



Journal Menu

- Abstracting and Indexing
- Aims and Scope
- Article Processing Charges
- Articles in Press
- Author Guidelines
- Bibliographic Information
- Contact Information
- Editorial Board
- Editorial Workflow
- Free eTOC Alerts
- Subscription Information

- Open Special Issues
- Published Special Issues
- Special Issue Guidelines

Call for Proposals for
Special Issues

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Research Article

Plant-Soil Relationships of *Bromus tectorum* L.: Interactions among Labile Carbon Additions, Soil Invasion Status, and Fertilizer

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Abstract

Invasion of western North America by the annual exotic grass *Bromus tectorum* L. (cheatgrass) has been an ecological disaster. High soil bioavailability of nitrogen is a contributing factor in the invasive potential of *B. tectorum*. Application of labile carbon sources to the soil can immobilize soil nitrogen and favor native species. We studied the interaction of labile carbon addition (sucrose), with soil invasion status and fertilizer addition on the growth of *B. tectorum*. Soils were noninvaded (BNI) and *B. tectorum* invaded (BI). Treatments were control, sucrose, combined fertilizer, and sucrose + fertilizer. The greenhouse experiment continued for 3 growth-cycles. After the 1st growth-cycle, sucrose addition reduced *B. tectorum* aboveground mass almost 70 times for the BI soil but did not significantly reduce growth in the BNI soil. *B. tectorum* aboveground mass, after the 1st growth-cycle, was over 27 times greater for BI control soils than BNI control soils. Although sucrose addition reduced soil-solution NO₃⁻, tissue N was not significantly lowered, suggesting that reduction of soil available N may not be solely responsible for reduction in *B. tectorum* growth. Noninvaded soil inhibits growth of *B. tectorum*. Understanding this mechanism may lead to viable control strategies.

1. Introduction

Soil nutrient availability is a principal determinant in structuring plant communities [1–3] and if excessive, it can facilitate invasion by weedy plant species [4, 5]. Availability of inorganic soil N is especially robust in determining winners and losers in plant competitive outcomes [6, 7], and high availability can enhance the competitive potential of fast-growing weedy species over slower-growing species [4, 8]. One can cause local extirpation or proliferation of particular plants and alter plant seral stage through manipulation of soil N resources, either through the addition of a soluble N form or sequestration of soil N via the addition of a labile C source such as sucrose [9–12]. Our research unit and others have demonstrated that multiple sucrose additions over time to the soil can extirpate fast growing exotic annuals and thereby allow more nutrient use efficient native species to establish [12–15]. The underlying mechanism for this restoration strategy is that sucrose stimulates the proliferation of soil microorganisms, which uptake and immobilize soil inorganic N resources away from plants [12, 16]. In this lowered available soil N regime, plants with greater N use efficiency, such as native perennials, have an establishment window without undue competition from fast growing annuals [11, 17, 18]. This mechanism, however, may not hold in all situations [19]. Although labile C addition to soil has been shown to lower available N [15, 20], there is no definitive evidence that decreased availability of soil N is the sole or principal determinant controlling competitive outcomes among exotic annuals and native species. For example, ortho-P, rather than N availability, may control competitive interactions for diffuse knapweed (*Centaurea diffusa* L.) [21]. Moreover, the

-  Abstract
-  Full-Text PDF
-  Full-Text HTML
-  Linked References
-  How to Cite this Article

utility of using a labile C source such as sucrose in restoration of exotic grass-dominated communities has pitfalls. If desirable plants do not establish during the period of lowered N-availability, eventually microbial turnover may release a flush of available N and heighten risk of weed reinvasion. In addition, it is unclear if one can generalize that greater available soil N facilitates more growth of invasive annuals relative to native plants [22, 23]. Finally, we are unaware of any studies that have explored the possibility that labile C additions affect plant growth in other ways besides reduced N availability.

