



Nitrogen dynamics in perennial- and annual-dominated arid rangeland

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It is often assumed that displacement of native perennial vegetation by exotic annuals will alter nutrient cycling. Nitrogen dynamics of native bunchgrass vegetation and adjacent stands of the exotic annual grass *Bromus tectorum* were compared on three sites in south-eastern Washington, U.S.A. The stands of *B. tectorum* had dominated the sites for at least 40 years. It should be emphasized that these sites were not prone to frequent wildfires as can be the case in some *B. tectorum*-dominated ecosystems. Over a 2-year period very few consistent differences were found between the two vegetation types in above-ground standing crop, root mass, *in situ* N mineralization, extractable soil N, or total soil C or N. *Bromus tectorum* above-ground plant mass and litter tended to have lower C/N ratios than did the native vegetation, but the results were not consistent over time or site. It appears that the exotic annual adapted to the resources on the site and, at least at the fairly gross level measured, had little impact on soil nitrogen. These results suggest that caution must be taken when assuming that a change in vegetation type and growth form will necessarily alter soil N levels.

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Introduction

A large portion of the Great Basin and Columbia Plateau in the northern United States was historically dominated by perennial bunchgrasses with varying proportions of the shrub, *Artemisia tridentata*. The Palouse Prairie of north-eastern Oregon and south-eastern Washington shares many species with the *Artemisia* steppe, but the plant communities tend to be grasslands more than shrub steppe. The vegetation of this region has been subject to climatic changes that have caused substantial shifts in vegetation patterns during the past 12,000 years (Miller & Wiegand, 1994). Species assemblages may be dynamic because plant species respond individually to climate changes (Tausch *et al.*, 1993). These authors suggested that the legacy of Quaternary climate change is plant communities that are not particularly stable. The lack of

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long-term evolutionary stability, in conjunction with indiscriminate grazing by domestic livestock during settlement may have opened this region to invasion by the non-indigenous alien annual, *Bromus tectorum* (L).

The chance introduction of *B. tectorum* approximately 100 years ago has profoundly influenced the vegetation of the region. Upadhyaya *et al.* (1986) assert that, 'Seldom in recent history has the vegetation of such a large area been transformed so rapidly and probably so permanently, as has been demonstrated by the invasion and spread of cheatgrass (*B. tectorum*) in the Great Basin and Columbia Basin area'. Billings (1990) suggested that *B. tectorum* may reduce the biotic diversity of the *Artemisia* biome by eliminating some plant and animal species, and probably altering entire ecosystems.

It is well-documented that *B. tectorum* disrupts the natural successional tendency of native rangeland communities (Mack, 1981; Billings, 1990). The ability of *B. tectorum* to extend roots at low soil temperatures and its intrinsic growth rate and efficiency have been used to explain the success of this species (Miller *et al.*, 1994). However, it is unclear whether *B. tectorum* maintains long-term site dominance through competition or whether this invasive annual alters site chemistry in its favour. Rangeland managers often assume that the inability to revegetate *B. tectorum*-dominated rangelands with native species is an indication that the site has been altered. Some of the earlier literature on this subject demonstrated that significant erosional loss of N could occur on *B. tectorum*-dominated rangeland (Haupt, 1956). In some areas of the western U.S., the invasion of *B. tectorum* has resulted in an increased fire frequency, which may increase the risk of erosion. However, Young (1943) reported that replacement of native vegetation with *B. tectorum* in the Palouse Prairie did not necessarily mean soil fertility had been affected, unless significant erosional losses had occurred.

In recent years there has been increasing recognition that soil processes in general (Whitford & Herrick, 1995) and specifically nitrogen cycling may play an important role in successional dynamics (McLendon & Redente, 1991; Tilman & Wedin, 1991). In an *Artemisia*-steppe community, McLendon & Redente (1991) demonstrated that annuals would dominate a disturbed site longer if nitrogen was added. Many studies of succession and nitrogen have focused on disturbance or relatively short-term effects of species composition. In the present study, *in situ* nitrogen dynamics of adjacent communities that were dominated by either *B. tectorum* or native bunchgrass species were compared. The annual community had been dominated by *B. tectorum* for at least 40 years, but fire was not a major factor in these communities. Because annuals cannot sequester N in live tissue between growing seasons as can the perennial species, it was hypothesized that: (1) the annual-dominated site would have a larger portion of its N pool subject to leaching and erosion; and (2) with time, the total N pool would be lower in the annual community compared to the perennial community.

