

# Cheatgrass Invasion Alters Soil Morphology and Organic Matter Dynamics in Big Sagebrush-Steppe Rangelands

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**Abstract:** Cheatgrass (*Bromus tectorum* L.) is an invasive annual grass that increases wildfire frequency, degrades native ecosystems, and threatens agriculture across vast areas of the Western United States. This research examines how cheatgrass invasion may alter physical and biological properties of soils. Proliferation of very fine roots and high production of low-quality litter by cheatgrass increases porosity and near-surface microbial activity, which may enhance decomposition of soil organic matter (SOM) similar to cultivated systems. This may enlarge active SOM pools (mineral and microbial biomass C and N) at the expense of slow pools and humus. To test this hypothesis, soil properties beneath long-term cheatgrass-invaded areas were compared with carefully matched soils under shrub canopies and grass-covered interspaces at seven undisturbed Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) plant communities in northern Utah and southeastern Idaho. Soils under cheatgrass had (1) higher porosity in surface horizons, (2) higher concentrations of mineral N throughout the soil profiles at the time of sampling, and (3) a larger proportion of mineralizable C and N in total SOM of surface horizons than soil under native shrub-steppe plant communities. These results support our hypothesis and suggest that long-term cheatgrass invasion may alter ecological stability and resilience by depleting slow and passive SOM pools. This research will contribute to improved understanding of fundamental ecosystem processes required for successful ecological restoration.

## Introduction

The exotic annual grass cheatgrass (*Bromus tectorum* L.) has invaded large areas of shrub-steppe ecosystems in the

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Western United States, and is now dominant on much of the Great Basin, Snake River Plain, and Columbia Plain physiographic provinces (Knapp 1996; Knick 1999; Mack 1981). The area covered by cheatgrass and its ecological impact on shrub-steppe plant communities rivals ecosystem conversion from grasslands to annual crops that took place in Central North American (Samson and Knopf 1994). Numerous investigations of native ecosystem conversion to croplands provide an understanding of agriculture-related environmental change, particularly of nutrient cycling and soil organic matter (SOM) dynamics in both natural and disturbed ecosystems (Parton and others 1987; Schimel 1986). As impacts of invasive plants on ecosystem processes begin to be understood (D'Antonio and Vitousek 1992; Ehrenfeld and Scott 2001), application of concepts from cropland conversion may further this understanding. In this paper, we describe research that compared soils under cheatgrass to those under native shrub-steppe grasslands. We discuss ecological parallels between annual crops and cheatgrass invasion and their implications for restoration of diverse native plant communities.

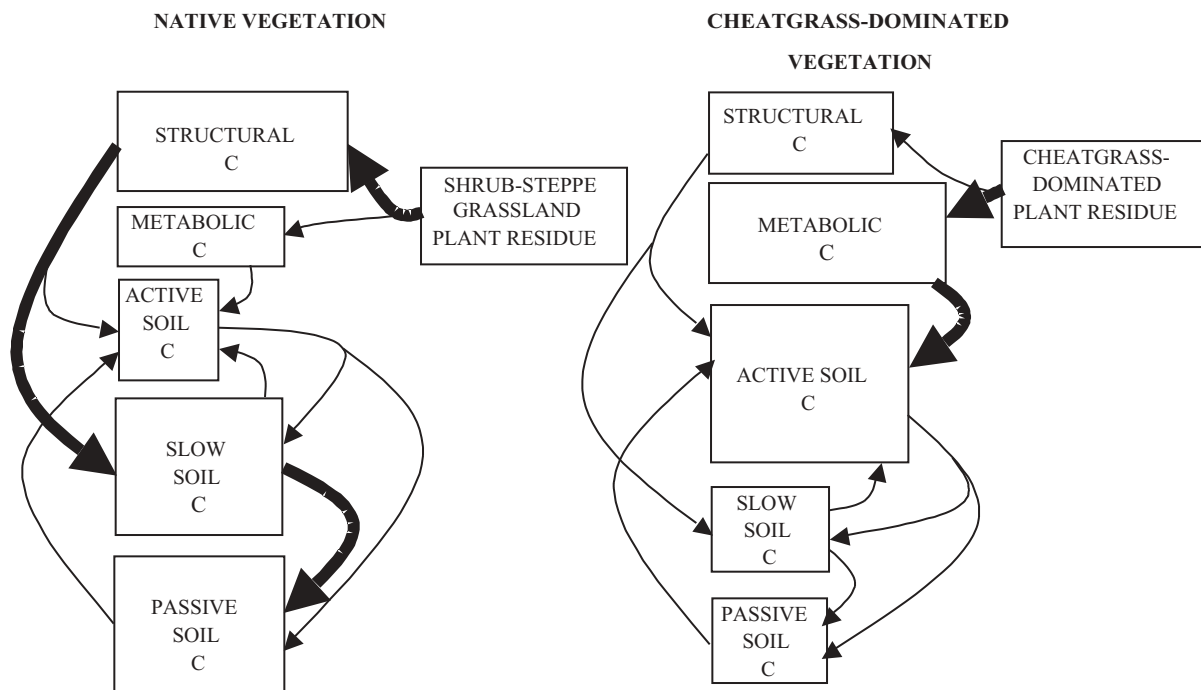
On a worldwide basis, conversion of native ecosystems to cropland results in about a 30-percent long-term decrease in soil organic carbon (SOC). Annually, such conversion accounts for nearly one-fifth of the net carbon (C) transfer from terrestrial ecosystems to the atmosphere from changing land uses (Davidson and Ackerman 1993). In general, cropland conversion is thought to change native ecosystems from net C sinks to important sources of atmospheric CO<sub>2</sub> (Schlesinger 1999). In semiarid shortgrass-steppe grasslands, the long-term decrease in SOC from conversion to cropland is often more than 60 percent (Aguilar and others 1988; Schimel 1986), most of which is lost in the first few years of cultivation (Bowman and others 1990). Cultivation also reduces labile C in soils as well as labile C as a proportion of SOC (Bowman and others 1990). Cropland soils typically have less total nitrogen (N), less labile N, and lower labile N:total N than their uncultivated counterparts. However, these N decreases with cultivation are proportionally less than that for SOC, resulting in narrowing C:N ratios in both total and labile fractions after cultivation of grassland soils (Bowman and others 1990). Inorganic N

