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RESEARCH ARTICLE

Effects of water additions, chemical amendments, and plants on in situ measures of nutrient bioavailability in calcareous soils of southeastern Utah, USA

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Abstract We used ion-exchange resin bags to investigate effects of water additions, chemical amendments, and plant presence on in situ measures of nutrient bioavailability in conjunction with a study examining soil controls of ecosystem invasion by the exotic annual grass *Bromus tectorum* L. At five dryland sites in southeastern Utah, USA, resin bags were buried in experimental plots randomly assigned to combinations of two watering treatments (wet and dry), four chemical-amendment treatments (KCl, MgO, CaO, and no amendment), and four plant treatments (*B. tectorum* alone, the perennial bunchgrass *Stipa hymenoides* R. & S. alone, *B. tectorum* and *S. hymenoides* together, and no plants). Resin bags were initially buried in September 1997; replaced in January, April, and June 1998; and removed at the end of the study in October 1998. When averaged across watering treatments, plots receiving KCl applications had lower resin-bag NO_3^- than plots receiving no chemical amendments during three of four measurement periods—probably due to NO_3^- displacement from resin bags by Cl^- ions. During the January–April period, KCl application in wet plots (but not dry plots) decreased resin-bag NH_4^+ and increased resin-bag NO_3^-. This interaction effect likely resulted from displacement of NH_4^+ from resins by K^+ ions, followed by nitrification and enhanced NO_3^- capture by resin bags. In plots not receiving KCl applications, resin-bag NH_4^+ was higher in wet plots than in dry plots during the same period. During the January–April period, resin-bag measures for carbonate-related ions HPO_4^{2-}, Ca^{2+}, and Mn^{2+} tended to be greater in the presence of *B. tectorum* than in the absence of *B. tectorum.* This trend was evident only in wet

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plots where *B. tectorum* densities were much higher than in dry plots. We attribute this pattern to the mobilization of carbonate-associated ions by root exudates of *B. tectorum*. These findings indicate the importance of considering potential indirect effects of soil amendments performed in conjunction with resource-limitation studies, and they suggest the need for further research concerning nutrient acquisition mechanisms of *B. tectorum*.

Keywords *Bromus tectorum* · Ion-exchange resin bags · Nutrient dynamics · Phosphorus · Potassium · *Stipa hymenoides*

Introduction

The vast majority of studies investigating soil-resource patterns in dryland ecosystems have focused on soil–water relations (Ehleringer et al. 2000). Comparatively little is known about dynamics and plant acquisition of mineral nutrients in drylands despite recognition that the nutrient status of soils can affect the structure and functioning of water-limited ecosystems (McClendon and Redente 1992; Bilbrough and Caldwell 1997; Havstad et al. 2000; Bowker et al. 2005). Soil-moisture status and nutrient uptake are not independent (Barber 1995; Marschner 1995), and effects of low soil moisture on nutrient availability to plants may be as significant as direct effects of water stress on plant performance (Chapin 1991). After reviewing the literature on resource limitations in dryland ecosystems, Hooper and Johnson (1999) concluded that there was no evidence for a shift from water to nutrient limitation along a geographic gradient of increasing water availability. Instead, their review supported the hypothesis that water and N generally are co-limiting in most dryland systems.

In efforts to understand the nature and degree of nutrient limitations in dryland ecosystems, fertilization experiments have become increasingly common. For example, Drenovsky and Richards (2004) combined water additions with additions of N (NH_4NO_3) and P (NaH_2PO_4) to determine whether foliar N–P ratios could be used to predict nutrient limitations in desert shrubland species. Schwinning et al. (2005) fertilized desert grasslands with N compounds ($(NH_4)_2SO_4$ in KCl solution, and KNO_3) to evaluate potential ecosystem responses to atmospheric N deposition. James et al. (2005) applied N and K (KNO_3), P (P_2O_5), Mg ($MgSO_4$), and Ca ($CaSO_4$) to evaluate nutrient limitations in a desert shrubland community. Each of these studies found significant responses to the chemical amendments that were applied, and results were interpreted in a straightforward manner as direct effects of nutrient additions or as combined effects of nutrient and water additions.

In these and other studies involving the manipulation of soil resources, relatively little attention has been devoted to evaluating treatment effects on in situ measures of nutrient status or bioavailability. This is surprising, given the potential for complex indirect effects of chemical amendments on soil equilibria involving ion-exchange processes, sorption–desorption reactions, and dissolution–precipitation reactions (Sparks 1995). Interpretations of experimental results and inferences concerning the nature of resource limitations in some cases may be confounded by biotic responses to indirect effects of experimental manipulations (DiTommaso and Aarssen 1989).

With this in mind, we investigated effects of resource manipulations that were conducted to examine soil controls of ecosystem invasion by the exotic annual grass *Bromus tectorum* L. in drylands of southeastern Utah, USA (Miller et al., in press). We used ion-exchange resin bags (Binkley and Matson 1983; Lajtha 1988; Lundell 1989) to characterize effects of water additions and chemical amendments (applications of KCl, MgO, and CaO) on in situ nutrient bioavailability over a 1-year period. We hypothesized that chemical amendments would affect dynamics of non-target nutrients such as N, that treatment effects on resin-bag measures would vary seasonally, and that effects would be influenced by the presence and identity of plants located in experimental plots.

