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Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA

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Abstract Semiarid sagebrush ecosystems are being transformed by wildfire, rangeland improvement techniques, and exotic plant invasions, but the effects on ecosystem C and N dynamics are poorly understood. We compared ecosystem C and N pools to 1 m depth among historically grazed Wyoming big sagebrush, introduced perennial crested wheatgrass, and invasive annual cheatgrass communities, to examine whether the quantity and quality of plant inputs to soil differs among vegetation types. Natural abundance δ^{15}N isotope ratios were used to examine differences in ecosystem N balance. Sagebrush-dominated sites had greater C and N storage in plant biomass compared to perennial or annual grass systems, but this was predominantly due to woody biomass accumulation. Plant C and N inputs to soil were greatest for cheatgrass compared to sagebrush and crested wheatgrass systems, largely because of slower root turnover in perennial plants. The organic matter quality of roots and leaf litter (as C:N ratios) was similar among vegetation types, but lignin:N ratios were greater for sagebrush than grasses. While cheatgrass invasion has been predicted to result in net C loss and ecosystem degradation, we observed that surface soil organic C and N pools were greater in cheatgrass and crested wheatgrass than sagebrush-dominated sites. Greater biomass turnover in cheatgrass and crested wheatgrass versus sagebrush stands may result in faster rates of soil C and N cycling, with redistribution of actively cycled N towards the soil surface. Plant biomass and surface soil δ^{15}N ratios were enriched in cheatgrass and crested wheatgrass relative to sagebrush-dominated sites. Source pools of plant available N could become ^{15}N enriched if faster soil N cycling rates lead to greater N trace gas losses. In the absence of wildfire, if cheatgrass invasion does lead to degradation of ecosystem function, this may be due to faster nutrient cycling and greater nutrient losses, rather than reduced organic matter inputs.

Keywords Invasive species (cheatgrass) · Ecosystem C and N storage · δ^{15}N natural abundance isotope ratio · Sagebrush rangeland

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Introduction

Sagebrush-dominated ecosystems comprise extensive land areas in the Great Basin and intermountain regions of the western US. These ecosystems are being altered by grazing, rangeland improvement techniques, exotic plant invasions, and altered wildfire regimes. These disturbances affect the composition and structure of native vegetation, typically by causing a shift in dominance from shrubs to introduced perennial or invasive annual grasses (Stewart and Hull 1949; D'Antonio and Vitousek 1992; West 1999). Differences in the distribution and turnover of biomass among plant life-forms, and the degree of internal versus external nutrient cycling in the plant-soil system are likely to play an important role in both short- and long-term ecosystem C and N storage and dynamics (Chapin et al. 1997). Given the large spatial extent of sagebrush ecosystems in the US (over 60 million hectares, West and Young 2000), even small changes in rates of biogeochemical cycling due to vegetation change may have large ramifications for regional and global C and N budgets. However, in spite of the extensive land area covered by sagebrush, surprisingly few data are available in the literature on ecosystem C and N pools and turnover rates in sagebrush-dominated systems.

Biogeochemical cycles in semiarid ecosystems are constrained by temporal and spatial variability (Burke 1989). Cold temperatures during the winter and low soil moisture in summer restrict the time frame for active plant growth and microbial activity to short periods in late spring and early autumn. When environmental conditions are adequate, rates of plant growth may be limited by soil N availability (James and Jurinak 1978; Bilbrough and Caldwell 1997; Duke and Caldwell 2001). Spatial patterns of plant cover and the life-form of vegetation types regulate soil organic matter accumulation and nutrient cycling rates (Charley and West 1977; Burke 1989; Vinton and Burke 1995; Schlesinger and Pilmanis 1998). The quantity and quality of plant organic matter inputs to soil via leaf litterfall and root turnover are key linkages driving soil microbial decomposition and plant nutrient availability. Increased C inputs, through differences in foliage and root turnover among different vegetation types (Caldwell et al. 1977; Gill and Jackson 2000; Belnap and Phillips 2001; Schenk and Jackson 2002), may increase N demand by soil microbes and reduce N available for plant uptake (Schlesinger and Peterjohn 1991; Hart et al. 1994). In contrast, increased quality of plant detrital inputs (i.e. lower litter C:N ratios) may increase N availability to plants via decreased microbial demand for inorganic N (Chen and Stark 2000; Carrera et al. 2003). What is not yet clear, is to what extent current shifts in dominant vegetation over large areas of the Great Basin and intermountain regions affect plant organic matter inputs, rates of soil organic matter turnover, and ecosystem C and N sequestration.

Shifts in vegetation type may alter the quantity and quality of organic matter inputs to soil through differences in biomass allocation and the magnitude of plant internal nutrient cycling. In semiarid systems, shrubs (such as sagebrush) appear to have more extensive root systems than annual or perennial grasses (Schenk and Jackson 2002), such that changes in dominant vegetation type may alter the depth distribution of organic matter and nutrients (Jackson et al. 2000; Jobbágy and Jackson 2000) and rates of soil nutrient cycling. For example, Vinton and Burke (1995) found that differences in quantity, quality, and biomass distribution (root:shoot ratio) of shortgrass steppe vegetation affected soil potential C mineralization rates. Carrera et al. (2003) reported that in the Patagonian Monte, perennial grass-dominated sites had greater plant internal N cycling (leaf N resorption), higher leaf litter C:N, and lower soil potential N mineralization rates compared to sites dominated by evergreen shrubs. Similarly, Evans et al. (2001) found that cheatgrass invasion of Colorado Plateau grasslands increased the size and C:N ratio of surface litter pools compared to uninvaded grasslands, and reduced potential N mineralization rates.

The larger-scale consequences of vegetation change may include direct losses of C and N from long-lived woody tissues as a result of wildfire (Bradley et al. 2006); and reduced ecosystem productivity of introduced grasses compared to intact sagebrush ecosystems (Schlesinger et al. 1990; Ivans 2005; Prater et al. 2006); but the magnitude of such effects are unclear (see Huenneke et al. 2002). Land degradation following cheatgrass invasion and dominance, or conversion of sagebrush to perennial forage grasses, might also accelerate ecosystem N losses over inputs, resulting in enriched natural abundance δ^{15}N signatures (Evans and Ehleringer 1993; Hogberg 1997; Evans and Belnap 1999).

In this study we compare ecosystem C and N contents (above- and belowground biomass, surface litter, and soil organic matter pools to 1 m depth) and the quantity and quality of plant organic matter inputs in a native sagebrush ecosystem with two vegetation types that represent the most common alternative stable states following disturbance (cheatgrass and crested wheatgrass dominated ecosystems) in Great Basin rangelands. We hypothesized that differences in plant life-form strongly affect plant biomass distribution and the magnitude of plant internal versus external nutrient cycling. Thus, the quality of plant organic matter inputs to soil would decrease, and litter quantity would increase in the order: cheatgrass, crested wheatgrass, and sagebrush. Consequently, we anticipated that plant biomass inputs would be lower in annual grass compared to native sagebrush ecosystems, leading to C and N losses from soil organic matter pools.

