



Soils mediate the impact of fine woody debris on invasive and native grasses as whole trees are mechanically shredded into firebreaks in piñon-juniper woodlands



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ABSTRACT

To stem wildfires, trees are being mechanically shredded into firebreaks with the resulting fine woody debris (FWD) potentially exerting immense control over soil and plants. We linked FWD-induced changes in microbial activity and nutrient availability to the frequency of *Bromus tectorum* and three native, perennial grasses across 31 piñon-juniper woodlands, UT, USA. Using a series of mixed models, we found that FWD increased the frequency of three of the four grasses by at least 12%. Deep, as opposed to shallow, soils mediated frequencies following FWD additions but only partially explained the variation in *Bromus* and *Pseudoroegneria spicata*. Although fertile areas associated with tree-islands elicited no response, FWD-induced increases in nitrogen mineralization in deep soils (15–17 cm) caused the frequency of the exotic and *Pseudoroegneria* to rise. Higher phosphorus availability in FWD-covered surface soils (0–2 cm) had no impact on grasses. FWD altered deep soil respiration, and deep and shallow microbial biomass structuring *Pseudoroegneria* frequencies, suggesting that microorganism themselves regulated *Pseudoroegneria*. The positive effects of FWD on grass frequencies intensified over time for natives but diminished for *Bromus*. Our results demonstrate that microorganisms in deeper soils helped mediate species-specific responses to disturbance both facilitating exotic invasion and promoting native establishment.

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1. Introduction

Terrestrial environments are exposed to a diverse array of disturbances that alter ecosystem characteristics and induce microbial-mediated biological changes belowground. Disturbances that alter the quantity and quality of carbon (C) resources entering environments, in particular, have the potential to exert immense control over soil processes (Zechmeister-Boltenstern et al., 2015). Wildfires, tree-fall, typhoons and/or anthropogenic activities related to timber harvesting (Tinker and Knight, 2000; Murphy et al., 2008) result in the addition of dead and downed wood that promotes soil C storage (Klopatek, 2002), stimulates and depresses the fluxes of trace gases to the atmosphere (Hafner and Groffman,

2005), and releases new sources of energy for trophic web interactions (Norden et al., 2004). Further, many of the effects of woody debris on soils may extend aboveground.

Linking potential shifts in microbial activity to plant performance is extremely difficult, but clearer relationships may arise following disturbances. Disturbances often lead to dramatic shifts in aboveground plant community composition, especially when promoting the invasion and dominance of exotic species (MacDougall and Turkington, 2005). Following woody additions, the cover of exotic understory species increases in many forested ecosystems (e.g., tropical and coniferous forests; Kerns et al., 2006; Murphy et al., 2008) in part due to sunlight reaching the once-shaded understory as downed wood opens gaps in the overstory canopy. Woody additions may also alter the belowground environment and impact plants. In surface soils, woody additions generally lead to the immobilization of inorganic nitrogen (N) as microorganisms decompose copious recalcitrant wood substrates (Laiho and Prescott, 2004). However, in the absence of an overstory

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utilizing N, N may accumulate and be exploited by germinating and emerging seeds, and established understory plants. Deeper in soils, the resulting dead root system from canopy species may decompose and stimulate N mineralization and availability (Ehrenfeld et al., 1997) aiding in seedling recruitment. Besides N dynamics, dead and downed wood may alter other aspects of the soil environment favoring plant invasion. For example, woody debris may cause microorganisms to: 1) elevate soil water availability as decomposition and the production of extracellular polymeric substances modify surface debris and/or soil structure (Or et al., 2007; Young et al., 2013); 2) increase the release rates of essential plant macronutrients, such as phosphorus (P; Richardson and Simpson, 2011); and 3) change in abundance with species specializing in degrading woody substrates becoming dominant, and growth promoting rhizobacteria (Hayat et al., 2010) and mycorrhizae (Vandenkoornhuysen et al., 2003) becoming rare. However, the extent that these disturbance-induced shifts extend deeper into soils away from woody materials or translate into plant responses remains relatively unclear.

The action of shredding semi-arid trees, coupled with one of the most prolific plant invasions occurring in any ecosystem, offers an unprecedented opportunity to understand the links between fine woody debris (FWD)-induced changes belowground and native and exotic plant responses aboveground. The annual exotic grass, *Bromus tectorum* (L.), is a prolific invader that degrades piñon-juniper woodlands by replacing native grass species and creating monocultures of continuous fuels leading to catastrophic wildfires (Brooks et al., 2004). To stem wildfires and create firebreaks in piñon-juniper woodlands (Owen et al., 2009), thousands of hectares of trees are being mechanically shredded into FWD and translocated to the soil surface. Most FWD is being deposited in place on existing “tree-islands of fertility” in contrast to interspaces containing grasses, forbs, and biological soil crusts. The mosaics of islands of fertility and interspaces are chiefly responsible for differences in microbial activity prior to FWD additions (Aanderud et al., 2008) and may serve to augment the effects of FWD on belowground processes. Soils beneath trees are enriched with C and other essential elements (e.g., N, P, and calcium) due to roots acquiring nutrients from interspace soils and depositing them on the soil surface via litter inputs. Even under this enrichment, microbial activity in tree-islands is low due to the low quality of pine needle litter, and this limitation may be enhanced as more recalcitrant C sources from FWD are added to surfaces. Also, N transformations can be higher beneath tree-islands than interspace soils (Schade and Hobbie, 2005), and the addition of woody C sources, such as lignin, may only serve to immobilize N and reduce N release (Bates et al., 2002).

