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Belowground response of prairie restoration and resiliency to drought

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ABSTRACT

Agricultural land use is a major threat to biodiversity and ecosystem functions in tallgrass prairies. However, there are proposed bioenergy systems that can use biomass harvested from restored tallgrass prairie, creating a potential free market incentive for landowners to restore prairies. These alternative management practices may alter associated soil microbial communities and their ecosystem services. We examined changes in soil microbial community structure, function, and resiliency to drought following two prairie restorations from row-crop agriculture and through subsequent succession in a fertilized and unfertilized tallgrass prairie. The soil microbial community structure was assessed through amplicon (16S and ITS) sequencing, function through potential extracellular enzyme activity, and resiliency indices were calculated for both microbial diversity measures and extracellular enzyme activity. We hypothesized that 1) distinct soil microbial communities in each management system will continue to develop over time reflecting the extent of divergence between the plant communities, due to the strong selective forces plant communities have on the soil microbiome. 2) Microbial extracellular enzymatic function will continue to diverge between the management systems across sampling years. 3) We will see increased resiliency to drought in the prairies potentially due to the greater diversity in this management system for the microbial and plant community, creating a possible enhancement in functional redundancy. Our experiment demonstrates that soil microbial communities continue to diverge from row-crop agriculture as prairie restoration progresses. Planted prairie bioenergy systems with higher plant diversity supported greater microbial diversity than corn systems. Corn monocultures were less resistant to drought stress, as evidenced by decreased microbial activity and richness. Prairies with increased microbial diversity exhibited increased functional resiliency than corn systems, as measured by cellulose-degrading enzyme activity. Prairies that received nitrogen fertilization maintained high microbial diversity and activity, even under drought. Our study demonstrates that diverse cropping systems may benefit from nitrogen fertilization to confer resiliency to disturbance events. Increasing resiliency, while maintaining productivity, is key to managing alternative crops that are sustainable systems for biofuel uses. Our multi-year study reveals the benefits of long-term experiments for capturing the dynamic range of microbial mediation of soil carbon and nutrients and the importance of resiliency in both developing sustainable management systems and modeling predictive biogeochemical models.

1. Introduction

Agricultural land use is a major threat to biodiversity and ecosystem functions such as regulating climate and maintaining water quality (Tilman et al., 2002). In the tallgrass prairie region of North America, conversion to row-crop agriculture has reduced the tallgrass prairie ecosystem by 86% (Samson and Knopf, 1996; Samson et al., 2004), making tallgrass prairie among the most “in crisis” ecosystems in the world (Hoekstra et al., 2005; Wright and Wimberly, 2013). In the past decade, there has been increased pressure to produce bioenergy sources from agricultural systems, continuing to threaten the remaining tallgrass prairies (Börjesson and Tufvesson, 2011; Fargione et al., 2008; Searchinger et al., 2008; Wright and Wimberly, 2013). However, there are proposed bioenergy systems that can use biomass harvested from restored tallgrass prairie, creating a potential free market incentive for land owners to restore prairie, particularly on marginal lands (Gelfand et al., 2013; Jarchow and Liebman, 2012; Tilman et al., 2006). These alternative management system practices are aimed to maximize aboveground productivity, while reducing the detrimental impacts of agriculture on the ecosystem as a whole (Tilman et al., 2002; Tscharntke et al., 2005; Turner et al., 2007). Investigation into how to successfully implement agricultural conversion to systems that support

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more biodiversity, increase carbon (C) storage, and promote nutrient retention is vital to learning how to manage biofuel agroecosystems for increased sustainability (Jarchow and Liebman, 2012; Kim et al., 2012). In addition, understanding the biogeochemistry occurring within biofuel agroecosystems could advance opportunities to support biofuel production on marginal lands; which traditionally have low C and nutrient storage and therefore could provide multiple benefits if converted to reconstructed prairie and appropriately managed to maximize ecosystem services (Gelfand et al., 2013; Isbell et al., 2015; Schulte et al., 2017).

Diverse prairies are being reconstructed on traditional agricultural fields to expand upon potential sustainable biofuel systems (Borsari et al., 2009; Jarchow and Liebman, 2012). During restoration from row-crop agriculture to diverse prairie communities, the abundance and chemistry of plant inputs to soil will change, reflecting plant community composition, phenology, and response to environmental cues (Anderson-Teixeira et al., 2009; De Deyn et al., 2008). For example, compared to diversified systems, traditional continuous corn agroecosystems have less abundant C inputs into the soil, reflected in lower root biomass and less diverse rhizodeposition (Allmaras et al., 2004; Collins et al., 1999; Dietzel et al., 2015; Dietzel et al., 2017). These changes in plant community ecology may affect soil microbial community composition, with potential cascading effects on C and nitrogen (N) cycling, which have important implications for the long-term fertility and productivity of corn biofuel systems (Barber et al., 2017; Klopf et al., 2017; Landis et al., 2008; McBride et al., 2011; Wieder et al., 2013). Tallgrass prairie restoration for biofuel services increases root biomass, soil C pools, and microbial biomass (Baer et al., 2010; Klopf et al., 2017); however, it is unclear how plant-microbe community interactions will change across time in restorations managed for biofuel.