concentrations are often reported to be higher in cropland than grassland soils, even without the effects of inorganic fertilizers (DeLuca and Keeney 1993a). Native grasslands are often described in terms of “tight,” conservative SOM cycling, wherein diverse and growing microbial communities immobilize limited amounts of N as fast as it mineralizes from decomposing SOM (DeLuca and Keeney 1993a; Schimel 1986). In contrast, cropland soils are thought to have decaying microbial communities that “leak” inorganic nutrients as SOM mineralization exceeds uptake of inorganic nutrients (Schimel 1986; Smith and others 1994). Previous studies of cheatgrass invasion found greater concentrations of inorganic N in soils beneath cheatgrass than native shrub-steppe vegetation (Evans and others 2001; Svejcar and Sheley 2001). Other studies reported changes in the amount of labile C as a proportion of TOC (Bolton and others 1990; Gill and Burke 1999; Smith and others 1994).

Conversion from grassland to cropland changes SOM dynamics in three ways: (1) reduced SOM inputs because of crop harvest, (2) lower root:shoot ratios in annual crops than perennial herbaceous and woody vegetation, and (3) increased decomposition rates from aeration and more labile organic substrates (Schimel 1986). Conversion of native shrub-steppe to dominance by cheatgrass impacts SOM dynamics in five similar ways: (1) reduced SOM inputs from frequent fires that volatilize litter almost annually in many areas (Knick and Rotenberry 1997; Whisenant 1990), (2) reduced root:shoot ratios compared to native grasses and shrubs (Monaco and others 2003), (3) higher litter decomposition rates from more labile litter

compared to native plants, (4) altered soil structural properties (Gill and Burke 1999) due to differences in root architecture between cheatgrass and native species (Arredondo and Johnson 1999), and (5) different assemblages of soil microbes (Kuske and others 2002) and fauna (Belnap and Phillips 2001) associated with cheatgrass and native soils. Conversion from perennial vegetation to annual vegetation may lead to larger active (inorganic and labile) SOM pools and smaller slow and passive (protected SOM and humus) pools (Parton and others 1987) (fig. 1). With cheatgrass invasion, these changes may result in feedback processes that progressively alter soil structure (Angers and Caron 1998), soil hydrology, and decomposition rates. Degradative feedbacks could ultimately lead to impoverished soils that may limit restoration alternatives.

Similarities between the impacts of annual crops and cheatgrass on SOM dynamics notwithstanding, clear differences in SOM content, composition, and cycling between soils underneath cheatgrass-dominated and shrub-steppe vegetation are difficult to detect (Bolton and others 1990; Svejcar and Sheley 2001). The objective of our study was to evaluate changes in soil morphology and the distribution and composition of SOM associated with cheatgrass invasion of sagebrush-steppe communities. Our underlying hypothesis is that soils under cheatgrass-dominated vegetation exhibit morphological characteristics and organic matter dynamics that facilitate depletion of slow and passive SOM that turns over in the timeframe of decades to centuries and enrich active SOM that turns over every 2 years or less (fig. 1).



**Figure 1**—Conceptual diagram of relative C flows in native shrub-steppe and cheatgrass-dominated vegetation (based on Parton and others 1987). Structural and metabolic C in plant residues have residence times of approximately 3 and 0.5 years, respectively. Active, slow, and passive soil C pools have approximate turnover rates of 1.5, 25, and 1,000 years.

