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Elevated enzyme activities in soils under the invasive nitrogen-fixing tree *Falcataria moluccana*

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Abstract

Like other N-fixing invasive species in Hawaii, *Falcataria moluccana* dramatically alters forest structure, litterfall quality and quantity, and nutrient dynamics. We hypothesized that these biogeochemical changes would also affect the soil microbial community and the extracellular enzymes responsible for carbon and nutrient mineralization. Across three sites differing in substrate texture and age (50–300 years old), we measured soil enzyme activities and microbial community parameters in native-dominated and *Falcataria*-invaded plots. *Falcataria* invasion increased acid phosphatase (AP) activities to $>90\,\mu mol\,g^{-1}\,soil\,h^{-1}$ compared to 30–60 $\mu mol\,g^{-1}\,soil\,h^{-1}$ in native-dominated stands. Extracellular enzymes that mineralize carbon and nitrogen also increased significantly under *Falcataria* on the younger substrates. By contrast, total microbial biomass and mycorrhizal abundance changed little with invasion or substrate. However, fungal:bacterial ratios declined dramatically with invasion, from 2.69 and 1.35 to <0.89 on the 50- and 200-year-old substrates, respectively. These results suggest that *Falcataria* invasion alters the composition and function of belowground soil communities in addition to forest structure and biogeochemistry. The increased activities of AP and other enzymes that we observed are consistent with a shift toward phosphorus limitation and rapid microbial processing of litterfall C and N following *Falcataria* invasion.
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Keywords: Nitrogen fixation; Extracellular enzyme; Phosphorus; Litter quality; Bacteria; Fungi; Invasive species; Acid phosphatase; Decomposition; Hawaii

1. Introduction

Nitrogen-fixing plants dramatically increase nitrogen (N) inputs and cycling rates in many ecosystems (Vitousek et al., 1987; Vitousek and Walker, 1989; Bowman et al., 1996; Maron and Connors, 1996). Because photosynthesis and productivity are often limited by N availability, N-fixers may increase ecosystem carbon (C) inputs as well (Binkley et al., 1992; Welsh, 2000). In sites where exotic N-fixers invade native ecosystems, they can alter vegetation structure and the quality of litter inputs (Vitousek and Walker, 1989).

Recently, Hughes and Denslow (2005) demonstrated that invasion by the exotic N-fixing tree *Falcataria moluccana* dramatically alters forest structure and litter inputs on young lava flows at low elevations on the island of Hawaii. Typically, these flows have minimal soil development and support native, open canopy forests dominated by *Metrosideros polymorpha*. On flows as young as 50 years, invading *Falcataria* can establish a closed canopy and thick organic root mat on top of the underlying substrate. Native vegetation declines under the dense canopy, and *Falcataria* facilitates invasion by other exotic species such as *Psidium cattleianum*. The biogeochemical effects of *Falcataria* invasion are dramatic: litterfall biomass inputs increase 1.3- to 8.6-fold, corresponding to four- to 55-fold increases in N inputs. *Falcataria* invasion also dramatically increases decomposition rates and soil nutrient availability by factors exceeding 10- and 100-fold, respectively, on the youngest lava flows (Hughes and Denslow, 2005; Hughes and Uowolo, in press). Compared to the native *Metrosideros*,

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N concentrations in *Falcataria* litter are four times greater, although lignin concentrations are also higher and cellulose concentrations are lower in *Falcataria* litter (Hughes and Uowolo, in press).

Aside from increasing rates of C and N cycling, N-fixers also affect phosphorus (P) cycling (Zou et al., 1995; Kaye et al., 2000). In plantations on the island of Hawai'i, *Falcataria* decreases available P pools more than adjacent, nonfixing plantation species with similar productivities (Binkley and Ryan, 1998; Binkley et al., 2000). Although Hughes and Denslow (2005) found elevated P availability with *Falcataria* invasion, the increase was not as strong as for N, suggesting that P supply may also be relatively limited in this system. Low P supply is consistent with the young age of these lava flows, where large available and organic P pools have not yet accumulated due to weathering processes (Raich et al., 1996). Under P limitation, plants and microbes may allocate resources toward P acquisition, particularly the production of phosphatase enzymes (Chróst, 1991; Olander and Vitousek, 2000; Treseder and Vitousek, 2001). Such changes in soil phosphatase activity can be driven by mycorrhizal fungi, and both *Falcataria* (Alexander et al., 1992) and the dominant native tree *M. polymorpha* are known to form associations with mycorrhizae.

