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Fire severity shapes plant colonization effects on bacterial community structure, microbial biomass, and soil enzyme activity in secondary succession of a burned forest

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ABSTRACT

The increasing frequency and severity of wildfires has led to growing attention to the effects of fire disturbance on soil microbial communities and biogeochemical cycling. While many studies have examined fire impacts on plant communities, and a growing body of research is detailing the effects of fire on soil microbial communities, little attention has been paid to the interaction between plant recolonization and shifts in soil properties and microbial community structure and function. In this study, we examined the effect of a common post-fire colonizer plant species, *Corydalis aurea*, on soil chemistry, microbial biomass, soil enzyme activity and bacterial community structure one year after a major forest wildfire in Colorado, USA, in severely burned and lightly burned soils. Consistent with past research, we find significant differences in soil edaphic and biotic properties between severe and light burn soils. Further, our work suggests an important interaction between fire severity and plant effects by demonstrating that the recolonization of soils by *C. aurea* plants only has a significant effect on soil bacterial communities and biogeochemistry in severely burned soils, resulting in increases in percent nitrogen, extractable organic carbon, microbial biomass, β-glucosidase enzyme activity and shifts in bacterial community diversity. This work propounds the important role of plant colonization in succession by demonstrating a clear connection between plant colonization and bacterial community structure as well as the cycling of carbon in a post-fire landscape. This study conveys how the strength of plant–microbe interactions in secondary succession may shift based on an abiotic context, where plant effects are accentuated in harsher abiotic conditions of severe burn soils, with implications for bacterial community structure and enzyme activity.

1. Introduction

As patterns of fire severity and frequency shift amidst climate change, understanding how fires may influence ecosystem structure and function is of growing importance (Niboyet et al., 2011; Reichstein et al., 2013). In particular, the western U.S. and Rocky Mountain regions are expected to face more frequent and severe fires (Westerling, 2006; Miller et al., 2009; Rocca et al., 2014). The details of ecological succession, including revegetation, can strongly influence ecosystem structure and function after such fire disturbance (Scheiner and Willig, 2011). Revegetation is a vital process for recovery of ecosystem function due to both direct and indirect effects on soil physical, chemical, and biological properties. While a vast body of research has described ecological consequences of fire to aboveground (DeBano et al., 1998; Bond et al., 2005) and belowground communities (Dooley and Treseder, 2012; Ferrenberg et al., 2013; Pourreza et al., 2014), a dearth of research has addressed the effect of colonizer plants on belowground soil microbial communities after fire disturbance (Hart

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et al., 2003; López-Poma and Bautista, 2014), or explicitly evaluated such interactions in the field. Nonetheless, interactions between soil bacteria and plants may themselves be drivers of ecosystem succession (Reynolds et al., 2003; Knelman et al., 2012; Jangid et al., 2013) and overall microbial communities (bacteria and fungi) are central to fundamental ecosystem soil processes including carbon (C) flux, nutrient (nitrogen (N) and phosphorous (P)) cycling, and soil fertility (Van Der Heijden et al., 2008; Schmidt et al., 2014).

Extensive research has also established that fire severity strongly influences the degree to which soil physical, chemical, and biological properties are altered. For example, the severity of a fire can alter the magnitude of chemical and biological changes experienced by soils, such as changes in C, microbial biomass, enzyme activity, ammonium, and/or pH (Neary et al., 1999; Certini, 2005). As well, fire severity can also strongly influence carbon chemistry (Certini et al., 2011; Knicker et al., 2013) and microbial community structure/activity (Hamman et al., 2007; Weber et al., 2014), and because fire severity affects a multitude of soil properties so strongly, it may also modulate the relative importance of plant–microbe interactions. While research continues to uncover aspects of when and where changes in plant communities may affect microbial community structure and function, existing theory suggests that links between microbes and plants may be strongest amidst harsh abiotic conditions (Van Der Heijden et al., 2008). In this way, fire severity may prove important in understanding plant–microbe interactions in secondary succession. In particular, since early successional heterotrophic microbial communities often face C and nutrient constraints both after fire-disturbance and in general (Zak et al., 1990; Treseder et al., 2004; Fierer et al., 2010), we expect plant colonization to alter microbial community structure and function via alterations in soil edaphic properties. Given existing research and theory that suggests the importance of plant–microbe interactions varies across different abiotic conditions, we hypothesize that fire intensity will modulate plant effects, in which soils experiencing severe burns will exhibit a greater response to plant colonization than soils experiencing light burn.