## Materials and Methods

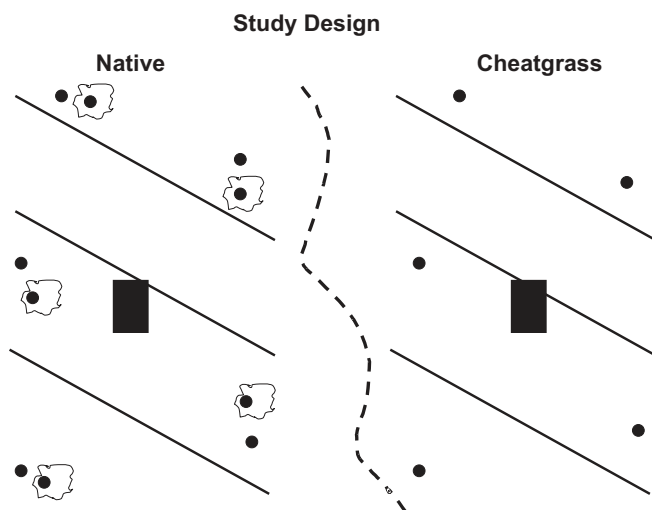
Soil morphology and SOM dynamics were compared in soils beneath cheatgrass-dominated and diverse Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & A.W. Young)-associated vegetation using a series of seven paired sites in Utah and Idaho. Soil samples and data were collected during summer and fall 2001 from soil profiles and replicated points randomly distributed within adjacent cheatgrass-dominated and Wyoming big sagebrush-associated vegetation (fig. 2). Soil-forming factors (such as, parent material, topography, climate, land use) at each paired site were similar between cheatgrass-dominated and adjacent sagebrush-steppe vegetation. Cheatgrass-dominated areas were nearly monocultures with documented dates of conversion from native vegetation. Cheatgrass invasion was not a result of livestock corrals, cultivation, excavation, or similar forms of severe disturbance.

Soil profiles were described and sampled following soil survey procedures (NRCS 1993). Soil profile descriptions are reported in Norton and others (in press). Soil pits in native vegetation were located with pit walls beneath grass and shrubs representative for the area within each site. One bulk soil sample was collected from three of the pit walls for each soil horizon and placed on ice for transport to the laboratory. Slope steepness, aspect, vegetation cover, description of landform and parent material, and likely cause of cheatgrass invasion were recorded at each soil pit. Replicated samples were collected from two depths (0 to 5 cm and 5 to 20 cm) at five random bearings (0 to 360 degrees) and distances (1 to 25 m) from each soil pit. Two distinct locations were sampled in the native half of each pair, including an area adjacent to the nearest perennial grass plants and an area beneath the nearest shrub canopy (fig. 2). Soil samples were homogenized shortly after collection, and about 10 g of

each sample was placed in a preweighed sample cup that contained 100 ml of 2M KCl for field extraction of nitrate-N ( $\text{NO}_3^-$ -N) and ammonium-N ( $\text{NH}_4^+$ -N). Cups were immediately capped and stored on ice for transport to the laboratory. Vegetation at each site was evaluated for areal cover (Daubenmire 1968) and frequency by species (Smith and others 1987) along three transects, each with a total of 20 quadrats 0.25-m x 0.25-m square (fig. 2).

Immediately upon returning to the laboratory, field extractions were reweighed to determine exact amount of soil sample, placed horizontally on a rotating shaker at 200 rpm for 30 minutes, and then allowed to settle overnight in a 4 °C refrigerator. Samples were filtered with Whatman no. 4 filters (Whatman International, Ltd., Maidstone, England) and wet-sieved through 2-mm screens to remove gravel. Gravel was dried, weighed, and the weight was subtracted from the field-moist weight of the extracted sample. KCl field extracts were frozen for further inorganic N analyses.

All soil samples were stored overnight in sealed sample bags maintained at 4 °C in a refrigerator, sieved through 2-mm screens (reserving at least three aggregates from each soil profile sample for bulk density analysis), and partitioned for determination of gravimetric moisture and mineralizable C and N. Mineralizable C was determined by aerobic incubation of ~20-g samples brought to 23 percent soil water content and incubated for 12 days in a 20 °C incubator in 0.95-L canning jars fitted with rubber septa. Gas in the headspace was sampled on days 1, 6, and 12 during the incubation (Zibilske 1994) and injected into a LI-COR 6400 infrared gas analyzer (LI-COR Corp., Lincoln, NE) for determination of  $\text{CO}_2$  concentration. Each jar was vacuum vented and returned to the incubator after  $\text{CO}_2$  measurements on day 1 and day 6. Inorganic N in the incubated ~20-g samples was determined by 2M KCl extraction after the 12-day incubation (Hart and others 1994). Concentration of  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N were determined with a Lachat flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI) for field samples and postincubation samples. Postincubation inorganic N concentration (the amount of inorganic N after the 12-day incubation) represents the active N pool and is reported as "active N." Bulk density was determined by the clod method (Blake and Hartge 1986). Total C and N were determined by dry combustion with a Leco CHN 2000 Autoanalyzer (Leco Corp., St. Joseph, MI). Inorganic-C concentration was determined gravimetrically (Loeppert and Suarez 1996) and subtracted from total-C concentration to determine organic-C concentration. Data from upper soil horizons were analyzed by paired difference t-test and correlation procedures using the Microsoft Excel Data Analysis Toolpak (Microsoft Corp., Redmond, WA). Cheatgrass-native comparisons for the native half of the replicated samples were based on weighted means derived from percent shrub cover and soil properties beneath grasses and shrubs.