Methods

Study sites

This study was conducted on three sites located in south-eastern Washington during 1993 and 1994. All sites lie within the *Artemisia tridentata*/*Agropyron spicatum* association (Franklin & Dyrness, 1973). This association occupies the centre of the Columbia Basin province and extends west to the foothills of the Cascade Range. Sites were selected that had discrete boundaries between native plant communities and communities dominated by nearly 100% *B. tectorum*. Native vegetation consisted of three layers: (1) a sparse: (1–3% cover) shrub layer composed primarily of *Artemisia tridentata*; (2) a middle layer of *Agropyron spicatum* and *Stipa comata* in equal proportion; and (3) a lower layer of *Poa sandbergii*. Based on species composition and the surface crust of crustose lichens (*Tortula brevipes* and *Tortula princeps*) and acrocarpous mosses (such as *Aloina rigida*),

native portions of the sites appeared near their climatic climax. The annual grassland portion of each site was historically similar to the native portion, but disturbance by either livestock over-grazing during the early 1900s, and/or the building of roads during the 1920s allowed *B. tectorum* to become the prominent grass species. Aerial photos available at the local U.S. Department of Agriculture-Natural Resources Conservation Service office indicate that by 1950 *B. tectorum* dominated substantial portions of the study area. Earlier photos are not available. Despite the dominance by *B. tectorum*, wildfires are infrequent.

Each study site encompassed about 0.1 ha and was selected in the spring of 1993 based on ocular estimates of density of autumn-germinated *B. tectorum* seedlings and the residual standing crop of *A. spicatum* and *S. comata*. Standing crop was our best indicator of potential species composition during the current growing season. All sites were within 30 km of each other. Topography ranged from gently sloping (< 2%) to level. The soils were silty and sandy, mixed with small amounts of windblown ash (USDA-NRCS, 1971). All sites have an effective rooting zone greater than 150 cm. Site 1 was located about 14 km west of Plymouth, WA (119°27' N; 45°55' W). Soils on this site were Quincy loamy sand (mixed, mesic Xeric Torripsamments). Annual precipitation ranges from 152 to 203 mm. Temperature extremes for this site range from 53 to -34°C with an average frost-free period of 165 days. Elevation is about 100 m. Site 2, located about 7 km north-west of Plymouth, WA (119°26' N; 46°03' W), was a well-drained Warden very fine sandy loam (coarse-silty, mixed, super-active, mesic Xeric Haplocambid). Annual precipitation ranges from 152 to 228 mm. Temperature extremes for this site range from 50 to -34°C with an average frost-free period of 150 days. Elevation is about 450 m. Site 3 was located 14 km north of Plymouth, WA (119°22' N; 46°06' W). Soils on site 3 were a Ritzville silt loam (coarse-silty, mixed, super-active, mesic Calcicidic Haploxeroll). Annual precipitation ranges from 228 to 304 mm. Temperature extremes for the sites range from 48 to -36°C with an average frost-free period of 145 days. Elevation is about 550 m. Temperature and precipitation were monitored daily at weather stations within 1 km of each site (Fig. 1). Weather data

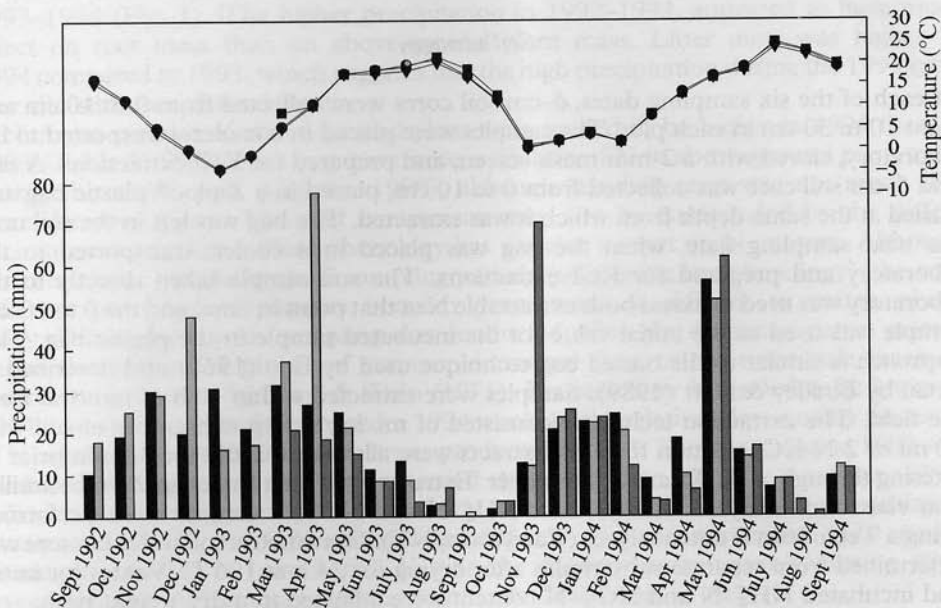


Figure 1. Monthly precipitation and temperature for the three sites used in this study. ■ Site 1; ▒ Site 2; ■ Site 3.

were obtained from the Public Agricultural Weather System (PAWS). Details on collection methods can be found at <http://index@prosser.wsu.edu/>.