In this study, we evaluated the extent that soils mediated the responses of exotic and native grass species to FWD. In a replicated field experiment, where FWD was manipulated across 31 piñon-juniper woodlands, we linked FWD-induced changes in microbial activity and nutrient availability to shifts in the frequency of the invasive *B. tectorum* and three native, perennial grasses in the Great Basin Desert and Colorado Plateau, UT, USA. The three perennial species included: *Elymus elymoides* (Raf.) Swezey, *Poa secunda* (J. Presl), and *Pseudoroegneria spicata* (Pursh) Á. Löve. To understand the ecological consequences of a single disturbance type occurring at different times across 30+ ecosystems, we used a series of mixed models. Specifically, we developed models to: 1) describe the effects of shredding whole *Juniperus osteosperma* (Torr.) and the subsequent addition of FWD on N mineralization, P availability, microbial respiration rates, microbial biomass, and dissolved organic C (DOC) in surface and subsurface soils; and, 2) relate these changes to grass species distribution. We also examined these potential links across tree-island soils covered in FWD and relatively

bare interspace soils. The perennial grass species we selected are often influenced by *B. tectorum* invasions (Mangla et al., 2011) and represent dominant grasses in piñon-juniper woodlands. Thus, by examining these natives in tandem with *B. tectorum*, our results may offer a more comprehensive understanding into the consequences of shredding on species invasion. We hypothesized that: 1) the effects of FWD on shallow soils, immediately below the disturbance in particular, will explain some of the variation in the frequency of all grasses; 2) tree-island microsites will influence FWD-induced links between soils and grasses; and 3) changes in the availability of essential plant nutrients (i.e., N and P) and not microbial activity will be the prominent processes dictating grass response following FWD additions.

2. Materials and methods

2.1. Woodland sites

We conducted our study across 31 piñon-juniper woodland sites in the Great Basin Desert, Utah, USA. Dominant tree species included *Juniperus osteosperma*, and *Pinus edulis* (Engelm.) along with the shrubs *Artemisia tridentata* Nutt. (ssp. *wyomingensis* Beetle and Young, *tridentata*, and *vaseyana* [Rydb.] Beetle). We selected woodland sites with at least 15–45% tree cover estimated using images from the National Agricultural Imagery Program at 1 m spatial resolution (USDA-FSA-APFO Aerial Photography Field Office, Salt Lake City, UT). To ensure that the sites were indicative of semi-arid soil in the western USA, we measured the following physiochemical characteristics: pH from soil pastes (Thermo Orion pH meter model 410, Thermo Scientific Orion, Beverly, MA); electrical conductivity from 1:1 w/v extracts (Beckman Conductivity Bridge model RC-16C, Beckman Coulter Inc., Brea, CA); soil %C and %N with dry combustion on a C to N analyzer (LECO TruSpec CN Determinator, LECO Corporation, St. Joseph, MI); and soil texture (% sand, silt, and clay) with a hydrometer. Basic soils characteristics were based on three soil samples from a combination of at least one surface and subsurface soil sample to capture the overall environment at each site. The mean annual temperature and precipitation in woodlands was based on a thirty-year period (1982–2012) from PRISM climate datasets (<http://www.prism.oregonstate.edu>).

2.2. FWD manipulation and soil sampling

To investigate the effects of FWD on soils, we created three, randomly-selected FWD addition and three control plots (33 × 30 m) in each site. In the addition plots, whole *J. osteosperma* trees were shredded with a toothed drum (Cline et al., 2010), and the resulting woody material was deposited on the soil surface 1–8 years prior to sampling (2003–2010), which occurred over a 2-year period during the summer months (April–August 2011–2012). Our FWD fits best within the definition of fine down and deadwood employed by researchers in multiple other ecosystems (Norden et al., 2004; Muller-Using and Bartsch, 2009). Following whole-tree shredding, the dead and downed materials fall under the classification of FWD (diameter < 10 cm) and do contain classic FWD components (e.g., needles, twigs, small branches). These materials also consist of extremely woody components (e.g., logs and large branches) generally reserved for FWD (diameter > 10 cm; Muller-Using and Bartsch, 2009) that are only reduced in size but not different in chemistry. Specifically, the diameter of FWD ranged from 0.1 to 7.5 cm (Young et al., 2014) and FWD was piled on top of tree-islands.

To begin to understand the effects of FWD on links between soils and grasses, we sampled soils in *J. osteosperma* tree-island microsites at the surface (0–2 cm depth) where seeds may germinate and

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