**Figure 2**—Schematic diagram of study design. Polygons represent shrubs, black dots represent two-depth replicated soil samples, black rectangles represent soil pits, and diagonal lines represent vegetation transects. See text for further description.

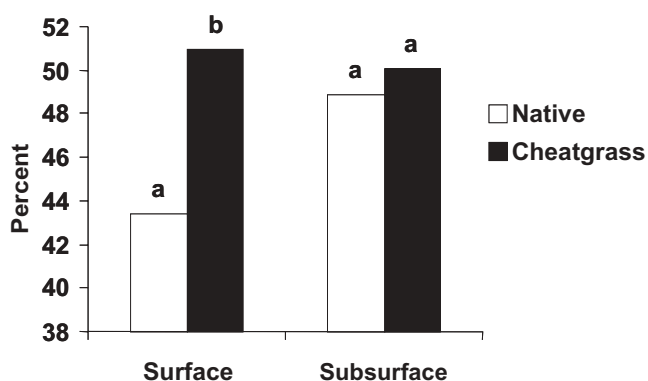
## Results and Discussion

Our results suggest that conversion of native shrub-steppe vegetation to cheatgrass dominance affects both the soil environment and SOM dynamics in ways that are analogous to grassland conversion to cropland. However, absolute, whole-solum SOM loss is not as distinct with

cheatgrass conversion as observed under cropland conversion (Bowman and others 1990; Davidson and Ackerman 1993).

Our analysis of vegetation cover shows that the native shrub-steppe areas were diverse, with up to 29 species in all three life forms (grass, shrub, and forb) well represented at the seven sites. Shrub cover ranged from 0 to 21 percent for the native areas. In contrast, cheatgrass areas had a maximum of 18 species, many of which were exotic annual weeds. Cheatgrass-dominated areas had very few shrubs, and most sites had nearly 100 percent cheatgrass, although sandberg bluegrass (*Poa secunda* J. Presl.) was well represented at some sites (maximum of 13 percent cover). Thus, vegetation at our sites was representative of cheatgrass-invaded areas (Mack 1981).

Soil porosity (the inverse of bulk density) was significantly higher in surface soil horizons under cheatgrass than native shrub-steppe vegetation, but this difference diminished in the subsurface (fig. 3). Higher porosity under cheatgrass is likely the result of the dense, very fine, and shallow root mass observed in A horizons under cheatgrass, which had 83 percent more very fine roots (<1 mm diameter) than A horizons under shrub-steppe vegetation. Fine-root density was the same beneath the two vegetation types below the A horizons. Cheatgrass soils had no roots coarser than 1 mm diameter, while size classes of very fine through coarse were well represented in shrub-steppe soils. Because cheatgrass dies each summer, decaying roots leave behind a high density of very fine tubular pores, which we observed in A horizons under cheatgrass. This combination of greater porosity and greater inputs of very fine roots accelerates decomposition by enhancing air and water movement in surface soils, and contributes to a relatively large and labile substrate each year. These changes induced by cheatgrass may facilitate pulses of microbial activity when moisture becomes available. These conditions may also enhance germination and establishment of cheatgrass seedlings. However, this relatively high porosity and labile SOM content is dependent on annual production by cheatgrass and may disintegrate



**Figure 3**—Percent porosity of soils beneath cheatgrass-dominated and native shrub-steppe vegetation based on means of seven cheatgrass sites and seven native sites. Different letters above columns indicate significant differences ( $P < 0.05$ ) resulting from paired-difference analysis.

rapidly if cheatgrass germination is prevented, as with pre-emergent herbicides that often precede planting of perennial species.

Differences in SOM distribution and composition beneath cheatgrass-dominated and shrub-steppe vegetation were analogous to differences beneath grasslands and croplands, but losses of SOM appeared to be less pronounced in shrub-steppe vegetation. The most significant differences occurred in soil N fractions with higher concentrations of total N, inorganic N, and active-pool N beneath cheatgrass than shrub-steppe vegetation, and lower  $\text{CO}_2\text{-C}:\text{active-pool N}$  ratios beneath cheatgrass than shrub-steppe soils.