At each site, five 10 × 3 m blocks were located along the community boundary. The blocks extended 5 m into each community and were spaced at least 10 m apart. Within each block 0.5 m² plots were randomly selected for sampling on each individual date. KCl extractable N and nitrogen mineralization were sampled on the following dates: 4 May, 28 June, and 18 August, 1993, and 27 March, 28 June, and 23 July, 1994. Above- and below-ground biomass and plant litter were sampled on the same dates, but in this study peak standing crop values were presented which occurred on 28 June 1993 and 28 May 1994. The wet growing season in 1993 delayed peak standing crop relative to the dry 1994 growing season.

Plant and litter

One 0.5 m² plot was clipped to ground level in each treatment/block/site combination on both sampling dates. All plant species were included in the clipping and care was taken to include only the current year's growth. Standing litter was added to litter from the ground surface within the 0.5 m² plot. Roots were harvested from 0 to 10 cm using a (7.6 cm) soil tube (Giddings Machine Co., Ft. Collins, CO)*. Roots were separated from soil in the field by sieving through a 4.0 mm mesh screen. The distinction between dead and living roots was made visually based on observation of their colour integrity. A separate root sample was harvested at each depth for chemical analysis. Root samples were analysed for length with a root length scanner (Comair Corp., Melbourne, Australia)

Above- and below-ground mass and litter were dried at 60°C for 48 h, and weighed. After weighing, the samples were ground in a Udy Mill (Udy Corp., Ft. Collins, CO) and analysed for C and N in a Perkin Elmer 2400 Series II CHNS/O analyser (Perkin Elmer, Norwalk, CT). Bulk soil collected at the end of the study (28 May 1994) was also analysed for total C and N.

Soil nitrogen

At each of the six sampling dates, 5-cm soil cores were collected from 0 to 10 cm and from 10 to 30 cm in each plot. The samples were placed in a cooler, transported to the laboratory, sieved with a 2-mm mesh screen, and prepared for KCl extractions. A second 5-cm soil core was collected from 0 to 10 cm, placed in a Ziploc[®] plastic bag and buried at the same depth from which it was extracted. The bag was left in the soil until the next sampling date, when the bag was placed in a cooler, transported to the laboratory and prepared for KCl extractions. The soil sample taken directly to the laboratory was used to assess both extractable N at that point in time, and the 0 to 10-cm sample was used as the initial value for the incubated sample in the plastic bag. This approach is similar to the buried bag technique used by Eno (1960) and described in detail by Binkley & Hart (1989). Samples were extracted within 10 h of removal from the field. The extraction technique consisted of mixing a 10 g subsample of soil with 50 ml of 2 N KCl solution for 1 h. Extracts were allowed to settle for 30 min prior to filtering through #42 Whatley filter paper. Extracts were then frozen in 20-ml scintillation vials until analysed. Analyses for NH₄⁺-N and NO₃⁻-N content were performed using a Technicon II autoanalyser (Tarrytown, NY). Gravimetric soil water content was determined from separate subsamples after drying for 24 h at 106°C. Values for initial and incubated NH₄⁺-N and NO₃⁻-N content were adjusted to a dry weight basis.

*Mention of trade name does not indicate endorsement by USDA or Montana State University.

Net N mineralization, net nitrification, and net ammonification were calculated by subtracting ambient levels of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ accumulated in the incubated samples at the end of the incubation period (Pastor *et al.*, 1984; Binkley & Hart, 1989). The following equations were used to determine net ammonification, net nitrification, and net N mineralization.

$$\text{Net ammonification} = \text{NH}_4^+_{(\text{incubated})} - \text{NH}_4^+_{(\text{initial})} \quad (1)$$

$$\text{Net nitrification} = \text{NO}_3^-_{(\text{incubated})} - \text{NO}_3^-_{(\text{initial})} \quad (2)$$

$$\text{Net N mineralization} = (\text{NH}_4^+ + \text{NO}_3^-)_{\text{incubated}} - (\text{NH}_4^+ + \text{NO}_3^-)_{\text{initial}} \quad (3)$$

Pastor *et al.* (1984) referred to the net change in $\text{NO}_3^-\text{-N}$ as 'net apparent nitrification'. It should be emphasized that the technique only measures net change over the incubation period and thus integrates over the various processes that control changes in $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$.

All variables measured only once during a year were analysed with paired-plot ANOVA techniques, and variables measured at multiple dates were analysed as split plots in time (Peterson, 1985). It was found that year tended to strongly interact with community, depth, and date within year, and there were also site interactions. Therefore, years and sites were analysed separately to help simplify the presentation of results. Statistical analyses were conducted using PROC GLM in the SAS software package (SAS, 1994). Arithmetic means and standard errors are presented.

