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Plant interactions with soils conditioned by different vegetation: A potential explanation of *Bromus tectorum* L. invasion into salt-deserts?

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ABSTRACT

Invasion by *Bromus tectorum* L. may condition the soil and increase nutrient availability. We hypothesized that nutrient poor soils of the arid Honey Lake Valley of northeastern California U.S.A., similar in physical and chemical properties, but conditioned by either *B. tectorum*, *Krascheninnikovia lanata*, or *Artemisia tridentata*, would differ as a rooting medium. These soil/vegetation types were placed in equal volumes in replicate 5400 cm^3 cylindrical containers, the template removed, and sown to *B. tectorum* or *Leymus triticoides*; controls were left unplanted. At harvest, root mass, root nutrient concentrations, and selected soil nutrients were quantified for each soil/vegetation type. Root mass was statistically similar among soil/vegetation types and seeded plants. After harvest, and relative to unplanted controls, *B. tectorum* invaded soil lost a greater proportion of several nutrients than the other soil/vegetation types suggesting greater nutrient uptake from that soil. Soil/vegetation types planted to *B. tectorum* had significantly greater depletion of soil nutrients compared to soils planted to *L. triticoides*. Soil invaded by *B. tectorum* had greater nutrient availability than similar soil conditioned by *A. tridentata* or *K. lanata* and offers a plausible explanation of why this exotic annual grass has been able to invade nutrient poor salt-desert ecosystems.

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1. Introduction

Arid salt-deserts of the intermountain west, once thought resistant to invasion by the exotic annual *Bromus tectorum*, have now become extensively invaded (Young and Tipton, 1990; Harper et al., 1996). What attributes of *B. tectorum* have allowed it to invade these harsh communities often characterized by coarse-textures, low organic matter, and low fertility? Elevated soil nutrient availability, particularly of nitrogen and phosphorus, often predicts successful plant invasion (Huenneke et al., 1990; Davis et al., 2000; Brooks, 2003). Indeed, the growth potential and competitive ability of *B. tectorum* is partially regulated by adequate soil availability of N and P (Kay and Evans, 1965; Wilson et al., 1966; Gundale et al., 2008). How then does *B. tectorum* invade and flourish in salt-desert soils relatively low in N and P availability? Unfortunately, even if a soil lacks nutrients favorable to exotic plants, some invasives are able to condition or "engineer" (increase nutrient availability) the soil in their new host environment to increase their competitive ability (Xingjun et al., 2005; Levine et al., 2006; Thorpe and Callaway, 2006; Jordon et al., 2008). *B. tectorum* is such a plant (Perkins and Nowak, 2013; Blank and Morgan, 2013). Can soils conditioned by an exotic plant, capable of increasing nutrient availability, also serve as a better substrate for other plants including natives? The evidence is mixed. Niu et al., 2007 reported that in China, areas heavily invaded by an exotic aster had elevated soil nitrogen and phosphorus availability relative to a recently invaded area; but growth of native plants including *Setaria plicata*, *Digitaria chinesis*, *Eupatorium fortunei*, *Stellaria chinesis*, *Lolium perenne*, *Rubus aculeatiflorus*, *Medicago sativa*, *Artemisia annua*, and *Chenopodium ambrosioides* were inhibited. In the same vicinity as this study, we compared plant tissue N concentrations for the natives *Krascheninnikovia lanata*, *Astragulus lentiginosus*, and *Achnatherum hymenoides* in areas invaded by *B. tectorum* for 1, 4, and >10 years (Blank and Morgan, 2011). Only *K. lanata* had significantly greater tissue N in areas invaded for >10 years relative to areas invaded for 1 year. To further refine our understanding of the nature of soil conditioning by *B. tectorum*, an experiment was conducted. This experiment tested if plant roots respond similarly to three soil types, which developed in similar soil parent material

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with similar textural characteristics, but differ in the vegetation they presently support and were conditioned by overtime. The soil/vegetation types include: 1) long-term occupation by *Artemisia tridentata*, 2) long-term occupation by *K. lanata* (non-invaded by *B. tectorum*), and 3) *K. lanata* invaded by *B. tectorum* for 10 years (also referred to as *B. tectorum* invaded soil). In the study area, *B. tectorum* first invaded canopies and interspaces of the *K. lanata* community, then *A. tridentata* canopies, and most recently *A. tridentata* interspaces. We hypothesized that roots of *B. tectorum* and the native perennial grass *Leymus triticoides* would proliferate to a greater extent in soil that had been previously conditioned through long-term occupation by *B. tectorum* growth, due to potentially greater nutrient availability, than similar soils conditioned by *A. tridentata* or *K. lanata*. We further hypothesized that roots of *B. tectorum* and *L. triticoides* will uptake a greater quantity of nutrients from the *B. tectorum* invaded soil due to elevated nutrient availability. We also hypothesized that *B. tectorum*, due to its rapid growth, will affect greater change in soil nutrients than will *L. triticoides*.