Methods

Study area

Resin-bag studies were conducted in a 2000-ha area in the southern portion of Canyonlands National Park (CNP) in southeastern Utah, USA. The study area is characterized by an arid climatic regime, with mean annual precipitation 215 mm and mean annual temperature 11.8°C between 1965 and 2001. During the period from September 1997 through October 1998, resin bags were used to investigate in situ patterns of nutrient bioavailability at five of 17 CNP sites used in studies of the annual C_3 grass *Bromus tectorum* L. and the perennial C_3 grass *Stipa hymenoides* R. & S. (Miller 2000; Miller et al., in press). Study sites measured approximately 40 m × 40 m and were selected to represent a range of soil characteristics and *B. tectorum* abundance. Sites were vegetated by sparse grassland communities, with total live plant cover ranging from 14 to 23% at the time of site selection in January 1997. All sites were located at approximately 1550 m in elevation, aspects varied, and slopes ranged from 2 to 5%. Study area landscapes are physically dominated by sedimentary rock formations consisting primarily of Permian-aged aeolian sandstones cemented by $CaCO_3$, and a fundamental characteristic of area soils is the presence of inherited carbonate compounds. Soils at three of the five sites were classified as coarse-loamy, mixed, mesic Ustollic Camborthids (fine sandy loams of the Begay series). Soils at the remaining two sites were classified as mixed, mesic Typic Torripsamments (loamy fine sands of the Sheppard series) (USDA Soil Conservation Service 1991).

Experimental treatments

At each of the five study sites, 24 circular *S. hymenoides*-centered plots measuring 1.2 m in diameter were established (16 in January 1997 and eight in September 1997). Plots were selected subjectively to contain *S. hymenoides* clones of similar size. All litter and plants except for the center *S. hymenoides* were removed by hand, and plots were caged with fencing to exclude vertebrates. Plots were assigned randomly to one of 24 treatment combinations consisting of three experimental factors—plants, chemical amendments, and water additions. Plant treatments consisted of (1) a single *S. hymenoides* clone grown in monoculture, (2) *B. tectorum* grown in monoculture, (3) *S. hymenoides* and *B. tectorum* grown together in mixture, and (4) no plants. In plots assigned to have *B. tectorum* alone or no plants, center *S. hymenoides* clones were removed by hand in January or September 1997. In plots assigned to the *B. tectorum* alone or mixture treatments, 1150 *B. tectorum* seeds (~2300 seeds/m^2) were mixed by hand in the top 1–2 cm of soil of the plot interior (0.8 m diameter) in September 1997. This seeding density was selected to approximate the maximum density of *B. tectorum* in the study area. Chemical amendments included (1) KCl (applied in solution at rate of 15 g per m^2 on 29–30 September 1997, 28 October 1997, 4 March 1998, and 2 April 1998), (2) CaO (applied in powder form at rate of 34.6 g per m^2 on 24 September 1997 and 2 March 1998), and (3) MgO (applied in powder form at rate of 25.0 g per m^2 on 24 September 1997 and 2 March 1998). These amendments were selected because of hypothesized effects of K availability and soil carbonate compounds (through effects on availability of P and micronutrients) on performance and spatial patterns of *B. tectorum* in the study area (Miller et al., in press). Calcium oxide and MgO were used rather than $CaCO_3$ and $MgCO_3$ because the former two compounds are more reactive than the latter two, although both the oxide and the carbonate forms first react in the soil to produce bicarbonate compounds (e.g., $Ca(HCO_3)_2$) (Brady and Weil 1996). Both CaO and MgO were used because we hypothesized that MgO would be more reactive in soils than CaO due to higher concentrations of Ca^{2+} than Mg^{2+} in CNP soils. The water treatment consisted of two levels, here referred to as ''wet'' and ''dry'' (Fig. 1). ''Wet'' plots were watered by hand biweekly from 1 October through 15 November, and again from 1 March through 15 May at rates that approximated 1.5–2.0 times the average amount of precipitation when combined with ambient precipitation levels. ''Dry'' plots also were watered biweekly or monthly in an effort to attain the average amount of precipitation. Even

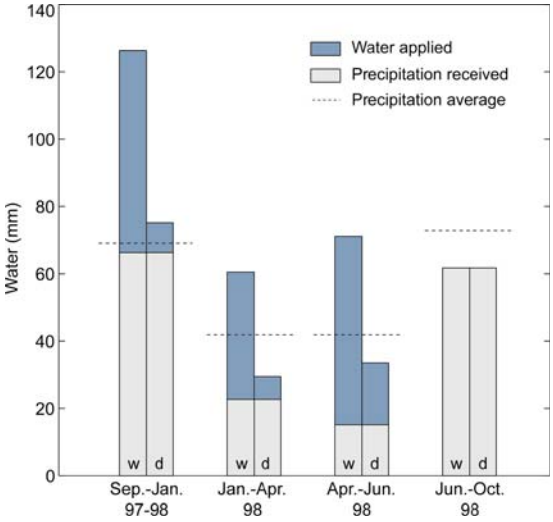


Fig. 1 Total water applied and precipitation received in wet (w) and dry (d) plots in comparison with average precipitation levels during the course of the study

with watering, dry plots received less than the average amount of precipitation over the course of this study. All treatments were crossed with one another with the exception of plots receiving CaO and MgO applications, which were assigned to the drier of the two watering treatments. At the end of the growing season in June 1998, aboveground *B. tectorum* biomass was harvested from plots seeded with *B. tectorum* in the previous fall. Treatment effects on *B. tectorum* performance are presented and discussed by Miller et al. (in press).

