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Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem

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Abstract. The exotic annual grass *Bromus tectorum* has replaced thousands of hectares of native perennial vegetation in semi-arid ecosystems of the western United States. Inorganic N availability and production were compared in soil from monodominant patches of *Bromus tectorum*, the perennial bunchgrass *Elymus elymoides*, and the shrub *Artemisia tridentata*, in Curlew Valley, a salt-desert shrub site in Northern Utah. *Bromus*-dominated soil had greater %N in the top 10 cm than *Artemisia* or *Elymus*-dominated soils. As determined by spring isotope-dilution assays, gross mineralization and nitrification rates were higher in *Bromus*-dominated than *Artemisia*-dominated soils, but gross rates of NH_4^+ and NO_3^- consumption were also higher. Litterbags had greater mass loss and N mineralization when buried in *Bromus* stands than in *Artemisia* stands, indicating the soil environment under the annual grass promotes decomposition. As determined by nitrification potential assays, nitrifier populations were higher under *Bromus* than under *Artemisia* and *Elymus*. Soil inorganic N concentrations were similar among vegetation types in the spring, but NO_3^- accumulated under *Bromus* once it had senesced. An *in situ* net mineralization assay conducted in autumn indicated that germinating *Bromus* seedlings are a strong sink for soil NO_3^-, and that net nitrification is inherently low in soils under *Artemisia* and *Elymus*. Results of the study suggest that differences in plant uptake and the soil environment promote greater inorganic N availability under *Bromus* than under perennial species at the site.

Introduction

In the Great Basin of the western United States, the widespread replacement of shrub and perennial bunchgrass communities by the exotic annual grass *Bromus tectorum* [L.] represents a fundamental shift in the dominant plant functional type, potentially affecting a number of factors important for ecosystem function. In particular, nutrient cycling may be affected by vegetation change in semiarid systems, which tend to have low soil organic matter and exhibit periods of intense soil nutrient processing alternating with periods of drought and stasis (Noy-Meir 1973; West 1991). Annual grass invasion could affect availability of inorganic N, the primary currency of the N cycle, in a variety of ways. Vegetation may indirectly influence the soil decompositional environment, and thus inorganic N availability, by affecting soil temperature and moisture regimes (West and Caldwell 1982; Pierson and Wight 1991; D'Antonio and Vitousek 1992). Plants directly influence soil inorganic N through uptake (Jackson et al. 1988; Wedin and Tilman 1990; Zak et al. 1990), and affect microbial production of inorganic N through the quality and amount of litter and root exudates released to the soil organic matter (SOM) pool (Melillo et al. 1982; Newman 1985; Biondini et al. 1988; Scott and Binkley 1997; Hooper and Vitousek 1998). Even within a functional type, the effect of individual species on SOM and inorganic N availability may be distinct (Wedin and Tilman 1990; Wedin and Pastor 1993), suggesting that a shift from perennial vegetation to annual grasses may produce substantial change.

Bromus occurs in the understory and as a monoculture on millions of hectares in the Intermountain West (Pellant and Hall 1994). *Bromus* typically germinates in response to autumn precipitation (Klemmedson and Smith 1964; Chiariello 1989), over-winters as a seedling, then sets seed and senesces by early summer (Klemmedson and Smith 1964). High growth and transpiration rates by the annual grass in the spring deplete soil moisture, impacting survival of both perennial seedlings (Harris 1967) and mature plants (Melgoza et al. 1990). Standing *Bromus* litter promotes fire (Stewart and Hull 1949; Upadhyaya et al. 1986), which further inhibits recovery of native vegetation and ultimately results in vast monodominant stands of the annual (Pellant 1990; Pellant and Hall 1994). Work in California annual grasslands suggests that the N cycle of annual systems should be more "open", thus leading to greater loss of N than in perennial systems, due to the ephemeral nature of annual grass plant cover and the yearly turnover of biomass (Jones and Woodmansee 1979; Jackson et al. 1988). The shift from perennial dominance to annual grass dominance may in fact influence a number of factors important for soil N cycling, including litter quantity and quality (Harris 1967; Evans et al. 2001), soil moisture depletion and recharge patterns (Cline et al. 1977; Kremer and Running 1996), and timing and amount of plant N uptake (Bilbrough and Caldwell 1997; Booth 2003). The current research was undertaken to characterize differences in N dynamics between annual-dominated and perennial-dominated soils, and to address the general hypothesis that inorganic N availability and production should be higher in *Bromus*-dominated than in perennial-dominated soils.

Methods

Site description and history

Work was conducted in Curlew Valley, a Great Basin desert site in Northern Utah, located at 41°52′ N, 113°5′ W at an elevation of 1,350 m. A thirty-year climate record from a station located 25 km from the site shows that the area receives about 310 mm of precipitation per year. Soils at the site are fine silty Xerollic Calciorthids (Thiokol series) of lacustrine origin (Skujins and West 1973), and are rock free in the lowest part of the valley where the study was conducted. The site contains mixed and monodominant patches of sagebrush (*Artemisia tridentata* [Nutt.] spp. *wyomingensis*), the perennial bunchgrass squirreltail (*Elymus elymoides* [Raf.]) and cheatgrass (*Bromus tectorum*). Transect sampling was undertaken to characterize vegetation communities at the site (Booth, unpub. data). Mature stands of *Artemisia* usually include *Elymus*, though monodominant patches of *Artemisia* also occur. Mixed *Artemisia/Elymus* stands include only small amounts of *Bromus*. Outside of shrub-dominated areas, *Elymus* occurs both in monodominant stands, and in mixed grass stands with *Bromus*. Small areas of monodominant *Bromus* also occur. Transect sampling indicates that aboveground density of *Artemisia* in shrub/grass stands reaches 50% and that of *Elymus* reaches 10%; maximum cover of *Elymus* in monodominant stands reaches 20%; and *Bromus* cover approaches 100% where it occurs alone. *Bromus* stands consist of dense vegetation and little if any cryptobiotic crust, probably due to its suppression by dense annual grass thatch (Lange 2001). Plants in *Artemisia/Elymus* and monodominant *Elymus* stands are separated by bare ground with some cryptobiotic crust cover and less aboveground litter than occurs in *Bromus* stands.