Materials and methods

Study site

This study was carried out on a Great Basin sagebrush rangeland in Rush Valley (Tooele County), Utah (112°28′ W, 40°17′ N, elevation 1,610 m). The site has extensive, nearly monodominant stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), crested wheatgrass (*Agropyron desertorum* (Fisch. ex. Link), var. 'Nordan'), and cheatgrass (*Bromus tectorum* L.), and has been moderately grazed for over 100 years (D. Johnson, personal communication). Mean annual precipitation and temperature measured on-site over a 5-year period (1999–2003) were 266 mm and 8.3°C, respectively, which is similar to nearby long-term climate records (Vernon, UT, 21.5 km from research site, 273.1 mm and 8.7°C, 1971–2000 means). Precipitation is distributed nearly evenly over the year, but soil water accumulation is restricted to the cooler autumn and winter months (November through March). Soils are derived from lacustrine (former Lake Bonneville) and alluvial sediments of primarily limestone deposits, have no root-restricting layer, and are classified as Erda silt loam, very deep, well drained, mixed, superactive, mesic Aridic Calcixerolls (A. Mitchell, personal communication). Soils are non-saline within the surface 100 cm (EC < 2.0 dS m^{-1}) (Table 1). Soil carbonates are mainly disseminated, with concentrations increasing from 10 to >25 g CO_3–C kg^{-1} soil with depth, and account for the majority (>70%) of total soil C to 100 cm depth.

Stands of both crested wheatgrass and cheatgrass vegetation were established in 1992 on areas formerly dominated by sagebrush. Crested wheatgrass was established to improve rangeland quality by disking to remove shrubs and then drill-seeding (30 cm row spacing). Cheatgrass established naturally with the onset of autumn rains after a summer wildfire consumed several large areas of sagebrush. Due to the long history of cheatgrass within the Great Basin (Pickford 1932; Mack 1981), it is likely that cheatgrass was already present in at least small amounts within the sagebrush stand at the time of disturbance.

In late 1998, four 22 × 22 m permanent plots were created in each vegetation type. Permanent plots were randomly located along two north–south and two east–west transects that crossed all three vegetation types. Transects were separated by at least 75 m, and plots of adjacent vegetation types within a transect were separated by approximately 40 m. All measurements were made from random locations within each of the permanent plots. Field sampling included measurement of aboveground biomass, surface litter, plant root biomass, and soil to a 1 m depth. Due to the large spatial heterogeneity in plant cover in Great Basin sagebrush communities, surface litter, belowground biomass and soil organic matter pools within sagebrush plots were sampled in randomly selected paired locations beneath shrub canopies and in the shrub-interspace (within 1 m of the canopy sampling point). The areal extents of shrub-canopy and shrub-interspace microsites (average 38 and 62%, respectively), determined by the line-intercept method, were used to scale results to an areal basis.

Aboveground biomass and surface litter

Crested wheatgrass and cheatgrass vegetation was sampled by harvesting live and dead biomass biweekly during the growing season (less frequently in summer and autumn) in 2001 and 2002. Biomass was harvested from five randomly located quadrats per plot on each sampling date; crested wheatgrass quadrats were 25 × 25 cm, and cheatgrass quadrats

Table 1 Site characteristics, Rush Valley, UT

Site characteristic	Cheatgrass	Crested wheatgrass	Sagebrush	
			Canopy	Interspace
Plant cover (%)[a]	80	37	15	<1
Root length density (mm cm^{-2})[b]	9.1	4.0	1.4	ND
Average root diameter (mm)[b]	0.20	0.22–0.24	0.26–0.30	ND
Textural class	Silt loam	Silt loam	Loam	Silt loam
Clay (%)	15.0	14.5	15.5	14.0
Silt (%)	52.5	53.0	48.0	48.0
pH[c]	7.5	7.5	7.2	7.7
Total soluble P (mg P kg^{-1} soil)[c]	0.25ab	0.30a	0.31a	0.15b
Electrical conductivity (dS m^{-1})[c]	0.50a	0.28b	0.55a	0.25b
Fine soil bulk density (Mg m^{-3})[d]				
0–10 cm	1.00	1.01	0.98	1.02
10–20 cm	1.13	1.16	1.12	1.20
20–40 cm	1.10	1.15	1.22	1.26
40–70 cm	1.18	1.31	1.25	1.25
70–100 cm	1.10	1.25	1.07	1.17

Sagebrush sites were stratified into areas beneath the outer extent of sagebrush canopies and interspace areas outside of sagebrush canopies. Canopy-affected areas represented 38% and interspace areas represented 62% of the total area of sagebrush ecosystems, based on line-intercept measurements

Within a row, values followed by same letter are not significantly different ($P > 0.05$)

ND—no data, root observation tubes were associated with individual sagebrush plants

[a] Percentage of plot area covered by live leaf tissue at maximum biomass

[b] For the 0–10 cm soil depth, based on minirhizotron data

[c] Saturated paste extracts, 0–10 cm soil depth

[d] Coarse fragments (>2 mm) accounted for 1.1–4.5% of soil mass, and increased with depth

were 10 × 10 cm. Plant samples were dried and prepared for elemental and isotopic analysis as described below. Peak aboveground biomass was used as an estimate of aboveground production in perennial and annual grass vegetation types. Aboveground production was estimated from the seasonal peak since the growing season is short for the annual grass, and growth is monotonic for the perennial grass in this semiarid ecosystem (see Sala and Austin 2000). Grazing management practices commonly include introducing cattle in mid- to late-summer; however, we excluded grazing from the site during the year that measurements were made to allow estimation of above-ground plant biomass production and to reduce grazing-induced variability in soil characteristics. Our estimates of aboveground biomass production assume that herbivory by other animals (antelope, rabbits, and Mormon crickets) was negligible.

