communities (Shade et al., 2012).

In addition to long-term changes in tallgrass prairie ecosystems, these regions have distinct seasonal changes in climate and plant phenology, ranging from hot, dry plant growing seasons to colder and wetter dormant periods (Knapp et al., 1998), which could also drive microbial community or population dynamics. In winter, freeze-thaw of surface soils might impose physiological limitations on cell survival to the summer season and affect the decomposition of soil organic matter (SOM), which could have variable feedbacks on N availability during the growing season (Bardgett et al., 2005; Schimel et al., 2007). Seasonal patterns of soil microbial turnover have been described in alpine and arctic ecosystems, and can be characterized such that saprophytic fungi and slow-growing bacteria with heightened depolymerization strategies dominate in winter, whereas mycorrhizal fungi and fast-growing bacteria dominate in summer (Schimel and Mikan, 2005; Schmidt et al., 2007). In grasslands, total soil microbial biomass tends to peak late in the growing season (Bardgett et al., 1997; Garcia and Rice, 1994), but less is known about how seasonal turnover is impacted by long-term changes in fire and fertilization management.

In a managed tallgrass prairie, drivers of microbial dynamics could also occur on relatively short time-scales. For example, event-based pulses of rhizodeposited soil carbon (C) from root growth, spikes of N availability from direct fertilization events, or mobilization of nutrients following rainfall, can stimulate microbial activity in the short-term, sometimes in association with community composition change (Armstrong et al., 2016; Fauci and Dick, 1994; Kuzyakov and Blagodatskaya, 2015; Stark et al., 2004). In addition to greater root production following spring burning (Johnson and Matchett, 2001), initial responses to fire can include higher microbial activity via increased soil temperature in the weeks following combustion of surface litter (Ojima et al., 1994; Treseder et al., 2004). However, microbial responses to events that modify nutrient availability may be ephemeral, or different from, longer-term responses (Bardgett et al., 2003; Kuzyakov et al., 2000; Ramirez et al., 2010). Altogether, there is currently a lack of understanding of how short, seasonal, and long-term management and change interact to alter soil microbial communities and populations, and how these interacting time-scales may impact the tallgrass prairie ecosystem.

The objective of this study was to assess microbial community and population dynamics, at event-based, seasonal and decadal resolutions, in response to two management practices that drive N availability in tallgrass prairie: prescribed annual fire and N fertilization. Fire volatilizes organic N in plant litter, maintaining an N-limited situation in which native prairie plants with low N demand are competitively dominant (Seastedt et al., 1991; Tilman and Wedin, 1991; Yu et al., 2015); in contrast, the lack of fire allows available soil N to accumulate (Blair, 1997; Johnson and Matchett, 2001; Turner et al., 1997). We sampled a 30-year field manipulation of annual burning and fertilization once per month for one year to address the following questions: 1) What is the response of the soil microbial community to event-based

(fire, resource pulse addition) and seasonal environmental variation? 2) Does long-term management of N availability impact the seasonal turnover of soil microbial communities, or modify the microbial community beyond the seasonal range of variability?

We predicted that: 1) Microbial populations would display distinct responses to fire and fertilization pulses, at both initial event-based and long-term time scales, with spring burning increasing microbial population sizes by promoting greater plant belowground production (Johnson and Matchett, 2001), and N pulses decreasing microbial population sizes through direct shifts in microbial community composition to favor a more “copiotrophic” community (Fierer et al., 2007; Ramirez et al., 2012), including a reduction in fungal populations (Treseder, 2008). Additionally, we expected to detect seasonal changes in population sizes, with higher microbial populations in the summer due to availability of labile C from plant rhizodeposition, and lower in the winter when heterotrophic microbes rely on decomposition of soil organic matter for energy and C (Schmidt et al., 2007). We also predicted that: 2) Microbial community composition would differ between winter and summer, due to a higher relative abundance of populations that grow well on complex soil organic matter in the winter turning over different populations that grow faster on labile C in summer. Also, we expected that increased N availability, through either fertilization or lack of fire, would create an environment that favors a greater proportion of fast-growing copiotrophic taxa, as opposed to slower-growing oligotrophic taxa, and as evidenced by a greater community mean rRNA operon copy number (Roller et al., 2016).

2. Materials and methods

2.1. Study site and experimental design

This study was conducted at Konza Prairie Biological Station (KPBS). Konza Prairie Biological Station is located in the Flint Hills region of Kansas (39°05'N, 96°35'W) and is characterized by warm, dry summers and wet, cool winters, with MAP of 835 mm and MAT of 26.6 °C. During the one-year sampling period, total monthly precipitation ranged from 6.2 mm in March 2015 to 147.3 mm during July 2015. Daily mean soil temperature ranged from 2.3 °C in December 2015 to 23.5 °C in July 2015, and daily mean air temperature ranged from 0.7 °C in January 2015 to 37 °C in July 2015. While mean temperatures were near or only slightly above average during the study period, the total annual precipitation of 1002.5 mm was 20% greater than average, reflecting a growing season with soil water content rarely much below field holding capacity (approximately 0.25 g·g⁻¹ (Zeglin et al., 2013)). Although specific micro-meteorological variables were not measured in each treatment, meteorological data for KPBS were collected for a site near the experimental plots. The vegetative cover of grasslands at KPBS is dominated by perennial C₄ grasses, such as *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*, while unburned plots feature more woody plants, such as *Juniperus virginiana*, *Cornus drummondii*, and *Rubus occidentalis* (Ratajczak et al., 2012).

The Belowground Plots Experiment (BGP) was established in May 1986 at KPBS as part of the Konza Prairie Long-Term Ecological Research (LTER) program. The experiment is located on Irwin silty clay loam (fine, mixed, mesic, Pachic Arguistolls), and arranged in a split-strip block design, where whole-plot treatments are manipulated by fire, a split-plot mowing treatment was randomly assigned to half of the whole-plot, and within each treatment split, the plots were stripped and randomly assigned a nutrient enrichment treatment (no fertilizer addition (control), N fertilizer addition (10 g N·m⁻² as NH₄NO₃), phosphorus (P) addition, or N and P fertilizer addition). For the purposes of this study, we sampled soils from just the control and the N fertilizer addition plots under annually burned and unburned management history.

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