Site history was established with the use of aerial photos and field observations from previous vegetation studies at the site (Gates et al. 1956; Baasher 1961; Mitchell 1965; Coyne 1969; Rice and Westoby 1978). The site was grazed by sheep from the 1870's to the 1960's (Rice and Westoby 1978), when sheep were replaced by cattle. Cattle presently graze the site from November to April. Ground and aerial photos indicate that in the 1950's and 1960's, the area employed in the current study contained scattered *Artemisia tridentata* stands adjacent to dense, homogenous stands of the half-shrubs *Atriplex nutallii* and *Ceratoides lanata* (now *Kreshnekovia lanata*) (Gates et al. 1956; Mitchell 1965). Previous workers at the site concluded that vegetation patterning did not relate to soil physical properties (Mitchell and West 1966), and that soil chemical properties (in particular salinity) were poorly correlated with vegetation distribution (Gates et al. 1956). Neither *Bromus* nor *Elymus* is visible in historical photos of shrub stands from the 1950's and 1960's (Gates et al. 1956; Mitchell 1965). However, both grasses have substantially increased at the site since the 1950's. In a study from the 1970's, *Elymus* was considered to be the "most important" perennial grass at the site, occurring in all vegetation communities, but no mixed or monodominant grass stands of any species were documented (Rice and Westoby 1978). Since the 1970's, there has been nearly complete replacement of half-shrub stands by mixed *Bromus/Elymus* stands and monodominant *Elymus* stands. The reasons for replacement of half-shrubs by grasses are not clear, though greater persistence of *Ceratoides* within than outside of grazing exclosures suggests that grass invasion may have occurred due to overgrazing of woody perennials (Booth 2001). Part of the site burned in 1983, but an eyewitness to the fire recounts that *Bromus* was already widespread by that time, and probably served to help carry the fire (Kevin Connors, pers. comm.). Areas burned in 1983 can be identified on aerial photos from that year by coloration differences, and on the ground by the persistence of burned *Artemisia* stumps. Aerial photos and ground surveying suggest that current *Bromus* and *Elymus* distribution is approximately equivalent in burned and unburned areas of the site (Booth 2001). *Bromus*-dominated areas (which generally include scattered *Elymus* tussocks) and monodominant *Elymus* patches range from about a meter to tens of meters in diameter, and are interspersed with *Artemisia/Elymus* patches across the site. The site is extremely flat, and the location of vegetation patches does not appear to be dictated by topography. Soil moisture-holding capacity and bulk density in the 0–20 cm layer do not differ among *Artemisia, Elymus*, and *Bromus* stands (Booth 2003). While grasses have completely replaced the formerly extensive stands of half-shrubs, the current distribution of *Bromus* and *Elymus* patches does not appear to relate to the former microscale distribution of half-shrubs at the site, since historical photos and data (Gates et al. 1956; Mitchell 1965; Rice and Westoby 1978) indicate that plants in shrub stands were separated by centimeters, not meters as are current vegetation patches. However, the possibility that current species distribution relates to patterns of nutrient distribution in the soil cannot be ruled out; it is possible that patterns of differential nutrient availability could even predate half-shrub stands documented in the 1950's.

Sampling for the current study was conducted over a total area of about 80 hectares, in areas where *Artemisia* stands are interspersed with *Bromus* and *Elymus* stands. Sampling on individual dates occurred in subsections of about 2 hectares within the larger site. Most sampling was conducted in the part of the site that did not burn in the 1983 fire, but where sampling was conducted in formerly burned areas, care was taken to sample only those grass-dominated areas that were formerly occupied by half-shrubs, and to avoid areas where burned *Artemisia* stumps occurred. Areas to be sampled were visually stratified by vegetation type, and then individual sampling locations within patches were randomly located by tossing a pin.

Methods overview

Inorganic N availability and production in *Bromus*- and perennial-dominated soils were compared using a variety of approaches. Since inorganic N production ultimately depends on substrate availability, total N was assessed in surface soils of all three vegetation types, and the isotopic signature of soil N was examined to draw inferences about relative N-fixation and loss rates (Evans and Ehleringer 1993). To evaluate differences in inorganic N availability, soil NH_4^+ and NO_3^- concentrations were compared in the spring, when all three plant species are actively taking up N, and in the autumn, long after *Bromus* senescence. To examine plant regulation of soil inorganic N concentrations in the autumn, around the time of *Bromus* germination, net mineralization and nitrification were compared among *in situ* undisturbed soil and root-exclusion cores in stands of all three species.

Soil concentrations are a simple measure of inorganic N availability, but reveal little about actual rates at which inorganic N is made accessible to plant and microbial consumers. To compare production and consumption rates between *Artemisia*-dominated and *Bromus*-dominated soils in the spring, gross rates of mineralization, nitrification, and microbial assimilation were assessed using isotope dilution assays. To compare the soil decompositional environment as influenced by vegetation type, decomposition of *Artemisia* foliage was assessed in litterbags buried in annual grass and shrub stands. Finally, certain soil microbial and faunal communities responsible for inorganic N production were compared among the vegetation types. Nitrification potential assays were conducted as a proxy for nitrifier population size in *Bromus, Artemisia* and *Elymus* soils, and nematode and amoebae populations were compared between the annual grass and shrub communities.

Total N, inorganic N and moisture content of surface soils

In June 2000, total nitrogen and $\delta^{15}N$ was assessed in soils collected from 0 to 2 cm and 3 to 10 cm at six sampling locations of each vegetation type. Soils were air dried, sieved to remove roots, and ground on a roller mill for 24 hours. Samples were analyzed for total N and $\delta^{15}N$ by direct combustion and mass spectrometry on an ANCA 2020 system (Europa Scientific, Cincinnati, Ohio). Data were analyzed with an ANOVA on species, using depth as a repeated measures factor (SYSTAT, version 2).