Total aboveground biomass of sagebrush vegetation was calculated from allometric equations (Rittenhouse and Sneva 1977; Uresk et al. 1977; Fransden 1983; Reiner 2004) based on measurements of each shrub >15 cm tall in the four 22 × 22 m permanent plots ($n = 2{,}660$ plants). The average of values from all four allometric equations was used to estimate sagebrush aboveground biomass, as this average was closely correlated with biomass measured directly from destructive harvest of eight sagebrush spanning a wide range of plant sizes (90–4,000 g/plant; $r^2 = 0.93$, slope $= 0.95$). Sagebrush aboveground biomass calculated in permanent plots ranged from 40 to 7,500 g/plant. The aboveground biomass of destructively harvested shrubs was separated into foliage plus four classes of woody tissue: small, medium, and large branches (<1.5, 1.5–3.0, and 3.0–4.0 cm circumference, respectively), and trunk (>4.0 cm). Harvested materials were dried and ground for elemental and isotopic analysis. The proportion of biomass in each size-class was found to be logarithmically related to total shrub mass (g):

$$\%\ \text{Small} = -0.043\ \ln(\text{shrub mass}) + 0.533$$
$$r^2 = 0.68$$
$$\%\ \text{Medium} = -0.014\ \ln(\text{shrub mass}) + 0.253$$
$$r^2 = 0.49$$
$$\%\ \text{Large} = 0.036\ \ln(\text{shrub mass}) - 0.122$$
$$r^2 = 0.55$$
$$\%\ \text{Trunk} = 0.042\ \ln(\text{shrub mass}) + 0.141$$
$$r^2 = 0.56$$
$$\%\ \text{Foliage} = -0.020\ \ln(\text{shrub mass}) + 0.207$$
$$r^2 = 0.69$$

These relationships were used to estimate the biomass of shrub components for each shrub measured in the four permanent plots. Aboveground biomass C and N contents (Mg C ha^{-1} and kg N ha^{-1}) were estimated by multiplying C and N concentrations of biomass components by the mass of the component, and summed for each shrub. Natural abundance N isotope ratios ($\delta^{15}N$) were calculated by multiplying the δ-value of each biomass component by the component's relative contribution to shrub total N content. Senesced plant foliage and root biomass (from surface soils, see below) were analyzed for lignin concentration (ash-free) following forage fiber methodology (Goering and Van Soest 1970).

Surface litter C and N contents were determined for ten dates during the snow-free season from April 2001 to 2002, and are presented as surface litter C and N content at the time of maximum plant aboveground biomass (late May for cheatgrass, mid-June for crested wheatgrass and sagebrush). Live and standing dead plant biomass was removed prior to collecting surface litter. Samples were brought back to the laboratory, dried (65°C) and weighed, ground (60 mesh) with a Wiley mill, and subsampled for analyses of C and N concentration and isotope ratios.

Soil sampling

Soils were collected with a 5 cm diameter 'King-tube' (Giddings Machine Co., Windsor, CO), on five sampling dates (April 2001–2002) from one randomly selected location in each of the four permanent plots of each vegetation type. Soil cores were separated into 0–10, 10–20, 20–40, 40–70, and 70–100 cm increments in the field, and stored in separate plastic bags on ice until returned to the laboratory. A second set of surface soil cores (0–10 and 10–20 cm) were collected within 30 cm of the first to provide sufficient soil for laboratory analyses.

Soils were sieved (<2, <1 mm) to collect coarse fragments and roots the day following sampling. Roots were rinsed with deionized H_2O and dried, weighed and ground for elemental and isotopic analysis. Coarse fragments were dried and weighed to calculate fine soil bulk density (assuming particle density of 2.65 Mg m^{-3}). Soil moisture content was determined by mass-loss after drying for 48 h at 105°C. A subsample of fine soil was dried and ground for determination of C and N concentrations and isotope ratios.

Soil organic C was determined following removal of carbonates by the acid fumigation procedure of Harris et al. (2001). Soil N concentrations and natural abundance $\delta^{15}N$ isotope ratios were determined using non-acid fumigated soil samples. Soil inorganic C was calculated as the difference in C from unfumigated (total C) and HCl-fumigated (organic C) samples. Total root biomass and soil C and N contents to 1 m soil depth were calculated by scaling pools to a mass per hectare basis for each depth, and summed for each plot; data presented are the average from five sampling dates. Total soil and root isotope ratios were calculated similarly, but values are weighted averages (based on C or N content) for each plot. All plant, litter, and soil C and N concentrations and isotope ratios were determined by continuous-flow direct combustion and mass spectrometry using a Europa 20/20 Mass Spectrometer (Europa Scientific, Crewe, UK). Analytical precision was approximately 0.15‰ $\delta^{15}N$ over all sample analyses, with duplicate analysis of 10% of samples.

Soil NH_4^+ and NO_3^- concentrations were measured in 2 M KCl extracts (1:10 soil:solution ratio), obtained in the field within 1 h of sample collection, and analyzed colorimetrically with a Lachat AE flow-injection Autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Microbial biomass C and N were determined on sieved, field-moist soils by the chloroform fumigation–extraction method following Haubensak et al. (2002), using k_{EC} of 0.35 (Voroney et al. 1991) and k_{EN} of 0.54 (Brookes et al. 1985). Paired fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4 (1:10 soil:solution ratio). Extracts were analyzed for organic C concentration with Phoenix 8000 TOC analyzer (Teledyne–Tekmar, Mason, OH, USA), and total soluble N (Lachat AE) following persulfate oxidation (Cabrera and Beare 1993).

Calculation of above- and belowground plant C and N inputs to soil

Aboveground plant C inputs to soil were assumed to equal maximum plant biomass for crested wheatgrass and cheatgrass vegetation. Sagebrush foliage C inputs to soil were assumed to equal foliage biomass C calculated from allometric equations described above, based on complete turnover of both ephemeral and over-wintering foliage on an annual basis (Evans and Black 1993; Welch 2005). Aboveground C inputs may be slightly overestimated if photodegradation results in significant mineralization of C from standing dead biomass and surface litter (Austin and Vivanco 2006; Brandt et al. 2007; Henry et al. 2008). No estimates of sagebrush woody litter inputs were made, since these inputs have very high spatial and temporal variability (West 1985) and contribute <8% to annual litterfall (Mack 1977).

Annual aboveground plant N inputs to soil were calculated as:

$$\text{N input} = (1 - \text{NRE}) \cdot f_N \qquad (1)$$

where NRE equals foliage N resorption efficiency, and f_N is foliage N content at peak biomass. Leaf N resorption efficiency was calculated directly based on differences in leaf N concentration at maximum plant biomass and in early autumn following leaf senescence (prior to autumn rainfall). The decline in cheatgrass foliage N concentration after maximum biomass was assumed to represent N translocated to maturing seeds. Cheatgrass aboveground N inputs were calculated with and without accounting for N translocated to seeds, but statistical analysis was restricted to the conservative estimate of leaf N input (after translocation), since cheatgrass seeds may reside in soil for several years before germinating or being decomposed (Hulbert 1955; Billings 1992), and cheatgrass soil detrital pools may not be at steady-state. Belowground C and N inputs were calculated as the product of mean root C and N pool size (five sampling dates) and root turnover rate. Belowground biomass turnover was assumed to equal 1.0 year^{-1} for cheatgrass, 0.5 year^{-1} for crested wheatgrass (Gill and Jackson 2000); and 0.3 year^{-1} for sagebrush (Caldwell et al. 1977). We assumed that there was no resorption of N from roots during senescence.

