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Tallgrass prairie soil fungal communities are resilient to climate change

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ABSTRACT

Climate models for central United States predict increasing temperatures and greater variability in precipitation. Combined, these shifts in environmental conditions impact many ecosystem properties and services. Long-term climate change experiments, such as the Rainfall Manipulation Plots (RaMPs), can be used to address soil community responses to simultaneous manipulation of temperature and temporal variability in precipitation. The RaMPs experiment is located in a native tallgrass prairie at the Konza Prairie Biological Station and has been operational since 1998 providing the potential to address responses to long-term environmental manipulations. To test whether community composition, richness, or diversity respond to environmental change, more than 40 000 fungal amplicons were analyzed from soil samples collected in 2006. The data suggest that soil fungal communities are compositionally resilient to predicted environmental change. This is the case both for the community composition overall as inferred from ordination analyses as well as analyses of variance for each of the most common Operational Taxonomic Units (OTUs). However, while this study suggests compositional resilience, further studies are required to address functional attributes of these communities and their responses to environmental manipulations.

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Introduction

Water and temperature are major abiotic factors that influence grassland carbon exchange on an ecosystem level both above and belowground (Xu et al., 2004; Davidson and Janssens, 2006). These factors are also fundamental drivers of the heterotrophic respiration that is estimated to account for 30–50% of the total soil respiration in most terrestrial systems (Raich and Schlesinger, 1992; Bond-Lamberty et al., 2004), although estimates may vary widely depending on biome/ecosystem (compare Hanson et al., 2000; Wan and Luo, 2003; Chen et al., 2009). The significance of the soil respiration and the large contribution of soil-inhabiting microbial communities to CO_2 flux emphasize their importance and underline the need to better understand the compositional and functional attributes of these communities, particularly so in the face of predicted future environmental conditions (Bardgett et al., 2008; Drigo et al., 2008).

Grasslands are important biomes. They comprise approximately 32% of the natural vegetation of earth's surface (Adams et al., 1990) and store 28–37% of the terrestrial organic soil carbon (Lal, 2004). The function and composition of the plant communities in grassland ecosystems have been proposed to be sensitive to variability in climatic conditions

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(Knapp and Smith, 2001; Gao and Reynolds, 2003). In grassland ecosystems, shifts in timing of precipitation – not in the total quantity – can be important controls of plant productivity (Knapp et al., 2002; Fay et al., 2011), soil respiration (Harper et al., 2005; Fay et al., 2011), as well as function and structure of soil communities (Zeglin et al., 2013). As soil moisture and its variability are major controls of the broad scale function and composition of the soil communities on various spatial (Brockett et al., 2012) and temporal scales (Zeglin et al., 2013), more detailed evaluation of community responses to long-term manipulations are timely.

IPCC (2007) predicted that effects of changes in extreme events – both increases in the duration of droughts and in the per event precipitation volumes - may exceed those expected for changes in average precipitation leading to more variable precipitation regime and soil moisture in mesic ecosystems (Knapp et al., 2008). While such changes in the per event volume of rainfall as well as in their frequency have been suggested to lead to rapid alterations in soil processes as well as aboveground community composition (Knapp et al., 2002; Fay et al., 2003; Harper et al., 2005; Swemmer et al., 2007; Fay et al., 2011), consequences of such alterations for belowground microbial communities have received comparatively less attention (Chou et al., 2008; Zeglin et al., 2013). This major gap prohibits our understanding of the soil community responses to changes in soil water that far exceed those witnessed for dominant plants (Huxman et al., 2004; Ogle and Reynolds, 2004; Schwinning and Sala, 2004), tend to be more dynamic, and responsive to pulse events (Austin et al., 2004; Ogle and Reynolds, 2004; Carbone et al., 2011).