To assess soil inorganic N concentration and gravimetric moisture content, 3-cm-diameter soil cores were collected from the 0 to 10 cm soil layer in six to eight randomly selected locations per vegetation type on several dates in the spring and fall, from November, 1996 through October, 1999. Sampling in 1997 was conducted primarily in *Bromus* and *Artemisia* stands; in 1998, soils from *Elymus*-dominated areas were added to the study. Soil cores were homogenized and a subsample immediately extracted in the field in 2-M KCl at a ratio of approximately 1:10 (soil:solution mass). Extractant was analyzed for NH_4^+ and NO_3^- using a flow-injection colorimetric analyzer (Lachat Instruments, Mequon, Wisconsin). Gravimetric soil moisture was determined by oven-drying soils at 105 °C for 36–48 hours. Data collected on each date were analyzed separately using a one-way ANOVA on species.

Litterbag study

Nylon bags of 1-mm mesh were filled with 11 g of mixed live and senesced *Artemisia* litter that had been collected at Curlew Valley in the fall of 1996 and subsequently air-dried. Duplicate bags were buried in June 1997 at each of eight random locations in *Bromus* and *Artemisia* stands, at 10 to 15 cm. An angled slit in the soil was made using a flat-bladed shovel and bags were inserted so as to minimize disturbance. Bags were recovered in late March 1998, and as much soil as possible was removed prior to drying the material for three days at 65 °C. Bag contents were weighed and ground in a Wiley mill using a 600-μm mesh screen, and subsamples were analyzed for N concentration using direct combustion and mass spectrometry. Mass of material was corrected for ash content. The proportional mass loss during incubation was calculated as the difference between the initial and final mass (ash-free weight of litter), divided by the original mass. Loss of total N from litter was calculated similarly. Results for duplicate bags were averaged, and values for bags buried in *Bromus* and *Artemisia* stands were compared using t-tests.

Gross N mineralization and nitrification rates

Gross mineralization and nitrification were determined in intact soil cores with the ^{15}N isotope dilution technique (Stark 2000). Experiments were carried out in early May, 1998, when soil inorganic N concentrations were relatively low. At each of six replicate locations in *Bromus* and *Artemisia* vegetation patches, two pairs of soil cores (3.7-cm diam. × 10 cm deep) were collected. Cores for determining rates of mineralization and NH_4^+ consumption were injected with 10 ml of 1-mM $(NH_4)_2SO_4$ (99 atom % ^{15}N), delivering 1.93 mg ^{15}N kg^{-1} soil. Cores for determining nitrification and NO_3^- consumption rates were injected with 10 ml of 4-mM $K^{15}NO_3$ (99 atom % ^{15}N) delivering 2.8 mg ^{15}N kg^{-1} soil. Solutions were injected throughout the core using multiple injections from 15-cm sideport needles (Popper and Sons, New York) to assist in uniform distribution of the added N. Added ^{15}N represented an 80% increase in NH_4^+ and a 871% increase in NO_3^- for the *Bromus* soils and a 109% increase in NH_4^+ and a 486% increase in NO_3^- in *Artemisia* soils. At the time of sampling, *Bromus* soils were slightly drier than *Artemisia* soils, and after injection moisture contents were 10% and 11%, respectively. One core of each NH_4^+ or NO_3^- pair was immediately extracted in 2-M KCl, to determine recovery efficiency of the added ^{15}N. The other was capped at one end and buried in a sealed jar at the location from which it was harvested. After 48 hours, buried cores were recovered and homogenized, then a subsample was immediately extracted in 2-M KCl for determination of NO_3^- and NH_4^+ pool sizes and ^{15}N enrichment. Isotope enrichment of $^{15}NH_4^+$ and $^{15}NO_3^-$ pools in KCl extracts was determined by a diffusion technique (Stark and Hart 1996) and continuous-flow direct combustion and mass spectrometry. Calculations to determine gross rates of production, consumption, and mean residence time (ambient pool size divided by gross production) for NH_4^+ and NO_3^- were conducted following Stark (2000). Microbial NH_4^+ immobilization was calculated as gross NH_4^+ consumption minus gross nitrification. All comparisons between vegetation types were carried out using t-tests.

Nitrification potential assay

Nitrification potential assays were carried out on soils from *Elymus, Bromus* and *Artemisia* stands using the shaken-soil-slurry assay described by Hart et al. (1994). A spring assay was conducted in late April of 1998, about a week prior to the pool dilution experiment, and a fall assay was conducted in early October of 1999. Soil cores were collected from the 0 to 10 cm layer at eight randomly chosen locations in each of the three vegetation types, and a subsample was immediately extracted in 2-M KCl for determination of inorganic N concentrations. At the lab, an additional subsample from each core was swirled for 24 h in a 50-mM $(NH_4)_2SO_4$ solution, and NO_3^- concentration was determined at 2,4, 22 and 24 h. Nitrification rates (mg NO_3^--N kg^{-1} soil day^{-1}) were calculated from the regression of NO_3^- concentration against time.

Soil fauna

To compare population sizes of nematodes, flagellates and amoebae, six replicate cores were collected from the upper 10 cm of soil in *Bromus* and *Artemisia* stands in mid-May 1997. Soil mesofaunal populations were estimated by Soil Foodweb Inc., Oregon, using the Most Probable Number method.

