Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities

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Abstract

Widespread cheatgrass (*Bromus tectorum* L.) invasion represents a major shift in species dominance that may alter ecosystem processes across much of the western US. To investigate differences following such conversion, soil morphology and organic matter under cheatgrass-dominated and native shrub-steppe vegetation were compared by standard soil analysis procedures at seven paired sites in Idaho and Utah. Results suggest that, following conversion to cheatgrass dominance, increased porosity and labile organic inputs enhance microbial decomposition in near-surface horizons beneath cheatgrass compared to adjacent soils under native vegetation. Enhanced decomposition could result in depletion of long-term SOM, leading to impoverished sites difficult to restore to native perennial vegetation.
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1. Introduction

Invasive, non-native species pose an ominous threat to natural ecosystems and represent one of the most important vectors of global environmental change

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(Pimentel et al., 2000). The ecology of exotic plant invasion has historically focused on identifying traits of invasive species and predicting ecosystem invasibility (Drake et al., 1989), while study of the impacts on ecosystem processes resulting from broad-scale alterations to plant community structure and function has begun only recently (Ehrenfeld and Scott, 2001). For example, plant species differ substantially in plant tissue and litter quality, their effects on soil water content and temperature, the amount and composition of root exudates, and their effects on the frequency and intensity of disturbance (Gill and Burke, 1999). Fundamental nutrient cycling processes are known to change following invasion by exotic plant species (Chapin et al., 1997) and understanding the nature and degree of these changes is necessary to successfully repair degraded ecosystems (Whisenant, 1999).

Exotic grass invasion is recognized as one of the most widespread and threatening types of ecosystem conversion because it often increases wildfire frequencies and reduces or eliminates long-lived woody vegetation that is integral to structure and function of arid to sub-humid ecosystems (D'Antonio and Vitousek, 1992). Conversion from shrub and tree canopy to grass dominance may even cause regional climate change as the albedo of the land surface is altered (Chapin et al., 1997). In shrub-steppe plant communities of the western US, the cool-season annual grass cheatgrass (*Bromus tectorum* L.) has become dominant by increasing the frequency of wildfires that remove long-lived perennial species (Whisenant, 1990; Knick, 1999). Cheatgrass phenology enables it to be an extremely effective competitor for limiting soil water and nutrients (Harris, 1967; Melgoza et al., 1990). Cheatgrass invasion and replacement of native shrub-steppe vegetation represents a fundamental shift to an alternative, self-enhancing stable-state domain (Laycock, 1991) that is very difficult to reverse.

One relatively unexplored consequence of cheatgrass invasion may be changes to basic belowground processes involved in nutrient cycling. For example, the type of vegetation covering the soil surface influences development of soil structure, which regulates air and water movement into and through the soil and rates of microbial decomposition (Angers and Caron, 1998). Cheatgrass invasion has been shown to change the composition and quantity of burrowing fauna, root pores, root exudates, mycorrhizal associations, and assemblages of microbial species (Belnap and Phillips, 2001; Kuske et al., 2002), each of which contribute to soil structure (Birkeland, 1984) and the rate of soil organic matter (SOM) decomposition. Cheatgrass invasion also changes the timing, distribution, and composition of organic matter inputs, as well as uptake of mineralized nutrients (Rickard, 1985; Bolton et al., 1990; Evans et al., 2001). Such shifts in SOM input and uptake may fundamentally alter partitioning of SOM among active, slow, and passive pools, which are thought to exert important influences on ecosystem structure and function (Parton et al., 1987; Gill and Burke, 1999).

Nutrient cycling in native shrub-steppe ecosystems is characteristically "tight" (i.e. net concentrations of plant-available nutrients are low) because broad spatial and temporal diversity of plants and soil microbes in rich mixtures of woody and herbaceous vegetation rapidly exploit nutrients as they are mineralized (Smith et al., 1994; Paschke et al., 2000). Combined livestock grazing and fire suppression starting

in the 19th century reduced the herbaceous understory and contributed to a more dense shrub cover with bare, depleted interspaces (Knapp, 1996; West, 1999). This loss of perennial herbaceous vegetation reduces spatial and temporal diversity in water and mineral uptake and results in accumulation of available N from decomposing shrub litter (West, 1999). Cheatgrass invades shrub interspaces in this type of degraded sagebrush-steppe plant community, increasing the amount and continuity of fine fuels until fire eliminates the shrub component and completes the conversion to near monocultures of cheatgrass that can apparently persist indefinitely (West, 1999).

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 intention was to compare soils beneath native vegetation to those beneath cheatgrass at the plant community level. We did not set out to describe differences among soils beneath individual shrub, grass, and interspace components of the complex and dynamic shrub-steppe ecosystem. Our underlying hypothesis was that soils under cheatgrass-dominated vegetation exhibit morphological characteristics and organic matter dynamics that facilitate depletion of slow and passive SOM that turns over on the order of decades to centuries and enrichment of active SOM that turns over at least once per year.

2. Materials and methods

Soil morphology and SOM dynamics were compared in soil profiles beneath cheatgrass- and big sagebrush-steppe-dominated vegetation using a series of paired sites in different landscape positions and with different ages of cheatgrass establishment, similar to work by Gill and Burke (1999) and many others. We focused on Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & A.W. Young)-associated vegetation because it is the most widespread of the big sagebrush-steppe plant communities in the intermountain west and the one most vulnerable to cheatgrass invasion (Shiflet, 1994). Seven paired sites located in central Utah, northern Utah, and southern Idaho (Fig. 1) were sampled during mid-summer and early fall of 2001. The following site selection criteria were used to maximize effective comparisons between the paired sites:

1. Cheatgrass-dominated areas had to be long-term, near-monocultures with dates of conversion from native vegetation documented by management records, previous research, aerial photography, fire history information, or other sources.
2. Cheatgrass invasion could not have been a direct result of severe disturbance (e.g. associated with livestock corrals and bedding grounds, cultivation, excavation, etc.).
3. Sites had to occur in a variety of landscape positions with a range of vegetation representative of Wyoming big sagebrush-associated vegetation.
4. Cheatgrass-dominated areas had to be adjacent to diverse Wyoming big sagebrush-native bunchgrass plant communities with similar natural soil
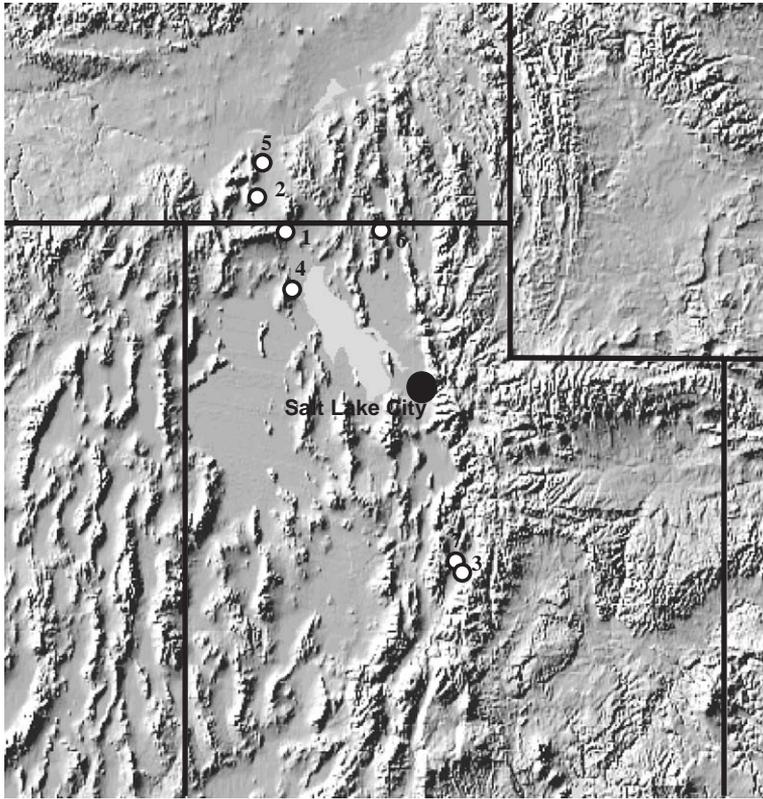
Fig. 1. Study site locations. Numbers correspond to Table 1.

development (e.g. parent material, slope steepness, aspect, etc.) and with similar management history (e.g. grazed by same class of livestock). No grazing exclosures were sampled.