On a whole-solum basis, soils beneath cheatgrass had less SOC and more total N than soils beneath shrub-steppe vegetation at five of the seven sites (table 1). Although the differences among averages for all sites were not significant ( $P > 0.05$ ), cheatgrass solums had 30 percent less SOC ( $P = 0.14$ ) and 4 percent more N ( $P = 0.40$ ) than shrub-steppe solums. SOC concentrations in surface soils beneath cheatgrass were equal to those under native shrub-steppe vegetation (figs. 4 and 5), while total N concentrations were higher in cheatgrass than shrub-steppe A horizons. This is opposite to observed changes in grassland soils following conversion to cropland (Bowman and others 1990). In our study, SOC levels declined more with soil depth under cheatgrass than under shrub-steppe vegetation at each of the sites (fig. 4). Average SOC concentration in the upper subsoil under cheatgrass averaged about half that of upper subsoils under shrub-steppe vegetation. The magnitude of the difference between SOC in A horizons and upper subsoils under cheatgrass correlates with the approximate age of cheatgrass invasion (fig. 6). Total N concentrations in the subsoil were equal for the two vegetation types. Subsoils of semiarid grasslands have higher decomposition rates than surface horizons because they hold more moisture for more of the year (Gill and others 1999). Higher soil water content, along with lower root inputs to subsoils and the possibility of a mineralization priming effect caused by large precipitation-induced pulses of microbial activity, may lead to depletion of subsoil SOC under cheatgrass-dominated vegetation. A mineralization priming effect is often observed in agricultural soils when a labile C source is combined with aeration caused by cultivation, which creates a large pulse of microbial activity. The C source is rapidly consumed, but enzymes remain capable of mineralizing SOM stored in slow and passive pools (DeLuca and Keeney 1993b). The result is uptake of more SOM mineralization products than in the original C source and depletion of SOM stored as slowly decomposing materials and humus. Gill and Burke (1999) found lower concentrations of slow-pool SOC beneath cheatgrass than under adjacent shrub-steppe vegetation.

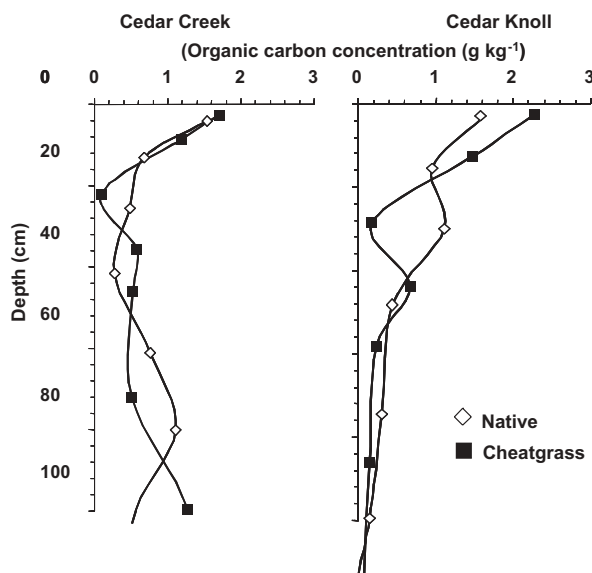
Field-extracted inorganic N differed significantly between vegetation type and soil depth (table 2). Cheatgrass-dominated areas had 75 percent more ( $P = 0.02$ )  $\text{NO}_3^- \text{-N}$  in the 0- to 5-cm soil depth and 66 percent more ( $P = 0.03$ ) in the 5- to 20-cm soil depth than shrub-steppe vegetation areas at the time of sampling (table 2). Ammonium N concentrations (not presented) followed similar trends, but were highly variable. Nitrate N also made up a higher proportion of total N at both soil depths (table 2). Higher inorganic N concentrations are often observed following conversion of grassland to cropland



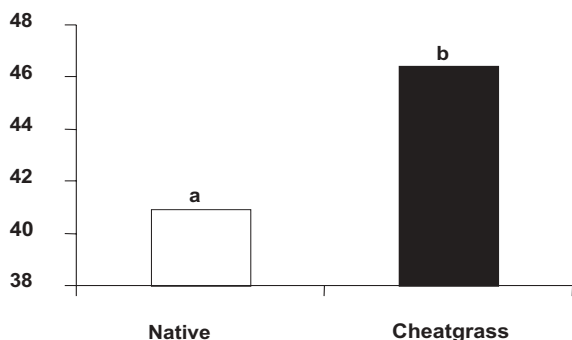
**Table 1**—Whole-solum organic C and total N under Wyoming big sagebrush steppe (native) and cheatgrass vegetation (CG).