Soil microbial communities are highly dynamic in membership (Buckley and Schmidt, 2003; Kuzyakov and Blagodatskaya, 2015). Therefore, understanding the soil microbiome response to prairie restoration requires multi-year evaluations relative to traditional agricultural systems. Changes in microbial community can lead to fluctuations in microbial C and N cycling activity and shape the local environment. Specifically, community level changes in extracellular enzymatic activity can lead to a feedback loop between the soil's physical properties, plant community, and microbial community (Braissant et al., 2003; Burns et al., 2013; Sasse et al., 2017). How rapidly microbial communities and their extracellular enzymes respond to this changing plant community, as well as the implications for coupled C-N cycling, needs to be further investigated to implement biofuel production that maximize ecological benefits (Averett et al., 2004).

Shifts in the plant communities in response to N fertilization can impact microbial community structure and diversity, with implications for microbial activity and function. The short-term effect of N fertilization is an increase in plant diversity and productivity, although this can change across time (Jarchow and Liebman, 2013). The long-term effect of N fertilization is a decrease in native plant diversity, as fast-growing plants, both exotic and native, arise in the community (Flores-Moreno et al., 2016; Harpole and Stevens, 2016; Morgan et al., 2016). The impacts of N fertilization on microbial communities are highly context dependent and often mediated by the response of the aboveground community to the N inputs (Leff et al., 2015; Kneller et al., 2018).

Nitrogen fertilization can also increase the sensitivity of the plant community to disturbance events, generating a compounded effect to potentially alter the plant community (Collins et al., 2017; Tognetti and Chaneton, 2015). Response to disturbance events or the resiliency of the community is often evaluated based on plant communities without consideration of how microbial community composition and function respond (Lau and Lennon, 2012; Sheik et al., 2011). Resiliency within the microbial community under natural disturbances has been investigated, and yet we know little of how microbial community changes affect belowground C and N cycling (Hawkes et al., 2005; van der Putten, 2010). In ecosystems managed for multiple ecosystem services, such as bioenergy feedstock systems, there is a tremendous need to evaluate how different management practices impact microbial resilience to current and predicted climatic events. Assessment of management practices like N fertilization on fungal and bacterial communities as well as their enzymatic activities is crucial to determine the long-term sustainability of these systems.

Using a microbial-focused approach, this study examined the long-term impact of N fertilization and management system (corn, prairie, and N fertilized prairie) on the microbial community structure and enzymatic function of restored grasslands used for biofuel production. Additionally, due to a natural drought occurrence, we were able to assess potential resiliency of these management systems within the microbial community and their enzymatic activity as well as the natural recovery afterwards. The Comparison of Biofuel Systems (COBS) field site is aimed at investigating potential biofuel cropping systems to increase plant diversity, sustainability, and maintain productivity. For this study, we evaluated three differing management systems: corn monoculture and restored native prairie with and without N fertilization. We seek to understand how management practices impacted fungal and bacterial community compositions, function, extracellular enzymes, and resiliency to drought across time in response to both the shifting plant communities and abiotic factors. We hypothesize that 1) distinct soil microbial communities in each management system will continue to develop over time reflecting the extent of divergence between the plant communities, due to the strong selective forces plant communities have on the soil microbiome. 2) Microbial extracellular enzymatic function will continue to diverge between the management systems across sampling years. 3) We will see increased resiliency to drought in the prairies due to the potentially greater diversity in this management system for the microbial and plant community, creating a potential enhancement in functional redundancy. To further inform sustainability efforts, the potential main drivers, plant community and N fertilization, and environmental cues of microbial community changes and function were studied across a 4-year sampling period.

2. Methods

2.1. Field Site Description and Soil Sampling Process

All samples were collected at the Comparison of Biofuel Systems (COBS) field study site (Boone County, IA). The COBS research site was established in 2008; prior, the site was used for corn-soybean rotations (Jarchow and Liebman, 2013). The COBS research site is a randomized complete block design comparing six bioenergy systems; plots measured 27×61 m^2. This study investigated three of these systems: continuous corn (maize; grain and 50% silage harvest for biomass), planted tallgrass prairie (~75% aboveground biomass harvest), and fertilized tall-grass prairie (~75% aboveground biomass harvest). Both tallgrass prairie systems were seeded with a mixture of 31 native genotype prairie species, in May 2008 (Jarchow and Liebman, 2013). The first fertilization of the fertilized prairie management system occurred on April 17th, 2009 and was applied as ammonium nitrate; following all annual nitrogen fertilization for all management systems was applied as urea-ammonium nitrate. Annually, the fertilized prairies received 84 kg N $ha^{-1}yr^{-1}$ in late March to mid April, and continuous corn systems received N inputs in accordance with spring nitrate tests (~168 kg N ha^{-1} yr^{-1}) applied immediately prior to corn planting (Jarchow and Liebman, 2012). The unfertilized prairie (referred to as the 'prairie' management in this study) did not receive any fertilizer inputs of any kind. The aboveground biomass is harvested to a height of 15-20 cm across all management systems annually in early November. Detailed COBS research site descriptions can be found in Jarchow and Liebman (2013). Soil samples were collected during peak growing season mid-August in 2011, 2012, and 2014. Soil cores were collected from the top 10 cm of soil using a 5 cm diameter slide-hammer coring device