2.1. Field procedures

Vegetation areal cover was characterized at each site (Daubenmire, 1968) by plant form and ground cover along three transects, each with a total of 20 quadrats (0.25 m × 0.25 m square). One soil pit in native vegetation at each site was located with pit walls beneath grass and shrubs representative for the site. Soil profiles were described and sampled as per procedures developed by the USDA Natural Resources Conservation Service (SSDS, 1993) in soil pits measuring 1 m wide × 2 m m long × 1.5 m deep (or to bedrock) that were excavated by hand or backhoe. Horizon depths, colors, root size and density, and other morphological features were described beneath grass-interspace portions of the soil pits. One soil pit in cheatgrass vegetation (nearly 100% cheatgrass cover) at each site was located as near as possible to the native vegetation sample area. One bulk soil sample was collected from three

of the pit walls for each soil horizon to reflect the shrub–grass-interspace composition of the site (Table 1). The soil survey techniques we used to describe and sample soils beneath the two vegetation types were designed to integrate site- or plant community-scale plant and interspace effects on soil properties (SSDS, 1993).

Soil samples were homogenized shortly after collection and about 10 g of each sample was placed in a pre-weighed sample cup that contained 100 ml of 2 M KCl for field extraction of nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N). Cups were immediately capped and stored on ice for transport to the laboratory. Soil samples were also placed on ice for transport to the laboratory. Site data, including slope steepness, aspect, vegetation cover, description of landform and parent material, and suspected cause of cheatgrass invasion were collected at each soil pit.

2.2. Laboratory procedures

Field extractions were placed horizontally on a rotating shaker at 200 rpm for 30 min immediately upon return to the laboratory, then allowed to settle overnight in a 4°C refrigerator. Samples were weighed to determine exact amount of soil sample, filtered with Whatman no. 4 filters, 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.

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 for bulk density analysis), and partitioned for determination of gravimetric moisture and mineralizable C and N. Mineralizable C was determined by aerobic incubation where $\sim$20-g samples were wetted to 23% soil water content and placed in 1 liter canning jars fitted with rubber septa. They were incubated for 12 days in a 20°C incubator. 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 analyser (LI-COR Corp., Lincoln, NE) for determination of CO_2 concentration. Each jar was vacuum vented and returned to the incubator after the Day 1 and Day 6 CO_2 measurements. Mineralized C values were calculated from CO_2 data. Mineral N in the incubated $\sim$20-g samples was determined by 2 M KCl extraction after the 12-day incubation (Hart et al., 1994). Concentration of NO_3^--N and NH_4^+-N were determined with a Lachat flow injection autoanalyser (Lachat Instruments, Milwaukee, WI) for field samples and post-incubation samples. Post-incubation mineral N concentration (the amount of mineral N after the 12-day incubation) represents the portion of total N that is most readily available for plant uptake and is reported as active-pool N (as opposed to mineralized N which includes only the portion mineralized during incubation).

Gravel removed from each soil sample was weighed, and the remainder of each soil sample was air-dried. Bulk density was determined by the clod method (Blake and Hartge, 1986) on soil clods removed from the bulk soil samples before sieving. Air-dried samples were analysed for particle-size distribution by the pipette method (National Soil Survey Center, 1996), and total C and N were determined by dry

Table 1
Soil and vegetation information for study sites

	Site	Soil series[a]	Native vegetation	Native Cover type (%)[b]	Landform	Parent material
1	Cedar Creek; Box Elder County, Utah	Hiko Peak gravelly loam	*Pseudoroegneria spicata/Artemisia tridentata wyomingensis*	Shrub 21 Grass 18 Interspace 23 Cheatgrass 11 Litter 46	Toeslope: mid alluvial fan	Stratified sands, gravels, & cobbles
2	Cedar Knoll; Cassia County, Idaho	Darkbull gravelly loam	*P. spicata/A. tridentata wyomingensis/ Juniperus spp.*	Shrub 18 Grass 22 Interspace 30 Cheatgrass 3 Litter 34	Footslope/ upper alluvial fan	Siltstone colluvium over fine-grained mudstone residuum
3	Five Mile Junction; Sanpete County, Utah	Quaker silty clay loam	*P. spicata*	Shrub 5 Grass 47 Interspace 19 Cheatgrass 4 Litter 42	Footslope/ upper alluvial fan	Stratified sand & gravel
4	Hogup Mountains; Box Elder County, Utah	Sitar silt loam	*P. spicata/Leymus salinus/A. tridentata wyomingensis*	Shrub 20 Grass 34 Interspace 25 Cheatgrass 4 Litter 15	Footslope/ upper alluvial fan	Gravelly calcareous mudstone colluvium & sandy alluvium
5	Horse Butte; Cassia County, Idaho	Trevino stony silt loam	*P. spicata/A. tridentata wyomingensis*	Shrub 18 Grass 25 Interspace 29 Cheatgrass 2 Litter 43	Loess capped basalt flow	Silty and very fine sandy eolian materials
6	Johnson Canyon; Box Elder County, Utah	Sandall cobbly silt loam	*P. spicata/ A. tridentata wyomingensis*	Shrub 17 Grass 18 Interspace 34 Cheatgrass 12 Litter 30	Mid slope	Shallow limestone colluvium
7	Mickel-Watson; Sanpete County, Utah	Atepic shaly clay loam	*P. spicata/ Juniperus spp.*	Shrub 0 Grass 23 Interspace 59 Cheatgrass 0 Litter 23	Ridge top	Very fine grained, slightly calcareous mudstone

[a] From USDA-NRCS Soil Surveys of Boxelder and Sanpete Counties, Utah, and Cassia County, Idaho (Chadwick et al., 1975; Swenson et al., 1981; Noe and Kukachka, 1994; Loerch et al., 1997).

[b] Grass includes minor native forb component; interspace includes bare soil, rock, and microbiotic crust; litter includes all plant detritus on soil surface.

combustion with a Leco CHN 2000 Autoanalyser (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 analysed by paired difference *t*-test (Steel and Torrie, 1980). This conservative approach was used to identify strongly consistent differences between soils beneath cheatgrass and native vegetation across our seven study sites, which had widely varying soil properties (see Tables 1 and 2).