Soil measures

Soils were characterized by analyses conducted on composite samples collected systematically from 0 to 10 cm at each study site with a 2.4-cm soil probe (30 subsamples per site) or an 8-cm bucket auger (10 subsamples per site). Soils were air dried and analyzed for pH (saturated paste extract); cation exchange capacity (CEC); organic matter (OM) content (Walkley and Black method); total Kjeldahl N; $NaHCO_3$-extractable P (P-Bicarb); amounts of micronutrients Mn, Fe, Cu, and Zn extractable with diethylenetriaminepentaacetic acid (Mn-Dtpa, Fe-Dtpa, Cu-Dtpa, and Zn-Dtpa); and amounts of exchangeable cations Ca^{2+}, Mg^{2+}, K^+, and Na^+ extractable with NH_4OAc buffered to pH 8.5 (Ca-Ex, Mg-Ex, K-Ex, and Na-Ex). Soil acid-neutralizing potential (ANP) was determined following the acid-neutralizing method of carbonate analysis (Allison and Moodie 1965), and carbonate content was determined gasometrically with a Chittick apparatus (Dreimanis 1962). Gypsum content was determined by the crystal water-loss method (Nelson 1982). The particle-size distribution of each composite sample was measured with a Malvern laser particle sizer following removal of carbonates and organic material by acid digestion.

Soil nutrient status also was characterized on the basis of laboratory extractions performed with ion-exchange resins (Skogley et al. 1990; Yang et al. 1991). All macronutrient ions K^+, HPO_4^{2-}, NH_4^+, NO_3^-, Ca^{2+}, Mg^{2+}, SO_4^{2-}, and micronutrient ions Mn^{2+}, Zn^{2+}, Fe^{2+}, and Cu^{2+} were extracted simultaneously from soils with mixed-bed (cation + anion) ion-exchange resin capsules manufactured by Unibest, Inc., Bozeman, Montana, USA. Each resin capsule consists of a 2-cm-diameter spherical ball with 4 ml of mixed-bed resin beads (H^+–OH^- saturated) contained within a plastic screen mesh. Capsule surface area is approximately 11.4 cm^2. For each sample, water and 50 g of dry soil were mixed to form a saturated paste, and a resin capsule was inserted into the center of the paste. After a 7-day incubation period, capsules were removed and washed free of all soil particles with a directed stream of deionized water. Adsorbed ions were stripped by placing the capsule in a small container with 20 ml of 2 M HCl and shaking on a reciprocal shaker for 20 min. The solution was collected, and the process repeated two additional times, yielding 60 ml of solution for analyses. Solution concentrations of all ions, with the exception of NH_4^+ and NO_3^-, were measured simultaneously by inductively coupled plasma (ICP) atomic emission spectroscopy. Ammonium and NO_3^- were recovered separately in a H_3BO_3 indicator solution by steam distillation with MgO and Devarda alloy, and were determined by titration with H_2SO_4 (Keeney and Nelson 1982). Ion concentrations are reported as μmol_c capsule^{-1} (Table S1, electronic supplemental material). Total exchange capacity is approximately 13,000 μmol_c capsule^{-1}.

Resin-bag measures

Effects of KCl applications, water applications, and plants on in situ bioavailability of NH_4^+, NO_3^-, K^+, HPO_4^{2-}, Ca^{2+}, and Mn^{2+} were measured with ion-exchange resin bags (Binkley and Matson 1983; Gibson et al. 1985; Lajtha 1988; Lundell 1989; Asner and Beatty 1996). Bags were made by placing 10 g of moist, mixed-bed ion-exchange resins (Sigma Dowex MR-3, H–OH form) in 70-cm^2 nylon-mesh tubes cut from undyed nylon stockings. Tube ends were closed with 10-cm plastic cable ties and excess materials were trimmed. Bags were cleaned and resins converted to H–Cl form by two 30-min shakes in 1 M HCl followed by one 30-min rinse with deionized water. Bags were spun dry in a hand centrifuge and stored in sterile plastic bags until placement.

In each experimental plot, four bags were buried 5–10 cm beneath the soil surface approximately 25 cm from plot centers, with one bag in each of the four intercardinal quadrants. Bags were placed initially in September 1997, and replaced in mid-January 1998, early April 1998, and late June 1998. The last set of bags was removed in early October 1998. Upon collection from the field, the four bags from each plot were placed in a single sterile bag and refrigerated until analysis. In the lab, bags were rinsed with deionized water to remove roots and soil particles, and the four bags collected from each plot were desorbed as a single composite sample by shaking together in 150 ml of 2 M HCl for 1 h. The solution was filtered, and concentrations of all ions with the exception of NH_4^+ and NO_3^- were measured simultaneously by ICP. Ammonium and NO_3^- were recovered and determined following methods described above for resin capsules. Results are reported as ion-adsorption rates in μmol$_c$ bag^{-1} 100 days^{-1} and interpreted as indices of in situ nutrient bioavailability. Based on per-unit-mass values reported by the manufacturer, total exchange capacity was approximately 17,000 μmol$_c$ bag^{-1}. To compare with post-deployment data from resin bags recovered from the field, background ion concentrations on a set of resin bags (n = 5) were measured after treatment with HCl following the same methods for ion desorption and determination.

Data analyses

Effects of watering treatments and KCl applications on seasonal resin-bag measures of NH_4^+, NO_3^-, and K^+ were analyzed in a factorial 2-way, fixed-effects, multivariate analysis of variance (MANOVA) design (Scheiner 1993; Underwood 1997). The same design was used to analyze for effects of plants and watering treatments on resin-bag measures of NH_4^+, NO_3^-, K^+, HPO_4^{2-}, Ca^{2+}, and Mn^{2+}. In both cases, preliminary analyses indicated that there were no interactions of soil type (relatively sandy versus relatively loamy soils) with effects of plants, watering treatments, or KCl applications on resin-bag measures. Data on among-soil patterns in resin-bag measures are presented and discussed by Miller et al. (in press). Following MANOVA, Tukey's honestly significant difference (HSD) post hoc procedure was used to test for differences among levels of factors with significant main or interactive effects (Zar 1999). All statistical analyses were conducted using STATISTICA^{TM} v5.5 on a PC platform (StatSoft 1999). Because of the relatively small sample sizes and large numbers of variables evaluated with the MANOVA procedure, P-values less than 0.10 were considered statistically significant. Applications of MgO and CaO had no detectable effects on any resin-bag measures, and results of these analyses are not presented here.