Results

It was difficult to establish consistent differences in mass attributes of the two communities (Table 1). For example, the native community tended to have higher root mass than *B. tectorum* on site 1, but not site 2. Results were dependent on year for site 3, although differences were not statistically significant ($p > 0.05$). It is surprising that the differences among years were not larger, given that crop year precipitation (September to September) was over twice as great in 1992–1993, compared to 1993–1994 (Fig. 1). The higher precipitation in 1992–1993, appeared to have more effect on root mass than on above-ground plant mass. Litter mass was higher in 1994 compared to 1993, which suggests that the high precipitation during the 1993 crop year did stimulate detrital inputs.

Nitrogen content of above-ground plant mass tended to be higher in 1994 than in 1993 (Table 2). The cause may have been a dilution of N in above-ground plant mass during the wetter year (Chapin, 1980), although standing crop was not much different between years. The year comparison may also be confounded by the difference in sampling dates. Plant phenology has a major impact on N content. Although per cent N was low during both sampling periods (suggesting late phenology), the very different precipitation patterns between years made it difficult to match phenology. During both years sampling was conducted when the dominant native grasses began showing initial phases of summer dormancy (leaf colour turns pale green to brownish) as defined by West & Wein (1971). Per cent litter N tended to be lower in 1994 than in 1993. The litter input for 1994 would be the relatively low-quality (in terms of N) above-ground plant mass that was produced in 1993. The litter input to 1993 was produced during a dry year that preceded the study (Fig. 1). The low litter values indicate that above-ground plant production was low in 1992. There were no consistent patterns of C, N, or C/N among the different plant communities. The native community tended to have higher N than the *B. tectorum* community during 1993 (except on site 1), but there were no significant differences in 1994.

There were also few significant differences in root C, N and root C/N ratios between the plant communities (Table 3). There was a significant main effect for

Table 1. Above- and below-ground plant mass, litter, and root length density of *Bromus tectorum* (BT) and native (NA) plant communities at several different locations ($n = 5$ for each mean value)*

Site and date	Community (g m^{-2})	Shoot mass (g m^{-2})	Litter (g m^{-2})	Root mass (g m^{-2})		Total	Root length density (cm cm^{-3})	
				0-10 cm	10-30 cm		0-10 cm	10-30 cm
Site 1	June 1993	BT	8.9	92.3	35.9	128.2	6.8	5.1
		NA	31.7 ^b	117.7	80.0	197.7	10.1	4.2
	May 1994	BT	41.9	25.1 ^b	7.8 ^b	32.9 ^b	5.6 ^b	0.5
		NA	24.3	100.7 ^a	29.3 ^a	130.0 ^a	21.1 ^a	0.7
Site 2	June 1993	BT	10.9	59.0	35.2	94.2	3.7	3.4
		NA	59.1	48.6	32.5	81.1	3.8	1.2
	May 1994	BT	34.6	30.0	10.5	40.6	3.8	0.3
		NA	67.3	34.0	8.7	42.6	5.4	0.3
Site 3	June 1993	BT	34.4	63.0	47.4	110.3	6.3	4.3 ^a
		NA	44.5	140.3	45.9	185.9	12.9	2.3 ^b
	May 1994	BT	27.8	37.0	13.4	50.4	4.7	0.9
		NA	31.4	49.2	8.6	57.8	9.6	0.3

*Superscript letters indicate significant differences ($p < 0.05$) between communities within site and year.

Table 2. Carbon, nitrogen, and C/N ratio of above-ground plant mass, and litter in *B. tectorum* (BT) and native (NA) plant communities at several locations (n = 5 for each mean value)*

Site and date	Community	Above-ground plant			Litter		
		% C	% N	C/N	% C	% N	C/N
Site 1							
June 1993	BT	43.4 ^a	0.56	80.2	34.5	1.34	25.6
	NA	44.0 ^b	0.51	89.1	29.5	0.86	36.5
May 1994	BT	40.5 ^b	1.00	41.5	32.4	0.83	38.6
	NA	43.9 ^a	0.72	73.7	18.6	0.54	34.6
Site 2							
June 1993	BT	43.0 ^b	0.40 ^b	119.7 ^a	32.4	0.72	45.1
	NA	44.2 ^a	0.64 ^a	73.0 ^b	23.8	0.60	39.5
May 1994	BT	39.9	0.58	70.2	28.1	0.52	54.0 ^a
	NA	42.0	0.79	56.1	16.3	0.71	24.2 ^b
Site 3							
June 1993	BT	42.7	0.41 ^b	118.2 ^a	34.1	0.67	50.7
	NA	42.7	0.68 ^a	65.3 ^b	40.4	0.90	45.6
May 1994	BT	40.8	0.82	50.7	—	—	—
	NA	42.0	0.78	57.5	—	—	—

* Superscript letters indicate significant differences ($p < 0.05$) between communities within site and year.

depth in some year/site combinations. When depth was significant for N, the upper profile roots (0–10 cm) tended to have higher N values than roots from the lower profile (10–30 cm).