3. Results

3.1. Soil morphology

The two uppermost horizons in the soil pedons were thinner in cheatgrass than native soils at five of the seven sites and similar at two sites (Tables 2 and 3). Below the second horizon, thickness was variable with no apparent pattern as related to vegetation cover. Soil color value in the A horizons was darker in the native than cheatgrass soils at five of the seven paired sites and similar to the cheatgrass soil at the other two sites (Table 2). Soil colors below the A horizons were equivalent in the native and cheatgrass soils. There were no consistent differences in soil texture or coarse-fragment contents among the paired profiles. The A horizons in the soil profiles were platy under cheatgrass but granular or fine subangular blocky under native vegetation at four of the seven paired sites. Bulk density of A horizons was lower beneath cheatgrass than native vegetation in five of the seven sites (Table 2) and significantly lower beneath cheatgrass than native vegetation when averaged across all sites (Table 3). Cheatgrass A horizons had significantly more very fine roots than those under native vegetation, but this difference diminished in lower horizons. Cheatgrass soils had no roots coarser than 1 mm, and most roots were much finer. By comparison, native soils had a diversity of root sizes, especially fine and medium roots. Cheatgrass soils also had many fine tubular pores, but few coarser pores (pore morphology and size distributions were estimated in each soil profile description but are not reported). Native soils had some very coarse pores associated with insect larvae, but cheatgrass soils did not. Calcium carbonate content was higher in A horizons of cheatgrass soils at five of the seven paired sites, but this difference diminished with depth (Table 2).

3.2. Soil organic matter dynamics

Total soil organic carbon (SOC) concentration was roughly equivalent in A horizons of native and cheatgrass soils, but decreased more sharply with increasing depth under cheatgrass (Fig. 2, Table 3). Soil organic C concentration dropped to significantly lower levels in the top 50 cm of cheatgrass soils than native soils (Table 4). Also in the top 50 cm of the soil profiles, the difference between the highest (in A horizons) and lowest SOC values was significantly larger in cheatgrass than

Table 2
Soil profile descriptions from paired sites[a]

Horizon	depth (cm)	Moist color	Text. class	Sand (%)	Silt (%)	Clay (%)	Rock Frags.[b] (%)	Structure			Bulk density (g cm^{-3})	Roots				pH	CaCO$_3$ (%)	Boun dary
								Grade	Size	Type		V. Fi	Fi	Med	Co			
Cedar Creek native; slope: 2%; aspect: 38°; coarse-loamy, mixed, superactive, mesic xeric haplocalcids																		
A	0–8	10YR 3/3	Sl	52	34	15	13	Mod	Med/fi	Sbk	1.41	Mn	Mn			7.64	19.7	CW
Bk	8–18	10YR 7/4	Gsl	52	31	17	20	Wk	Med	Pl, pr	1.33	Mn	Cm			7.58	21.7	CS
Btk	18–33	10YR 5/4	Gsl	58	26	16	21	Mod	Med/fi	Sbk	1.52	Cm	Cm			7.77	25.8	CS
BC	33–50	10YR 5/3	Gsl	61	24	15	25	Mod	Fi	Sbk	1.56	Cm			Fw	8.10	27.9	GS
C1	50–72	10YR 6/3	Vgsl	59	23	17	40	Ms			1.68	Fw				8.68	28.7	CS
2C2	72–88	10YR 6/3	Gls	82	9	9	31	V. wk	Fi	Sbk		Cm				9.62	30.5	CS
2C3	88–118	10YR 5/3	Ls	89	5	5	3	V. wk	Fi	Sbk		Fw	Fw			9.35	35.4	AI
3C4	118–150+	10YR 4/3	Vgls	89	6	5	43	V. wk	Fi	Sbk						9.60	34.8	
Cedar Creek cheatgrass; slope: 2%; aspect: 42°; coarse-loamy, mixed, superactive, mesic xeric haplocalcids																		
A	0–5	10YR 4/3	Sl	62	22	16	13	Wk	Med	Pl	1.34	Mn				8.52	25.5	CS
ABt	5–12	10YR 4/4	Sl	58	23	19	13	Mod	Co/med	Pl, pr	1.31	Cm				8.04	25.8	CS
Bt	12–32	10YR 5/3	Sl	63	20	16	4	Mod	Med	Sbk	1.27	Cm				7.82	35.8	AW
2BC1	32–39	10YR 5/3	Vgsl	74	13	13	51	Wk	Fi	Sbk		Mn				7.77	33.7	AW
2BC2	39–43	10YR 4/3	L	54	28	18	6	Str	Med	Pl	1.30	Fw				8.31	26.4	AW
2BC3	43–48	10YR 5/3	Gl	51	31	17	22	Wk	Fi	Sbk	1.44	Cm				8.02	26.6	AW
2BC4	48–53	10YR 4/3	L	54	28	18	6	Str	Med	Pl	1.30	Fw				8.31	26.4	AW
3BCk	53–91	10YR 4/2	Gl	51	31	17	22	Mod	Med	Sbk	1.44	Cm				8.02	26.6	CS
3C1	91–108	10YR 5/3	Gl	54	30	16	27	Ms			1.64	Fw				7.82	29.0	GS
4C2	108–132	10YR 5/4	Gsl	60	25	15	28	Ms			1.70					8.01	30.9	AW
5C3	132–150+	10YR 4/3	Vgls	81	11	8	44	Sg								8.24	30.4	
Cedar Knoll native; slope: 5%; aspect: 100°; coarse-loamy, mixed, superactive, mesic xeric haplocalcids																		
A	0–7	10YR 3/3	Gl	33	46	21	23	Mod	Fi	Gr	1.20	Mn	Fw			6.82	1.9	CW
AB	7–24	10YR 4/3	Sil	28	52	20	11	Mod	Med	Pr	1.23	Cm	Cm	Fw		7.32	5.2	CS
Bk	24–36	10YR 4/3	Sil	27	54	19	8	Mod	Med	Pr	1.34	Cm	Cm	Fw		7.45	10.2	CS

Horizon	Depth (cm)	Color	Texture	Sand	Silt	Clay	>2mm	Grade	Size	Shape	Db				pH		Boundary
Btk	36–60	10YR 5/3	Gsil	26	55	19	15	Str	Med	Sbk	1.46	Fw			7.60	10.6	CS
2CB	60–89	2.5Y 7/2	L	39	35	26	—	Wk	Med	Sbk	1.28	Fw			7.49	20.1	CS
2Cr	89–110	2.5Y 8/3	L	48	29	23	—	Ms				Fw			7.35	16.4	CS
2R	110–115+	2.5Y 8/3	L	44	35	21	—	Mudstone							7.67	8.4	

Cedar Knoll cheatgrass; slope: 5%; aspect: 125°; coarse-loamy, mixed, superactive, mesic xeric haplocalcids

Horizon	Depth (cm)	Color	Texture	Sand	Silt	Clay	>2mm	Grade	Size	Shape	Db				pH		Boundary
A	0–5	10YR 4/4	L	34	38	28	0	Mod	Co/Med	Pl	1.27	Mn			6.85	4.2	AS
Btl	5–20	10YR 4/3	L	28	45	28	0	Wk	Med	Pr	1.22	Cm			7.20	2.1	CS
Bt2	20–37	10YR 4/3	Gcl	27	35	37	24	Wk	Med/Fi	Pr	1.34	Cm			7.62	5.7	CS
Btk1	37–50.5	10YR 4/4	Gcl	28	41	31	22	Str	Med/Fi	Sbk	1.45	Cm			7.83	2.1	CS
Btk2	50.5–66	10YR 5/4	Vgl	32	40	28	37	Wk	Fi	Sbk		Fw			8.23	17.1	AS
2Crl	66–106.5	2.5Y 6/3	Sl	56	26	18	—	Ms							8.65	21.3	CS
2Cr2	106.5–120	5Y 6/2	Sl	56	27	17	—	Ms							8.70	12.5	CS
2R	120–122+	Mudstone													8.64	4.6	