Statistical analysis

We used repeated measures analysis to evaluate the depth-distribution of soil C and N pools and isotope ratios, among vegetation types using PROC MIXED (SAS version 9.0, Cary, NC). Vegetation type and sample depth were fixed effects, plots were random, with plot × vegetation type as the subject of repeated measure. We used information criteria (AICC and BIC) from several covariance structures to obtain the best model for each variable. Most variables conformed to split-plot residual design with regard to covariance of the error matrix. Variables were transformed when necessary to comply with model assumptions; data were most commonly natural log transformed. The SLICE command was used to evaluate significant differences among vegetation types for each soil depth, and when significant, pairwise differences were used to compare each vegetation type at a specific soil depth. Analysis of variance was used to determine whether vegetation types differed for total ecosystem pools. Statistical differences were considered significant for $\alpha = 0.05$.

Results

Distribution of ecosystem C and N

Total ecosystem C content averaged 258 ± 11 Mg C ha^{-1} (mean ± 1 SE) to a 1 m depth across vegetation types, and was dominated by soil inorganic C pools. Organic C accounted for 29% of total ecosystem C storage, with no significant differences among vegetation types ($P = 0.21$). Similarly, total ecosystem N content did not differ significantly among vegetation types ($P = 0.17$), averaging 7,936 ± 409 kg N ha^{-1}.

Aboveground biomass C pools in sagebrush were roughly three times those in cheatgrass or crested wheatgrass vegetation types, while N pools were only 36% greater in sagebrush compared to the grasses (Tables 2, 3). Sagebrush foliage accounted for nearly half of aboveground N, but only 16% of aboveground C. The remaining N and C was found in live and standing dead woody biomass. Peak aboveground biomass C and N contents in cheatgrass and crested wheatgrass vegetation types were greater than sagebrush foliage ($P < 0.002$ and $P < 0.03$ for C and N contents, respectively). Aboveground biomass C:N ratios were highest for sagebrush woody biomass (89.2), while C:N ratios of live and senesced foliage did not differ significantly among vegetation types (Table 4). Lignin concentrations and lignin:N ratios in sagebrush foliage were nearly three times those in cheatgrass or crested wheatgrass foliage ($P < 0.001$).

Surface litter C and N pools in cheatgrass-dominated sites were significantly larger than in crested wheatgrass, while sagebrush surface litter was intermediate ($P < 0.02$ and $P < 0.01$, for C and N, respectively; Tables 2, 3). Spatial heterogeneity of surface litter C and N was large in sagebrush dominated sites. Litter pools beneath shrub-canopies (1.1 Mg C ha^{-1} and 61.6 kg N ha^{-1}, respectively) were approximately ten times those of shrub-interspaces (0.1 Mg C ha^{-1}, and 6.2 kg N ha^{-1}). Surface

Table 2 Ecosystem C pools in three vegetation types in Rush Valley, UT

Ecosystem pool	Cheatgrass	Crested wheatgrass	Sagebrush			Model SE (depth)[b]
			Areal average[a]	Beneath canopy	Interspace	
	(Mg C ha^{-1})					
Aboveground plant biomass C	1.2 (0.1)b	1.3 (0.1)b	3.8 (0.7)a			
Wood	n.a.	n.a.	3.2 (0.5)			
Foliage	1.2 (0.1)a	1.3 (0.1)a	0.6 (0.1)b			
Surface litter C	0.9 (0.1)a	0.4 (0.1)b	0.6 (0.1)ab			
Root C (0–100 cm)	2.0 (0.3)	3.1 (0.4)	2.4 (0.3)			
Soil organic C (0–100 cm)	72.1 (3.9)	69.1 (3.1)	62.0 (4.2)			
Root C (kg C m^{-3})						
0–10 cm	1.00	0.69	0.81	1.40	0.46	(0.22)
10–20 cm	0.26b	0.48a	0.42a	0.48	0.36	(0.11)
20–40 cm	0.15b	0.37a	0.20b	0.27	0.15	(0.07)
40–70 cm	0.09b	0.26a	0.18a	0.15	0.20	(0.06)
70–100 cm	0.01c	0.14a	0.06b	0.07	0.05	(0.02)
Soil organic C (kg C m^{-3})						
0–10 cm	15.92a	14.28ab	12.90b	14.24	12.15	(2.84)
10–20 cm	10.51	10.99	9.59	9.75	9.47	(2.19)
20–40 cm	7.72	7.25	6.64	7.07	6.40	(1.52)
40–70 cm	6.08	5.93	5.01	5.43	4.76	(1.19)
70–100 cm	4.11	3.86	3.63	3.38	3.75	(0.79)
Microbial C (kg C m^{-3})						
0–10 cm	0.52	0.41	0.39	0.50	0.32	(0.18)
10–20 cm	0.31	0.24	0.27	0.35	0.22	(0.10)
20–40 cm	0.18	0.28	0.24	0.29	0.20	(0.08)
40–70 cm	0.14	0.15	0.14	0.18	0.12	(0.05)
70–100 cm	0.08	0.08	0.09	0.11	0.08	(0.03)

Values represent vegetation type means for five dates

[a] Weighted average of sagebrush canopy and interspace microsites based on the areal extent of the two microsites

[b] Back-transformed standard error for differences among vegetation types within a soil depth, from repeated measures ANOVA

Within a row, means with the same lowercase letter are not significantly different ($P > 0.05$)