Root exclusion experiment

To examine the influence of perennials and germinating *Bromus* on soil inorganic N concentrations, net rates of mineralization and nitrification were compared in the presence and absence of root uptake by *Bromus, Elymus*, and *Artemisia* in September, 1998. To exclude roots, a set of three PVC tubes (10-cm-diam. × 10-cm-deep, total volume 785 cm^3) was installed at six locations in each vegetation type. Tubes were pounded into the soil until flush with the soil surface in *Bromus* patches, between tussocks in the *Elymus* areas, and within *Artemisia* stands. Just after tube installation, a large precipitation event stimulated *Bromus* germination and foliage proliferation by *Elymus*. Root-exclusion tubes were kept free of vegetation, but by mid-October, *Bromus* seedlings were growing densely in adjacent undisturbed soils. At the time of installation on September 12, a soil sample was immediately extracted in 2-M KCl for inorganic N determination. At two-week intervals between late September and late October, one root exclusion core was harvested from each location, and adjacent undisturbed soils were also cored to 10 cm. Soil samples were immediately homogenized and extracted in 2-M KCl and analyzed for inorganic N. Net mineralization and nitrification were calculated as the difference in inorganic N content on a date minus that from the previous extraction, divided by the number of days in the interval. Soil moisture content and inorganic N concentrations on specific dates, and net mineralization and nitrification rates in the two-week intervals between measurements, were compared using species and core type (root-exclusion vs. unconfined) as factors and utilizing Tukey multiple comparisons tests for pairwise comparisons. Repeated-measures ANOVA was employed to compare absolute N concentrations among dates, treating the bi-weekly core collections as subsamples from a block.

Results

Total N, inorganic N and moisture content of surface soils

Total soil %N was higher in *Bromus* soils than in *Artemisia* or *Elymus* soils, which did not differ from each other ($p < 0.001$; Figure 1a). Soils from the 0 to 2-cm

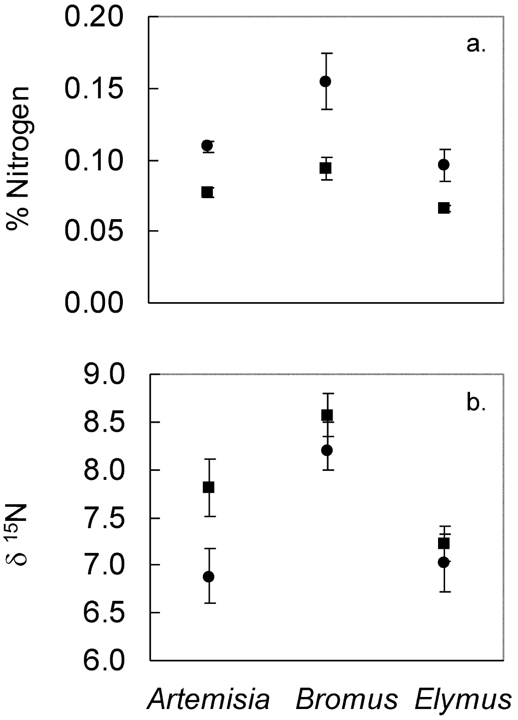

Figure 1. Total soil N (a) and $\delta^{15}N$ (b) in soils of *Bromus, Artemisia* and *Elymus*. Circles represent 0 to 2 cm soil depth; squares 2 to 10 cm. Error bars are standard error of the mean; n = 6.

layer had higher total %N than those from the 2 to 10 cm layer ($p < 0.001$). *Bromus* soils had higher $\delta^{15}N$ values than soils of either perennial species, which did not differ from each other ($p < 0.001$; Figure 1b). Soil from the 0 to 2 cm layer had a higher $\delta^{15}N$ than soil from the 3 to 10 cm layer ($p = 0.02$).

Soil inorganic N concentrations were generally low in spring of 1997 and 1998 (Figure 2a). Nitrate concentrations tended to be less than 1 mg NO_3^--N kg^{-1} soil and NH_4^+ concentrations were between 1.5 and 3 mg NH_4^+-N kg^{-1} soil, except for samples collected in late March 1998, which showed slightly elevated NH_4^+ concentrations. Soils collected in late November of 1996 also had low inorganic N concentrations (Figure 2a). In late summer and fall, NH_4^+ concentrations did not differ between vegetation types, but NO_3^- concentrations in *Bromus* soils were up to ten times higher those in *Artemisia*-dominated soils in 1997 (Figure 2a). Nitrate concentrations in *Bromus* soils also exceeded those in *Artemisia* and *Elymus* soils in September 1998 and October 1999.

Soil moisture in the 0 to 10 cm layer tended to be slightly higher under perennials than under *Bromus* in the spring (Figure 2b). In the autumn, however, *Bromus*-dominated soils were usually moister than perennial-dominated soils.

