

Plant nitrogen uptake drives rhizosphere bacterial community assembly during plant growth



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ABSTRACT

When plants establish in novel environments, they can modify soil microbial community structure and functional properties in ways that enhance their own success. Although soil microbial communities are influenced by abiotic environmental variability, rhizosphere microbial communities may also be affected by plant activities such as nutrient uptake during the growing season. We predicted that during the growing season, plant N uptake would explain much of the variation in rhizosphere microbial community assembly and functional traits. We grew the invasive C₃ grass *Bromus tectorum* and three commonly co-occurring native C₃ grasses in a controlled greenhouse environment, and examined rhizosphere bacterial community structural and functional characteristics at three different plant growth stages. We found that soil N availability and plant tissue N levels strongly correlated with shifts in rhizosphere bacterial community structure. It also appeared that the rapid drawdown of soil nutrients in the rhizosphere during the plant growing season triggered a selection event whereby only those microbes able to tolerate the changing nutrient conditions were able to persist. Plant N uptake rates inversely corresponded to microbial biomass N levels during periods of peak plant growth. Mechanisms which enable plants to influence rhizosphere bacterial community structure and function are likely to affect their competitive ability and fitness. Our study suggests that plants can alter their rhizosphere microbiomes through influencing nutrient availability. The ways in which plants establish their rhizosphere bacterial communities may now be viewed as a selection trait related to intrinsic plant species nutrient demands.

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1. Introduction

When plants establish in soils, they immediately interact with soil microbial communities and begin to profoundly alter the habitat within the rhizosphere—the rooting zone where soil microbes quickly assimilate plant-derived carbon and compete with plants for available nutrients (Schimel and Bennett, 2004; Mendes et al., 2013; Philippot et al., 2013). Plants affect the physical and chemical conditions within the rhizosphere in several ways, such as altering the soil environment through root growth (Bever et al., 2010; Padilla et al., 2013) increasing organic carbon availability

through root exudation (Nannipieri et al., 2008; Kuzyakov, 2010; Bird et al., 2011) and decreasing water and nutrient availability through uptake (Jackson et al., 1989; Herman et al., 2006; Marschner et al., 2011). Clearly, these myriad changes can drive rapid and fundamental shifts in the rhizosphere microbiome. Not surprisingly, rhizosphere microbial communities differ in structure and function from bare soils and even bulk soils within any environment (Knelman et al., 2012; Bell et al., 2014a; Ciccazzo et al., 2014). But which of these many plant-mediated changes are most important in structuring microbial communities?

While soil microbial communities often differ among plant species (Grayston et al., 1998; Donn et al., 2014) and even among plant genotypes (Zancarini et al., 2012; Mariotte et al., 2013), in some cases plant species do not explain the variation among rhizosphere microbiomes (Arenz et al., 2014; Bell et al., 2014a). This

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raises the question of whether plant species differ in their ability to modify their rhizosphere microbiome, and if so, what are the mechanisms underlying these differences? One challenge is that observational studies of mature field plants offer little insight into the mechanisms by which plants affect rhizosphere microbiomes, as any differences could be due to establishment in favorable microsites. Mounting evidence that rhizosphere bacterial community composition changes throughout plant developmental stages (Houlden et al., 2008; Micallef et al., 2009; Ziegler et al., 2013) suggests that plants do have an important role in structuring soil bacterial communities throughout the growing season (Kourtev et al., 2002; Marschner et al., 2004; Fierer et al., 2013). But again, we are left to wonder how plant species may differentially influence their rhizosphere microbiomes.

Plant – microbe – soil feedbacks play a fundamental role in plant community establishment and success (Reynolds et al., 2003). When plant species establish in novel environments, they appear to shift rhizosphere microbial community structural and functional associations in ways that enhance their success (Ehrenfeld et al., 2005; Turan et al., 2012; Wang et al., 2012). By establishing positive soil feedbacks (Levine et al., 2006; Diez et al., 2010; Bever et al., 2012) plants are sometimes able to stimulate increased nutrient mineralization which may improve their ability to compete with other plant species. For example, when the exotic C_3 annual grass *Bromus tectorum* invades habitats in western North America upon disturbance, it appears to support soil bacterial communities within its rhizosphere that are capable of higher N mineralization rates relative to rhizosphere communities associated with native plants (Hawkes et al., 2005; Schaeffer et al., 2011). This positive plant-soil feedback contributes to *B. tectorum*'s ability to outcompete native plants for available nutrients (Sperry et al., 2006; Vasquez et al., 2008).