Table 3 Ecosystem N pools in three vegetation types in Rush Valley, UT

Ecosystem pool	Cheatgrass	Crested wheatgrass	Sagebrush			Model SE (depth)[b]
			Areal average[a]	Beneath canopy	Interspace	
	(kg N ha^{-1})					
Aboveground plant biomass N	53.8 (5.9)b	48.1 (1.9)b	68.3 (11.5)a			
Wood	n.a.	n.a.	35.7 (11.5)			
Foliage	53.8 (5.9)a	48.1 (1.9)a	32.7 (5.7)b			
Surface litter N	43.4 (5.2)a	13.2 (3.2)b	27.1 (4.3)ab			
Root N (0–100 cm)	76.8 (14.1)	85.9 (12.2)	76.3 (8.1)			
Soil N (0–100 cm)	8072 (351)	7977 (354)	7255 (268)			
Root N (g N m^{-3})						
0–10 cm	44.6	25.4	41.1	74.8	20.2	(9.1)
10–20 cm	10.3	12.3	9.5	11.2	8.1	(3.1)
20–40 cm	4.4b	7.7a	3.7b	4.8	3.1	(1.5)
40–70 cm	3.8	6.2	3.1	2.8	3.3	(1.3)
70–100 cm	0.5c	4.8a	1.8b	1.8	1.8	(0.4)
Soil N (kg N m^{-3})						
0–10 cm	1.57a	1.37ab	1.21b	1.25	1.18	(0.19)
10–20 cm	1.00	1.04	0.94	0.95	0.93	(0.15)
20–40 cm	0.80	0.85	0.82	0.89	0.79	(0.13)
40–70 cm	0.81	0.79	0.67	0.72	0.64	(0.11)
70–100 cm	0.54	0.50	0.43	0.42	0.48	(0.07)
Microbial N (g N m^{-3})						
0–10 cm	79.4	70.9	72.6	90.9	61.6	(10.6)
10–20 cm	61.3	53.1	45.7	52.4	41.3	(6.5)
20–40 cm	27.8	35.2	31.7	35.6	29.3	(3.7)
40–70 cm	19.3	28.5	22.4	20.6	23.9	(2.6)
70–100 cm	18.1	15.7	14.4	14.6	14.1	(1.7)
Soil NH_4^+ (g N m^{-3})						
0–10 cm	1.66	1.56	1.32	1.45	1.25	(0.20)
10–20 cm	0.86	0.97	1.24	1.27	1.24	(0.19)
20–40 cm	0.64	0.74	0.89	0.91	0.81	(0.08)
40–70 cm	0.45	0.56	0.62	0.61	0.64	(0.08)
70–100 cm	0.36	0.33	0.37	0.35	0.37	(0.04)
Soil NO_3^- (g N m^{-3})						
0–10 cm	3.70a	2.61ab	2.00b	2.11	1.98	(0.22)
10–20 cm	2.13	2.00	1.67	1.77	1.62	(0.11)
20–40 cm	2.00	2.07	1.57	1.72	1.50	(0.13)
40–70 cm	2.12a	1.25b	1.07b	1.18	1.01	(0.08)
70–100 cm	2.29a	1.12b	0.98b	1.07	0.91	(0.12)

Values represent vegetation type means for five dates

[a] Weighted average of sagebrush canopy and interspace microsites based on the areal extent of the two microsites

[b] Back-transformed standard error for differences among vegetation types within a soil depth, from repeated measures ANOVA

Within a row, means with the same letter were not significantly different ($P > 0.05$)

Table 4 Characteristics of organic matter quality across vegetation types

Ecosystem pool	Cheatgrass	Crested wheatgrass	Sagebrush
Aboveground biomass C:N	22.9	26.9	55.7
Wood C:N			89.2
Live foliage C:N	22.9	26.9	21.6
Senesced foliage C:N	46.9	52.3	55.8
Foliar lignin (g/kg)	44.6b	42.9b	119.1a
Foliage lignin:N	4.93b	5.60b	12.50a
Surface litter C:N	21.2	29.7	21.3
Root biomass			
0–10 cm C:N	27.1	28.8	23.8
0–100 cm C:N	27.4b	37.5a	27.7b
Root lignin (g/kg)	121.1ab	90.01b	164.8a
Root lignin:N	7.30ab	6.60b	10.41a
Soil organic matter C:N (0–10 cm)	10.4	10.6	10.7

Values are means from four field plots

C:N ratio of live foliage represents values at peak plant biomass

Lignin concentrations (ash-free) were measured on senesced foliage; root lignin concentrations were measured on a composite sample from the 0–10 cm soil depth over five sampling dates

Within a row, values followed by same letter are not significantly different ($P > 0.05$)

litter C:N ratios did not differ significantly among vegetation types.

Total root C and N pools to 1 m depth did not differ significantly among vegetation types, but the distribution of root C and N with soil depth varied among vegetation types (vegetation type × soil depth interaction $P < 0.0001$) (Tables 2, 3). More than 60% of total root C was found within the surface 0–20 cm soil beneath cheatgrass vegetation, compared to 51% in sagebrush and 38% in crested wheatgrass vegetation types. In the subsoil, cheatgrass root C was less than half that of crested wheatgrass and sagebrush vegetation types (Table 2). Root C:N ratios were not significantly different among vegetation types within the surface soil (0–10 cm, $P < 0.05$) (Table 4), but C:N ratios of perennial plant roots doubled (>50:1) with increasing soil depth, and were significantly greater than cheatgrass roots between 10 and 40 cm (data not shown). Root lignin concentrations and lignin:N ratios in surface soil (0–10 cm) were significantly higher in sagebrush roots compared to crested wheatgrass, while cheatgrass was intermediate ($P < 0.01$ for lignin and lignin:N ratios; Table 4).

We found no significant differences in total soil C or N pools among vegetation types within 1 m depth. In addition, the distribution of soil bulk density (Table 1), coarse fragment content, and inorganic C with depth did not differ significantly among vegetation types. Coarse fragments (>2 mm) accounted for only 1.1% of soil mass in surface (0–10 cm) soil and 4.5% in subsoil (70–100 cm), averaging 2.4 ± 1.1% across all soil samples collected. However, surface soils (0–10 cm) of cheatgrass dominated sites had significantly larger organic C ($P < 0.019$) and N ($P < 0.012$) pools compared to sagebrush soils, and crested wheatgrass soil C and N pools were intermediate (Tables 2, 3). Soil organic C:N was highest in the surface soil (approximately 10.7) and decreased with depth to approximately 7.8 at 70–100 cm.

Microbial biomass C and N content to 1 m accounted for approximately 2.8 and 4.0% of soil organic C and soil N pools, respectively, but did not differ significantly among vegetation types. Microbial C and N contents declined significantly with depth ($P < 0.0001$ for both), with no significant difference among vegetation types (Tables 2, 3). Inorganic N pools ($NH_4^+ + NO_3^-$) declined significantly with soil depth (Table 3). Averaged across all five sampling dates, NH_4^+ accounted for 48% of soil inorganic N in surface soil, and 27% in the subsoil. There was little difference in soil NH_4^+ pools among sampling date or among vegetation types ($P > 0.2$),