Site	Organic C				Total N			
	Native	CG	Diff. <sup>a</sup>	P	Native	CG	Diff.	P
	----- g m <sup>-2b</sup> -----		percent		----- g m <sup>-2</sup> -----		percent	
Cedar Creek	10,894	13,689	26		931	1,418	52	
Cedar Knoll	6,933	6,179	-11		1,196	1,666	39	
Five Mile Junction	36,625	15,135	-59		3422	2,328	-32	
Horse Butte	4,821	3,517	-27		847	700	-17	
Hogup Mountains	11,187	6,282	-44		1,076	1,230	14	
Johnson Canyon	4,961	6,125	23		502	627	25	
Mickel-Watson	10,672	9,547	-11		1,079	1,480	37	
Mean	12,299	8,639	-30	0.14	1,293	1,350	4	0.40

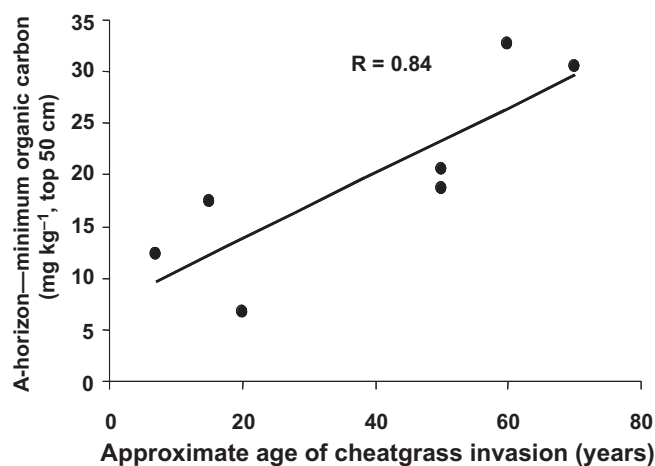
<sup>a</sup> Percent differences based on "native" values.  
<sup>b</sup> Calculated from bulk density of soil samples from each horizon.



**Figure 4**—Soil organic carbon concentration in paired soil profiles under cheatgrass-dominated and Wyoming big sagebrush-steppe vegetation at two of the seven study sites. SOC concentrations followed similar trends at each of the seven study sites.



**Figure 5**—Percent difference in SOC concentrations between the 0- to 5-cm soil depth and the 5- to 20-cm soil depth based on means from all replicated points. Different letters above columns indicate significant differences ( $P < 0.05$ ) resulting from paired-difference analysis.



**Figure 6**—Difference in SOC concentration between A-horizons (maximum in upper 50 cm) and minimums within the top 50 cm in each of seven cheatgrass soil profiles as a function of approximate time since cheatgrass became the dominant vegetation.

and are considered indicative of decaying, C-limited SOM systems that “leak” mineralized nutrients after short-lived pulses of microbial activity drive mineralization of stored SOM (Schimel 1986). A similar explanation may apply to higher inorganic-N concentrations beneath cheatgrass than native shrub-steppe vegetation.

Active-pool C (C mineralized during 12-day incubations) was nearly the same under the two vegetation types. Active-pool N (postincubation inorganic N) concentrations, however, were 39 percent higher ( $P = 0.04$ ) in the 0- to 5-cm soil depth and 34 percent higher ( $P = 0.12$ ) in the 5- to 20-cm soil depth in cheatgrass-dominated areas than shrub-steppe areas (table 2). Mineralized C accounted for about the same proportion of total SOC in both vegetation types, but active N accounted for a higher proportion of total N in cheatgrass-dominated than shrub-steppe soils at both depth increments (table 2). These proportions suggest that cheatgrass-dominated vegetation creates a mineralizing environment

**Table 2**—Paired difference analysis<sup>a</sup> of selected soil properties under Wyoming sagebrush-teppe (native) and cheatgrass-dominated vegetation (CG).

Depth	Organic C			Total N			Field NO <sub>3</sub> <sup>-</sup> -N			Active-pool C		
	Native <sup>b</sup>	CG	Diff. <sup>c</sup>	Native	CG	Diff.	Native	CG	Diff.	Native	CG	Diff.
<i>cm</i>	---	<i>g kg<sup>-1</sup></i>	---	<i>percent</i>	---	<i>g kg<sup>-1</sup></i>	---	<i>percent</i>	---	<i>mg kg<sup>-1</sup></i>	---	<i>percent</i>
0 to 5	20.53	21.85	6.5	2.14	2.34	9.6	5.33	9.31	74.8 <sup>d</sup>	190.48	210.31	10.4
5 to 20	12.13	11.71	-3.5	1.44	1.36	-6.0	2.17	3.61	65.9 <sup>d</sup>	64.33	60.50	-6.0

	Active-pool N			NO <sub>3</sub> <sup>-</sup> -N/Total N			Active-pool N/Total N			Active-pool C:N		
	Native	CG	Diff.	Native	CG	Diff.	Native	CG	Diff.	Native	CG	Diff.
	--	<i>mg kg<sup>-1</sup></i>	--	<i>percent</i>	<i>mg NO<sub>3</sub><sup>-</sup>-N g<sup>-1</sup> TN</i>	<i>percent</i>	<i>mg NO<sub>3</sub><sup>-</sup>-N g<sup>-1</sup> TN</i>	<i>percent</i>				<i>percent</i>
0 to 5	23.71	33.05	39 <sup>d</sup>	2.54	4.07	60 <sup>d</sup>	12.05	15.59	29 <sup>e</sup>	9.29	10.19	10
5 to 20	5.60	7.52	34	1.53	2.92	91 <sup>d</sup>	4.04	6.36	57 <sup>d</sup>	17.33	8.39	-52 <sup>d</sup>

<sup>a</sup> Means from seven study sites, each with 10 native samples (five grass and five shrub) and five cheatgrass samples at each depth.