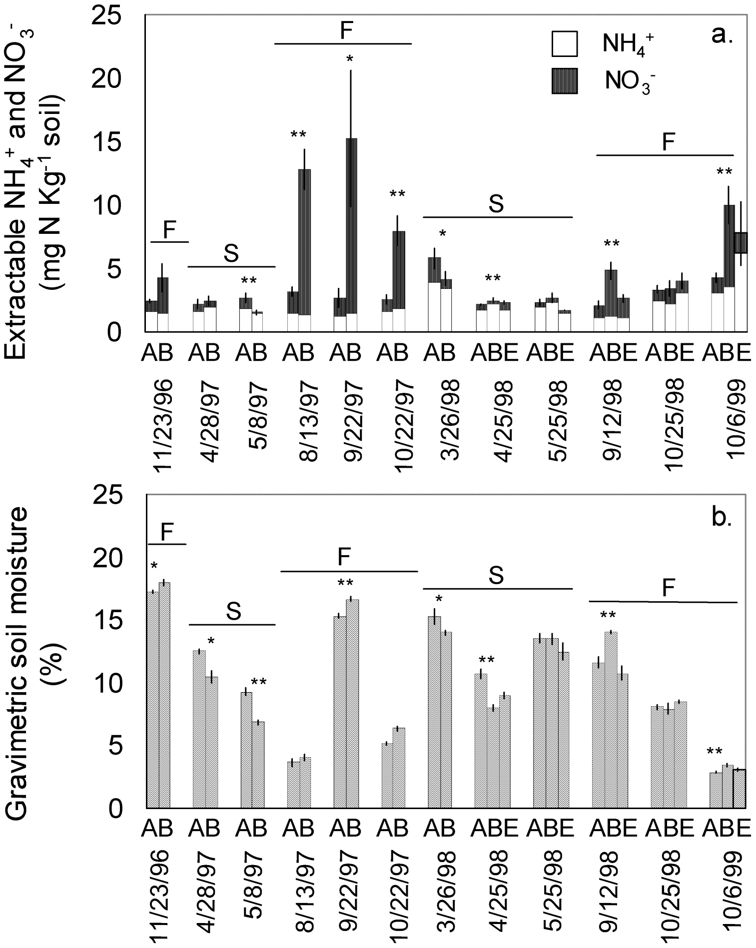

Figure 2. Changes in inorganic N and soil moisture through time in surface soils collected from fall 1996 to fall 1999. A = *Artemisia*, B = *Bromus*, E = *Elymus*. For (a), error bars are standard error of mean total inorganic N. Measurements are grouped by season (Fall and Spring). One asterisk denotes a difference in NO_3^- or water significant at $p < 0.05$; two asterisks denote $p < 0.01$.

Litterbag study

Litter decomposed more rapidly in *Bromus* stands than in *Artemisia* stands. Litterbags buried in the *Bromus* patches lost 53% of their original mass between June and March, and total N decreased by 24%, while those in the *Artemisia* stands lost 43% of mass and 4% of total N (both significant at $p < 0.001$).

Table 1. Mean N-cycling rates, inorganic N concentrations and water content of *Bromus* and *Artemisia* soil cores in spring of 1998. Total NH_4^+ consumption (not shown) is the sum of nitrification and NH_4^+ assimilation. Standard error of the mean in parentheses; n = 6.

		KCl extractable		Gross rates				MRT	
	Soil water content	NH_4^+	NO_3^-	Mineralization.	NH_4^+ assimilation	Nitrification	NO_3^- consumption	NH_4^+	NO_3^-
	g H_2O g^{-1} soil	mg N kg^{-1} soil		mg N kg^{-1} soil day^{-1}				days	
Artemisia	7.3	1.65	0.54	0.73	0.65	0.34	0.34	3.35	1.68
	(0.3)	(0.11)	(0.06)	(0.22)	(0.17)	(0.08)	(0.07)	(1.12)	(0.25)
Bromus	5.6	2.25	0.30	1.52	1.34	0.49	0.82	1.79	0.66
	(1.8)	(0.21)	(0.02)	(0.21)	(0.15)	(0.05)	(0.05)	(0.21)	(0.10)
p	0.00003	0.02	0.001	0.03	0.02	0.15	0.0004	0.21	0.004

Gross N mineralization and nitrification rates

Gross mineralization, NH_4^+ assimilation, and total NH_4^+ consumption rates (assimilation plus nitrification) in *Bromus* soils were double those in *Artemisia* soils, but NH_4^+ pool mean residence time did not differ significantly between soils of the two vegetation types (Table 1). Consumption rates for both vegetation types exceeded production rates ($p = 0.1$), a phenomenon typically observed following addition of inorganic N to N-limited soils (Davidson et al. 1990).

Gross nitrification rates in *Bromus* soils as measured by $^{15}NO_3^-$ addition were higher than those in *Artemisia* soils, but a single high outlier in the *Artemisia* samples (which came from beneath a senescing shrub) rendered the difference significant at only $p = 0.15$ (Table 1). The set of samples collected in healthy shrub stands had a mean nitrification rate half that found in *Bromus* stands ($p < 0.01$). After NO_3^- injection, soil NO_3^- pool sizes did not differ significantly between the two species ($p = 0.3$), but gross NO_3^- consumption was twice as high in *Bromus* as *Artemisia* soils, and mean residence time for NO_3^- was significantly shorter. Nitrate consumption rates in *Artemisia* soils did not differ from production rates, but consumption was significantly higher than production in *Bromus* soils ($p < 0.01$).

Nitrification potential assay

Nitrification potential rates measured in spring and fall were 40–100% higher in *Bromus* soils than in soils of the two perennial species ($p < 0.001$; Figure 3). Rates in *Elymus* and *Artemisia* soils did not differ in either season. Overall, rates on the fall sampling date were slightly higher than on the spring sampling date ($p = 0.04$).

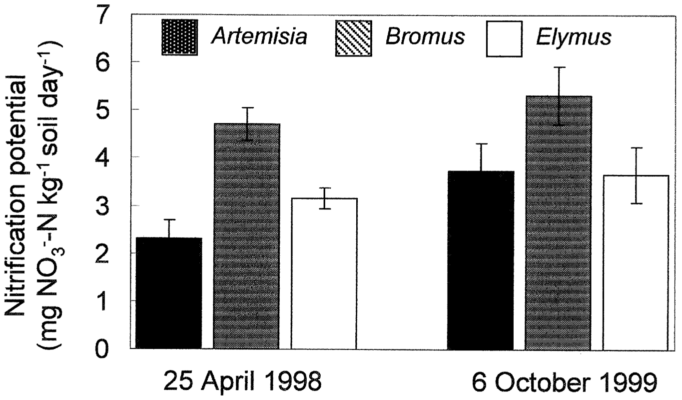

Figure 3. Effect of vegetation type on nitrification potential rates in spring 1998 and fall 1999. Error bars are standard error of the mean; n = 8.

Moisture content of soils collected for the assay in spring was higher than in fall in all vegetation types (Figure 2b; sampling dates 4/25/98 and 10/6/99).

Soil fauna

Soil faunal populations differed significantly between *Artemisia* and *Bromus* soils. Total nematode numbers were significantly higher in *Artemisia* soils (16 ± 3 g^{-1} soil) than *Bromus* soils (6 ± 3 g^{-1} soil; $p = 0.04$), with numbers primarily concentrated in fungal- and bacterial-feeding groups. However, amoebae populations were significantly higher in *Bromus* soils (359 ± 57 g^{-1} soil) than in *Artemisia* soils (44 ± 12 g^{-1} soil; $p < 0.001$). There was no significant difference in the number of flagellates (overall mean 11 ± 5 g^{-1} soil).