There were also no community differences for soil C, N, or C/N ratio for soil sampled at the end of the study (Table 4). When averaged over the three sites, values for the *B. tectorum* and native communities were very similar.

There were no differences in rates of ammonification between communities, nitrification, or total N mineralization on any site during either year (Fig. 2). The most active period of N mineralization was spring of 1993.

There were also no differences between communities for extractable NH_4^+ (Fig. 3). There was an accumulation of extractable NO_3^- in upper profile soils beneath *B. tectorum* during the summer of 1994. On sites 2 and 3, the upper profile soil under the native community also exhibited increased NO_3^- levels during the latter part of 1994. On site 2 there was also an increase in NO_3^- during July 1994 in the lower depth (10–30 cm) under the *B. tectorum* community. Total extractable N tended to be lowest during the spring sampling of each year.

Discussion

No substantial evidence was found in this study that more than 40 years of dominance by the annual *B. tectorum* has altered total soil N, extractable N, or N mineralization. In fact, we found very few differences between native bunchgrass and *B. tectorum* communities for any of the variables measured. Our results contrast with those of Joffre (1990) who compared annual and perennial grassland in south-western Spain. This author found that compared to the annual site, the perennial site had higher

Table 3. Carbon, nitrogen, and C/N ratio for roots of *B. tectorum* (BT) and native (NA) plant communities at two soil depths. Within site and year, we listed all cases where plant community (trt), depth, or trt \times depth interactions were significant ($p < 0.05$) or approached significance ($p < 0.10$)

Site and date	Community	Depth	% C	% N	C/N		
Site 1 June 1993	BT	0-10	trt $p = 0.04$ 39.8	0.72	58.3		
	NA	0-10		0.74	43.9		
	BT	10-30		0.68	49.0		
	NA	10-30		0.50	58.7		
	May 1994	BT	0-10	trt $p = 0.07$ 22.1	1.17	19.5	
		NA	0-10		0.89	24.8	
		BT	10-30		1.02	28.2	
		NA	10-30		0.72	39.1	
		BT	0-10		depth $p = 0.04$ 41.4	0.81	54.4
		NA	0-10			1.00	38.1
	Site 2 June 1993	BT	10-30	35.3	0.58	62.9	
		NA	10-30		0.61	54.9	
BT		0-10	depth $p = 0.03$ 23.7	0.93	24.3		
NA		0-10		1.03	—		
BT		10-30		—	—		
NA		10-30		1.0	31.3		
Site 3 June 1993	BT	0-10	depth $p = 0.02$ 41.5	0.90	47.0		
	NA	0-10		0.65	50.1		
	BT	10-30		0.50	69.2		
	NA	10-30		0.56	70.7		
	May 1994	BT	0-10	depth $p = 0.01$ 18.6	0.71	26.6	
		NA	0-10		0.87	29.2	
		BT	10-30		1.03	39.8	
		NA	10-30		0.95	38.5	
		BT	0-10		trt depth $p = 0.07$ 25.6	0.71	26.6
		NA	0-10			0.87	29.2
	May 1994	BT	10-30	40.6	1.03	39.8	
		NA	10-30		0.95	38.5	

Table 4. Total soil carbon (C), total soil nitrogen, and C/N ratio for *B. tectorum* (BT) and native (NA) plant communities. Soil was sampled at the end of the study (23 July 1994)*

Site	Community	% C	% N	C/N
1	BT	0.38	0.039	9.4
	NA	0.28	0.031	9.8
2	BT	0.46	0.043	12.6
	NA	0.44	0.043	13.6
3	BT	0.34	0.021	18.0
	NA	0.29	0.020	19.0
Mean	BT	0.39	0.034	13.5
	NA	0.33	0.032	13.4

* Samples were taken at 0–10 cm and 10–30 cm, but depth was not significant and did not interact with treatment. Thus, means are averaged over depth.

N mineralization, higher immobilization of N in biomass, and lower leaching of mineral N. However, Bolton *et al.* (1990) found no difference in N mineralization potential between a perennial sagebrush steppe community and a *B. tectorum* annual grassland. Their study site was within 120 km of the present site in a similar climatic zone, and they concluded that the shrub steppe and annual grassland had similar soil N dynamics. The contrasting results for south-eastern Spain and the north-western U.S. may be a result of differences in plant growth and climatic patterns. Joffre (1990) states that in Spain, autumn rains leach mineral N from soils supporting annual species because the annuals had just begun to germinate and could not sequester soil N. In our situation, germination also tends to occur in the autumn, but the majority of precipitation is received during winter and spring (Fig. 1). Low temperatures limit the growth of both the annual and perennial species during winter, and *B. tectorum* initiates root growth earlier than the native species (Harris, 1967). *Bromus tectorum* has sufficient shoot and root growth by early spring to begin using available soil N, which probably explains the similarity in extractable soil N for *B. tectorum* and the native community during spring (Fig. 3). There is a tendency for the *B. tectorum* soil to have slightly higher extractable N than native community soil after mid-summer. Peak above-ground standing crop normally occurs by mid-June and there would be little demand for N after peak standing crop. The late summer increase in extractable N, especially during the dry year (1994) probably results from the fact that annuals cannot store N in perenniating structures as can the native bunchgrasses.