Thus, in order to generate a better understanding of plant–microbe interactions following fire disturbances of varying severity, we examined patterns of soil chemistry, bacterial communities, microbial biomass, and overall extracellular enzyme activity of C, N, and P-acquiring enzymes, in four soil categories: severe burn unvegetated soils, severe burn revegetated soils, light burn unvegetated soils, and light burn revegetated soils from approximately one year after a major wildfire. We examined bacteria to assess a higher resolution picture of soil biotic responses to plant colonization during secondary succession revegetation processes, but we also assayed changes to total microbial biomass and enzyme activity – metrics that also integrate over the fungal community which may play a prominent role in post fire soil dynamics (Treseder et al., 2004; Gartner et al., 2012; Holden et al., 2012). Here, we investigated how plant recolonization after fire may vary in its impact on soil biogeochemistry under conditions of varying fire severity.

2. Materials and methods

2.1. Site description and sampling

We sampled soils from the High Park fire burns outside of Ft. Collins, CO, in July 2013. Soils were collected at the Buckhorn Camp property on the Colorado Front Range, which sits at ~2377 m above sea level. Samples were collected approximately one year after the fire, which occurred in June 2012 and is the 3rd largest fire in Colorado's recorded history to date based on area burned. The site included both severely and lightly burn areas within a continuous area of forest dominated by Ponderosa Pine *(Pinus ponderosa)* on similar slope and aspect, and with similar tree cover (in the area of latitude: 40.59 N; longitude: 105.32 W). General characteristics of these Front Range ponderosa pine forests are described by Veblen et al. (2000). Severe burn was defined as areas with no soil litter layer and trees that were fully scorched to the crown (Fig. S1). Light burn areas had a litter layer of 0.5–3.5 cm and partially scorched trees (55–286 cm scorch height) (Fig. S1). All trees were dead in the severe burn areas while live and dead trees were mixed in light burn areas. Eight replicate revegetated and unvegetated soil samples were collected from both severe and light burn areas at least 5 m apart across transects spanning 50 m in both light and severe burn landscapes. Revegetated soil samples were collected under *Corydalis aurea* plants, a native plant that is a common member of communities after fire disturbance and was dominant in both light and severe burn areas. Vegetated soil samples were taken from under *C. aurea* plants that were free of any other vegetation within a radius of at least 32 cm from the sampled soil. Unvegetated samples were free of vegetation within a 1.5 m radius. Soils were collected using a 5 cm diameter coring device to 5 cm depth and, for light burn soils, pine litter was removed prior to sampling. Thus, all samples included the top 5 cm of soil. Soils were immediately transported to labs at the University of Colorado at Boulder, passed through 2 mm mesh size sieves, and subsampled to be stored at 4 °C for soil chemical and enzyme analysis. A subsample was stored at −70 °C for molecular analysis.

2.2. Soil properties

Soils were dried at 100 °C for 48 h to determine gravimetric soil moisture, and soil pH was determined on fresh soils using a ratio of 2 g soil to 4 mL DI H_2O. Thirty milligrams of dried, ground soils were packed in tin capsules and then run on a Thermo Finnigan EA 1112 Series Flash Elemental Analyzer (Thermo Fisher Scientific, Inc., Waltham, MA, USA) to determine % C and % N of samples (Matejovic, 1997). Within a day of collection, ~8 g fresh soil were extracted in 40 mL 0.5 M K_2SO_4 to determine NH_4^+ and NO_3^-/NO_2^- extractable N, total extractable non-purgeable organic carbon (extractable carbon excluding carbonates) (NPOC), and total dissolved nitrogen (TDN). Microbial biomass C was ascertained through a paired set of extractions on 72-h chloroform-fumigated samples as per standard methods (Brookes et al., 1985). Microbial biomass-C as reported was adjusted for extraction efficiency based on the literature correction value of 0.45 (Beck et al., 1997). All extractions included shaking for 1 h and filtering with Whatman no.1 paper (Whatman Incorporated, Florham Park, NJ, USA). Extracts were frozen until chemical analysis. NH_4^+ was measured on a BioTek Synergy 2 Multidetection Microplate Reader (BioTek, Winooski, VT, USA) and NO_3^-/NO_2^- were measured on a Lachat QuikChem 8500 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA) from pre-fumigation extracts. NPOC in pre and post fumigation soils were measured on a Shimadzu TOC-V CSN Total Organic Carbon Analyzer (Shimadzu TOCvcpn, Kyoto, Japan).

To determine changes in carbon chemistry via humification, fluorescence spectroscopy was employed (Fellman et al., 2010). For each sample, 5 g fresh soil were extracted in nanopure H_2O, shaken for 1 h at 250 rpm and filtered through combusted (4 h at 450 °C) Whatman GF/F filters (Whatman Incorporated, Florham Park, NJ, USA) into combusted amber viles. First, UV–vis analysis was performed using an Agilent 8453 spectrophotometer (Agilent Technologies, Santa Clara, CA, USA). For fluorescence analysis, a 1:10 dilution of extract:water was completed so that UV absorbance at 254 nm fell between 0.1 and 0.2 cm^{-1}. These diluted samples were then used for fluorescence analysis on a Fluoromax-3 spectrofluorometer (Horiba Jobin Yvon, Kyoto, Japan). A three dimensional