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### Cover Page Footnote

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# Evidence that Invasion by Cheatgrass Alters Soil Nitrogen Availability

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## ABSTRACT

We hypothesized that cheatgrass (*Bromus tectorum*), an exotic invasive annual, may alter soil nitrogen availability. In the Honey Lake Valley of northeastern California, we have monitored soil and vegetation along a chronosequence of cheatgrass invasion. In 2007, we measured total C, total N, and  $\delta^{15}\text{N}$  in tissue of cheatgrass, winterfat (*Krascheninnikovia lanata*), freckled milkvetch (*Astragalus lentiginosus*), and Indian ricegrass (*Achnatherum hymenoides*) in areas invaded for 1, 4, and >10 years. As time since invasion increased, tissue N increased and C/N decreased significantly for cheatgrass and winterfat. Time since invasion significantly affected  $\delta^{15}\text{N}$ , which declined significantly for winterfat and increased significantly for Indian ricegrass and freckled milkvetch. These data suggest that cheatgrass invasion has altered soil nitrogen availability and that other plants respond to this altered availability.

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## INTRODUCTION

Plants that can engineer the soil or create positive plant-soil feedbacks to enhance nutrient availability can elevate their competitive stature (Ehrenfeld 2003; Kulmatiski and others 2008). Such tipping of competitive stature may be responsible for turning an exotic species into an invasive one (Crooks 2002). The invasive success of *Bromus tectorum* (cheatgrass) is predicated on myriad factors, but soil nutrient availability, particularly of nitrogen (N), is an important determinant (Adair and others 2007; Vasquez and others 2008). The literature is conflicting regarding the effects of cheatgrass invasion on soil N resources. Rimer and Evans (2006) reported that after 2 years invasion by cheatgrass in Canyonlands National Park, Utah, the labile N pool decreased 50 percent. Over a 2-year period, few consistent differences in N mineralization, extractable soil N, or total soil C or N were found between native and cheatgrass invaded sites in Oregon (Svejcar and Sheley 2001). On the other hand, in northern Utah, soil beneath cheatgrass was shown to increase N availability relative to native species (Booth and others 2003).

We have monitored the invasion of a winterfat community in the Honey Lake Valley of northeastern California, beginning in 1998. A systematic measurement of surface soil properties was begun in 2000 utilizing a transect of 13 points, 50 m apart, that extended from the points first invaded by cheatgrass

(1-4) to points not yet invaded (5-13). By 2007, all plots had become invaded by cheatgrass, albeit the most recently invaded only had small sparsely-spaced plants. The chronological resolution of this monitoring program allows detailed information on how cheatgrass has affected soil N dynamics and its relationship to plant N uptake. We hypothesize that cheatgrass invasion alters the availability of soil nitrogen.

## MATERIALS AND METHODS

The study was undertaken in the Honey Lake Valley of northeastern California (40° 08' N; 120° 04' W). Since 1998 we have monitored the invasion of a winterfat (*Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit) community by cheatgrass (*Bromus tectorum*). We define invasion to be when small isolated plants of cheatgrass in winterfat canopies expand to fill shrub interspace positions. Soils are uniform throughout the winterfat vegetation zone and are classified as coarse-loamy, Xeric Haplocalcids (Blank 2008). Annual precipitation averages 230 mm. In March of 2000, a transect of 13 sites, 50 m apart, was laid out beginning at the initial focus of cheatgrass invasion (first 4 sites) to areas yet non-invaded. Several times a year, surface soil (0-30 cm) was collected randomly, in interspace microsites, within 5 m of each study plot. In May 8, 2007, following a winter and early spring of below normal