The research of McLendon & Redente (1991), Tilman & Wedin (1991) and Wedin & Pastor (1993) has demonstrated that soil N can play a critical role in plant succession. McLendon & Redente (1991) found that the dominance of a site by annuals during the early stages of secondary succession was related to high nutrient availability. In fact, the addition of N altered the successional pattern by lengthening the period of annual dominance. This research was conducted in a semi-arid sagebrush steppe community in north-western Colorado. In a mesic prairie in Minnesota, Tilman & Wedin (1991) found that the higher successional stage prairie grasses were able to reduce soil solution N levels more effectively than early successional species. They concluded that early successional species may be superior colonists, but inferior nitrogen competitors compared to the high successional prairie grasses. The present comparison between native grassland and annual grassland is conceptually different from the successional studies. In this situation, the annual grassland is a different 'steady state', rather than

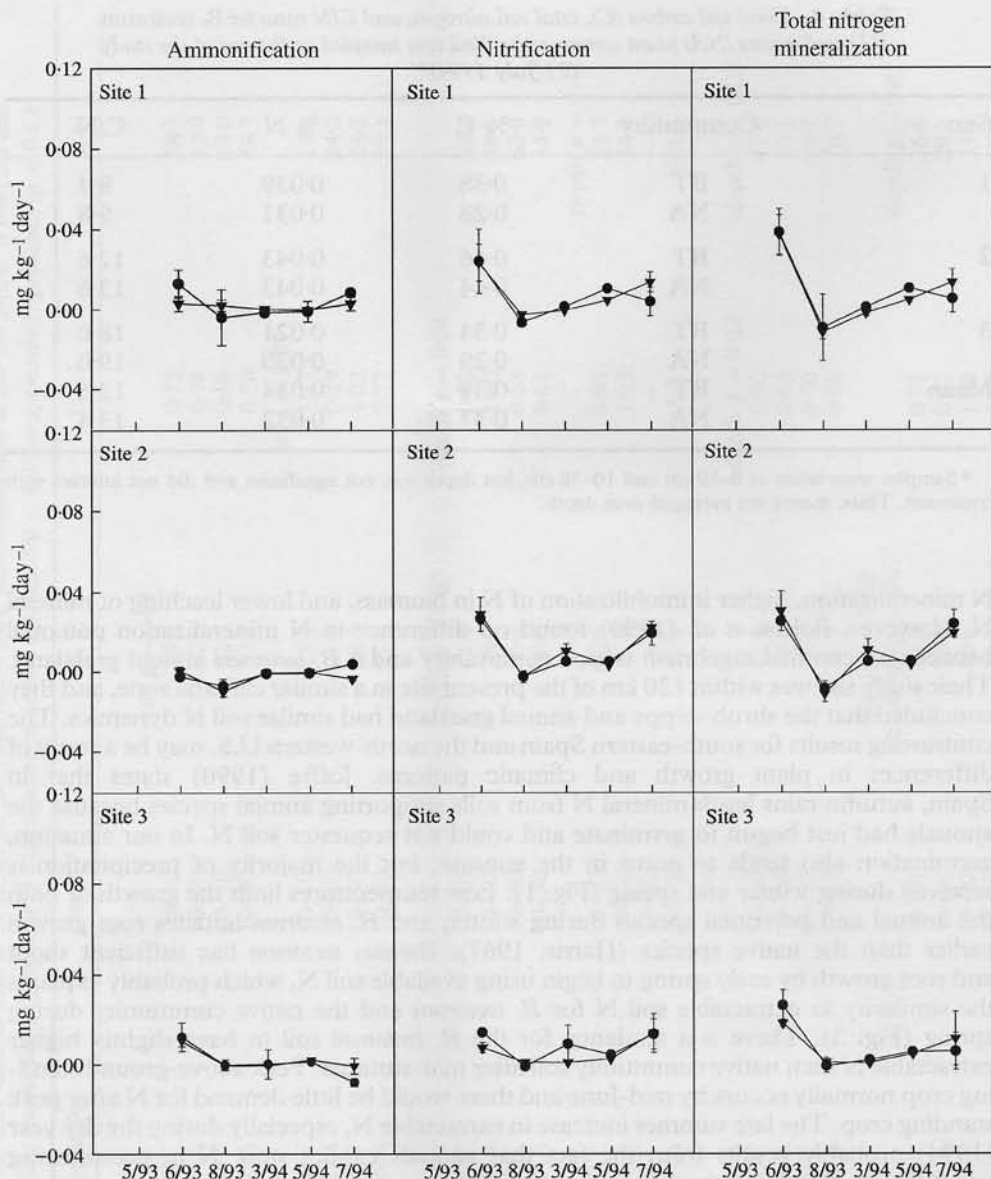


Figure 2. Seasonal patterns in net ammonification, net nitrification and total net nitrogen mineralization for cheatgrass (*Bromus tectorum*) and native bunchgrass communities on the three study sites. Units are expressed as mg N kg⁻¹ day⁻¹ over the sampling period. ●— cheatgrass; ▼— native.