While both water and temperature are major abiotic controls of grassland ecosystem carbon exchange (Xu et al., 2004; Davidson and Janssens, 2006; Fay et al., 2011), the effects of altered precipitation are not as well understood as those of elevated CO₂ or temperature (Weltzin et al., 2003). Studies focusing on the interactions of multiple global change drivers may be fewer yet (Bardgett et al., 2008). The responses to interacting climatic drivers of soil communities and their function tend not to be additive (Shen et al., 2009; Hayden et al., 2012; Matias et al., 2012). Accordingly, experimental manipulations that combine multiple global change factors are necessary to elucidate the potentially synergistic responses of soil systems. Increased soil temperatures tend to stimulate soil respiration directly through positive responses by acceleration of both autotrophic and heterotrophic metabolism (Rustad et al., 2001; Melillo et al., 2002; Shen et al., 2009). Alternatively, higher soil temperatures may shift soil function indirectly through increases in nitrogen mineralization, primary production, and litter production (Stromgren and Linder, 2002; Pendall et al., 2004). Warming may also reduce overall microbial biomass (Frey et al., 2008) and increase (Castro et al., 2010) or decrease (Allison and Treseder, 2008; Hayden et al., 2012) fungal abundance. Overlaid with changing average temperatures, changes in soil water potential may directly and indirectly control soil community metabolic and physiological activities by affecting substrate availability via litter production and substrate diffusion (Skopp et al., 1990; Davidson and Janssens, 2006; Bardgett et al., 2008). Warming may amplify these effects - potentially as a result of greater rate of water loss from the soil

profile. Sheik et al. (2011) reported that with elevated temperatures, water budgets regulated microbial populations. More importantly, they concluded that timing of the precipitation events is critical for microbial populations.

In contrast to broad microbial community responses to environmental manipulations, few studies have explored the responses of general soil fungal communities - particularly to interacting environmental factors. Fungal community responses to warming would be expected, because fungal respiration tends to increase with temperature (Hacskaylo et al., 1965; Malcolm et al., 2008) although in the long-term the communities may adapt to the changing environmental conditions (Malcolm et al., 2008). Studies that have targeted the effects of elevated temperature have reported different and contrasting responses (Bardgett et al. 1999; Compant et al., 2010): experimental warming may increase diversity of soil fungi (Allison and Treseder, 2008), decrease (Allison and Treseder, 2008; Hayden et al., 2012) or increase (Castro et al., 2010; Ziegler et al., 2013) fungal abundance or biomass, change relative taxon abundances (Allison and Treseder, 2008; Deslippe et al., 2011; Anderson et al., 2013), or have minimal effects on richness, diversity, and community composition (Allison et al., 2010; Papanikolaou et al., 2010) depending on the ecosystem. In addition to the ecosystem level context dependencies (Compant et al., 2010), interacting environmental drivers may further modulate the fungal community responses (Hayden et al., 2012). For example, Rygiewicz et al. (2000) showed that soil fungal community responses to elevated temperature differed between [CO₂] treatments. Heterotrophic fungal communities and their responses to shifts in environmental conditions are particularly important, because they are essential in carbon and nutrient cycling (Dighton, 2003), comprise a large recalcitrant belowground carbon sink (Treseder and Allen, 2000), and may be affected directly by the shifts in the environmental drivers or indirectly through the responses in plant communities (Cregger et al., 2012). Anderson et al. (2013) observed that both elevated CO_2 and elevated temperature influenced the fungal community composition. These authors emphasized the importance of considering the community responses in the context of the plant host, as decoupling direct effects of environmental conditions and indirect effects modulated via plant communities are essential to understand the complexities of soil community dynamics (Bardgett et al., 2008). The plant community dependent responses are particularly important for root-colonizing mycorrhizal communities. Studies focusing on those fungal guilds have reported increases in ecto- and arbuscular mycorrhizal mycelium, species richness, as well as root colonization in response to experimental warming (Staddon et al., 2003; Clemmensen et al., 2006; Heinemeyer et al., 2006; Hawkes et al., 2008; Deslippe et al., 2011; Büscher et al., 2012), although these responses are unlikely to be universal (Olsrud et al., 2010). Experimental warming may also lead to shifts in the relative abundances of soil-inhabiting fungi and bacteria (Zhang et al., 2005; Rinnan et al., 2007; Frey et al., 2008).

Soil moisture also strongly influences fungal communities structurally and functionally (Toberman et al., 2008; Bell et al., 2009; Baldrian et al., 2010; Castro et al., 2010; Hawkes et al., 2011; Schmitt and Glaser, 2011; Cregger et al., 2012).

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