Root exclusion experiment

At the time of tube installation on 12 September, soil NH_4^+ did not differ among the three species, but soil NO_3^- concentrations were higher under *Bromus* than under perennials (Figure 4). From 12–27 September (Weeks 0–2), soil NH_4^+ concentrations generally increased ($p < 0.001$) in root-exclusion tubes and unconfined soils alike, while there was no significant change in NO_3^- concentrations over the same period. Between 27 September and 12 October (Weeks 2–4), soil moisture decreased fastest in *Bromus* unconfined soils ($p = 0.03$) and NO_3^- concentrations also declined, presumably due to uptake by recently germinated *Bromus* seedlings. Net nitrification was highest in *Bromus* root-exclusion tubes (0.30 ± 0.11 mg NO_3^--N kg^{-1} soil day^{-1}; $p < 0.001$), but was negligible in *Artemisia* (0.03 ± 0.02 mg NO_3^--N kg^{-1} soil day^{-1}) and *Elymus* (0.008 ± 0.03 mg NO_3^--N kg^{-1} soil day^{-1}) root-exclusion tubes.

Net ammonification showed the opposite pattern from net nitrification in Weeks 2–4, with higher rates in unconfined soils (0.22 ± 0.03 mg NH_4^+-N kg^{-1} soil day^{-1})

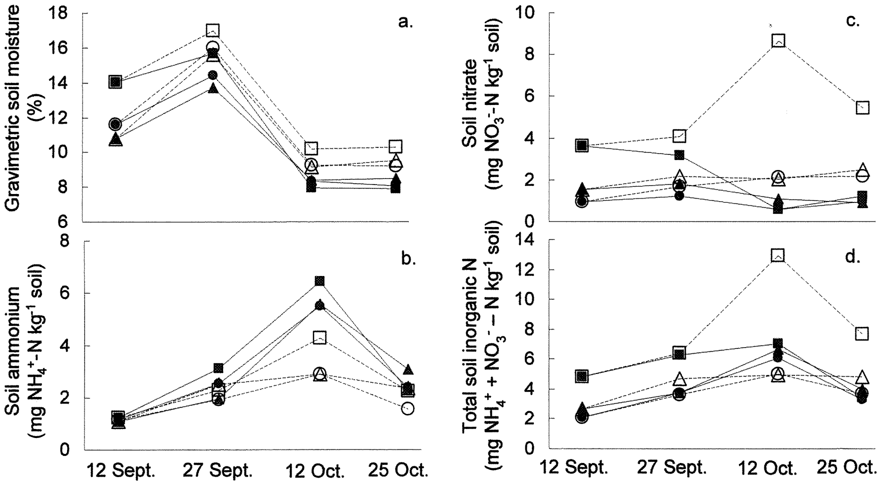

Figure 4. Effect of root exclusion and vegetation type on soil moisture content, ammonium, nitrate, and total inorganic N concentrations in stands of *Artemisia* (circles) *Bromus* (squares) and *Elymus* (triangles) at Curlew Valley in autumn 1998. Open symbols represent unconfined soils; filled symbols represent root exclusion cores. Error bars omitted for clarity.

than in root-exclusion tubes (0.07±0.02 mg NH_4^+-N kg^{-1} soil day^{-1}; $p < 0.001$). For *Bromus*, total net mineralization rates were higher in root-exclusion tubes than in unconfined soils, but the opposite was true in *Artemisia* and *Elymus* soils, where net mineralization was highest in unconfined soils ($p = 0.002$).

Total inorganic N peaked in all cores on 12 October. The highest overall values were found in *Bromus* root-exclusion tubes (12.92 mg inorganic N kg^{-1} soil). Total soil inorganic N concentrations in perennial stands on that date were less than half those in annual stands, and did not differ significantly between root-exclusion tubes and unconfined soils. Soil NO_3^- concentrations in perennial stands also did not differ significantly between root-exclusion tubes and unconfined soils.

Between 12 October and 25 October (Weeks 4–6), NH_4^+ concentrations declined in all treatments, though concentrations generally declined more quickly in unconfined soils (–0.23 mg NH_4^+-N kg^{-1} soil day^{-1}, ± 0.04) than in root-exclusion tubes (–0.09 mg NH_4^+-N kg^{-1} soil day^{-1} ± 0.02; $p = 0.004$). Over this period, NO_3^- concentrations in *Bromus* root-exclusion tubes declined substantially (–0.23 mg NO_3^--N kg^{-1} soil day^{-1} ± 0.11), while NO_3^- concentrations in other treatments remained low and relatively stable ($p = 0.006$ for the species-by-core-type interaction).

Discussion

Bromus-dominated soils had higher total N, higher autumn NO_3^- concentrations, higher decomposition rates, distinct soil faunal communities, higher potential nitrification rates, and higher spring gross mineralization and nitrification rates than soils from *Artemisia* and *Elymus* stands. Total soil N in surface soils under *Bromus* was variable, but was on average about 20% higher than under perennials. Three scenarios might account for this result. First, higher soil N under *Bromus* could be related to manure and urine deposition by cattle during the winter months when the site is grazed. However, vegetation patches are small and closely intermixed at Curlew Valley, and transect surveys revealed no differences in manure deposits among vegetation types (Booth, unpub. data). Second, higher total soil N could predate *Bromus* invasion and instead relate to former plant or cryptobiotic crust distribution. While this possibility cannot be excluded, historical photographs and data indicate that the scale of vegetation patchiness at the site has increased greatly with grass invasion (Gates et al. 1956; Mitchell 1965; Rice and Westoby 1978). Former stands of half-shrubs were dense and homogenous, and plants were separated by just centimeters, whereas *Bromus* and *Elymus*-dominated areas now range from a meter to tens of meters in extent. Furthermore, the high overall δ^{15}N of *Bromus* soils is not consistent with N derived from cryptobiotic N fixation. Atmospherically derived N is operationally defined as having a δ^{15}N of 0‰, and its fixation into soils tends to decrease soil δ^{15}N.