Invasion by exotic plants can fundamentally alter soil characteristics relative to those characteristics that evolved during pedogenesis under native vegetation. Biogeochemical cycling, the soil biotic community, and N dynamics may be so changed by plant invasion that the soil begins to follow a different pedogenic trajectory [24–27]. Cheatgrass (*Bromus tectorum* L.) is the most prevalent exotic invasive plant in the Great Basin of the western United States [28]. This annual grass forms tufts up to 2-feet (0.6 m) tall and can germinate in the fall or spring. *B. tectorum* has the potential to completely alter ecosystems by replacing native vegetation and fostering large-scale catastrophic wildfires. Moreover, invasion by *B. tectorum* disrupts food-webs, alters soil N dynamics, lowers species diversity, and decreases fungi populations [29, 30]. It is reasonable, then, to suspect that a particular soil invaded by *B. tectorum* for a period of time might respond differently to treatments such as addition of labile C and fertilizer than that same soil not invaded by *B. tectorum*. *Bromus tectorum* invasion increased porosity, altered soil organic matter dynamics, and enhanced microbial decomposition relative to noninvaded sites [31]. Given the potential of *B. tectorum* to alter soil properties, a reasonable conjecture is that long-term invaded soil may function differently as a growth media than noninvaded sites.

Since 1998, we have monitored an invasion of a winterfat (*Krascheninnikovia lanata* (Pursh) A.D.J. Neeuse & Smit) community by *B. tectorum* in the Honey Lake Valley of northeastern California. New colonizations, spreading from the invasion front, are small and widely spaced and often recruit in the canopy of *K. lanata*. At the same time, in adjacent areas that have been invaded for several years, plants of *B. tectorum* are far larger and denser. It is only in the 2nd and 3rd years of invasion that plant stature increases markedly and plants become more prevalent in interspace positions. From these observations, it appeared that there was a soil factor in noninvaded areas that was inhibiting initial populations of *B. tectorum* and that the inhibitory factor was muted upon invasion. The previous observations are consistent with the “biological inertia” theory of plant community invasibility [32]. Based on these observations and previous research the following null hypotheses were proposed for testing.

- (1) Immobilization of N, upon sucrose addition, is the controlling factor in the reduction of *B. tectorum* growth.
- (2) Growth of *B. tectorum* will be alike in soils invaded by *B. tectorum* for several years relative to a similar soil not yet invaded.

2. Materials and Methods

Soil was collected from a winterfat (*Krascheninnikovia lanata* (Pursh) A.D.J. Neeuse & Smit) community in the Honey Lake Valley of northeastern California, USA (40°08'N, 120°04'W) that is presently being invaded by cheatgrass (*Bromus tectorum* L.). The A horizon (0–20cm) was collected from shrub interspace microsites at 2 sites from an area that has been invaded by *B. tectorum* for at least 4 years (BI) and a nearby noninvaded area (BNI). General properties of soils, taken from a contemporaneous research project at the same study site, are provided in Table 1. Values are average of 4 samples taken throughout the year. Textural class was determined by hand texturing. Organic C quantified after removal of CaCO₃ with acid. Available N is NO₃⁻ and NH₄⁺ extracted with KCl [33]. Net N mineralization was determined by the difference of total N after 30-day moist aerobic incubation minus that initially present. At each site, soil was obtained by compositing over 100 subsamples from an area of about 100m². The two disturbed soils were transported to the greenhouse, homogenized, and immediately filled into tapered containers (15cm upper diameter, 13.5cm lower diameter, 16cm depth, 3kg for each soil type). Treatments were “control” (only planted and watered), “sucrose” (20g applied to the soil surface), “fert”, and “sucrose + fert”. Fert was applied as 80mL of aqueous solution containing 4.6g N as ammoniacal-N (23%), nitrate-N (22%), and urea-N (55%). Five seeds of *B. tectorum* were sown near the center of each container, and germinating seeds plucked to allow only one to grow. Soil was kept near field capacity with deionized water but watered sparingly to avoid leaching. Aboveground and root mass were harvested after 72-day growth, the soil homogenized, and a 10g subsample from each container was reserved for soil analyses. Containers were refilled with the same soil, sown with multiple seeds of *B. tectorum* as before, and grown and harvested for 2 more times. In the 2nd and 3rd growth-cycles, also 72-day total growth, no sucrose was added but fertilizer was added at the same rate. After each harvest, the following parameters were measured: (1) aboveground mass and root mass after drying 48 hours at 60°C, (2) leaf tissue N concentration by the Kjeldahl procedure, and (3) soil-solution concentration of NO₃⁻, and acetate by immiscible displacement [34] with quantification by gradient elution ion chromatography with suppressed conductivity detection. We also randomly collected 4 replicate A horizon samples from BI and BNI areas and sent to a commercial laboratory for microbial characterization by phospholipid fatty acids (PLFA). At the time samples were collected, BI sites had been invaded for at least 4 years. PLFA characterizes the entire microbial community including viable biomass concentrations, community composition, and metabolic status [35].