2. Materials and methods

To test the hypotheses, three soil types were freshly-collected from the Honey Lake Valley (40°08′N; 120°04′W; elevation 1242 m) of northeastern California, U.S.A. Remnant of pluvial Lake Lahontan, these soils have been influenced by deltatic sedimentation and Holocene eolian reworking of those deposits. The soil types are: 1) *K. lanata* (Prush) A.D. J. Meeuse & Smit invaded by *B. tectorum* L. for over 10 years; 2) *K. lanata* not invaded by *B. tectorum*; and 3) *A. tridentata* Nutt. Soils are classified as coarse-loamy, mixed, superactive, mesic durinodic, Xeric Haplocalcids (Soil Survey Staff, 2015), but soils supporting *A. tridentata* are slightly deeper to carbonate-bearing soil horizons. Surface soil (0–20 cm), roughly corresponding to the A horizon, was collected from each vegetation type. Random samples were taken over a 100 m^2 area from soil between shrubs (interspace soil). Each soil/vegetation type was collected and returned to the greenhouse, and ran through a 4-mm opening sieve to remove coarse woody debris and homogenized (soil does not contain coarse fragments). A subsample of each soil type was analyzed for pH, particle size distribution, organic C and N (Leco Truspec® calibrated with a NIST certified soil standard, no carbonates present in collected soils), and extractable Ca^{+2}, Mg^{+2}, K^{+}, and Na^{+} (pH 7.0 ammonium acetate method, Thomas, 1982). From the extractable data, the molar proportions of Ca^{+2}, Mg^{+2}, Na^{+}, and K^{+} were derived.

A steel template was constructed to divide cylindrical growth containers (5400 cm^3) into three equal volume partitions. Partitions were filled with an equal volume of each soil/vegetation type and the template removed. The center of each container was sown to either *B. tectorum*, *L. triticoides* (Buckley) Pilger (creeping wildrye), or left unseeded (control). We chose the native perennial grass *L. triticoides* because it occurs extensively in the environment the soil types were collected from. Planted treatments were replicated seven times; control treatments were replicated five times. Planted and unplanted containers were watered as needed with de-ionized water to maintain the soil near field capacity; unplanted controls did not need to be watered as often. Plants were sown on March 7 and harvested on June 16. No artificial lighting was used. Greenhouse cooling was set to not exceed 27 °C in daylight and heating was set not to go below 10 °C at night. As roots grew, they were free to move through each soil type and proliferate.

At harvest, above-ground biomass was clipped at the soil surface, dried at 70 °C for 48 h, and weighed. Next, the steel template was reinserted to correspond to each partition, and hammered into the soil until the container bottom was reached. The template was sharpened at the bottom to cut through the roots easily. Roots in each soil type were quantitatively extracted, washed, dried at 70 °C for 48 h, weighed, and milled. Root tissue was analyzed for total C and N using a LECO TruSpec® analyzer (calibrated with EDTA). Another portion of tissue was ashed at 550 °C, solubilized in HCl and HNO_3 (Kalra, 1997) and analyzed for P (Lachat QuikChem® system using molybdovanadate chemistry) and Ca, Mg, and Mn (atomic absorption spectroscopy). Post-harvest soil was stored at 2 °C until analyzed - within one week. A subsample of soil was dried at 105 °C and moisture content was used to correct all weights to an oven dry basis. Attributes measured included: mineral N by 1.5 M KCl-extraction (Keeney and Nelson, 1987), mineral N after 30-day moist aerobic incubation in the dark (lab temperature is a constant 23 °C) (Bundy and Meisinger, 1994), bicarbonate-extractable P with quantification using molybdenum-blue chemistry (Olsen and Sommers, 1982), and immiscibly displaced Ca^{+2}, Mg^{+2}, K^{+}, Na^{+} (quantified by atomic absorption/emission spectroscopy) and ortho-P (quantified by ion chromatography) (Mubarek and Olsen, 1976). Immiscible displacement extracts solution-phase anions and cations. Derived metrics included the molar proportion of NH_4^{+} in mineral N and in 30-day mineralizable N. For each soil/vegetation type, changes in soil nutrient availability were quantified by calculating the percentage loss or gain of a particular nutrient relative the unplanted controls.

The experiment was completely randomized. To assure normality, some data were square root or log transformed. Using JMP® (Cary, North Carolina), post-harvest plant data and soil data from planted treatments were analyzed using a mixed effect ANOVA model with catagorical variables Plant (*B. tectorum*, *L. triticoides*), Soil/Vegetation Type (*K. lanata* invaded by *B. tectorum*, *K. lanata* non-invaded, and *A. tridentata*), and their interaction with replication within Soil/Vegetation Type and Plant as the random variable. Post-harvest soils data from unplanted controls was analyzed by ANOVA, with categorical variable Soil/Vegetation Type with replication within Soil/Vegetation Type as the random variable. Tukey's Honest Significant Difference test was used to compare means.

3. Results

3.1. Variation in plant biomass and root nutrient concentrations

At harvest, average aboveground biomass of *B. tectorum*, was 3.50 g (s.e. = 0.17), which greatly exceeded that of *L. triticoides* (2.14 g, s.e. = 0.09). Root mass was statistically similar among soil/vegetation types and plant species (Table 1); although *B. tectorum* root mass tended to be higher in the *B. tectorum* invaded soil and *L. triticoides* root mass tended to be higher in the *A. tridentata* soil (Table 2). Of all root nutrient concentrations quantified, only Ca was affected by a significant main effect due to soil/vegetation type; it was greatest for the *B. tectorum* invaded soil (Tables 1 and 2). Except

Table 1
ANOVA analyses for root weight and root nutrient concentrations.

Attribute	Soil/vegetation	Plant	Interaction
Root mass	0.8891	0.1331	0.2731
Nitrogen	0.2313	**0.0017**	0.3481
Carbon	0.3058	**<0.0001**	0.7053
Phosphorus	0.5820	**<0.0001**	0.7053
Calcium	**0.0156**	0.1710	0.0763
Magnesium	0.9593	**<0.0001**	0.6477
Potassium	0.5108	0.0933	0.5440
Manganese	0.1199	**<0.0001**	0.1877
Iron	0.9593	**<0.0001**	0.6278

Bolded numbers denote significant differences.