Five Mile Junction native; slope: 3%; aspect: 336°; fine, mixed, superactive, mesic xeric haplocalcids

Horizon	Depth (cm)	Color	Texture	Sand	Silt	Clay	>2mm	Grade	Size	Shape	Db				pH		Boundary
A	0–9	10YR 4/2	Sil	21	57	22	0	Mod	Med/fi	Pl	1.46	Cm	Cm		7.98	35.2	CS
Btkl	9–24	10YR 6/2	Cl	24	45	32	4	Mod	Med/fi	Sbk	1.46	Cm		Cm	8.19	37.9	GS
Btk2	24–38	10YR 5/2	Sicl	13	52	35	8	Wk	Med	Pl	1.34	Cm	Cm		8.18	40.7	GS
Btk3	38–72	10YR 5/2	Cl	27	42	31	4	Wk	Med	Pr	1.52	Cm	Fw	Fw	8.20	42.0	AS
BtC1	72–103(gr)	10YR 6/3	Cl	21	43	36	6	Wk	Fi	Pl		Fw			8.36	49.7	CS
BtC2	72–103(s)	10YR 6/3	Cl	12	47	41	4	Mod	Med	Pr	1.35	Fw			8.28	42.8	CS
C	103–160+	10YR 5/3	Cl	22	44	34		Ms			1.33	Fw	Fw		8.39	42.1	

Five Mile Junction cheatgrass; slope: 5%; aspect: 343°; fine, mixed, superactive, mesic xeric haplocalcids

Horizon	Depth (cm)	Color	Texture	Sand	Silt	Clay	>2mm	Grade	Size	Shape	Db				pH		Boundary
A	0–7	10YR 4/2	Sicl	9	56	35	3	Str	Med	Pl	1.07	Mn			7.95	37.5	CS
Btk	7–23	10YR 4/2	Sicl	20	51	29	5	Mod	Med	Pr	1.22	Cm			8.30	45.6	GS
BCk	23–35	10YR 4/2	Cl	17	48	35	7	Mod	Co/fi	Sbk	1.31	Cm			8.31	45.5	GS
BCk	35–150	10YR 5/3	Sicl	8	53	39	7	Wk	Co/fi	Sbk	1.30	Fw			8.39	46.2	CS
CB	150–155+	10YR 6/3	Cl	8	47	45	2	Mod	V. fi	Sbk	1.27	Fw			8.74	44.5	

Hogup Mountains native; slope: 20%; aspect: 54°; loamy-skeletal, mixed, superactive, mesic xeric calciargids

Horizon	Depth (cm)	Color	Texture	Sand	Silt	Clay	>2mm	Grade	Size	Shape	Db				pH		Boundary
A	0–5	10YR 3/2	Gl	51	32	17	31	Mod	Med	Pl	1.44	Mn	Mn	Cm	8.27	26.0	CW
Btk	5–33	10YR 5/3	Gl	51	33	16	32	Mod	Med/fi	Sbk	1.41	Cm	Cm	Fw	8.55	29.9	CS
Bt	33–55	10YR 5/3	Vgl	51	24	25	38	Wk	Med/fi	Sbk	1.42	Mn	Cm		8.57	34.8	GS
BtC	55–75	10YR 5/3	Vgsl	58	19	23	42	Str/Mod	Med	Sbk	1.80	Cm			9.61	38.7	CS

Table 2 (*continued*)

Horizon depth (cm)	Moist color	Text. class	Sand (%)	Silt (%)	Clay (%)	Rock Frags.[b] (%)	Structure Grade	Size	Type	Bulk density (g cm^{-3})	Roots V. Fi	Fi	Med	Co	pH	CaCO$_3$ (%)	Boundary
C1	75–94	10YR 5/4	Gsl	56	19	24	34	Wk	Med	Sbk	1.72	Mn	Fw	Fw		9.86	38.8	GS
C2	94–110	10YR 5/3	Vgsl	56	19	25	46	Wk	Med	Sbk	1.74	Cm	Fw			9.96	34.3	CS
C3	110–124	10YR 5/3	Vgsl	55	21	24	55	Ms			1.38	Fw				9.81	34.1	CS
C4	124–160+	10YR 6/3	Gsl	55	19	26	33	Sg			1.79	V. Fw				9.55		

Hogup Mountains cheatgrass; slope: 23%; aspect: 49°; loamy-skeletal, mixed, superactive, mesic xeric haplocalcids

A	0–6	10YR 3.5/3	Vgsl	54	34	12	35	Wk	Med/fi	Sbk	1.38	V. Mn				7.69	29.7	AS
Bt1	8–27	10YR 4/3	Vgsl	55	33	12	42	Mod	Fi	Pl	1.31	Cm				8.05	31.5	CW
Bt2	27–44	10YR 5/3	Vgl	51	35	14	35	Str/Mod	Med/fi	Sbk	1.40	Fw				8.23	27.6	GS
Bt3	44–53	10YR 5/3	Vgsl	55	32	13	36	Mod	Fi	Sbk	1.41	Fw				8.57	29.6	GS
Bt4	53–65	10YR 5/3	Vgsl	57	31	12	42	Mod	Fi	Sbk		Cm				8.50	30.5	GS
C1	65–94	10YR 5/3	Vgsl	63	28	9	52	Wk	Med/fi	Sbk	1.47	Fw				8.60	31.2	GS
C2	94–150+	10YR 5/3	Vgsl	55	15	30	51	Ms			1.59	Fw				9.70	36.3	

Horse Butte native; slope: 9%; aspect: 205°; coarse-loamy, mixed, superactive, mesic xeric haplocalcids

A	0–6	10YR 4/3	Gl	38	46	15	26	Mod	Fi	Pl	1.84	Cm	Cm	Cm		6.85	2.2	CS
Bt	6–25	10YR 4/2	Sil	27	55	17	8	Mod	Med	Pr	1.47	Cm	Cm	Fw		7.65	2.8	CS
Btk	25–35	10YR 5/3	Gsil	29	54	16	17	Wk	Med	Sbk	1.69	Cm	Cm			7.51	10.1	CS
BCk	35–75	10YR 5/4	Gl	45	44	11	16	V. wk	Med	Sbk	1.15	Fw		Fw		7.70	23.2	AI
2R	75–80+	Basalt																

Horse Butte cheatgrass; slope 8%; aspect: 205°; coarse-loamy, mixed, superactive, mesic xeric calciargids