Table 1: Initial properties of the soils.

The greenhouse experiment was completely randomized as pots were periodically moved through the course of the experiment. The ANOVA was a mixed model with repeated measures on growth-cycle and random error term of pot within soil and treatment [36]. The experiment had 6 replicates \times 2 soil invasion types (BNI and BI), \times 4 treatments (control, sucrose, fert, sucrose + fert) \times 3 growth-cycles = 144 total pots. Data normalization required transformation of some variables. Confidence intervals at the 95% level were derived for the highest order significant ($P \leq .10$) interactions. Initial soil and PLFA data were analyzed using an unpaired t -test.

3. Results

3.1. Initial Properties of Soils

Soil occupied by *B. tectorum* (BI) for at least 4 years was grossly similar in properties to soil not yet invaded (BNI) (Table 1). BI soil had higher concentrations of C and N, but the C/N was very similar between the two soils. BI soil had a lower pH than BNI soil. BNI and BI soil had very similar N availability and net N mineralization potentials.

After 4-year invasion by *B. tectorum*, the soil microbial community has been considerably altered as elucidated by phospholipid fatty acids (PLFAs). BI soil has significantly greater total microbial biomass, eukarya biomass, and a greater ratio of bacteria to eukarya than BNI soil (Table 2).

Table 2: Selected results of PLFA analyses for BNI and BI soils.

3.2. Plant Parameters

An interaction among treatment, soil invasion status, and growth-cycle influenced aboveground ($P = .0005$) and root mass ($P = .0652$) of *B. tectorum* (Table 3). In the 1st growth-cycle, aboveground mass of *B. tectorum* grown in controls was over 27 times less in the BNI soil relative to the BI soil. Overall, this growth differential was reduced in the 2nd growth-cycle and could be partially overcome by addition of fertilizer, especially in the 3rd growth-cycle. For the BNI soil only, sucrose addition did not significantly reduce aboveground or root mass of *B. tectorum* relative to the controls. Soil treatments had a large impact on *B. tectorum* growth in the BI soil. Relative to the BI controls, sucrose addition negatively affected *B. tectorum* growth for the 1st growth-cycle only; aboveground mass was reduced over 68 times and root mass was reduced over 56 times. The sucrose + fert treatment produced similar, albeit less, decline in plant mass relative to the controls, reducing aboveground mass over 14 times and root mass over 18 times. Following the 2nd and 3rd growth-cycles, aboveground and root mass of *B. tectorum* were statistically similar between sucrose amended and control soils. The sucrose + fert treatment, however, resulted in much higher growth after the 2nd cycle than the corresponding controls; aboveground mass was over 40 times greater for the BNI soil and over 3 times greater for the BI soil. This significant trend continued after the 3rd growth-cycle, but differences were lower. Growth of *B. tectorum* tended to be higher upon fertilizer additions relative to controls; but significant increases in aboveground and root biomass only occurred after the 2nd growth-cycle for the fert treatment and only for the BNI soil.

Table 3: Influence of treatment, soil invasion status, and growth-cycle on *B. tectorum* growth and leaf N concentration.