A third possibility that may account for higher N in *Bromus* soils is that system N is distributed differently, or is more concentrated, under the annual grass than under *Elymus*. At Curlew Valley, *Bromus*-dominated soils are covered with a dense thatch, and aboveground litter inputs appear to be more homogenous than under perennials, where litter is concentrated beneath plants and interspaces are mostly bare. Results of other studies suggest that annuals may concentrate organic material in near-surface soils. At the Arid Lands Reserve in eastern Washington, the highest inorganic N concentrations in *Bromus* soils were found at the 0–5 cm depth, whereas perennial stands showed greater distribution of soil N with depth (Bolton et al. 1990). In a California annual grassland, Jackson et al. (1988) found the highest overall soil N concentration in the 0–4 cm layer, with 75% of root material in the top 10 cm, and concluded that at peak standing crop, only half of vegetative N was aboveground. A study in Southern Utah found that perennial grass stands recently invaded by *Bromus* had greater litter inputs than uninvaded stands (Evans et al. 2001).

The contrast in N distribution between the *Bromus* and *Elymus* systems may have consequences for N retention in the system as a whole. As grasses replaced half-shrubs at the site, some of the N formerly held in woody biomass was probably incorporated into grass biomass. Annual senescence by *Bromus* means that all such N is returned to the soil decompositional system a yearly basis. Microbial preferences for ^{14}N, and trace gas production associated with nitrification and denitrification which favors loss of the lighter ^{14}N isotope (Paul and Clark 1989; Shearer and Kohl 1993), could contribute to the concentration of ^{15}N in *Bromus* soils, particularly since inorganic N turnover and production rates appear to be higher under *Bromus* than under perennials. Because nitrogen fixation by cryptobiotic crust tends to decrease the δ^{15}N of soils, the differing isotopic signature of soil N in *Bromus* and perennial-dominated areas suggests that net loss of ^{14}N may exceed its replacement by symbiotic fixation in the annual system (Evans and Belnap 1999).

Because senescing perennial vegetation resorbs N for storage in belowground biomass (Clark 1977; Killingbeck and Whitford 1996), *Elymus* may retain and recycle N formerly held in woody biomass more effectively than does *Bromus*. *Elymus* relies on substantial retranslocation of carbohydrates (Coyne 1969) and N (Booth 2003) for regrowth of foliage, taking up relatively little inorganic N from the soil in autumn. Thus, the difference between *Elymus*-dominated and *Bromus*-dominated areas of about 43 g N m^{-2} in the top 10 cm of soil is probably partly accounted for by N held in perennial biomass. However, it is also possible that N loss in *Elymus*-dominated areas could contribute to the discrepancy between the two grass systems. In a grazed system, having relatively more N tied up in SOM, as it is in the annual system, may protect N stocks better than having N held in aboveground biomass. Without an assessment of total above- and belowground N pools in the different vegetation types, however, it is not possible to conclude whether one of the vegetational systems contains greater N stocks than the other.

Inputs to the SOM pool derived from annuals may increase soil microbial biomass, as was found in a California study (Hooper and Vitousek 1998), which may in turn account for the higher populations of bacterial grazers found in *Bromus* soils than perennial-dominated soils. The significance of higher nematode numbers in *Artemisia* soils than in *Bromus* soils is unclear, since nematodes were primarily of the bacterial- and fungal-feeding groups, with very few of the root grazers that might be expected in a perennial system. However, amoebae populations were eight-fold higher in *Bromus* soils than in *Artemisia* soils. Bacterial grazing by amoebae could contribute to the higher gross mineralization rates that were observed in *Bromus* soils. Because bacterial and mesofaunal C:N ratios are similar, a relatively large portion of N consumed by grazers is excreted, potentially enhancing soil NH_4^+ production (Clarholm 1981; Paul and Clark 1989). Nitrifiers are generally considered poor competitors for NH_4^+ relative to heterotrophs (Verhagen et al. 1992), and soil NH_4^+ availability appears to be the primary control on nitrification rates in many systems (Robertson 1982; Zak et al. 1990; Chen and Stark 2000). High gross mineralization rates in *Bromus*-dominated soils may enhance substrate supply to nitrifiers, allowing maintenance of a population that is almost double that in perennial-dominated soils and the higher gross nitrification rates that were observed under *Bromus*. Higher inorganic N production under *Bromus* implies greater N availability, even when soil inorganic N pools are small, due to a greater rate of pool replenishment.

The balance of inorganic N production and consumption

Even though gross mineralization and nitrification rates were higher under *Bromus*, soil inorganic N concentrations tended to be similar between the annual and perennial systems in the spring (Figure 2a), probably partly due to uptake by the annual grass. Germinating *Bromus* seedlings controlled soil NO_3^- concentrations in the fall root exclusion experiment, and *Bromus* continues to be a strong sink for N even when mature (Bilbrough and Caldwell 1997; Booth 2003). Microbial consumption also regulates inorganic N availability; high gross consumption rates in *Bromus* soils suggest that the microbial community is relatively carbon-rich and NH_4^+-limited in the spring (Chen and Stark 2000). This also appears to be the case in recently invaded perennial grass stands in Southern Utah, where the high C:N ratio of *Bromus* litter apparently has increased N immobilization relative to uninvaded stands (Evans et al. 2001).

At Curlew Valley, it is likely that microbial respiration through the spring reduces the C:N ratio of decomposing plant residues, permitting a net increase of inorganic N in drying soils concomitant with the cessation of plant N uptake following *Bromus* senescence. Environmental factors may also influence the balance of production and consumption. Heterotrophic NO_3^- assimilation appears to be more inhibited than nitrification by low soil water potentials, so that net nitrification can actually increase as soil moisture content decreases (Low et al. 1997). In 1997, the difference in NO_3^- consumption and production led to an increase in *Bromus* soils of 0.11 mg NO_3^--N kg^{-1} soil day^{-1} between 8 May and 13 August.

