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REGULAR ARTICLE

Fire effects on the mobilization and uptake of nitrogen by cheatgrass (*Bromus tectorum* L.)

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Abstract Cheatgrass (*Bromus tectorum* L.), an invasive annual grass, is displacing native species and causing increased fire frequency in the Great Basin of the southwestern United States. Growth and nitrogen uptake patterns by cheatgrass were examined in a greenhouse study using soils from sites with the same soil type but different fire histories: 1) an area that burned in 1999 that is now completely invaded with cheatgrass (CG); 2) an area that has not burned recently and is now dominated by Wyoming big sagebrush (*Artemisia tridentata*ssp.*wyomingensis* Beetle and Young) and Sandberg's bluegrass (*Poa secunda* J. Presl) (WBS); and 3) a Wyoming big sagebrush area that burned in August of 2008 just prior to soil collection (NB). Cheatgrass seedlings had higher leaf numbers, height and mass in the NB soil. Ammonium-N mobilized by fire in the NB soil had significantly enriched ^{15}N than soils from CG or WBS sites and this pattern was reflected in the isotopic signatures of the plants. Fire-mobilized mineral N accounted for only 58% of N taken up by cheatgrass in the NB soil, suggesting fire enhanced the ability of cheatgrass to assimilate more recalcitrant soil organic N.

Keywords Bromus tectorum · Fire · Nitrogen · Ammonium nitrate · 15N

Introduction

The invasion of non-native species is a growing concern in many ecosystems. In the Great Basin of the southwestern United States, cheatgrass (*Bromus tectorum* L) is a rapidly spreading invasive species that is out-competing the native species in many areas. It is a native of Europe that was introduced to the United States at multiple locations in the mid-late 1800s. Cheatgrass is an erect annual grass that has a competitive advantage over many natives because it often germinates earlier (Roundy et al. 2007) and can maintain higher growth and nutrient uptake rates than many of the native grasses (Monaco et al. 2003).

The literature on cheatgrass effects on soil nitrogen (N) is conflicting. Sperry et al. (2006) suggests that cheatgrass is primarily accessing subsurface N, rede-

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positing it at the soil surface as litter and thus causing an increase in surface soil mineral N. In contrast, Blank (2008) reported that subsurface soil pools did not appear to be a well utilized resource by cheatgrass. MacKown et al. (2009) found that cheatgrass takes up 1.5 to 2.2 times more N than many of the other perennial grasses. Blank and Young (2004) found that cheatgrass can, over numerous growth cycles, extract more labile N from soils than other invasive grasses. Rimer and Evans (2006) found that cheatgrass has the capacity to decrease the labile N pool by up to 50% in the first 2 years of invasion. The leaching of NO_3^- from the soil surface during rain or snowmelt events is hypothesized to be one of the main causes for the depletion of soil N over time under cheatgrass stands (Hooker et al. 2008). Norton et al. (2008) also showed that N_2O emissions can be significantly elevated during nitrification following wetting of soils invaded with cheatgrass. On the other hand, a buildup of NO_3^- under cheatgrass is often seen both in surface soils (Blank 2008; Boxell and Drohan 2009; Norton et al. 2004) and at depth, the latter as a result of leaching from surface horizons (Hooker et al. 2008; Sperry et al. 2006). The foliage of cheatgrass has higher lignin: N ratios and C:N ratios than many natives, suggesting that it can slow the natural cycling of N (Blank 2008; Hooker et al. 2008; Norton et al. 2004; Rimer and Evans 2006). On the other hand, some studies have observed shallow and rapid cycling of organic matter (OM) attributed to increased fire frequencies, rhizosphere priming effects and increased microbial activity (Blank 2008; Norton et al. 2004).

Once cheatgrass is established, it causes an increase in fire frequency due to the creation of an abundance of fine fuel (MacKown et al. 2009; Monaco et al. 2003). In sagebrush ecosystems, natural fire cycles range from 60 to 500 years but cheatgrass-dominated systems can burn as often as every 3–5 years (Chambers et al. 2007; Knapp 1996). These changes in the fire cycle have significant impacts not only for native plant reestablishment but also for the rising costs of fire management. In 1996, it was estimated that half of the annual cost of fire in the Great Basin can be directly attributed to cheatgrass invaded sites. This figure corresponds to approximately $10 million that is being spent per year on cheatgrass fires alone (Knapp 1996).