Plant nutrient uptake can stimulate soil bacterial N mineralization (Bever et al., 2010, 2012). Any reduction in soil nutrient availability increases C:N stoichiometry within the rhizosphere, which can initiate microbial extracellular enzyme production to oxidize or hydrolyze soil organic matter to release otherwise unavailable nutrients (Allison et al., 2007; Kuzyakov, 2010; Drake et al., 2013). Although it is clear that plant nutrient uptake can influence changes in soil N availability by inducing soil microbial enzyme production, we do not yet know if plant nutrient uptake also influences rhizosphere bacterial community composition.

Due to the relatively narrow stoichiometric flexibility of soil bacteria (Anderson et al., 2005; Cherif and Loreau, 2013), rapid shifts in N availability within the rhizosphere resulting from plant nutrient uptake could strongly alter soil bacterial community structure (Hessen et al., 2004; Ramirez et al., 2012; Sardans et al., 2012). Plant N uptake coupled with root C inputs (via exudation or root sloughing) during the growing season (Fig. 1) could impose strong N limitation within the rhizosphere (Phillips et al., 2011; Perveen et al., 2014), favoring only those microbes that can tolerate the altered nutrient conditions (Sinsabaugh et al., 2009; Sistla and Schimel, 2012; Fanin et al., 2013). Although plant and soil microbial communities often appear to be closely linked (Bell et al., 2014a; Courty et al., 2014; Schmidt et al., 2014), few studies have directly observed plant influences on bacterial community assembly and function at multiple points throughout the growing season within the rhizosphere.

If plant N uptake and subsequent declines in available N within the rhizosphere influence bacterial community composition, then this may be a key mechanism by which plants affect bacterial community structure and function throughout the plant growing season. The main objective of this research was to study how plant nutrient uptake and soil C and N dynamics within the rhizosphere and in unvegetated soils influence bacterial community structure

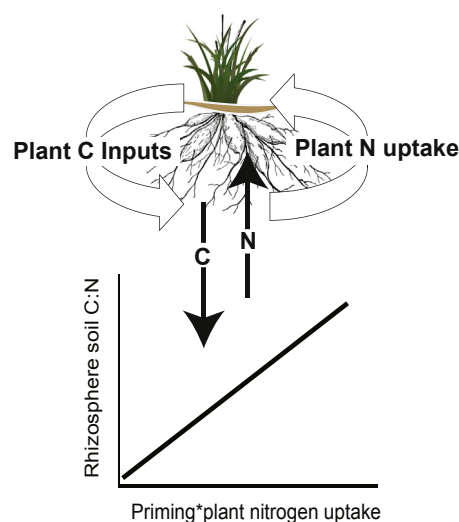


Fig. 1. During periods of rapid plant growth, high nutrient uptake may impose nutrient constraints within the rhizosphere zone that can act as a filter on microbial community characteristics.

during different plant growth stages. We grew plants in a controlled greenhouse environment, and examined bacterial community composition and biomass within the plant rhizosphere as well as plant N uptake and soil N availability at three time points throughout the growing season to represent early, mid, and peak plant growth. We predicted that plant N uptake would explain much of the variation in rhizosphere bacterial community assembly and functional traits among plant species, directly corresponding to timing and nature of plant growth. We also predicted that soil and microbial biomass C:N would inversely correlate with their respective enzyme activities. More specifically, since the invasive grass *B. tectorum* exhibits higher N uptake rates compared to native grass species (Miller et al., 2006; Sperry et al., 2006; Perkins et al., 2011), we predicted that soil enzyme activities and soil nutrient availability would increase more quickly in the rhizosphere of *B. tectorum* during the early stages of the growing season compared to the other native grass species. We also predicted that *B. tectorum* would alter bacterial community structure within the rhizosphere more quickly than the other native grasses.

2. Materials and methods

2.1. Experimental design

This study focused on elucidating the influence of actively growing plants on soil nutrient availability and bacterial community structure by characterizing species-specific rhizosphere microbe traits across a growing season. We selected four C_3 grass species, including: *B. tectorum* L. (Cheatgrass), *Koeleria macrantha* (prairie Junegrass; (Ledeb.) Schult.), *Pascopyrum smithii* (western wheatgrass (Rydb.) Á. Löve), and *Vulpia octoflora* (Sixweeks fescue; (Walter) Rydb.) to observe at three different stages throughout the growing season. These plant species use the same photosynthetic pathway, but differ in life history (phenology) and root structural traits, which could influence rhizosphere bacterial associations. For example, *B. tectorum* is an invasive winter annual grass introduced to North America with a fibrous rooting pattern. *K. macrantha* is a native perennial bunchgrass with a fine fibrous rooting pattern. *P. smithii* is a native perennial with a rhizomatous rooting pattern. Lastly, *V. octoflora* is a winter annual native to North America also with a fibrous rooting pattern. Seeds for all three native grass

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