A	0–6	10YR 4/4	L	38	49	12	11	Str	Med	Pl	1.56	Mn				7.62	1.2	AS
Bt	6–14.5	10YR 4/2	Vgl	33	44	23	44	Str	Fi	Pl	1.51	Cm				8.08	2.7	CS
Btk1	14.5–33	10YR 5/4	Vgl	32	51	17	48	Wk	Med	Pr	1.28	Cm				8.51	5.7	CS
Btk2	33–55	10YR 6/4	Sil	20	54	26	4	Str	Med	Sbk	1.28	Fw				8.79	22.2	AS
BtC	55–71	10YR 6/4	Sil	28	67	4	7	Ms			1.30	Fw				7.97	7.5	GS
C	71–99	10YR 6/4	Gsil	33	53	14	30	Ms				Fw				7.99	10.7	AS
2R	99–107+	Basalt																

Johnson Canyon native; slope: 30%; aspect: 204°; clayey-skeletal, carbonatic, superactive, mesic lithic xeric haplocalcids

A	0–5	10YR 3.5/3	Gsicl	0	71	29	19	Mod	Fi	Gr	1.35	V. Mn	Cm	7.30	1.3	CW
Bt	5–20	10YR 3/4	Vgsicl	0	64	36	36	Str	Fi	Sbk	1.29	Cm	Cm	7.44	1.4	AI
2R	20–40+	Limestone												8.57	56.1	

Johnson Canyon cheatgrass; slope: 33%; aspect: 209°; clayey-skeletal, carbonatic, superactive, mesic lithic xeric calciargids

A	0–5	10YR 4/3	Gsicl	10	59	31	30	Mod	Fi	Pl	1.15	Mn		7.46	2.1	CW
AB	5–20	10YR 4/3					47	Mod	Med/fi	Sbk	1.28	Cm		7.70	1.4	CW
Bt	20–30	10YR 4/4	Gsil	22	51	27	15	Str/Mod	Fi	Sbk	1.19	Cm		7.53	2.7	AI
2R	30–40+	Limestone												8.39	75.7	

Mickel-Watson native; slope: 8%; aspect: 343°; fine, mixed, superactive, mesic xeric calciargids

A	0–11	10YR 3/4	Sicl	17	49	34	12	Wk	Fi	Sbk	1.58	Cm	Cm	8.00	34.1	CS
ABtk	11–24	10YR 5/4	Gsic	13	47	40	20	Str/Mod	Fi	Sbk	1.30	Cm	Fw	8.11	42.1	AS
Btk1	24–39	10YR 8/3	Sic	6	45	49	1	Str	Med/fi	Abk	1.35	Fw		8.08	60.6	CS
Btk2	39–53	10YR 8/4	Gsicl	9	51	39	29	Mod	Med	Sbk	1.21	Fw		8.20	60.1	AS
2R	53–60+	Mudstone										Fw	Fw		56.5	

Mickel-Watson cheatgrass; slope: 8%; aspect: 328°; fine, mixed, superactive, mesic xeric calciargids

A	0–8	10YR 4/4	Sicl	18	52	29	3	Mod	Med/fi	Pl	1.97	Mn		7.96	39.7	CS
ABtk	8–20	10YR 5/6	Sicl	15	48	37	8	Mod	Med/fi	Sbk	1.42	Cm		8.23	40.6	Cl
Btk1	20–27	10YR 4/4	C	14	37	49	8	Str	Med/fi	Sbk	1.53	Cm		8.31	49.6	AW
Btk2	27–37	10YR 8/6	Sicl	8	57	35	12	Str	Med/fi	Abk		Fw		8.48	66.8	AW
Cr	37–51	10YR 6/4					—	Mod	Fi	Sbk	1.35	Fw		8.74	46.3	AS
2R	51–54	Mudstone						Rock						9.25	8.4	AS
3Cr	54–57	10YR 6/8	C	19	35	46	—	Ms						8.92	42.3	AS
4R	57+	Mudstone														

[a] Abbreviations: A, abrupt; Abk angular, blocky; C, clear; C, clay; Cl, clay loam; Cm, common; Co, coarse; Fi, fine; Fw, few; G, gradual; Gcl, gravelly clay loam; Gl, gravelly loam; Gr, granular; Gsic, grvelly silty clay; Gsicl, gravelly silty clay loam; Gsil, gravelly silt loam; Gsl, gravelly sandy loam; L, loam; Ls, loamy sand; Med, medium; Mn, many; Mod, moderate; Ms, massive; Pl, platy; Pr, prismatic; Sl, sandy loam; S, smooth; Sbk, subangular blocky; Sicl, silty clay loam; Sil, silt loam; Sl, sandy loam; Str, strong; Vgl, very gravelly loam; Vgls, very gravelly loamy sand; Vgsl, very gravelly sandy loam; W, wavy; Wk, weak.

[b] Not appropriate for paralithic (Cr) horizons.

Table 3
Paired difference analysis of means for selected soil properties in soils under diverse sagebrush communities (native) and cheatgrass-dominated communities (CG)[a]

	Thickness			Bulk density			Very fine roots[c] (<1 mm)			Fine roots[c] (1–2 mm)			Clay		
	Native (cm)	CG (cm)	Diff.[b] (%)	Native (g cm^{-3})	CG (g m^{-3})	Diff. (%)	Native (dm^{-2})	CG (dm^{-2})	Diff. (%)	Native (dm^{-2})	CG (dm^{-2})	Diff. (%)	Native (%)	CG (%)	Diff. (%)
A horizon	7.3 (0.8)	6 (0.4)	−18**	1.45 (0.09)	1.3 (0.07)	−10.7**	109 (19.2)	200 (0)	83***	75 (20.6)	0	−100***	29 (6.5)	26 (4.8)	−11
Subsurface 1	17 (2.2)	13 (1.6)	−21**	1.36 (0.03)	1.32 (0.04)	−2.4	61 (16.8)	76 (21)	25	48 (7.1)	0	−100***	28 (6.4)	26 (6.2)	−6
Subsurface 2[d]	15 (1.7)	15 (2.0)	4	1.44 (0.06)	1.36 (0.04)	−5.9	63 (19.3)	55 (0)	−12	46 (9.2)	0	−100***	29 (6.2)	30 (6.6)	5

	pH			CaCO3			Organic C			Total N			C:N		
	Native	CG	Diff (%)	Native (%)	CG (%)	Diff. (%)	Native (g kg^{-1})	CG (g kg^{-1})	Diff. (%)	Native (mg kg^{-1})	CG (mg kg^{-1})	Diff. (%)	Native	CG	Diff. (%)
A horizon	7.6 (0.2)	7.7 (0.19)	2.3	17.2 (5.8)	20 (6.4)	16.3***	21 (0.25)	23 (0.40)	10	2017 (245)	2523 (371)	25**	10 (2.2)	9 (0.4)	−14**
Subsurface 1	7.8 (0.2)	7.9 (0.14)	1.4	20.1 (6.5)	21.4 (7.2)	6.1	11 (0.28)	12 (0.21)	12	1218 (151)	1263 (148)	4	7 (2.2)	8 (2.9)	16
Subsurface 2	7.9 (0.2)	8.1 (0.14)	2.6	30.4 (7.9)	28.3 (7.8)	−6.7	6 (0.19)	3 (0.29)	−55*	998 (146)	1075 (134)	8	6 (19.4)	3 (4.7)	−54*