Such elevated NO_3^- availability may have been one factor contributing to the greater litterbag decomposition observed under *Bromus* than under *Artemisia*, since decomposers may have been less dependent on N contained in the decomposing material itself (Melillo et al. 1982). Additionally, microclimatic conditions or soil moisture availability in *Bromus* surface soils may have promoted decomposition, since microbial respiration is enhanced by even small increases in soil moisture content at summer temperatures (Wildung et al. 1975). Although *Bromus*-dominated soils tend to be drier than perennial-dominated soils in the spring, soil moisture from late season storms can accumulate in *Bromus*-dominated soils once the grass has senesced (Evans and Young, 1970; Figure 2b). Curlew Valley soils are extremely fine-textured, and the steepness of the soil moisture content/moisture potential relationship for the site means that small differences in water content in dry soils can translate to relatively greater differences in soil moisture potential (Dani Or, unpub. data).

Both plant uptake and microbial immobilization appear to be important for regulating inorganic N availability in autumn. In the root exclusion experiment, high net nitrification rates in *Bromus* root-exclusion tubes between Weeks 2 and 4 were matched by a large capacity for N uptake by germinating seedlings in unconfined soils. Similar patterns of increased late-summer N availability are also typical in California annual grasslands, where elevated soil NO_3^- concentrations decrease after annual grasses germinate (Jones and Woodmansee 1979; Jackson et al. 1988; Schimel et al. 1989), and NO_3^- can constitute 50–75% of N uptake by germinating seedlings (Schimel et al. 1989). In contrast, net nitrification appeared to be inherently low in *Artemisia* and *Elymus* soils, barely differing in root-exclusion tubes and unconfined soils. It is possible that roots growing from beneath the open-bottom tubes may have reduced soil NO_3^- concentrations in *Artemisia* and *Elymus* root-exclusion tubes. However, previous work using tubes of the same dimension at Curlew Valley indicated that *Artemisia* roots inside the tubes were effectively kept at one-sixth the density of roots outside the tubes from May to October (Reichenberger and Pyke 1990), thus it seems unlikely that significant root invasion had occurred after only four weeks of the current experiment. Generally lower NH_4^+

concentrations in root-exclusion tubes than in unconfined soils on 12 October (Figure 4) may have been due to uptake by nitrifiers which had increased in the absence of plant root competition (Zak et al. 1990). However, NH_4^+ production also may have been stimulated in unconfined soils, if C exudates from proliferating roots promoted microbial population growth, and thus protozoan grazing and excretion of NH_4^+ (Elliot 1978; Clarholm 1985).

Significance of altered N dynamics in Bromus soils

Aside from the increased risk of fire in annual-dominated systems, a shift to *Bromus* dominance may have important consequences for ecosystem function in unburned systems. Whether *Bromus* itself has caused a concentration of N in surface soils, or whether the annual colonized areas of already increased soil N, the absence of plant uptake following senescence appears to allow accumulation soil NO_3^- relative to perennial-dominated areas. Typical NO_3^- concentrations for *Bromus* soils in autumn (5 to 15 mg NO_3^--N kg^{-1} soil, but sometimes much higher) represented from 0.5 to 1.4% of total soil N. In contrast, *Artemisia* and *Elymus* soil NO_3^- concentrations were usually less than 2 mg kg^{-1} soil, representing about 0.25% of total soil N in those communities. Increased gaseous loss of N could be one consequence of the shift in ecosystem N dynamics associated with *Bromus* dominance. Nitrification in California annual grasslands has been shown to induce emission of NO and N_2O, particularly in recently wetted soils (Davidson 1992; Hungate et al. 1997), and denitrification of accumulated NO_3^- occurs even in semi-arid systems (Peterjohn and Schlesinger 1990; Matson et al. 1991). Nitrate can also be lost in overland flow or leached to lower soil horizons in semi-arid systems (Jones and Woodmansee 1979). Losses of inorganic N have been recorded for annualized watersheds in California (Jackson et al. 1988), and a study in southwestern Spain found greater inorganic N losses under newly germinated annual grasses than perennial grasses, which mobilized N uptake quickly with the onset of autumn rains (Joffre 1990). In the autumn root-exclusion experiment at Curlew Valley, net immobilization in *Bromus* root-exclusion tubes occurred significantly later than NO_3^- uptake by seedlings in unconfined soils, highlighting the possibility of N loss prior to plant germination.

The role of fire is unquestionably of paramount importance for the spread of *Bromus* in the Intermountain West. However, autogenic factors may contribute to the stability and spread of *Bromus* in burned and unburned systems alike. *Bromus* is extremely responsive to NO_3^- (McLendon and Redente 1992), showing decreased seedling germination and growth following addition of the nitrification inhibitor nitrapyrin, or high-C substrates that promote NO_3^- immobilization (Young et al. 1995, 1997). High autumn NO_3^- concentrations in *Bromus*-dominated soils may favor continued recruitment and vitality of the annual grass and promote a nutrient regime that favors other opportunistic invaders (Bazzaz 1986; Maron and Connors 1996). Increasing atmospheric CO_2 may also favor the spread of the annual. Mayeux et al. (1994) reported that *Bromus* leaf area and tillering rates responded to elevated CO_2 more than those of several other C_3 species, including some perennial grasses. Furthermore, decreased transpiration under elevated CO_2 may increase soil moisture, thus increasing gross mineralization rates, as was found in a California annual grassland (Hungate et al. 1997). Since N limitation can attenuate plant response to increased CO_2 (Field et al. 1992; Polley 1997; Rastetter et al. 1997), feedbacks by *Bromus* on soil inorganic availability may extend annual grass response in a changing climate.

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