Results

Soil properties

Shallow study area soils (0–10 cm depth) were calcareous loamy fine sands and fine sandy loams with sand contents ranging from 77.3 to 89.0% by mass (mean = 83.2%). Carbonate contents ranged from 5.0 to 6.5% $CaCO_3$ equivalent by mass (mean = 5.7%), pH ranged from 8.2 to 8.4 (mean = 8.1), OM content ranged from 0.14 to 0.39% (mean 0.3%), and CEC ranged from 3.0 to 8.7 cmol$_c$ kg^{-1} soil (mean 5.7 cmol$_c$ kg^{-1} soil; Table S1, electronic supplemental material). Resin-capsule data indicated that Ca^{2+} was the most abundant cation in the soil environment, with a mean value (1046.5 μmol$_c$ capsule^{-1}) that was more than 10 times higher than the mean value (97.7 μmol$_c$ capsule^{-1}) of Mg^{2+}. Together, these two accounted for approximately 94% of measured cation charges.

Effects of KCl and water applications on seasonal measures of N and K bioavailability

Main effects of added KCl (Wilk's lambda = 0.32, $F = 11.67$, effect df = 12, error df = 65, $P < 0.01$) and interactive effects of KCl and water (Wilk's lambda = 0.64, $F = 3.10$, effect df = 12, error df = 65, $P < 0.01$) were significant for resin-bag measures of NH_4^+, NO_3^-, and K^+ adsorption rates. Main effects of water applications were statistically insignificant ($P = 0.19$). In plots treated with KCl, K^+ levels on resin bags were greater during the January–April period (mean ± 1 SE = 12.85 ± 0.80 μmol$_c$ bag^{-1} 100 days^{-1}, $P < 0.001$) and the June–October period (10.64 ± 1.11 μmol$_c$ bag^{-1} 100 days^{-1}, $P < 0.001$) than in plots that received no chemical amendments (4.98 ± 0.28 μmol$_c$ bag^{-1} 100 days^{-1} and 3.18 ± 0.27 μmol$_c$ bag^{-1} 100 days^{-1} during the January–April and June–October periods, respectively). During the June–October period, NH_4^+ levels on resin bags also were higher in plots receiving KCl treatments (43.09 ± 2.20 μmol$_c$ bag^{-1} 100 days^{-1}, $P = 0.04$) than in plots receiving no chemical amendments (37.79 ± 1.38 μmol$_c$ bag^{-1} 100 days^{-1}). NO_3^- levels on resin bags were lower in KCl-treated plots than in control plots during the September–January period (4.77 ± 0.48 versus 7.06 ± 0.59 μmol$_c$ bag^{-1} 100 days^{-1}, $P = 0.004$), the April–June period (4.10 ± 0.39 versus 5.72 ± 0.47 μmol$_c$ bag^{-1} 100 days^{-1}, $P = 0.01$), and the June–October period (3.39 ± 0.39 versus 5.37 ± 0.75 μmol$_c$ bag^{-1} 100 days^{-1}, $P = 0.02$).

Water and KCl applications had interactive effects on resin-bag measures of NH_4^+ and NO_3^- during the January–April period (Fig. 2). Wet plots with KCl applications had significantly lower NH_4^+ adsorption rates ($P = 0.01$) than dry plots with KCl applications. The opposite was true for NO_3^-, with higher adsorption rates in wet plots treated with KCl than in dry plots treated in KCl ($P < 0.01$).

Effects of water applications and plants on seasonal measures of N, K, P, Ca, and Mn bioavailability

Water (Wilk's lambda = 0.39, $F = 3.14$, effect df = 24, error df = 49, $P < 0.001$) and plants (Wilk's lambda = 0.21, $F = 1.40$, effect df = 72, error df = 147, $P = 0.04$) both had significant effects on seasonal measures of nutrient bioavailability, but the interaction between these two factors was statistically insignificant ($P = 0.43$). During the September–January period, NH_4^+ adsorption rates were lower in wet plots than in dry plots ($P = 0.06$), and mean NH_4^+ values for field-deployed resin bags were lower than background concentrations measured on resin bags that were never buried in plots (Fig. 3). During the January–April period, NH_4^+ adsorption rates were higher in wet plots than in dry plots ($P = 0.06$). The opposite pattern was observed for resin-bag measures of NO_3^- and K^+ during the same period. Although differences between wet and dry plots were statistically insignificant for these ions, there was a tendency for lower NO_3^- ($P = 0.14$) and lower K^+ ($P = 0.12$) adsorption on resin bags in wet plots relative to dry plots (Fig. 3). During the April–June period, K^+ adsorption on resin bags in wet plots was significantly greater than in dry plots ($P = 0.03$), and there was no effect of water treatment on NH_4^+($P = 0.61$) and NO_3^- ($P = 0.92$). Post hoc analyses indicated that the watering treatment did not have significant effects on seasonal measures of HPO_4^{2-}, Ca^{2+}, and Mn^{2+} on resin bags.