	Field inorganic N			Mineralized C			Active-pool N			Active-pool C:N		
	Native (mg kg^{-1})	CG (mg kg^{-1})	Diff (%)	Native (mg kg^{-1})	CG (mg kg^{-1})	Diff. (%)	Native (mg kg^{-1})	CG (mg kg^{-1})	Diff. (%)	Native	CG	Diff. (%)
A horizon	8.1 (2.3)	11 (3.8)	39	278 (42.5)	291 (68.0)	5	23 (4.45)	34 (7.6)	46**	13 (1.6)	10 (2.3)	−20*
Subsurface 1	1.4 (0.2)	2.6 (0.5)	85**	44.4 (6.8)	42.7 (9.4)	−4	1.8 (0.42)[e]	6.2 (1.4)	244**	39 (12.6)[e]	6 (1.3)	−83**
Subsurface 2	0.8 (0.2)	3.1 (1.7)	277*	26.6 (7.4)	52.5 (26.5)	97	0.6 (0.12)[f]	3.4 (1.8)	467*	59 (24.2)[f]	44 (33.9)	−25

Standard errors for means are in parentheses ($n = 7$ except where noted).
*, **, and *** significant at the 0.1, 0.05, and 0.01 levels, respectively.
[a] Based on mean values in the top three horizons across the seven study sites.
[b] Percent difference based on "native" values.
[c] Root density based on midpoints of visually estimated ranges.
[d] $n = 6$ because Johnson Canyon native profile has only two horizons.
[e] $n = 6$.
[f] $n = 5$.
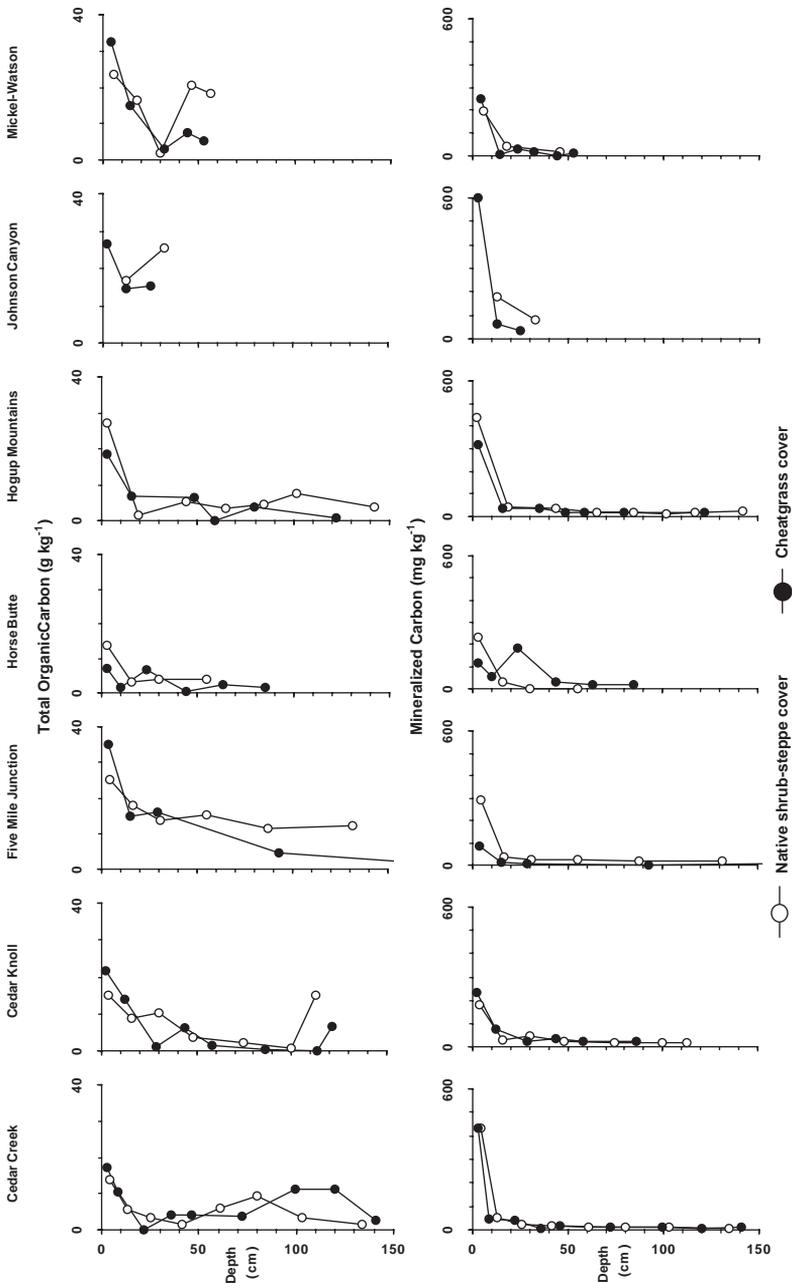
Fig. 2. Concentration of soil organic C (top) and cumulative mineral C released during 12-day incubation (mg CO_2-C kg soil^{-1}) (bottom) by horizon in paired soil profiles.

Table 4
Differences between highest and lowest concentrations of soil organic carbon in top 50 cm of soil profiles under diverse sagebrush communities (native) and cheatgrass-dominated communities (CG)

Site	A horizon org. C (highest), 0–50 cm			Lowest org. C, 0–50 cm			Difference (high-low), 0–50 cm		
	Native (g kg^{-1})	CG (g kg^{-1})	Diff. (%)	Native (g kg^{-1})	CG (g kg^{-1})	Diff. (%)	Native (g kg^{-1})	CG (g kg^{-1})	Diff. (%)
Cedar Creek	14	17	25	1	0[a]	−100	12	17	39
Cedar Knoll	15	22	43	4	1	−69	11	21	79
Five Mile	25	35	39	14	5	−66	11	30	166
Horse Butte	14	7	−49	3	0.2	−92	11	7	−37
Hogup Mtns	27	19	−31	1	0[a]	−100	26	19	−28
Johnson Canyon	25	27	5	17	14	−14	9	12	42
Mickel-Watson	24	33	38	2	0[a]	−100	22	33	49
Mean	21	23	10	6	3	−51**	15	20	36*
Standard error	2.2	3.7		2.5	2.0		2.5	3.5	

* and ** significant at the 0.1 and 0.05 levels, respectively, by paired difference analysis.
[a] Values below the detection level of the method.

native soils (Table 4). The size of the mineralizable fraction of total SOC varied considerably among the seven study sites (Fig. 2), but was similar beneath cheatgrass and native vegetation within each site, with no significant differences observed in the top three horizons (Table 3).

Total N content in the A horizons was significantly higher in cheatgrass than native vegetation and decreased sharply in subsurface horizons to equivalent levels for cheatgrass and native soils (Fig. 3, Table 3). Nitrate-N concentrations were generally higher beneath cheatgrass than native cover, with significant differences between cheatgrass and native subsurface horizons (Fig. 3, Table 3). Ammonium-N concentrations (data not shown) were low and variable, and generally followed the same trends as NO_3^--N. Concentration of active-pool N (i.e. mineral N concentration after the 12-day incubation) in surface and uppermost subsurface horizons was greater under cheatgrass than native cover at five of the seven sites (Fig. 4, Table 3). Each of the N forms analysed (total N, mineral N at field sampling time, and inorganic N after a 2-week incubation) increased slightly below the third horizon in at least four of the seven cheatgrass soils. Concentrations of N showed a similar, but less pronounced trend in some of the native soils.

