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Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure

Andrew Kulmatiski [a,*], Karen H. Beard [b]

[a] Department of Biological Sciences, University of Alaska, Anchorage, AK 99508, USA
[b] Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322-5230, USA

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ABSTRACT

Plant–soil feedbacks are gaining attention for their ability to determine plant community development. Plant–soil feedback models and research assume that plant–soil interactions occur within days to weeks, yet, little is known about how quickly and to what extent plants change soil community composition. We grew a dominant native plant (*Pseudoroegneria spicata*) and a dominant non-native plant (*Centaurea diffusa*) separately in both native- and non-native-cultivated field soils to test if these species could overcome soil legacies and create new soil communities in the short-term. Soil community composition before and after plant growth was assessed in bulk and rhizosphere soils using phospholipid fatty acid analyses. Nematode abundance and mycorrhizal colonization were also measured following plant growth. Field-collected, native-cultivated soils showed greater bacterial, Gram (−), fungal, and arbuscular mycorrhizal PLFA abundance and greater PLFA diversity than field-collected, non-native-cultivated soils. Both plant species grew larger in native- than non-native-cultivated soils, but neither plant affected microbial composition in the bulk or rhizosphere soils after two months. Plants also failed to change nematode abundance or mycorrhizal colonization. Plants, therefore, appear able to create microbial legacies that affect subsequent plant growth, but contrary to common assumptions, the species in this study are likely to require years to create these legacies. Our results are consistent with other studies that demonstrate long-term legacies in soil microbial communities and suggest that the development of plant–soil feedbacks should be viewed in this longer-term context.

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1. Introduction

The interactions between plants and surrounding soil communities have been a topic of intense research in the past decade (Kulmatiski et al., 2008; Bever et al., 2010). Plant–microbial interactions, in particular, are thought to decrease plant growth, increase the rate of succession, and explain non-native plant success (Kardol et al., 2006; Reinhart and Callaway, 2006; Kulmatiski et al., 2008). These effects are due in large part to negative (i.e., plant–pathogen) plant–soil interactions (Bever, 1994; Van der Putten and Peters, 1997; Klironomos, 2002) though positive plant–soil interactions have also been recognized (Van der Heijden et al., 1998; Kourtev et al., 2003; Hawkes et al., 2005). For example, mycorrhizal associations and plant–growth promoting bacteria have been shown to increase plant growth and change plant community composition (Van der Heijden et al., 1998; Compant et al., 2005). Interactions among plants, microbes, and other soil organisms, such as nematodes, are only beginning to be explored (Fu et al., 2005; Wurst et al., 2008; Hol et al., 2010).

Plants are not only affected by soil communities but they also affect soil community composition. However, due to the difficulty of measuring plant effects on soil communities, plant–soil feedback (PSF) research has taken a bioassay or black-box approach to measuring differences in soil communities (Bever et al., 1997). More specifically, plant–soil feedback research measures plant growth on soils cultivated by 'self' and 'other' plant species to determine the net effect that a plant species has on the soil community. This experimental approach has revealed the ability of plants to create soils that increase or decrease plant growth, yet relatively little is known about the specific changes plants cause in microbial community composition (Westover et al., 1997; Eisenhauer et al., 2010; Maul and Drinkwater, 2010).

Plant–soil feedbacks are typically measured under greenhouse conditions and often in sterilized soils (Kulmatiski and Kardol, 2008). Relatively little is known about how plant–soil feedbacks develop in soils with fully developed soil communities. For

* Corresponding author. Tel.: +1 907 786 1676; fax: +1 907 786 1314.
E-mail address: afak@uaa.alaska.ed (A. Kulmatiski).

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example, it is not known if different soils are more or less resistant to changes in microbial composition (Murakami et al., 2000). An important, unanswered question in the plant–soil feedback literature, therefore, is how long plants require to cultivate their soil type in soils with established soil communities (Murakami et al., 2000; Kourtev et al., 2003; Kulmatiski and Kardol, 2008; Maul and Drinkwater, 2010). Addressing this question is critical to plant–soil feedback models because these models assume that plants change microbial structure and function continuously (Bever et al., 1997; Kourtev et al., 2003; Maul and Drinkwater, 2010).

The primary goal of this study was to determine if, over approximately one growing season, target plants could overcome plant growth legacies and recreate identifiable soil communities (i.e., provide experimental support for previously observed patterns). Previous research at the study site demonstrated that over the long-term, non-native plants produce soils with small, low diversity microbial communities as indicated by phospholipid fatty acid (PLFA) analyses and that these effects were independent of agricultural legacies (Kulmatiski and Beard, 2008). Consistent with strong plant effects on microbial composition, we predicted that plants would cause rapid changes in microbial composition especially in the rhizosphere because of differences in root sloughing, root exudation and susceptibility to soil pathogens and symbionts. More specifically, we predicted that when plant species were grown on soils historically cultivated by conspecifics, soil microbial community composition would not change; conversely, we expected that the soil microbial community would be altered when plant species were grown on soils historically cultivated by different plant taxa.

In this study, we describe the long-term effects of plant growth on soil communities, we then grow the dominant native plant *Pseudoroegneria spicata* (Pursh.) and the dominant non-native plant *Centaurea diffusa* (Lam.) in self- and other-cultivated soils to assess the short-term effect of the growth of these species on the whole-soil and rhizosphere PLFA, aboveground plant biomass, mycorrhizal colonization, and nematode abundance. We hypothesized that plant effects would be observable in rhizosphere soils but weak in bulk soils because plants presumably affect microbial composition primarily through sloughing and root exudation which is concentrated in the rhizosphere.