Plant effects on resin-bag measures of nutrient bioavailability were statistically significant only for Ca^{2+} during the January–April period (Fig. 4). During this period, Ca^{2+} levels on resin bags in plots with *B. tectorum* alone were significantly greater than in plots with *S. hymenoides* alone ($P = 0.096$), and they tended to be greater than in plots with no plants. Plant effects were statistically insignificant for seasonal measures of NH_4^+, NO_3^-, K^+, HPO_4^{2-}, and Mn^{2+}, but January–April trends for HPO_4^{2-}, Mn^{2+}, and Ca^{2+} were similar (Fig. 4). During this period, resin-bag measures for these ions all tended to be greater in plots with *B. tectorum* alone and with *B. tectorum* and

Fig. 2 Interactive effects of added water and KCl on seasonal NH_4^+, NO_3^-, and K^+ adsorption rates (means ± 1 SE) in plots at Canyonlands field sites from Sep. 1997 through Oct. 1998 (*n* = 20 plots per point). Within each sampling period, treatment means identified by different letters were significantly different by Tukey's HSD multiple-comparison test. Dashed horizontal lines indicate mean background concentrations of ions on resin bags

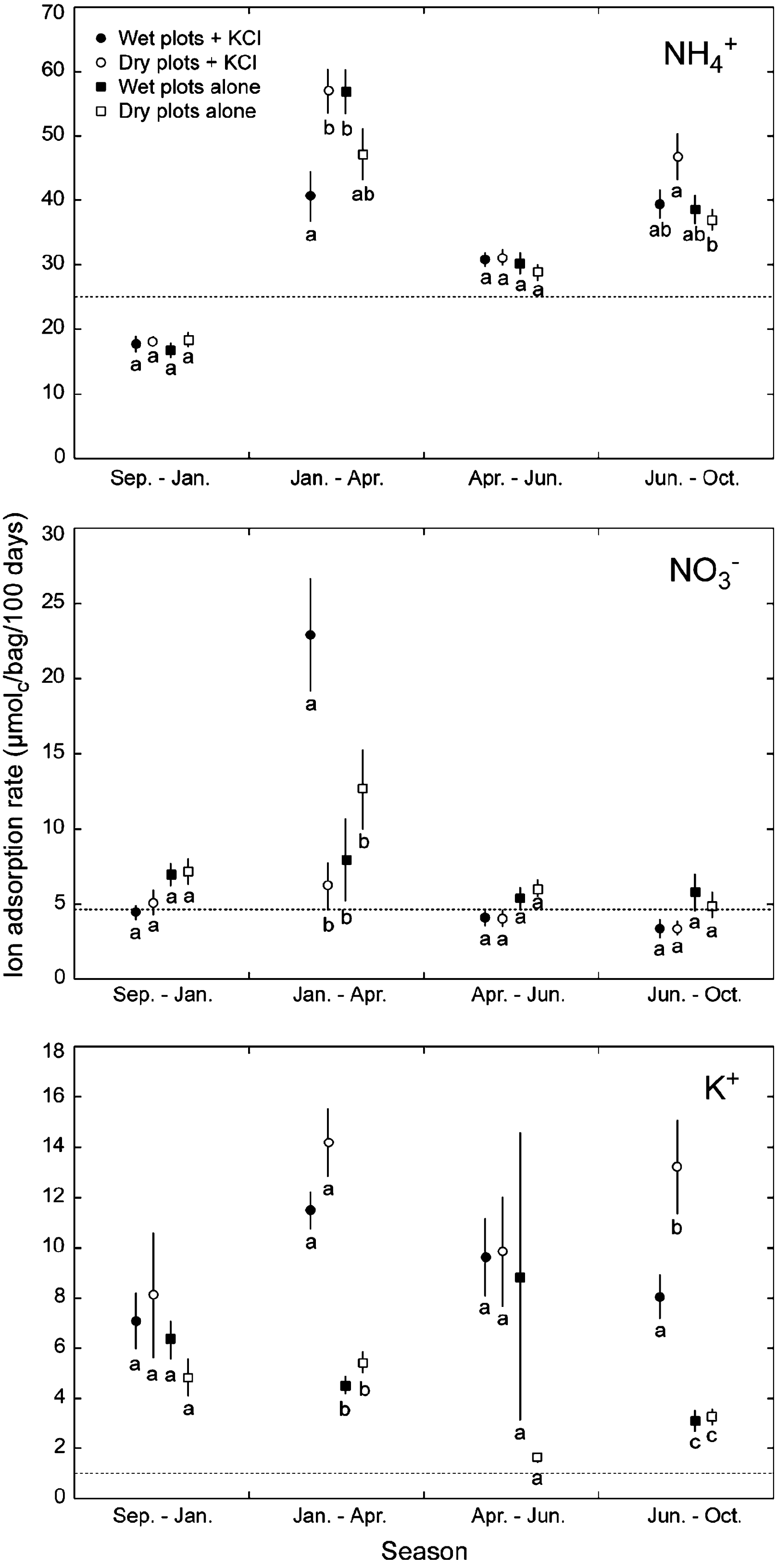
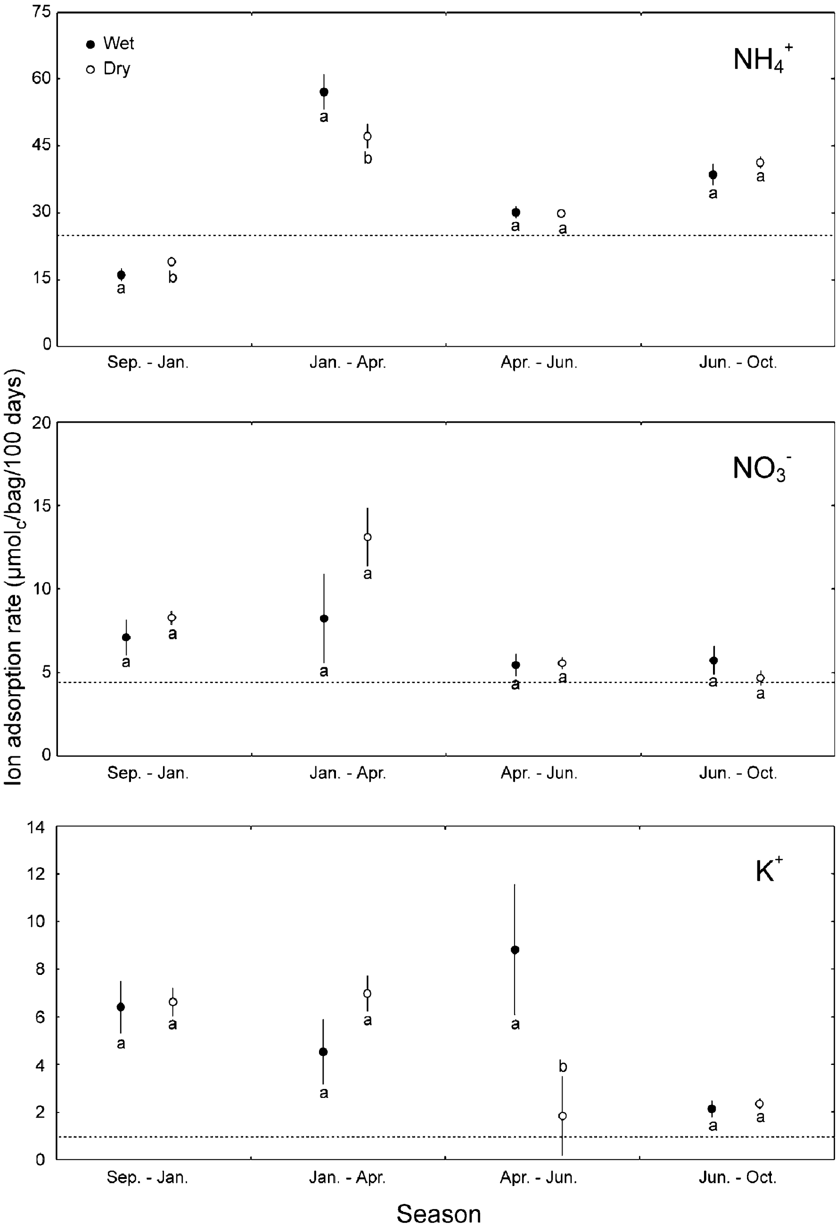