Lower C:N ratios in cheatgrass than native soils (Table 3) reflect the relatively higher N concentrations but similar SOC concentrations in cheatgrass compared to native soil profiles. This relationship is particularly pronounced in active-pool C:N ratios (mineral C and N concentrations after incubation) below surface horizons at all sites except the Horse Butte site (Table 3, Fig. 4).

4. Discussion

Our data for soil morphology and SOM indicate that there are fundamental differences between soils below Wyoming big sagebrush-steppe and cheatgrass-dominated vegetation. These differences are similar in type and scale to effects of cultivation on grassland soils (Davidson and Ackerman, 1993; DeLuca and Keeney, 1994). Native shrub-steppe soils appear to have tight, complex organic-matter cycles while those of cheatgrass-dominated soils show signs of decaying SOM systems, similar to cultivated soils (Schimel, 1986). Both annual crop systems and cheatgrass-dominated vegetation enhance SOM mineralization as they reduce SOM inputs compared to native perennial vegetation (Schimel, 1986; Monaco et al., 2003). The differences hold true across the seven sites we analysed, including five where native vegetation consisted of mixed shrubs and bunch grasses and two with only a minor shrub component in the native vegetation (see Table 1). This suggests that the differences we observed are attributable to conversion of sagebrush-steppe vegetation to cheatgrass dominance, rather than to the absence of shrubs on the cheatgrass sites.

Thinner A horizons under cheatgrass-dominated vegetation likely reflect functional differences between cheatgrass and native grasses that lead to differences in SOM distribution. Cheatgrass allocates proportionally more resources to aboveground shoot biomass relative to roots on an annual basis compared to
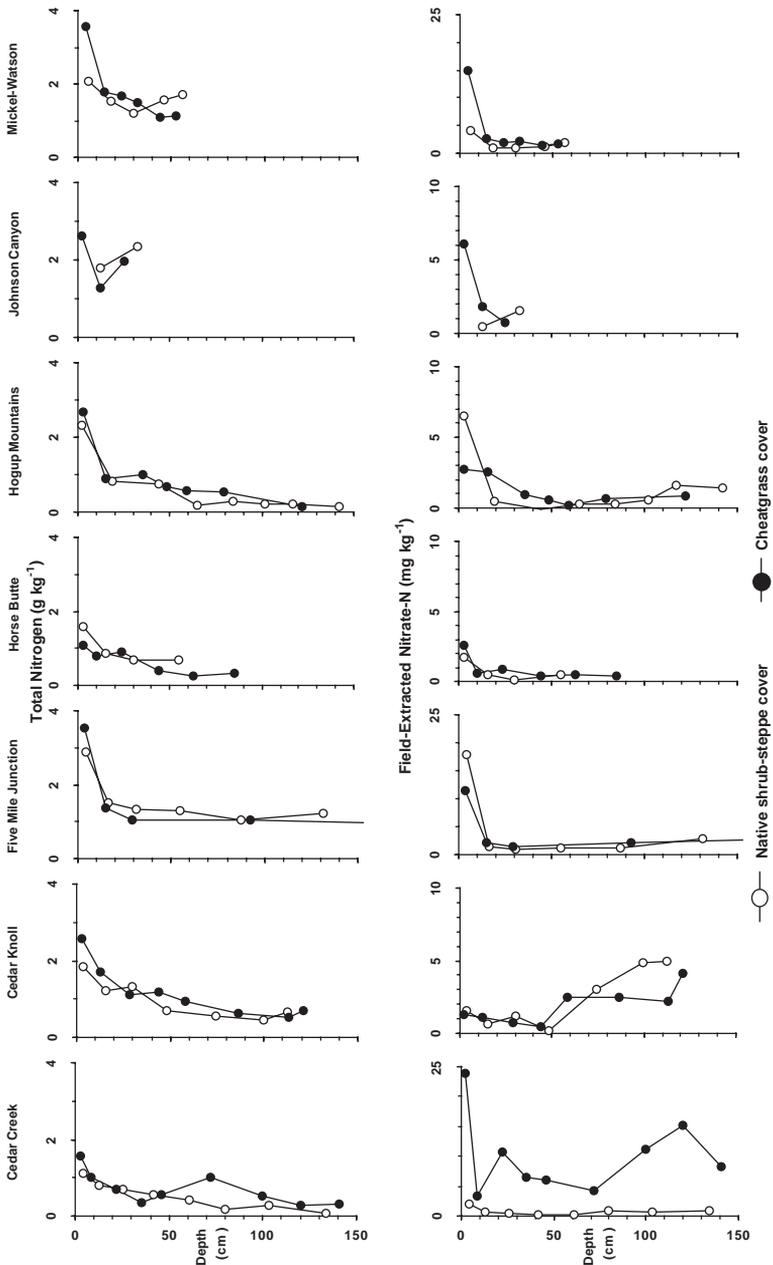
Fig. 3. Concentration of total N (top) and nitrate-N (extracted at time of sampling) (bottom) by horizon in paired soil profile samples. Note that nitrate-N *x*-axis has two different scales, 0–10 and 0–25.
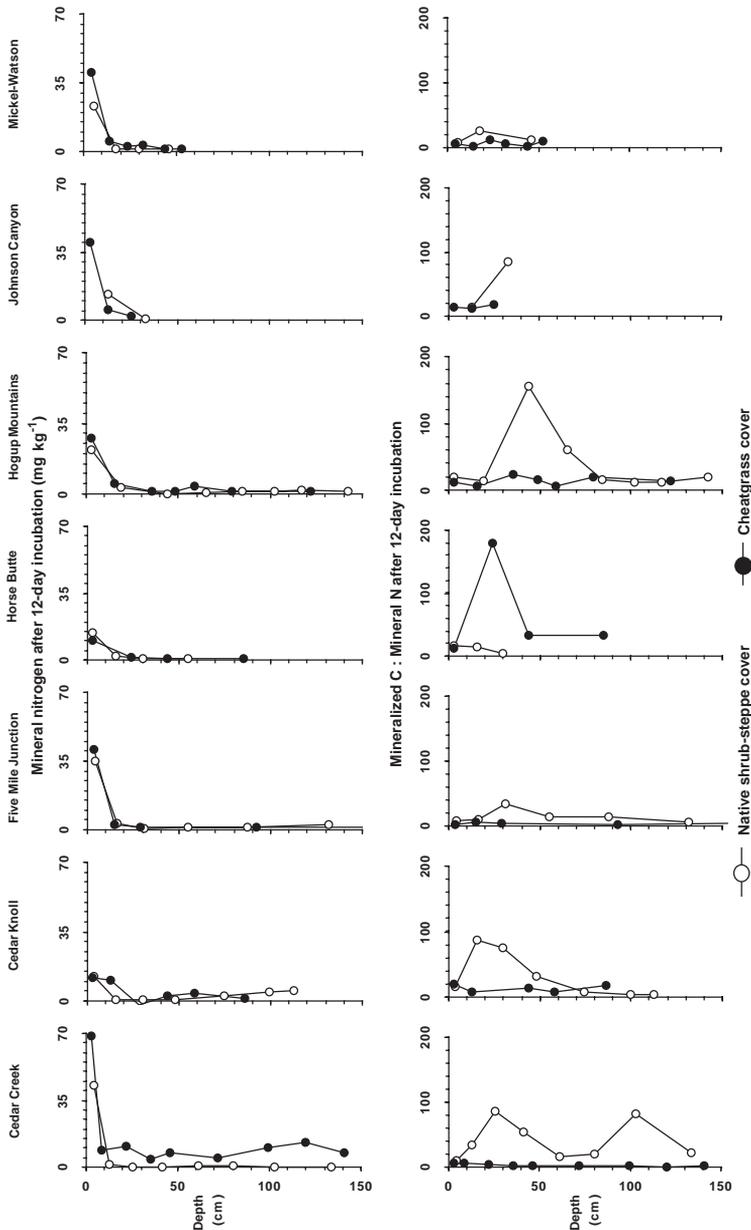
Fig. 4. Concentration of active-pool N (top) and active-pool C:N ratios (bottom) extracted from subsamples incubated for 12 days by horizon in paired soil profiles.