Nitrogen in the inorganic form of ammonium (NH_4^+) usually increases following fire due partial organic matter combustion and denaturing of proteins in soils (Certini 2005). Although both NH_4^+ and NO_3^- are very soluble, NH_4^+ is adsorbed on the negatively charged surfaces of minerals and organics and does not readily leach. These increases in NH_4^+ can lead to short-term increases in post-fire plant production (Certini 2005). Within 1 year of fire, a pulse of NO_3^- can appear in runoff and soil solution due to the reestablishment of nitrifying bacteria and the subsequent nitrification of the initial NH_4^+ pulse (Korb et al. 2004; Certini 2005; Johnson et al. 2007; Miller et al. 2006). Fire often causes substantial increases in soil erosion, resulting in the loss of soil fertility (Certini 2005) On the other hand, the longer-term effects of fire may include fostering the establishment of N-fixing vegetation, resulting in increases in soil fertility (e.g., Johnson et al. 2005).

Högberg (1997) hypothesized that fire consumes the upper ^{15}N-depleted part of the litter and soil profile, hich, combined with post-fire increases in nitrification, may result in ^{15}N-enriched NH_4^+. This in turn may result in the enrichment of ^{15}N in the post-fire plant community. This hypothesis was supported by the results of Grogan et al. (2000), who found increases in post-fire foliar ^{15}N compared to unburned forests. Saito et al. (2007) hypothesized that burning would cause enrichment of ^{15}N in soils due to volatilization of the lighter isotopes. This hypothesis was supported by results of a muffle furnace study, but results of field sampling in a wildfire were inconclusive.

In this study, we investigated the effects of fire on soil N availability and cheatgrass growth in a greenhouse experiment. Specifically we examined effects of wildfire on 1) soil mineral N levels, 2) cheatgrass growth and N uptake, and 3) the ability of cheatgrass to access native soil organic N. To achieve these objectives, we grew cheatgrass in soils from a newly burned site, a site that was burned 10 years previously, and a site that had not been burned in at least the last 50 years. We measured pre- and post-growth soil mineral N, plant biomass and N uptake, and ^{15}N in both soils and plants.

We hypothesized that:

1. The recent fire event will result in elevated levels of mineral N in soils which is also isotopically enriched when compared to the other two soils.
2. Due to the higher amounts of mineral N in the newly burned soil, cheatgrass growth and N

uptake will be greater as well in this soil and the plant N will reflect the enriched ^{15}N signal of the soil mineral N pool.

3. Finally, we hypothesize that the nitrogen uptake by cheatgrass will exceed soil N mineralization in the absence of plants in all three soils due to the ability of cheatgrass to access native soil organic N (Blank 2008).

Materials and methods

Field site description

The soils were collected from Eden Valley, Nevada USA. Soils in the area are coarse-loamy, mixed, superactive, mesic Xeric Petrocambids (Denny 2002). The soils used in this study were taken from a Wyoming Big Sagebrush (*Artemisia tridentata*ssp. *wyomingensis* Beetle and Young) and Sandberg's bluegrass (*Poa secunda* J. Presl)-dominated area which has not burned within the last 50 years (hereafter referred to as "WBS"), an area that burned in 1999 that is presently invaded by cheatgrass (hereafter referred to as "CG"), and a Wyoming big sagebrush area that burned in August of 2008 just prior to soil collection (hereafter referred to as "NB") (Fig. 1).

Field and laboratory procedures

Initial soils were analyzed for total N (TN), total C (TC), total mineral N (TMN, NH_4^++NO_3^-) and pH. The TN and TC of the initial soil samples were determined using Dumas combustion through a LECO TruSpec (LECO U.S.A., St. Joseph, MI). To find initial TMN content, 10 g soil samples were extracted (30 mL of 1 M KCl), filtered, and run through a Lachat QuikChem® Autoanalyzer (Hach Company, Loveland, CO). The pH of the soil was found in a 25 mL soil and 20 mL of 1.9 M $CaCl_2$ slurry.