<sup>b</sup> Weighted means based on proportion of grass and shrub cover on sites.

<sup>c</sup> Percent difference based on "native" value.

<sup>d</sup> Significant at the *P* < 0.05 level.

<sup>e</sup> Significant at the *P* < 0.10 level.

where uptake is limited by shortage of labile C caused by rapid decomposition and relatively low root:shoot ratios.

Ratios of SOC to total N were equal in soils of the two vegetation types. The C:N ratios in the active SOM pool were also equal in both A horizons and in the 0- to 5-cm depth of both vegetation types (table 2). However, active-pool SOM of cheatgrass soils had much lower C:N ratios in upper subsurface horizons (fig. 7) and in the 5- to 20-cm depth increment (table 2) than those of native shrub-steppe soils. These differences in active-pool C:N ratios are analogous to comparisons between grassland and cropland soils (DeLuca and Keeney 1993a; Schimel 1986). This pattern suggests conservative, "tight" N cycling dominated by immobilization in soils under shrub-steppe vegetation compared to more net

mineralization in a "leaky" N cycle under cheatgrass-dominated vegetation. Smith and others (1994) found that soils beneath shrub-steppe vegetation had much tighter, more efficient N cycling compared to cropland, forest, and annual grass ecosystems they analyzed.

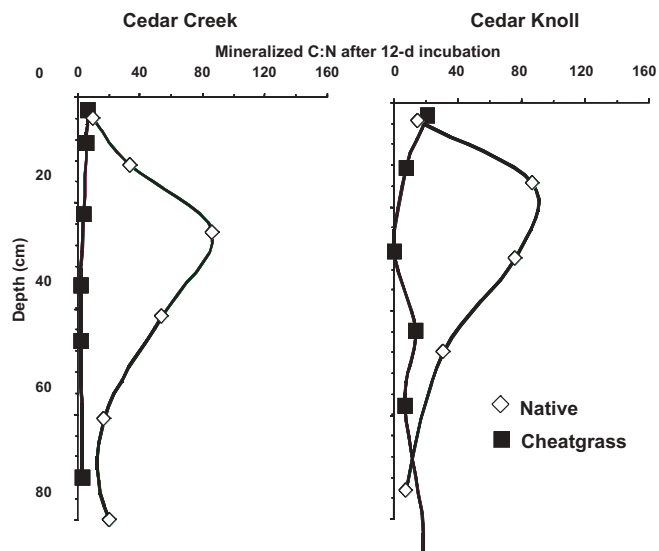
## Conclusions

This research contributes basic knowledge about how extensive annual grass invasion alters soil properties recognized as foundations of ecological stability and resilience (Coleman and others 1983). Our results suggest that conversion of diverse native plant communities to cheatgrass, which is now the dominant vegetation on most of three major physiographic provinces in the Western United States, leads to losses of SOM and changes in its composition and distribution. These changes may be analogous to changes brought about by crop cultivation in central grasslands of North America, which are known to have altered basic ecosystem functions such as cycling of C, N, and water. These basic ecosystem functions are even more difficult to restore in the arid and semiarid West because inherent fragility of altered ecosystems (Tausch and others 1993) makes reversal uncertain and very expensive. The magnitudes of these changes may intensify with the time that cheatgrass dominates, limiting the prospects for restoring these areas. Our results suggest that successful restoration of diverse native vegetation in cheatgrass-dominated areas may require use of transition species that are capable of competing with cheatgrass while contributing slow-pool SOC to the soil.

## References

Aguilar, R.; Kelley, E. F.; Heil, R. D. 1988. Effects of cultivation of soils in Northern Great Plains rangeland. *Soil Science Society of America Journal*. 52: 1081–1085.

Angers, D. A.; Caron, J. 1998. Plant-induced changes in soil structure: processes and feedbacks. In: van Breeman, N., ed. *Plant-induced soil changes: processes and feedbacks*. Dordrecht, The Netherlands: Kluwer Academic Publishers: 55–72.



**Figure 7**—Active-pool C:N ratios (mineralized C:N after 12-d incubation) in paired soil profiles under cheatgrass-dominated and Wyoming big sagebrush-steppe vegetation at two of the seven study sites. Active-pool C:N ratios followed similar trends at six of the seven study sites.