simply a lower successional stage of the perennial grassland. Thus, the concepts that apply to successional sequences appear not to apply to the present situation.

The results of this study have implications for the debate over steady states and thresholds in rangeland ecology (Westoby *et al.*, 1989; Friedel, 1991; Laycock, 1991). It has often been assumed that changes in steady states and the crossing of thresholds is related to woody plant dominance and/or soil degradation (Friedel, 1991). The shift to annual dominance may also be viewed as a threshold shift, but the mechanism is unclear.

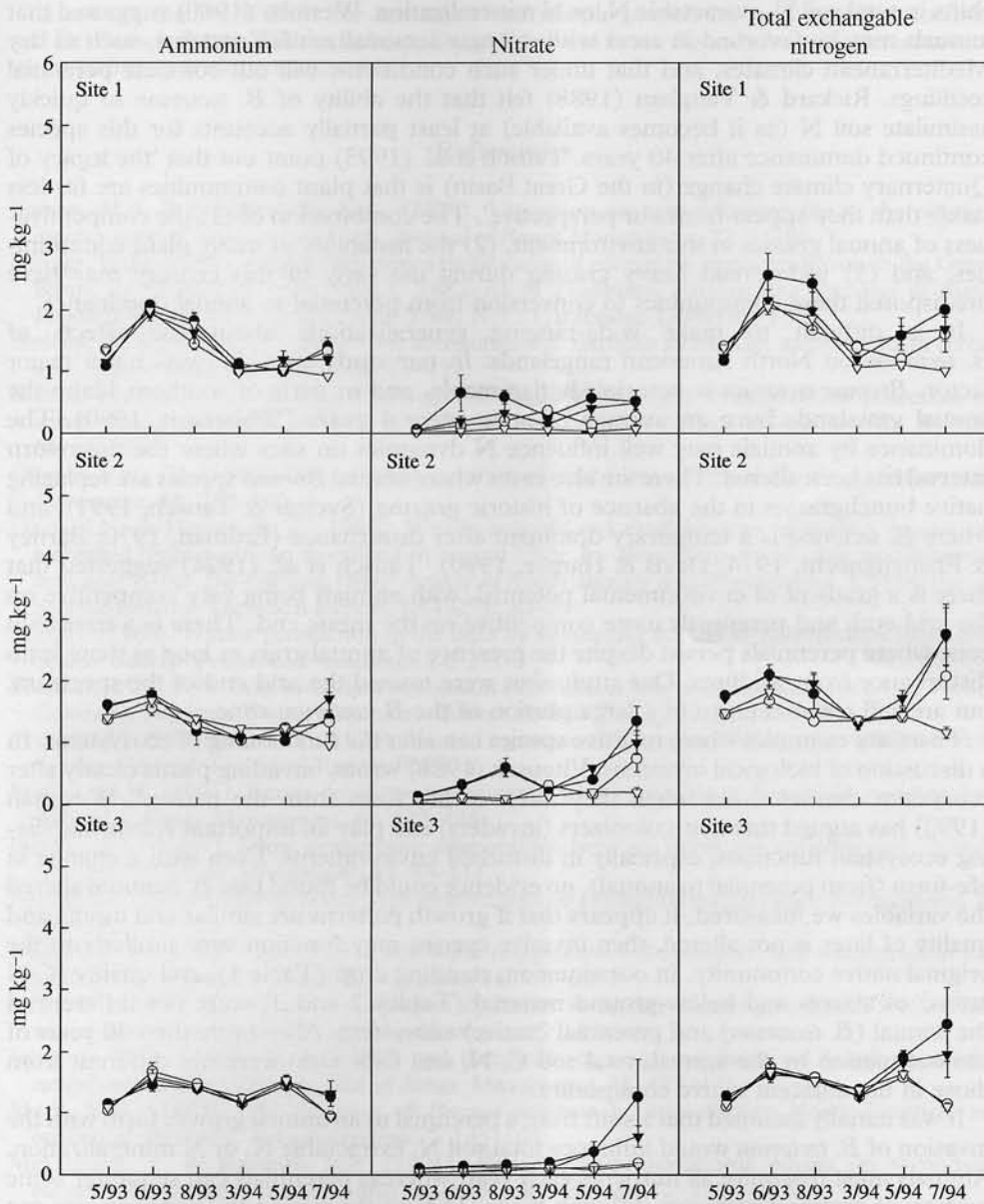


Figure 3. Seasonal patterns in KCl extractable ammonium ($\text{NH}_4^+\text{-N}$), extractable nitrate ($\text{NH}_4^+\text{-N}$), and total extractable nitrogen at two depths (0–10 and 10–30 cm) for cheatgrass (*Bromus tectorum*) and native bunchgrass communities on the three study sites. Units are mg N kg soil⁻¹ at each individual sampling time. —●— cheatgrass 0–10 cm; —○— cheatgrass 10–30 cm, —▼— native 0–10 cm; —▽— native 10–30 cm.