Leaf N concentration was affected by significant soil \times growth-cycle and treatment \times growth-cycle interactions (Table 3). For all growth-cycles, control and sucrose treatments have statistically similar leaf N concentrations. For both soils, the sucrose + fert treatment significantly increased tissue N concentration for all growth-cycles relative to the corresponding controls. For the 1st growth-cycle, fertilizer additions did not affect tissue N concentration relative to the control. Relative to controls, the fertilizer treatment significantly increased tissue N concentration after the 2nd and 3rd growth-cycles.

3.3. Soil Parameters

Treatment \times soil \times growth-cycle interaction significantly affected soil-solution NO_3^- concentration (Table 4). After the 1st growth-cycle, NO_3^- was significantly less in the BNI soil for every treatment except sucrose and sucrose + fert compared to the corresponding BI treatments. This response pattern continued after the 2nd growth-cycle except that NO_3^- was now statistically similar to the fert treatment. After the 3rd growth-cycle, soil-solution NO_3^- was statistically similar between BI and BNI soils for all treatments, except for the fert treatment. Sucrose addition caused a significant decline in soil-solution NO_3^- relative the control, but only for the BI soil after the 1st growth-cycle, although there was a strong trend lower for both BI and BNI soil after the 2nd growth-cycle (Table 4). Except for the BNI soil after the 1st growth-cycle, the fert application rate significantly increased soil-solution NO_3^- for both soils and all growth-cycles, relative to controls. Acetate in the soil-solution was influenced by a treatment main effect (Table 4). Soil-solution acetate concentration was significantly greater for the sucrose and sucrose + fert treatment compared to the other treatments.

Table 4: Influence of treatment, soil invasion status, and growth-cycle on soil-solution nitrate and acetate.

4. Discussion

In this container experiment, growth of *B. tectorum* was strongly affected by treatment, growth cycle, and whether the soil was not yet invaded or invaded for about 4 years by *B. tectorum*. Myriad traits contribute to the competitive stature of plants and considerable effort has been expended to decipher those traits most predictive of invasive success [37, 38]. A robust predictor of invasion success for some plants is rapid growth during the seedling stage [39]. Thus, the huge variability of *B. tectorum* growth brought about by sucrose addition, fertilizer addition, and if the soil was previously invaded has enormous ecological significance for its potential control.

In the 1st growth cycle following sucrose addition to a soil previously invaded by *B. tectorum* (BI), aboveground mass of *B. tectorum* was reduced, an astonishing 98 percent relative to the control soil. The magnitude of growth reduction of this invasive annual grass is illustrative of why labile carbon sources have been tested in the field as a potential tool to restore invaded rangelands in the western United States [40]. The fact that the growth reduction properties of sucrose were lost after the 1st growth cycle vividly displays that sucrose addition to control invasive weeds like *B. tectorum* has a very short window of efficacy. It is generally assumed that sucrose and other labile C sources stimulate microbial activity and immobilize mineral N [16, 41, 42]. Moreover, all references that we are aware of implicate this decrease in available soil N as the causative factor in explaining how labile C sources extirpate fast growing exotic annuals from ecosystems [9, 10, 12, 15]. In the present study, we do not dispute that a major cause in the reduction in *B. tectorum* upon sucrose addition is a consequence of reduced availability of N. Indeed, after the 1st growth cycle, leaf N of *B. tectorum* grown in sucrose-amended soil was much less than that of *B. tectorum* grown in control soil. Our data, however, suggest that the sucrose addition causes additional reduction in *B. tectorum* growth via another mechanism, thus forcing rejection of hypothesis 1. Firstly, after the 2nd and 3rd growth-cycles, *B. tectorum* growth in sucrose-amended soil was statistically similar to controls; yet soil-solution NO_3^- was considerably less than in the control soils. These findings suggest that although soil-solution pools of NO_3^- are likely suboptimal for maximal growth in the sucrose amended soils, *B. tectorum* was still able to acquire N in similar concentrations as plants grown in the control soils. Secondly, in the 1st growth-cycle, sucrose + fert addition to the BI soil significantly reduced the growth of *B. tectorum* and depressed levels of NO_3^- in the soil-solution, compared to the corresponding controls; yet, tissue N concentration was statistically greater. Clearly, *B. tectorum* was able to access a portion of the added N fertilizer, but it did not aid its growth.