Approximately 0.02 m^3 of soil was collected from each site at a depth of 0–20 cm and transported to the greenhouse. Soil collection in the NB area was performed within 1 week of the burn before any precipitation event. Soils from the other two areas were collected during the same sampling period as the newly burned area. In the WBS area, soils were collected in plant interspaces and directly below sagebrush. In the CG area, standing vegetation was removed before soils were taken. Soils were well-homogenized but not sieved before planting. The greenhouse experiment used a completely randomized block design with three soil types, two treatments (planted or not planted) and 15 replicates (pots) of each treatment (n=90). Pots that were not planted

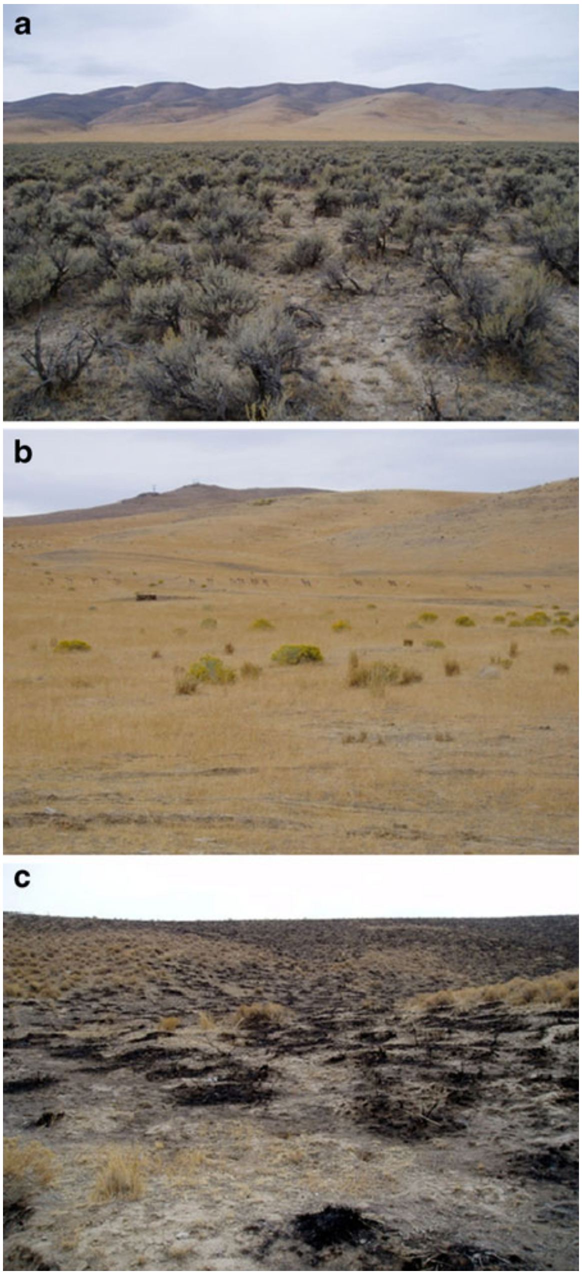

Fig. 1 Site photos at the Wyoming Big Sage (WBS), cheatgrass (CG) and newly burned (NB) sites (**a**, **b** and **c**, respectively)

were used to monitor natural losses/gains during the growing period.

Bromus tectorum L. seeds were harvested from the invaded portion of the field site in the fall of 2008 and planted shortly after in small, conical pots each containing 80 g of unsieved soil. The bottom of each pot was covered with mesh and were placed on an elevated platform to allow free drainage. Plants were thinned to one plant per pot. The plants were grown in a non-water limited environment with no added fertilizer so that the limiting growth factor was the nutrient availability in the soil. The pots were watered with 100 mL of filtered tap water on alternating days. Plants were grown under natural light with a maximum daily temperature of 80°F and minimum nightly temperature of 45°F for 90 days.

The pot locations were randomized every 2 weeks to reduce edge and neighbor effects. Once a month during the 3-month growth period, height and number of tillers were recorded to determine the effect of resource availability on seedling growth. After 90 days, plant roots and shoots were harvested, dried at 100°F for 2 weeks and weighed.