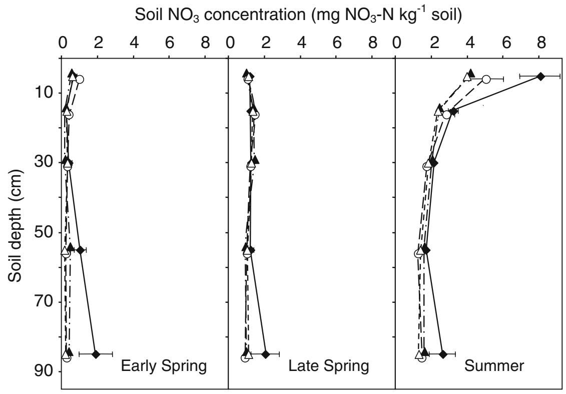

Fig. 1 Seasonal changes in soil NO_3^- concentrations in three vegetation types. Symbols: cheatgrass (*solid diamonds*), crested wheatgrass (*circles*), sagebrush-canopy (*solid triangles*), sagebrush-interspace (*hollow triangles*). *Error bars* (±1 SE; $n = 4$), may be smaller than symbols

but NO_3^- increased during the summer dry-season (Fig. 1), particularly in surface and subsurface soils beneath cheatgrass. Soil gravimetric water content, averaged across the five sampling dates, differed significantly with soil depth ($P < 0.0001$) and among vegetation types ($P < 0.003$) (data not shown). Soil water content was highest in cheatgrass and lowest in crested wheatgrass within the surface soil (0–10 cm) and subsoil (below 20 cm).

Estimates of plant above- and belowground inputs to soil

Total plant detrital C inputs to soil were greatest in cheatgrass and crested wheatgrass compared to sagebrush vegetation types (0–10 cm, $P < 0.02$; 0–100 cm, $P < 0.01$; Table 5). Similarly, plant N inputs were significantly greater in cheatgrass versus the other vegetation types, particularly for the surface soil (0–10 cm, $P < 0.016$; 0–100 cm, $P < 0.03$).

Natural abundance $\delta^{15}N$ stable isotope ratios

Cheatgrass aboveground biomass $\delta^{15}N$ (at peak biomass) was significantly enriched (6.6‰, $P < 0.001$) relative to crested wheatgrass (5.2‰), and sagebrush whole plant biomass (2.9‰) and foliage (3.6‰, $P < 0.001$; Fig. 2). Across the growing season, $\delta^{15}N$ of cheatgrass foliage declined from 8.5‰ in spring to approximately 5.5‰ shortly after plant senescence, while crested wheatgrass and sagebrush foliage $\delta^{15}N$ ratios declined by 1.0‰ (data not shown). Surface litter pools were slightly enriched beneath cheatgrass compared to the other vegetation types (Fig. 2), but this difference was not significant ($P = 0.15$). Root biomass $\delta^{15}N$ signatures were also significantly higher in cheatgrass and crested wheatgrass versus sagebrush dominated soils overall ($P < 0.014$). Differences in root $\delta^{15}N$ among vegetation types were greatest in surface soil (0–10 and 10–20 cm, $P < 0.0001$, $P < 0.02$), where cheatgrass and crested wheatgrass roots were 1.1–2.9‰ enriched relative to sagebrush roots. Soil $\delta^{15}N$ isotope ratios were not significantly different among vegetation types overall ($P = 0.11$), and were nearly constant with depth ($P = 0.07$). However, in surface soil cheatgrass and crested wheatgrass soil $\delta^{15}N$ signatures were up to 1.1‰ enriched relative to sagebrush soils (Fig. 2, $P < 0.03$). Root biomass $\delta^{15}N$ was significantly correlated ($r = 0.77$, $P < 0.001$) with surface soil $\delta^{15}N$ across vegetation types. Weighted average $\delta^{15}N$ of ecosystem N pools were slightly, but not significantly, enriched in cheatgrass and crested wheatgrass sites (9.0 ± 0.3‰) compared to sagebrush sites (8.5 ± 0.3‰).

Discussion

Influence of vegetation type on the quantity and quality of plant organic matter inputs to soil

We found substantial differences in the quantity of plant organic matter inputs to soil among monodominant stands of sagebrush, crested wheatgrass, and cheatgrass vegetation types. Interestingly, the quantity of plant C inputs to soil (comparable to net primary production, NPP) was nearly twice as large in cheatgrass and crested wheatgrass systems as in sagebrush systems (Table 5). This pattern strongly contrasts with our initial hypothesis, that C inputs to soil would be lower in cheatgrass versus sagebrush dominated sites, and is driven by greater foliage and root turnover in annual and perennial grasses compared to sagebrush. Our results are similar to estimates of plant inputs derived from literature data (Table 6) and to NPP of sagebrush-steppe using eddy covariance methods in Idaho (Gilmanov et al. 2003). Between vegetation types, Huenneke et al. (2002) reported slightly greater aboveground NPP in grass versus shrub dominated areas in the Chihuahuan desert, and

Table 5 Estimates of aboveground and belowground plant C and N inputs to soil

	Cheatgrass	Crested wheatgrass	Sagebrush
Biomass turnover (AG / BG)[a] (year^{-1})	1.0/1.0	1.0/0.50	1.0/0.30
C inputs to soil		(Mg C ha^{-1} year^{-1})	
Aboveground inputs (AG)	1.23	1.29	0.62
Belowground inputs (BG)			
0–10 cm	1.08	0.34	0.25
0–100 cm	1.96	1.54	0.70
Total C inputs			
AG + 0–10 cm	2.31a	1.63ab	0.87b
AG + 0–100 cm	3.19a	2.83a	1.32b
N Resorption Efficiency[b]	0.54	0.58	0.56
N inputs to soil		(kg N ha^{-1} year^{-1})	
Aboveground inputs (AG)	19.9	17.3	15.35
Belowground inputs (BG)			
0–10 cm	44.6	12.7	13.13
0–100 cm	76.8	43.0	22.88
Total N inputs			
AG + 0–10 cm	64.5a	30.0b	28.49b
AG + 0–100 cm	96.7a	60.3ab	38.24b

[a] Shows turnover rates assumed for calculations of inputs; aboveground input assumes that all leaf C is returned to soil surface annually; belowground turnover rates are based on literature estimates

[b] Foliar resorption efficiency estimated from leaf harvests. We assume no root N resorption during plant senescence

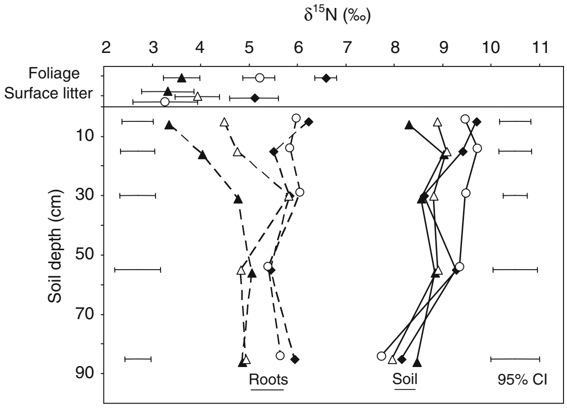

Fig. 2 Natural abundance δ^{15}N for plant biomass, detritus and soil N pools. Symbols as in Fig. 1. Symbols connected by *dashed lines* indicate root δ^{15}N ratios; *solid lines* indicate soil δ^{15}N ratios. *Error bars* represent 95% confidence intervals ($n = 4$). Symbols adjusted along the vertical (soil depth) axis for clarity

Stewart and Hull (1949) found comparable production between crested wheatgrass and cheatgrass in Idaho.