Fig. 3 Main effects of watering treatment on seasonal NH_4^+, NO_3^-, and K^+ adsorption rates (means ± 1 SE) in plots at Canyonlands field sites from Sep. 1997 through Oct. 1998 (*n* = 20 wet plots, 60 dry plots). Plots receiving KCl applications were excluded due to potential plant responses to interactive effects of KCl and water on N dynamics. Dashed horizontal lines indicate mean background concentrations of ions on resin bags



S. hymenoides together than in plots with *S. hymenoides* alone and without plants.

Discussion

Effects of KCl and water additions on measures of N bioavailability in this study indicate the importance of considering indirect consequences of nutrient amendments in studies investigating resource limitations. During three of four measurement periods, plots receiving KCl applications had lower resin-bag NO_3^- than plots receiving no chemical amendments. This probably resulted from displacement of NO_3^- ions from resin bags by Cl^-. NO_3^- generally has greater affinity for anion-exchange resins than Cl^-, but both are high-affinity ions and ion capture and retention by resins also are strongly controlled by mass-action effects (Skogley and Dobermann 1996). During the January–April period, KCl applications in wet

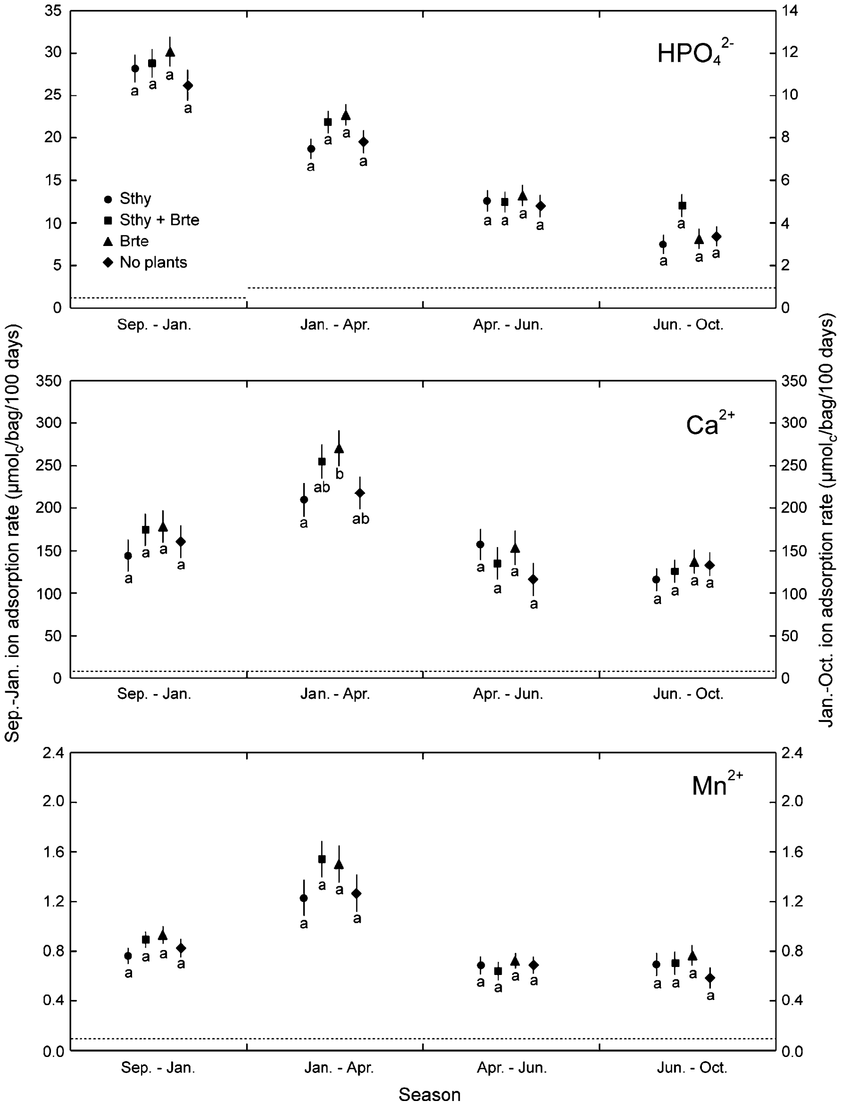


Fig. 4 Main effects of plants (*Stipa hymenoides* = Sthy; *Bromus tectorum* = Brte) on seasonal HPO$_4^{2-}$, Ca^{2+}, and Mn^{2+} adsorption rates (means ± 1 SE) in plots at Canyonlands field sites from Sep. 1997 through Oct. 1998 (n = 20 plots per point). Note the different y-axis scales for HPO$_4^{2-}$ adsorption during Sep.–Jan. and the following three seasons. Plots receiving KCl applications were excluded due to potential plant responses to interactive effects of KCl and water on N dynamics. Dashed horizontal lines indicate mean background concentrations of ions on resin bags

plots resulted in lower resin-bag NH$_4^+$ relative to wet plots not treated with KCl (Fig. 2). This effect did not occur in dry plots, where instead there was a tendency for higher resin-bag NH$_4^+$ in plots receiving KCl applications. In dry plots, the tendency for greater capture of NH$_4^+$ on resin bags in KCl-treated plots may have resulted from the displacement of NH$_4^+$ from soil colloids by K$^+$ ions. In wet plots, the decrease in resin-bag NH$_4^+$ in KCl-treated plots was accompanied by a significant increase in resin-bag NO$_3^-$ in the same plots (Fig. 2). The implication is that the combined application of KCl and water resulted in NH$_4^+$ displacement followed by nitrification and enhanced NO$_3^-$ capture by resin bags.

Despite two applications of KCl during the September–January period, effects of KCl addition on K$^+$ adsorption by resin bags were not evident until the January–April period (Fig. 2). This is likely attributable to the fact that KCl applications were applied to the soil surface and resin bags were buried 5–10 cm beneath the soil surface. It may have taken several weeks before diffusion and downward transport by water applications resulted in elevated K$^+$ concentrations in the soil zone where resin bags were placed.

Although plant effects on resin-bag measures of nutrient bioavailability were statistically insignificant in nearly all cases, we found some evidence for positive effects of *B. tectorum* on resin-bag measures of carbonate-related ions. During the January–April period, resin-bag measures of HPO_4^{2-}, Ca^{2+}, and Mn^{2+} tended to be greater in the presence of *B. tectorum* than in the absence of *B. tectorum* (Fig. 4). January–April patterns depicted in Fig. 4 are for data averaged across wet and dry plots, but inspection of the data in greater detail indicates that these patterns are solely attributable to results from wet plots where *B. tectorum* densities (mean = 1517.8 plants m^{-2}) were much higher than in dry plots (mean = 735.4 m^{-2}; Miller et al., in press). In wet plots with high root densities, *B. tectorum* may have affected HPO_4^{2-} dynamics through phosphatase production and the stimulation of organic-P mineralization (Paul and Clark 1996). Other studies have reported high phosphatase activity beneath *B. tectorum* (Bolton et al. 1993). However, it is unclear how phosphatase production might have produced similar trends in resin-bag HPO_4^{2-}, Ca^{2+}, and Mn^{2+}.

An alternative hypothesis is that *B. tectorum* affected dynamics of these ions in wet plots through effects of root exudates on carbonate dissolution processes. In calcareous soils, dynamics of HPO_4^{2-}, Ca^{2+}, and Mn^{2+} ions commonly are controlled by dissolution and precipitation reactions of the carbonate compounds with which they are associated (McBride 1979; Krauskopf and Bird 1995; Schlesinger 1997). Rhizosphere acidification by root exudates (organic acids) is one mechanism by which plants can mobilize sparingly soluble mineral nutrients (Illmer and Schinner 1995; Hinsinger 1998). *B. tectorum* exhibits considerable below-ground growth in winter (Harris 1967), and winter growth may translate into production of root exudates and the mobilization of carbonate-bound nutrients. In contrast with *B. tectorum*, *S. hymenoides* is not active during winter and resin-bag measures for HPO_4^{2-}, Ca^{2+}, and Mn^{2+} in plots with *S. hymenoides* alone were indistinguishable from those observed in plots without plants. This latter finding also may have been due to the placement of resin bags 5–10 cm beneath the soil surface approximately 25 cm from plot centers. No *S. hymenoides* roots were observed in this zone.