For plant nutrient analyses, roots and shoots were combined as the analyses required a relatively large amount of plant material. The samples were ground using a Wig-L-Bug (Rinn®, Elgin, IL) and sent to the UC Davis Stable Isotope Facility for analysis for N content and ^{15}N isotopic signature. Plant samples were combusted at 1,020°C in a reactor packed with chromium oxide and silvered colbatous/cobaltic oxide. Oxides were removed in a reduction reactor (reduced Cu at 650°C) and the He carrier flowed through a water trap (magnesium perchlorate) and a CO_2 trap. Nitrogen and CO_2 were separated on a Carbosieve GC column (65°C, 65 mL/min) before entering the PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Soil samples were analyzed for total mineral nitrogen (NH_4^+ and NO_3^-) after the growing period using the same method as the pre-growth soils. Total mineral nitrogen in the pre-growth and post-growth non-planted soils was also analyzed isotopically in the Colorado Plateau Analytical Laboratory at Northern Arizona University. These soils were analyzed for $^{15}NO_3$ following the protocol of the USGS Techniques and Methods 10-C17 (Determination of the $\delta(^{15}N/^{14}N)$ and $\delta(^{18}O/^{16}O)$ of Nitrate in Water: RSIL Lab Code 2900). This procedure used bacteria (*Pseudomonas chororaphis* in this case) which denitrified the NO_3^- in the system into N_2O but does not continue to N_2. The samples were analyzed via a ThermoQuest Finnegan Delta Plus Isotope Ratio Mass Spectrometer (IRMS, Thermo Fisher Scientific, Waltham, MA) for mass/charge ratios of 44 ($^{14}N^{16}O_2$), 45 ($^{15}N^{16}O_2$) and 46 ($^{15}N^{16}O^{18}O$). Soil samples were also analyzed for $^{15}NH_4$ using the method of Brooks et al. (1989). The NH_4^+ was analyzed via a DELTA V Advantage IRMS (Thermo Fisher Scientific, Waltham, MA).

Statistical analysis

Differences in soil N, plant height and leaf number were analyzed in SAS 9.2 (SAS Institute Inc., Cary, NC) using PROC GLIMMIX models. For plant height and leaf numbers, mixed models were used where date measured, site (WBS, CG or NB) and their interaction were fixed factors. For soil ^{15}N, the fixed factors were site, treatment (pre-growth or post-growth not planted) and their interaction. In the case of total mineral N and total pot N, site, treatment (planted or not planted), time (pre- or post-growth) and their interactions served as fixed factors. In all models, the residual term served as the random factor in order to compensate for over-dispersion within the replications. Tukey's post-hoc tests were performed to examine significant differences within the fixed factors. Due to the fact that there was only one fixed factor (site) for plant dry weight, plant N and plant ^{15}N, statistics were performed using one-way ANOVA in DataDesk 6.1 (Data Description Inc. Ithaca, NY).

Results

When comparing soil initial conditions, the Wyoming big sage (WBS) soil contained the lowest amounts of

Table 1 Initial soil total C (TC), total N (TN), C:N ratio and pH levels prior to experiment in the Wyoming big sage (WBS), cheatgrass (CG) and newly burned (NB) soils

Soil	TC (mg g^{-1})	TN (mg g^{-1})	C:N	pH$_{CaCl2}$
WBS	5.36±0.09	0.69±0.02	7.77±0.09	6.14±0.03
CG	19.53±0.68	1.76±0.04	11.06±0.68	6.75±0.04
NB	22.10±0.43	2.08±0.02	10.61±0.43	7.23±0.08

Table 2 Soil nitrogen (NH_4^+, NO_3^- and total mineral N (TMN)) levels and ^{15}N signals prior to and following experiment as well as the mineralization in the unplanted and net change in the planted pots in the Wyoming big sage (WBS), cheatgrass (CG) and newly burned (NB) soils