2. Materials and methods

2.1. Field sites

This study was conducted using soils from the northern shrub-steppe of the Methow Valley, Washington, USA (48°27′N, 120°12′W, 550–700 m a.s.l.). Nine formerly-agricultural (ex-arable) fields with adjacent, never-cultivated areas (undisturbed) of similar topography were selected for sampling. Prior to abandonment, ex-arable fields had been tilled for non-irrigated production of alfalfa and wheat, with minimal fertilizer use. Soils were on the Newbon-Conconully association, consisting of coarse-loamy, mixed mesic Typic Haploxerolls (Lenfesty, 1980). In several fields in the study area soil organic matter ranges (48–64 g kg^{-1}), extractable nitrogen (22–28 mg kg^{-1}), and extractable phosphorus (20–27 mg kg^{-1}) were greater in ex-arable, non-native-dominated than undisturbed, native-dominated soils (Kulmatiski et al., 2006b). Fine-root mass is greater in undisturbed (4.6 ± 2.0 mg g^{-1}) than ex-arable fields (1.6 ± 0.5 mg g^{-1}; Kulmatiski et al., 2006a). Across the 0–120 cm depths, there was no difference in particle size and soils contained 72.3 ± 3.0% sand and 10.9 ± 1.4% clay (Kulmatiski et al., 2006a). Mean annual precipitation is 350 mm, with 68% falling between October and March (NCDC, 2006).

The growing season begins with snowmelt, usually in March or April, and continues until snowfall in November, though most plant growth occurs in two months (May and June) and seasonal senescence occurs in June and July. Vegetation in the ex-arable fields consists primarily of persistent non-native plant communities, whereas the adjoining undisturbed areas are dominated by natives (Kulmatiski, 2006). The non-native species include grasses *Bromus tectorum* (L.) and *Poa bulbosa* (L.), and forbs *C. diffusa*, *Cardaria draba* (L.), *Sisymbrium altissimum* (L.), and *Sisymbrium loeselii* (L.). Native species include perennial grasses *P. spicata*, *Festuca idahoensis* (Elmer), and *Hesperostipa comata* (Trin. & Rupr.), forbs *Balsamorhiza sagittata* (Pursh.), *Lupinus arbustus* (Dougl. ex Lindl.), *Lupinus aridus* (Dougl.), and *Lupinus caudatus* (Kellogg), and shrubs *Purshia tridentata* (Pursh.) and *Artemisia tridentata* (Nutt.). Root biomass in both ex-arable fields and undisturbed areas is concentrated in the upper soil layers; on average, 52% of total root biomass in the top 120 cm of soil is found in the upper 15 cm (Kulmatiski et al., 2006a).

2.2. Experimental design

In June of 2005, 360 soil cores, 5 cm width × 15 cm depth, were taken from nine fields. In each field, five cores were taken for PLFA analyses from each of four soil types: ex-arable areas growing non-natives (predominantly *C. diffusa*), ex-arable areas growing natives (predominantly, *P. spicata*), undisturbed areas growing non-natives, and undisturbed areas growing natives. This factorial sampling design allowed us to distinguish plant-history effects from agricultural history effects (Kulmatiski and Beard, 2008). The two species used in this study are the dominant native- and non-native species, so it was not difficult to locate soil cores adjacent to individuals from these species. Cores were field-collected, so the samples are not from monocultures, but the soils were always taken from the presumed rooting zone of an individual from the target species. These samples were analyzed without growing plants to assess the long-term effects of plant growth on PLFA composition. An additional ten cores were taken from the ex-arable areas growing non-natives and the undisturbed areas growing natives. These samples were used to determine the short-term effects of *C. diffusa* and *P. spicata* growth on these soils.

Individual cores were left inside transparent plastic sleeves used to extract them, and were immediately stored in the dark, at −20 °C. Microbial activity was assumed to be negligible because the soils were extremely dry (water potentials < −30 MPa) when collected (Kulmatiski et al., 2006a). Cores were transported frozen to Utah State University, and all but the tops were wrapped in aluminum foil to block out light. All cores were wetted to field capacity and stored at room temperature for one week. Four (±0.01) gram subsamples were then removed for PLFA analyses (see below) from cores used to measure long-term legacies of plant growth and agricultural management (i.e., survey cores). Cores used to assess short-term effects of plant growth (i.e., experiment cores) received five germinated seeds. After three weeks, the two smallest plants were removed so that each pot contained three target individuals. Plants grew in a growth chamber (Precision Scientific, Inc., Chicago, IL) with 16 h of light at 300 foot candles for two months. Temperatures were maintained at 15 °C during the night and 25 °C during the day. Cores were watered every three days to maintain moisture but not saturate soils or allow leaching. Cores were rotated weekly to minimize microsite effects.

After two months, which represents the growing season (May and June) plants began to show signs of nutrient stress (i.e., yellowing), presumably due to becoming root-bound in relatively small soil cores. At this time, aboveground biomass was clipped, dried at 70 °C, and weighed. Plant roots from each pot were separated by hand from soil. A 4.00 ± 0.01 g bulk soil sample was

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