native perennial species (Monaco et al., 2003). Consequently, cheatgrass produces more leaf litter and a more shallow, very fine root system (Tables 2 and 3) than the native sagebrush-steppe community. Cheatgrass shoots and roots also have higher

C:N ratios (Paschke et al., 2000; Evans et al., 2001; Monaco et al., 2003). Lighter color of A horizons under cheatgrass suggests less humus in these soils, but it could also reflect elevated $CaCO_3$ concentrations (perhaps a result of denser soil cover capturing $CaCO_3$ dust particles) in A horizons under cheatgrass (Table 2). This could be a result of increased erosion beneath the cheatgrass cover exposing upper Bk horizons. However, differences in clay content between surface and subsurface horizons do not support this possibility; enough leaching to form A horizons would also leach $CaCO_3$. No other signs of severe erosion are present at the sites. Platy structure, which has been associated with freeze–thaw conditions (discussion in Gerrard et al., 1992, pp. 187–188), is evident in many of the A horizons under cheatgrass and suggests more extreme effects of climate in surface soils under cheatgrass than native sagebrush-steppe vegetation. Harsher environmental conditions in A horizons could result from relatively low concentration of humus beneath cheatgrass and/or from the short lifespan of cheatgrass and absence of living biomass during some of the extreme temperature fluctuations and drying–rewetting events in Great Basin summer and fall seasons. Humus and living biomass enhance both soil-water holding capacity and specific heat that moderate environmental extremes.

Allocation of resources to fine shoot material above the soil surface and a dense, fine root mass in surface soil horizons beneath cheatgrass result in similar total SOC concentrations in surface horizons of cheatgrass and intact native plant communities (Table 3, Fig. 2). However, the very low SOC levels in upper subsurface horizons of cheatgrass soils (Fig. 2) suggests that cheatgrass contributes less SOM at this depth.

Gill et al. (1999) observed higher decomposition rates in the 10- to 15-cm depth range than at the surface of shortgrass-steppe soils in Colorado and attribute this to higher available water in the subsurface than at or near the soil surface. Combined with decreased SOM inputs below shallow A horizons, subsurface decomposition after conversion to cheatgrass could contribute to the low SOC levels we observed in the 10- to 50-cm depth range beneath cheatgrass-dominated vegetation.

The readily available carbohydrate source created when C-rich plant materials are exposed to frequent wetting–drying and freeze–thaw cycles on or near the soil surface (Schimel and Parton, 1986; Cui and Caldwell, 1997), along with the lack of appreciable root OM input below 15–20 cm beneath cheatgrass (Table 2), may result in the mineralization of SOM stored through millennia of shrub-steppe vegetation cover. This suggests the possibility of a mineralization priming effect, where increased microbial biomass, altered microbial composition, and enzymatic activity created by the labile C source break down not only the fresh, labile C, but also previously protected, resistant SOM. A mineralization priming effect, where substrate amendments stimulate plant and microbial uptake of more C and N than is present in the added substrate, is often observed when a labile nutrient source is introduced to soils with previously conservative SOM turnover (DeLuca and Keeney, 1993). Gill and Burke (1999) found lower concentrations of particulate organic matter C (a slowly cycling pool of SOC) beneath cheatgrass than perennial shrubs on northern Utah rangelands and attributed the difference to loss of stored SOM after cheatgrass invasion of shrub-steppe vegetation.

In contrast to SOC, total N concentrations were higher in surface horizons beneath cheatgrass than native sagebrush-steppe vegetation, but the same in subsurface horizons under the two vegetation types. The higher NO_3^--N concentrations we observed under cheatgrass (Table 3, Fig. 3) supports the scenario of more rapid, shallow SOM turnover. Bolton et al. (1990) and Svejcar and Sheley (2001) also observed higher mid-summer levels of inorganic N in soils beneath cheatgrass than native shrub-steppe vegetation, which they attributed to the absence of organic N storage in the annual cheatgrass.

Spring moisture and warm temperatures on rangelands of the Intermountain West lead to a pulse of mineralization that coincides with plant growth (Cui and Caldwell, 1997). For cheatgrass, which senesces very early in the growing season, mineralization may extend beyond the period of plant uptake. The out-of-phase mineralization and uptake, along with mineralization of deeper, stored SOM discussed above, may contribute to the higher mid-summer NO_3^- levels we observed in cheatgrass soils (Table 3, Fig. 3). Consequently, this scenario might facilitate rapid growth of cheatgrass after fall precipitation or in early spring. In contrast, a diverse assemblage of native perennial grass and shrub vegetation likely continues uptake of mineralized N because of greater spatial and temporal exploitation by both plants and soil microbes. Repeated sampling through the course of one or more years would be necessary to confirm these observations.

The composition of active-pool SOM mineralized during our 12-day incubations also supports the concept of shallower SOM that turns over more rapidly under cheatgrass compared to native vegetation. Although concentrations of mineralizable C were about the same under cheatgrass and native vegetation, the concentration of active-pool N was greater in upper horizons under cheatgrass than native vegetation. The resulting lower C:N ratio of the active SOM pool in cheatgrass soils suggests a mineralizing, C-limited microbial environment compared to an immobilizing, N-limited microbial environment beneath native plant communities. This may be caused by more spatially and temporally diverse inputs of SOM and uptake of mineral N by the native perennial vegetation. The Horse Butte site showed the opposite trend, perhaps because of high $CaCO_3$ in the third soil horizon, which may have caused a rapid increase of CO_2-C during the incubation.

Smith et al. (1994) also reported differences between ratios of metabolic quotients of C (qCO_2, or basal production of CO_2-C per unit of biomass) and N (qN, or net N mineralized per unit of biomass) in shrub-steppe (qCO_2:qN = 20) and annual grass-dominated soils (qCO_2:qN = 5). Their results indicate that the shrub-steppe ecosystem stores appreciable amounts of recalcitrant C and has the tightest, most efficient N cycling (higher immobilization and lower mineralization) compared to crop, forest, and annual grass ecosystems they evaluated (Smith et al., 1994).

5. Conclusions

The results of our study showed important differences in soil morphology and the distribution and composition of SOM in soils underneath intact and

cheatgrass-invaded Wyoming big sagebrush-steppe plant communities. These differences suggest that soils under cheatgrass-dominated plant communities have shallow, rapidly cycling SOM pools. Together with other recent studies (e.g. Gill and Burke, 1999; Evans et al., 2001), these results suggest that cheatgrass invasion has led to a loss of SOM, which may affect important soil structural attributes. Loss of SOM could create ecologically impoverished sites that are very difficult to restore to functionally diverse perennial plant communities.

Acknowledgements

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