Plant N inputs to soil were more than twice as large in cheatgrass compared to perennial grass and sagebrush systems (Table 5). The greater N inputs in cheatgrass-dominated soils was largely due to greater root N turnover (45 versus 13 kg N ha^{-1} year^{-1}), since foliar N resorption efficiencies (Table 5) and plant biomass C:N ratios (Table 4) were similar among vegetation types. This is consistent with greater biomass turnover and more ‘open’ nutrient cycling in annual grass versus perennial plant dominated ecosystems (Jones and Woodmansee 1979), and may explain the faster soil N cycling rates in cheatgrass versus sagebrush reported by others (Booth et al. 2003; Saetre and Stark 2005). Other studies have reported foliar N loss in annual grasses during the growing season (Woodmansee and Duncan 1980; Evans et al. 2001; Svejcar and Sheley 2001; Eviner 2004); we interpret this as primarily translocation of N to maturing seeds. Volatile N losses are unlikely to explain the seasonal decline in cheatgrass foliar N. Cheatgrass foliar δ^{15}N declined by approximately 3‰ during the growing season, but NH_3 volatilization should result in leaf δ^{15}N enrichment (Hogberg 1997).

The similarity in the quality (as C:N ratio) of both live and senesced plant foliage and roots among

Table 6 Carbon and nitrogen pools of semiarid ecosystems reported in the literature

Site	MAT/MAP (°C/mm)	Soil depth sampled (cm)	C pools (Mg C ha^{-1})				N pools (kg N ha^{-1})			
			Above-ground biomass	Surface litter	Roots	Soil	Above-ground biomass	Surface litter	Roots	Soil
Annual grass										
CA[a]	9/486	30	0.8–2.0	0.8–2.2	2.2–3.6		43–65	49	61	3185
CA[b]	16/300	100	2.7		4.5	92	100		220	8900
WA[c]	7/220	20	0.6–1.0	0.6–0.9			14–51	13–28		2200
WA[d]	8/250	30	0.25	0.35	0.64	17.7				
This study	8/240	100	1.2	0.9	2.0	72.1	54	43	77	8073
Perennial grass										
WA[d]	8/250	30	0.34	0.3	0.99	15.2				
UT[e]	7/244	40	1.1	1.8	4.6		26	70	240	
ID[f]	8/300	90	0.7–1.4		5.3		44–67		53–80	
Arg.[g]	15/600	100	1.5	0.5	3.8		22	15	140	6400
This study	8/240	100	1.3	0.4	3.1	69.1	48	13.2	86	7977
Sagebrush										
CO[h]	7/270	45	2.7 (0.5)	2.2	3.8	41.3	61 (16)	43	61	5293
ID[i]	7/250		6.5		5.2					
UT[e,j]	7/244	90	3.0 (0.3)	4.5	4.2	52	57 (17)	35	157	5200
This study	8/240	100	3.8 (0.6)	0.5	2.4	62.0	68 (33)	27	76	7255

Numbers in brackets represent sagebrush foliage, if reported

[a] Jones and Woodmansee (1979), Woodmansee and Duncan (1980)

[b] Brenner et al. (2001) California chronosequence <10,000 year old soils

[c] Rickard (1985); data reported as range of low and high elevation sites

[d] Svejcar and Sheley (2001)

[e] Shinn et al. (1975); six grass and six shrub dominated sites in Curlew Valley

[f] Hull and Klomp (1974); crested wheatgrass biomass 5–10 years after sagebrush removal at high and low productivity sites (range)

[g] Montani et al. (1996), Brevedan et al. (1996); perennial grass in semiarid Argentina

[h] Redente et al. (1985)

[i] Pearson (1965); Snake River sagebrush and *Stipa*

[j] West and Klemmedson (1978)

vegetation types is surprising compared to work from other semiarid ecosystems (Vinton and Burke 1995; Evans et al. 2001; Carrera et al. 2003) and given the large differences in plant functional type in this study. However, sagebrush foliage and fine roots had greater lignin concentrations and lignin:N compared to cheatgrass or crested wheatgrass (Table 4), which could affect accumulation of surface litter. Woody litter inputs beneath sagebrush canopies, although not evaluated in terms of plant inputs in this study, might be expected to increase surface litter accumulation compared to grass dominated sites. Instead, both surface litter pools and aboveground inputs in sagebrush sites were one-half those in cheatgrass stands, suggesting that neither higher lignin concentrations or woody litter inputs had much effect on surface litter turnover and accumulation in this ecosystem.

Greater C and N inputs in grass- versus sagebrush-dominated ecosystems may be responsible for the larger surface soil C and N pools observed in this study (Tables 2, 3). Alternatively, larger surface soil N pools could be due to greater N_2-fixation by cryptobiotic crusts; however, if this were the case then natural abundance ^{15}N isotope ratios would be expected to be less enriched (closer to 0‰) in surface soils with greater N content (Evans and Ehleringer 1993). Instead, cheatgrass and crested wheatgrass soils had more enriched δ^{15}N signatures than sagebrush soils (Fig. 2). This is similar to results of Booth et al. (2003) and suggests greater losses of ^{15}N depleted N-forms (Hogberg 1997; Amundson et al. 2003). Given our results, the ecosystem-level response to vegetation change may be more complicated than simply greater retention of actively cycled N or increased trace gas N loss.

Differences in the quantity of plant inputs to soil among vegetation types may also affect the retention and cycling of organic matter within deeper soil layers. Our calculations of subsoil C inputs suggest greater inputs in crested wheatgrass sites compared to sagebrush or cheatgrass dominated sites (indicated by the difference between C inputs in 0–10 and 0–100 cm increments in Table 5). Smaller subsoil C inputs were due to small root biomass pools in cheatgrass, and both small root biomass and slow root turnover estimates in sagebrush soils. Over time, ecosystem C storage could increase in crested wheatgrass compared to sagebrush sites, since decomposition rates are slower at depth, and a greater proportion of recalcitrant C remains compared to surface soils (Gill and Burke 2002).