What mechanisms, beside immobilization of available N, could reduce *B. tectorum* growth in sucrose-amended soil? There are myriad interactions with the soil microbial community when a labile C source such as sucrose is added [16]. Organisms capable of utilizing a particular substrate proliferate [43]. These organisms in kind may produce secondary metabolites that can negatively affect plant growth [44]. We suspect that sucrose addition stimulates production of an inhibitory factor that retards the growth of *B. tectorum*. One possibility is that production of acetate and other metabolites of fermentation, typical of sucrose-amended soil [45], hinders *B. tectorum* growth. Fermentation metabolites have been shown to retard root elongation and inhibit root initiation [46, 47]. Data from our study indicate a strong relationship between sucrose addition and acetate levels in the soil-solution after the 1st growth cycle (Table 4). Moreover, at least for the 1st growth cycle, the greatest concentrations of acetate corresponded to the greatest reduction in *B. tectorum* growth (Tables 3 and 4).

Soil invasion status significantly influenced *B. tectorum* growth therefore forcing rejection of null hypothesis 2. After the first, second, and third growth cycles, respectively, *B. tectorum* aboveground mass in BNI control soil was 96, 92, and 59 percent less than in the BI control soil. Given the similarity in initial soil properties (Table 1) and that both soils were collected from a similar pre-existing plant community, the growth dichotomy is perplexing. Invasive plants are known to increase soil nutrient availability, particularly N [48]. Long-term occupation of a soil by *B. tectorum* may have altered or "engineered" the soil to mineralize N at a faster rate than a similar soil initially planted to *B. tectorum*. Indeed, BI soil has far greater microbial biomass and a greater proportion of eukarya to bacteria than does BNI soil (Table 2). Perhaps the greater abundance of microbes in the BI soil fosters greater availability of N through elevated mineralization. Elevated availability of N greatly increases *B. tectorum* growth [3, 49], and under most treatments in this study, availability of N was greater for the BI soil (Table 3). If available soil N was the sole factor explaining the dichotomy in *B. tectorum* growth between the BI and BNI soil, then why did not addition of fertilizer N to the BNI soil in the 1st growth cycle overcome any potential N deficiency? Furthermore, the C/N ratios of both soils are similar and quite low (Table 1) suggesting that N will be available for plant growth as mineralization occurs. As an alternative hypothesis, we propose that soil not yet invaded by *B. tectorum* has an inhibitory factor. Moreover, this suspect inhibitory factor decreases as time of occupation by *B. tectorum* increases (Table 3). Our hypothesis is consistent with the Von Holle et al. [32] theory of "biological inertia," which may involve allelopathic chemicals released by the native community thereby suppressing invading plants. Apparently this suspect inhibitory factor in the BNI soil can be mediated by a combination of sucrose + fertilizer as witnessed by the large increase in *B. tectorum* biomass in the 2nd growth-cycle (Table 3). Such a response suggests that sucrose addition may have encouraged the growth of microorganisms that lessened (decomposed?) the inhibitory factor (see [50] e.g.). At this time, however, we lack

If noninvaded soil is, at least initially, inhibitory to *B. tectorum*, how does it establish? One possibility is that initial populations of *B. tectorum* albeit small in stature and widely spaced facilitate alteration of the soil such that the factor(s) responsible for growth inhibition is reduced or eliminated. Invasion by *B. tectorum* has been shown to alter soil microbial communities and soil food webs relative to what occurs under native species [30]. Greater understanding of the inhibitory effect of fresh noninvaded soil and the pathways by which invasion decreases the inhibitory factor(s) may offer new avenues for control for *B. tectorum* and other invasive plants.

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