Because of its abundant, N-rich litter inputs and effects on nutrient cycling, invasion by *Falcataria* is likely to affect soil microbiological and biochemical processes (Sinsabaugh et al., 1991; Ratledge, 1994; Sinsabaugh, 1994). Specifically, we hypothesized that elevated nutrient availabilities under *Falcataria* would cause a shift in the microbial community from fungal to bacterial dominance, since some fungi compete poorly under high N conditions (Fog, 1988). Since the relative availability of P may decline under *Falcataria*, we predicted that mycorrhizal abundance and acid phosphatase (AP) activity would increase. We also hypothesized that *Falcataria* litter inputs would provide resources for microbes to increase production of enzymes that degrade organic C compounds, while the synthesis of N-degrading enzymes would decrease due to higher N availability (Chróst, 1991; Sinsabaugh and Moorhead, 1994; Allison and Vitousek, 2005). Finally, we predicted that the microbial and enzymatic effects of invasion would diminish with flow age because differences in stand structure and litter inputs were smallest on the oldest lava flow (Hughes and Denslow, 2005).

2. Methods

2.1. Site description

We used study sites established by Hughes and Denslow (2005) in the Malama Ki (19°26′53″N, 154°51′40″W) and Keauohana (19°25′11″N, 154°57′14″W) State Forest Reserves on the Island of Hawaii. Mean annual precipitation at the sites is ~2500 mm (Giambelluca et al., 1986), and mean annual temperature is ~23 °C. The climate is aseasonal, with no less than 100 mm of precipitation falling in any given month, and monthly mean temperatures varying by <3 °C (NOAA, 2002). The Malama Ki site is located on a 213 year-old (y.o.) pahoehoe lava flow, while the Keauohana sites are located on 48 and 200–400 y.o. a′a flows. For simplicity, we refer to the sites as 50 y.o. a′a, 200 y.o. pahoehoe, and 300 y.o. a′a. The native vegetation at these sites is dominated by the ubiquitous Hawaiian tree *M. polymorpha*, with the diversity of understory shrubs and trees increasing with flow age. Forests on the two younger flows have open canopies, with lichens (50 y.o. a′a) or grasses (200 y.o. pahoehoe) covering the volcanic substrate between *Metrosideros* individuals. At the 50 y.o. site, soils are sparse and classified as a′a lava flows (Sato et al., 2005). Soils at the 200 y.o. site are classified as Opihikao extremely rocky mucks, with pahoehoe lava outcrops occupying 30–50% of the land area, while soils at the 300 y.o. site are classified as Malama extremely stony mucks. Both of these soil types have thin (~5 cm) organic horizons that are strongly acidic (Sato et al., 2005).

At each site, we set up 10 circular 0.01 ha plots in the native forest ('control') and 10 plots in adjacent *Falcataria*-invaded ('invaded') areas. To ensure that plot locations were comparable in vegetation cover, substrate type, and disturbance history prior to *Falcataria* invasion, we examined aerial photos of the invaded plots prior to invasion and compared size-class distributions of dead *Metrosideros* trees in the invaded plots with those of live trees in adjacent control plots (Hughes and Denslow, 2005).

2.2. Soil collection

In January 2003 and January 2004, we randomly chose five of 10 control and five of 10 invaded plots at each site for soil sampling. We used a trowel to remove five 10×10 cm samples to a depth of 5 cm near the center of each plot. Within each plot, we took samples at random locations 1–2 m apart, except in the 50 y.o. site where we only found soil accumulating in low spots between a′a blocks. Samples were composited, kept cool, and shipped to Stanford University within 2–3 days for further processing. We passed the samples through a 4 mm sieve to remove coarse roots, organic debris, and lava pieces, and homogenized the soil by hand for use in microbial and enzyme analyses. Soils were subsampled to determine water and nutrient contents (oven drying, 65 °C) and refrigerated (4 °C) for a maximum of 10 days before analyses.

Samples for phospholipid fatty acid (PLFA) analyses were collected similarly in July 2003, except that three cores were composited from within each of three control and three invaded plots. The composited samples were sieved to 2 mm and freeze-dried prior to analysis.

2.3. Soil nutrient concentrations

We determined total soil N and P concentrations using Kjeldahl digestion followed by colorimetric analysis on an