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References

Allison LE, Moodie CD (1965) Carbonate. In: Black CA (ed) Methods of soil analysis, part 2: chemical and microbiological properties. American Society of Agronomy, Madison, pp 1379–1396

Asner GP, Beatty SW (1996) Effects of an African grass invasion on Hawaiian shrubland nitrogen biogeochemistry. Plant Soil 186:205–211

Barber SA (1995) Soil nutrient bioavailability: a mechanistic approach. John Wiley & Sons, New York, p 414

Bilbrough CJ, Caldwell MM (1997) Exploitation of springtime ephemeral N pulses by six Great Basin plant species. Ecology 78:231–243

Binkley D, Matson P (1983) Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci Soc Am J 47:1050–1052

Bolton H Jr, Smith JL, Link SO (1993) Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biol Biochem 5:545–552

Bowker MA, Belnap J, Davidson DW, Phillips SL (2005) Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. Ecol Applic 15:1941–1951

Brady NC, Weil RR (1996) The nature and properties of soils, 11th edn. Prentice-Hall, Upper Saddle River, NJ, p 740

Chapin FS III (1991) Effects of multiple environmental stresses on nutrient availability and use by plants. In: Mooney HA, Winner WE, Pell EJ (eds) Responses of plants to multiple stresses. Academic Press, San Diego, pp 67–88

DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. Vegetatio 84:9–29

Dreimanis A (1962) Quantitative gasometric determination of calcite and dolomite by using Chittick apparatus. J Sediment Petrol 32:520–529

Drenovsky RE, Richards JH (2004) Critical N:P values: predicting nutrient deficiencies in desert shrublands. Plant Soil 259:59–69

Ehleringer JR, Schwinning S, Gebauer R (2000) Water use in arid land ecosystems. In: Press MC, Scholes JD, Barker MG (eds) Physiological plant ecology. Proceedings of the 39th symposium of the British ecological society, 7–9 September 1998, University of York. Blackwell Science, Boston, pp 347–365

Gibson DJ, Colquhoun IA, Greig-Smith P (1985) A new method for measuring nutrient supply rates in soils using ion-exchange resins. In: Fitter AH, Atkinson D, Read DJ, Usher MB (eds) Ecological interactions in soil: plants, microbes, and animals. Blackwell Scientific, Oxford, pp 73–79

Harris GA (1967) Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecol Monogr 37:89–111

Havstad KM, Herrick JE, Schlesinger WH (2000) Desert rangelands, degradation and nutrients. In: Arnalds O, Archer S (eds) Rangeland desertification. Kluwer, Dordrecht, pp 77–87

Hinsinger P (1998) How do plants acquire mineral nutrients? Chemical processes involved in the rhizosphere. Adv Agron 64:225–265

Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. Biogeochemistry 46:247–293

Illmer P, Schinner F (1995) Solubilization of inorganic calcium phosphates—solubilization mechanisms. Soil Biol Biochem 27:257–263

James JJ, Tiller RL, Richards JH (2005) Multiple resources limit plant growth and function in a saline-alkaline desert community. J Ecol 93:113–126

Keeney DR, Nelson DW (1982) Nitrogen—inorganic forms. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis. Part 2. Chemical and microbiological properties. ASA/SSSA, Madison, WI, pp 643–698

Krauskopf KB, Bird DK (1995) Introduction to geochemistry, 3rd edn. McGraw-Hill, Boston, p 647

Lajtha K (1988) The use of ion-exchange resin bags for measuring nutrient availability in an arid ecosystem. Plant Soil 105:105–111

Lundell Y (1989) In situ ion exchange resin bags to estimate forest site quality. Plant Soil 119:186–190

Marschner H (1995) Mineral nutrition of higher plants. 2nd edn. Academic Press, London, p 889

McBride MB (1979) Chemisorption and precipitation of Mn^{2+} at $CaCO_3$ surfaces. Soil Sci Soc Am J 43:693–698

McLendon T, Redente EF (1992) Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91:312–317

Miller ME (2000) Effects of resource manipulations and soil characteristics on *Bromus tectorum* L. and *Stipa hymenoides* R. & S. in calcareous soils of Canyonlands National Park, Utah. Unpublished dissertation, University of Colorado, Boulder, CO, p 159

Miller ME, Belnap J, Beatty SW, Reynolds R (in press) Performance of *Bromus tectorum* L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of southeastern Utah, USA. Plant Soil

Nelson RE (1982) Carbonate and gypsum. In: Page AL, Miller RH, Keeney DR (eds) Methods of soil analysis, part 2. Chemical and microbiological properties. ASA/SSSA, Madison, pp 181–198

Paul EA, Clark FE (1996) Soil microbiology and biochemistry. 2nd edn. Academic Press, San Diego, p 340

Scheiner SM (1993) MANOVA: Multiple response variables and multispecies interactions. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman & Hall, New York, pp 94–112

Schlesinger WH (1997) Biogeochemistry: an analysis of global change. 2nd edn. Academic Press, San Diego, p 588

Schwinning S, Starr BI, Wojcik NJ, Miller ME, Ehleringer JR, Sanford RL Jr, (2005) Effects of nitrogen deposition on an arid grassland in the Colorado Plateau cold desert. Rangeland Ecol Manage 58:565–574

Skogley EO, Dobermann A (1996) Synthetic ion-exchange resins: soil and environmental studies. J Env Qual 25:13–24

Skogley EO, Georgitis SJ, Yang JE, Schaff BE (1990) The phytoavailability soil test-PST. Commun Soil Sci Plan 21:1229–1243

Sparks DL (1995) Environmental soil chemistry. Academic Press, San Diego, p 267

StatSoft, Inc. (1999) STATISTICA for Windows. StatSoft, Tulsa, OK

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, p 504

USDA Soil Conservation Service (1991) Soil survey of Canyonlands area, Utah: parts of Grand and San Juan Counties, p 293

Yang JE, Skogley EO, Georgitis SJ, Schaff BE, Ferguson AH (1991) Phytoavailability soil test: development and verification of theory. Soil Sci Soc Am J 55:1358–1365

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upple Saddle River, NJ, p 663