We observed accumulation of soil NO_3^- during the summer in all vegetation types (Fig. 1), but the largest pools were found in cheatgrass surface and subsurface soils. This appears to be a general phenomenon in semiarid ecosystems (Jones and Woodmansee 1979; Jackson et al. 1988; Davidson et al. 1990; Svejcar and Sheley 2001; Booth et al. 2003; Sperry et al. 2006). Soil NO_3^- accumulation may be a consequence of enhanced microbial activity after infrequent summer precipitation events (Cui and Caldwell 1997; Austin et al. 2004) and lower rates of inorganic N consumption as soils dry (Low et al. 1997), while greater NO_3^- accumulation in surface soils beneath cheatgrass versus perennial vegetation could be due to the lack of plant N uptake after annual grass senescence. The mechanisms resulting in greater subsoil NO_3^- beneath cheatgrass are not clear, but could result from: (a) leaching of NO_3^- from surface soils during cold-season soil water recharge, or (b) in situ net nitrification in deeper soil horizons due to microbial C limitations. Unfortunately, the relative importance of these mechanisms has not been determined. In any case, leaching of elevated NO_3^- pools below the shallow rooting zone during soil water recharge may be an important mechanism for ecosystem N loss from cheatgrass stands over time. Results from other work reveal a large potential for NO_3^- accumulation below the rooting zone in arid and semiarid systems (Walvoord et al. 2003; Jackson et al. 2004).

Integrating the N cycle with ecosystem δ^{15}N

Ecosystem N pools in this study exhibit enriched δ^{15}N signatures (9.0‰) compared to other temperate ecosystems (Martinelli et al. 1999), which may be a consequence of semiarid climate, historical land use, or soils derived from lacustrine sediments. Amundson et al. (2003) and Austin and Vitousek (1998) suggest that drier climates display enriched δ^{15}N signatures because ^{15}N-depleted gaseous losses (e.g. NH_3 volatilization, and NO and N_2O emissions) exceed leaching losses (Peterjohn and Schlesinger 1990). A history of grazing may also be a factor (Sparks et al. 1990; West 1999), with loss of cryptobiotic crust communities after disturbance (Skujiņš and West

1974; West and Skujinš 1977) resulting in enriched δ^{15}N signatures of plant available N over time (Evans and Belnap 1999). Lacustrine sediments are a common soil parent material in the Great Basin and may contain older ^{15}N-enriched organic matter. This might explain the lack of a pattern in soil δ^{15}N with depth (Fig. 2), in contrast to nutrient poor aeolian-derived soils of the Colorado plateau that display strong ^{15}N enrichment with depth (see Evans and Ehleringer 1993; Sperry et al. 2006).

The differences in plant δ^{15}N among vegetation types observed in this study are unlikely to be due to differences in plant physiological isotopic fractionation during N assimilation. While plants may fractionate against ^{15}N when plant N assimilation rather than soil N availability is the rate limiting step (Mariotti et al. 1982; Evans 2001), inorganic N pools during periods of active growth were smaller than concentrations where physiological fractionation is expected to be significant (Kolb and Evans 2003). Differences in plant uptake of NH_4^+ versus NO_3^- are also unlikely to explain the observed patterns. Cheatgrass soils have the largest NO_3^- pools when germination begins in autumn (Fig. 1, see also Booth et al. 2003). However, δ^{15}N of NO_3^- is depleted relative to NH_4^+ (Handley and Raven 1992), while cheatgrass foliage δ^{15}N signatures were significantly enriched compared to crested wheatgrass or sagebrush (Fig. 2). Instead, differences in plant δ^{15}N signatures among vegetation types likely reflect differences in δ^{15}N of labile (plant available) N pools.

We propose two possible mechanisms that could result in ^{15}N enrichment of plant available N in grass- versus sagebrush-dominated ecosystems. The first mechanism involves NO_3^- accumulation during the dry-season and translocation of the more ^{15}N-depleted NO_3^- below the rooting zone during cold-season soil water recharge. Nitrification results in isotopically depleted NO_3^- but enriched NH_4^+ pools (Handley and Raven 1992). While the magnitude of NO_3^- movement into subsoils of Great Basin ecosystems remains unknown, work in other semiarid and arid systems suggests that NO_3^- transport below the rooting zone may be substantial (Walvoord et al. 2003; Jackson et al. 2004).

The second mechanism involves stimulation of soil C and N cycling rates in response to greater plant C and N inputs. Since nitrification consumes a substantial proportion of gross N mineralization in semiarid systems (Schimel et al. 1989; Davidson et al. 1990; Smart et al. 1999; Booth et al. 2003; Saetre and Stark 2005), accelerated N cycling rates could increase trace gas loss of ^{15}N-depleted NO and N_2O (from nitrification, nitrifier–denitrification, or denitrification processes; Firestone and Davidson 1989; Hogberg 1997; Smart et al. 1999; Stark et al. 2002), and result in isotopic enrichment of actively cycled N. This mechanism may also be consistent with observed shifts in the distribution of actively cycled organic matter towards the soil surface after vegetation change. Over longer time-scales, both mechanisms could lead to ecosystem degradation due to a reduction in the amount of actively cycled N.

Cheatgrass invasion has been shown to substantially increase wildfire frequency (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks and Pyke 2001). The cheatgrass stands examined in this study did not burn during the 10 years since the initial cheatgrass invasion, and thus our discussion has focused on differences in C and N cycling unrelated to repeated burning. Increased wildfire frequency could have important impacts on nutrient pools and cycling rates; however the magnitude of these effects will be highly dependent on the return interval and intensity of fires. Assuming that wildfires consume all senesced aboveground plant tissue and surface litter and that all of the N contained in these components is lost from the cheatgrass system, N loss from a single fire would be approximately 70 kg N ha^{-1}, or <1% of the total ecosystem N. The fire return interval would determine whether sufficient time occurred to allow replenishment of this N through wet and dry N deposition and biological N fixation. The long-term impact of indirect effects of fire (e.g. increased N mineralization rates) are even more difficult to predict since they can have both positive effects (e.g. increased plant production and N uptake; increased N-fixation) and negative effects (e.g. increased denitrification and gaseous N loss; erosion). Therefore, it is not clear how increased wildfire frequencies associated with cheatgrass will contribute to loss of nutrients and ecosystem degradation.

In conclusion, our results suggest that plant detrital inputs and cycling of labile C and N may be accelerated in disturbed ecosystems dominated by introduced grasses such as cheatgrass and crested wheatgrass compared to native sagebrush. If cheatgrass invasion and dominance does lead to degradation of ecosystem function, this may be due to faster nutrient cycling and greater losses, rather than reduced organic matter inputs. The increase in wildfire frequency and severity associated with the cheatgrass-wildfire cycle may in turn affect ecosystem C and N cycling through direct C and N losses, while accelerated rates of nutrient cycling may amplify already substantial trace gas emissions to the atmosphere from semiarid rangelands (Bowden 1986; Schlesinger et al. 1990).

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