B. tectorum is a very effective competitor against seedlings of perennial species (Hull, 1963; Harris, 1967), and has displaced native bunchgrasses in large areas of the Great Basin and interior Pacific North-west. However, it is unclear whether the heavy grazing that may have initially caused the reduction in bunchgrasses and favoured the shift to *B. tectorum* also caused changes in N cycling. Our results suggest that the *B. tectorum* annual grassland is maintained through competitive interaction, rather than

shifts in total soil N, extractable N, or N mineralization. Westoby (1980) suggested that annuals may be favored in areas with strongly seasonal rainfall patterns, such as dry Mediterranean climates, and that under such conditions, will out-compete perennial seedlings. Rickard & Vaughan (1988) felt that the ability of *B. tectorum* to quickly assimilate soil N (as it becomes available) at least partially accounts for this species continued dominance after 40 years. Tausch *et al.* (1993) point out that 'the legacy of Quaternary climate change (in the Great Basin) is that plant communities are far less stable than they appear from our perspective'. The combination of (1) the competitiveness of annual grasses in this environment, (2) the instability of many plant communities, and (3) widespread heavy grazing during the early of this century may have predisposed these communities to conversion from perennial to annual dominance.

It is difficult to make wide-ranging generalizations about the effects of *B. tectorum* on North American rangelands. In our study sites, fire was not a major factor. *Bromus tectorum* is notoriously flammable, and in parts of southern Idaho the annual grasslands burn an average of once every 4 years (Whisenant, 1990). The dominance by annuals may well influence N dynamics on sites where the fire return interval has been altered. There are also cases where annual *Bromus* species are replacing native bunchgrasses in the absence of historic grazing (Svejcar & Tausch, 1991), and where *B. tectorum* is a temporary dominant after disturbance (Erdman, 1970; Barney & Frishcknecht, 1974; Davis & Harper, 1990). Tausch *et al.* (1994) suggested that there is a gradient of environmental potential, with annuals being very competitive on the arid end, and perennials more competitive on the mesic end. There is a transition zone where perennials persist despite the presence of annual grass as long as there is no disturbance from wildfires. Our study sites were toward the arid end of the spectrum, but are still representative of a large portion of the *B. tectorum* zone.

There are examples where invasive species can alter the functioning of ecosystems. In a discussion of biological invasions, Vitousek (1986) wrote, 'invading plants clearly alter ecosystem characteristics when they differ in life form from the natives'. Westman (1990) has argued that new colonizers (invaders) can play an important role in stabilizing ecosystem functions, especially in disturbed environments. Even with a change in life-form (from perennial to annual), no evidence could be found that *B. tectorum* altered the variables we measured. It appears that if growth patterns are similar and inputs and quality of litter is not altered, then invasive species may function very similarly to the original native community. In our situation, standing crop (Table 1), and quality (C/N ratios) of above- and below-ground material (Tables 2 and 3) were not different in the annual (*B. tectorum*) and perennial (native) ecosystem. After more than 40 years of site occupation by the annual, total soil C, N, and C/N ratio were not different from those in the adjacent native community.

It was initially assumed that a shift from a perennial to an annual growth form with the invasion of *B. tectorum* would influence total soil N, extractable N, or N mineralization. Annuals must reacquire all nutrients each year, whereas perennials can sequester some portion of required nutrients in living tissue. During the period the nutrients are not bound in tissue, they may be susceptible to leaching (e.g. Joffre, 1990), or erosional losses (Haupt, 1956). Over time, loss of nutrient capital might deplete the fertility of a site. There is also evidence that increased N availability can extend the period during which annuals dominate a disturbed site (McLendon & Redente, 1991). It might be possible to have a situation where fertility is gradually depleted and yet available N remains fairly high, since available N is a small proportion of total N. In fact, neither were found to be the case. Site fertility or at least total soil C, N, and C/N ratio were not affected by annual dominance, and neither was extractable nor mineralizable N. The invasive species adapted to the resources available and had little consistent impact on any of the parameters we measured. That is not to say that other components of N cycling may not be influenced. But at the gross level of total soil N, N mineralization, and extractable N, the two growth forms functioned in a similar fashion.

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