- Arredondo, J. T.; Johnson, D. A. 1999. Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. *New Phytologist*. 143: 373–385.
- Belnap, J.; Phillips, S. L. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications*. 11: 1261–1275.
- Blake, G. R.; Hartge, K. H. 1986. Bulk density. In: Klute, A., ed. *Methods of soil analysis. Part 1: physical and mineralogical methods*. 2d ed. Madison, WI: American Society of Agronomy: 363–375.
- Bolton, H., Jr.; Smith, J. L.; Wildung, R. E. 1990. Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. *Soil Science Society of America Journal*. 54: 887–891.
- Bowman, R. A.; Reeder, J. D.; Lober, R. W. 1990. Changes in soil properties in a Central Plains rangeland soil after 3, 20, and 60 years of cultivation. *Soil Science*. 150: 851–857.
- Coleman, D. C.; Reid, C. P. P.; Cole, C. V. 1983. Biological strategies of nutrient cycling in soil systems. *Advances in Ecological Research*. 13: 1–55.
- D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*. 23: 63–87.
- Daubenmire, R. 1968. *Plant communities: a textbook of plant synecology*. New York: Harper & Row, Publishers. 300 p.
- Davidson, E. A.; Ackerman, I. L. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry*. 20: 161–193.
- DeLuca, T. H.; Keeney, D. R. 1993a. Soluble organics and extractable nitrogen in paired prairie and cultivated soils of central Iowa. *Soil Science*. 155: 219–228.
- DeLuca, T. H.; Keeney, D. R. 1993b. Glucose induced nitrate assimilation in prairie and cultivated soils. *Biogeochemistry*. 21: 167–176.
- Ehrenfeld, J. G.; Scott, N. 2001. Invasive species and the soil: effects on organisms and ecosystem processes. *Ecological Applications*. 11: 1259–1260.
- Evans, R. D.; Rimer, R.; Sperry, L.; Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*. 11: 1301–1310.
- Gill, R. A.; Burke, I. C. 1999. Ecosystem consequences of plant life form changes at three sites in the semiarid United States. *Oecologia*. 121: 551–563.
- Gill, R. A.; Burke, I. C.; Milchunas, D. G.; Lauenroth, W. K. 1999. Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. *Ecosystems*. 2: 226–236.
- Hart, S. C.; Stark, J. M.; Davidson, E. A.; Firestone, M. K. 1994. Nitrogen mineralization, immobilization, and nitrification. In: Weaver, R. W.; Angle, S.; Bottomley, P., eds. *Methods of soil analysis. Part 2: microbiological and biochemical properties*. Madison, WI: Soil Science Society of America: 985–1018.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert. *Global Environmental Change*. 6: 37–52.
- Knick, S. T. 1999. Requiem for a sagebrush ecosystem? *Northwest Science*. 73: 53–57.
- Knick, S. T.; Rotenberry, J. T. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (U.S.A.). *Landscape Ecology*. 12: 287–297.
- Kuske, C. R.; Ticknor, L. O.; Miller, M. E.; Dunbar, J. M.; Davis, J. A.; Barns, S. M.; Belnap, J. 2002. Comparison of soil bacterial communities in rhizospheres of three plant species and the interspaces in an arid grassland. *Applied and Environmental Microbiology*. 68: 1854–1863.
- Loeppert, R. H.; Suarez, D. L. 1996. Carbonate and gypsum. In: Sparks, D. L., ed. *Methods of soil analysis. Part 3: chemical methods*. Madison, WI: Soil Science Society of America: 437–474.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agro-Ecosystems*. 7: 145–165.
- Monaco, T. A.; Johnson, D. A.; Norton, J. M.; Jones, T. A.; Connors, K. J.; Norton, J. B.; Redinbaugh, M. B. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management*. 56: 282–290.
- Norton, J. B.; Monaco, T. A.; Norton, J. M.; Johnson, D. A.; Jones, T. A. [In press]. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *Journal of Arid Environments*.
- NRCS. 1993. *Soil survey manual*. Washington, DC: USDA Natural Resource Conservation Service.
- Parton, W. J.; Schimel, D. S.; Cole, C. V.; Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*. 51: 1173–1179.
- Samson, F. B.; Knopf, F. L. 1994. Prairie conservation in North America. *BioScience*. 44: 418–421.
- Schimel, D. S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry*. 2: 345–357.
- Schlesinger, W. H. 1999. Carbon sequestration in soils. *Science*. 284: 2095.
- Smith, J. L.; Halvorson, J. J.; Bolton, H. J. 1994. Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. *Soil Biology Biochemistry*. 26: 1151–1159.
- Smith, S. D.; Bunting, S. C.; Hironaka, M. 1987. Evaluation of the improvement in sensitivity of nested frequency plots to vegetational change by summation. *Great Basin Naturalist*. 47: 299–307.
- Svejcar, T.; Sheley, R. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. *Journal of Arid Environments*. 47: 33–46.
- Tausch, R. J.; Wigand, P. E.; Burkhardt, J. W. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: Legacy of the Quaternary? *Journal of Range Management*. 46: 439–447.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, D. E.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. *Proceedings of the symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-276*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.
- Zibilske, L. M. 1994. Carbon mineralization. In: Weaver, R. W.; Angle, S.; Bottomley, P., eds. *Methods of soil analysis. Part 2: microbiological and biochemical properties*. Madison, WI: Soil Science Society of America: 15–40.