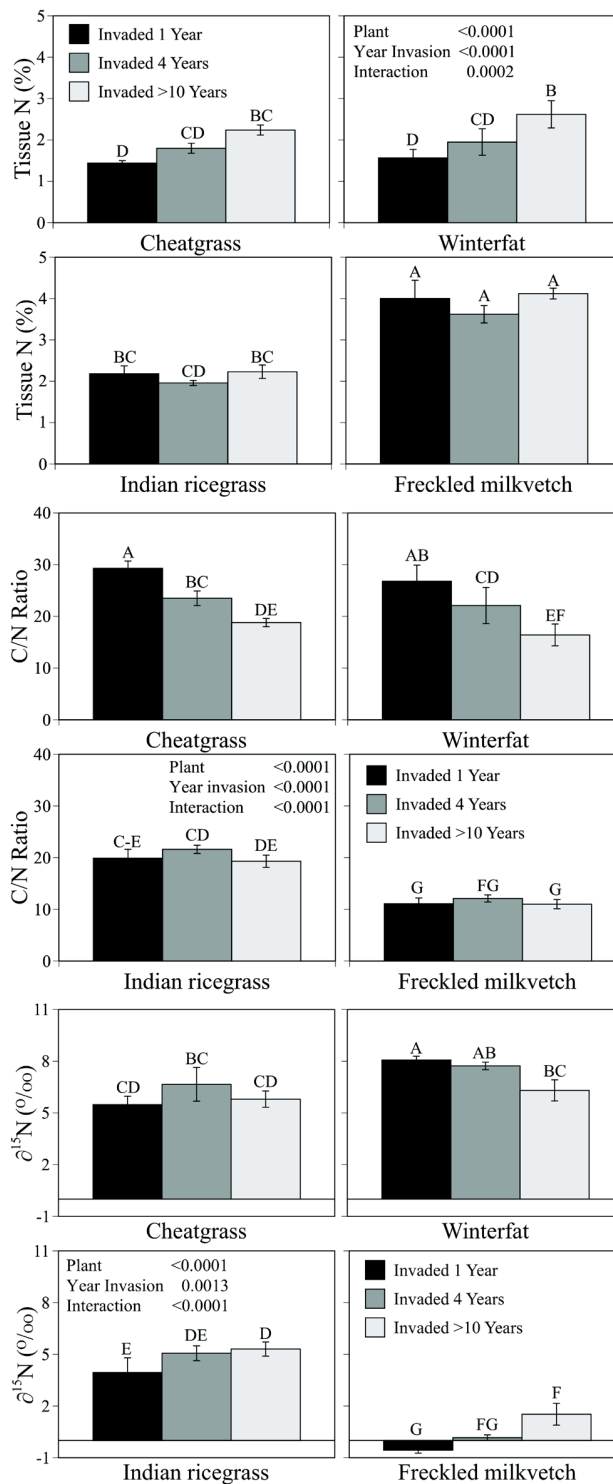
precipitation, we collected total above-ground biomass for the four most common plant species: cheatgrass, winterfat, freckled milkvetch (*Astragalus lentiginosus* Douglas ex Hook.), and Indian ricegrass (*Achnatherum hymenoides* Roem. & Schult. Barkworth). Collected sites were replicated four times in areas separated by at least 50 meters in three invasion zones: invaded by cheatgrass for 1, 4, and >10 years. Plant material was dried for 48 hrs at 60°C, milled, and sent to the Colorado Plateau Stable Isotope Laboratory at University of Northern Arizona for analysis of tissue N and C concentrations and of tissue  $\delta^{15}\text{N}$ .

All data were normalized as necessary and analyzed by ANOVA with categorical variables invasion class and plant species, using Tukey's Honest Significance Test at the  $p \leq 0.05$  level to separate means.

### RESULTS AND DISCUSSION

A significant interaction between cheatgrass invasion status and plant species affected plant tissue N concentrations, plant tissue C/N ratios, and values of  $\delta^{15}\text{N}$  (figure 1). Tissue N concentrations significantly increased and C/N ratios significantly declined for cheatgrass and winterfat and remained statistically similar for Indian ricegrass and freckled milkvetch with increasing time since cheatgrass invasion. As time since invasion increased, tissue  $\delta^{15}\text{N}$  declined significantly for winterfat and increased significantly for Indian ricegrass and freckled milkvetch.

The natural abundance of  $\delta^{15}\text{N}$  data lent support to the hypothesis that cheatgrass invasion has altered soil nitrogen availability. If cheatgrass is accessing a more recalcitrant N pool from soil organic matter, which is less available to natives before invasion, then the newly available pool may have a unique  $\delta^{15}\text{N}$  signature that will be reflected in plant tissue N of all species (Högberg 1997). Indeed, the three native species tested differed significantly in  $\delta^{15}\text{N}$  among invasion classes. Winterfat has an extensive fibrous root system and a deep penetrating taproot. Its  $\delta^{15}\text{N}$  tissue signature, when growing without much competition from cheatgrass, was greater than that of cheatgrass which suggests it is partially accessing a different soil N pool, perhaps deeper in the soil profile.



**Figure 1.** Percent concentration of N, C/N ratios, and  $\delta^{15}\text{N}$  in above-ground tissue of cheatgrass, winterfat, Indian ricegrass, and freckled milkvetch as affected by time since cheatgrass invasion. ANOVA results presented in panels. For all panels, bars with different letters are significantly different ( $p \leq 0.05$ ). Data were collected in 2007.

After >10 years of invasion by cheatgrass,  $\delta^{15}\text{N}$  of winterfat tissue declined significantly and was statistically similar to that of cheatgrass, which suggests the plant is uptaking a greater proportion of that pool of N associated with cheatgrass invasion. The  $\delta^{15}\text{N}$  signature of Indian ricegrass was significantly lower than that of cheatgrass, in plots only recently invaded. Indian ricegrass can fix  $\text{N}_2$  in its rhizosheath (Wullstein 1980; Wullstein 1991), which can explain its lower  $\delta^{15}\text{N}$ . In plots invaded for >10 years, Indian ricegrass tissue  $\delta^{15}\text{N}$  significantly increased to an average value similar to that of cheatgrass, again suggesting it may be partially obtaining N resources associated with invasion. The effect of cheatgrass invasion on the  $\delta^{15}\text{N}$  signature of the symbiotic nitrogen fixing species, freckled milkvetch, is apparent. Tissue  $\delta^{15}\text{N}$  in newly invaded soils averaged near 0 suggesting most N is obtained via fixation of atmospheric  $\text{N}_2$ , and increased  $\delta^{15}\text{N}$  values in soils invaded for >10 years suggests the plant is using more N from mineralized soil sources after invasion.

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