	^{15}N Signal Initial Pre-planting (‰) Avg ± Std Err	^{15}N Signal Final Unplanted (‰) Avg ± Std Err	Soil Concentration Initial Pre-planting (mg kg^{-1}) Avg ± Std Err	Soil Concentration Final Unplanted (mg kg^{-1}) Avg ± Std Err	Soil Concentration Final Planted (mg kg^{-1}) Avg ± Std Err	Net Change Final-initial Unplanted (mg kg^{-1}) Avg ± Std Err	Net Change Final-initial Planted (mg kg^{-1}) Avg ± Std Err
WBS soil							
NO_3^--N	−4.2±0.1	−2.3±0.3	2.1±0.4	8.4±0.6	5.2±0.5	6.3±0.7	3.1±0.6
NH_4^+-N	3.3±0.5	−0.8±1.8	2.6±0.1	2.5±0.1	2.6±0.1	−0.1±0.1	0.0±0.1
TMN			4.7±0.4	10.9±0.6	7.8±0.5	6.2±0.7	3.1±0.6
CG soil							
NO_3^--N	−4.3±0.1	−5.3±0.2	5.3±0.4	4.2±0.5	2.1±0.2	−1.1±0.6	−3.2±0.5
NH_4^+-N	2.5±0.7	−1.7±1.5	2.9±0.6	6.0±0.1	5.8±0.2	3.1±0.6	2.9±0.7
TMN			8.2±1.0	10.2±0.5	7.9±0.3	2.0±1.1	−0.3±1.1
NB soil							
NO_3^--N	−0.8±0.1	1.9±0.6	2.6±0.1	34.2±6.1	3.7±1.4	31.6±6.1	1.1±1.4
NH_4^+-N	8.0±0.5	4.2±0.3	47.4±7.9	3.7±0.1	4.1±0.2	−43.7±7.9	−43.3±7.9
TMN			50.1±7.8	37.9±6.1	7.8±1.4	−12.1±9.9	−42.2±8.0

total C, total N, NO_3^--N and NH_4^+-N as well as the lowest pH (Tables 1 and 2). The cheatgrass (CG)soil fell between the WBS and newly-burned (NB) soils for pH, TC and TN but had the highest amounts of NO_3^--N and the highest C:N ratio (Tables 1 and 2). The soils from the NB site contained the highest amounts of TC, TN and NH_4^+-N but had the lowest C:N ratio and the mid-level NO_3^--N amount (Tables 1 and 2). As hypothesized, soils from the NB site contained greater mineral N concentrations by nearly six-fold and the mineral N in this soil was also enriched in ^{15}N when compared to the soils from the other two sites (Table 2). The NB soil showed a significant net loss of TMN over the course of the experiment in the unplanted treatment (Table 2, Fig. 2). Although the total soil mineral N (TMN) in the WBS soil doubled in the absence of plants, this difference was not statistically significant (Fig. 2). The isotope data also shows that the pre-growth samples in all three soils had an isotopically enriched pool of

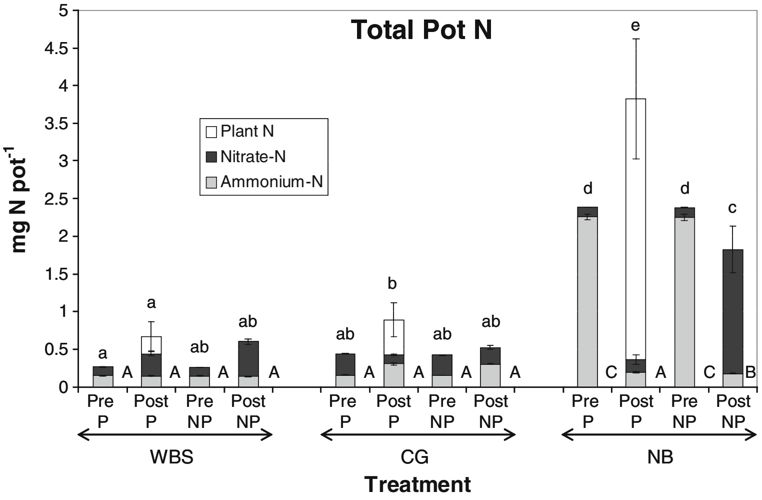

Fig. 2 Total Pot N (soil NH_4^+ + soil NO_3^-+plant N) for Wyoming big sage (WBS), cheatgrass (CG) and newly burned (NB) soils. *Lower-case letters* indicate differences in total pot N differences among site by treatment by time interactions while capital letters represent significant differences among soil total mineral N, TMN, amounts between site by treatment by time interactions. Values are mean ± S.E.

Table 3 Statistical table for ANOVAs examining the effects of site and treatment on soil ^{15}N and those on the effects of site, treatment and time on total pot N and total mineral N, TMN. Statistically significant values are in bold ($p<0.05$)

Soil statistics					
Den DF=24		Soil $^{15}NO_3$		Soil $^{15}NH_4$	
Effect	Num DF	*F* value	*P* value	*F* value	*P* value
Site	2	154.22	**<.0001**	17.10	**<.0001**
Treatment	1	21.58	**0.0001**	22.21	**<.0001**
Site* Treatment	2	19.18	**<.0001**	0.02	0.9818
		Total Pot N (den DF=166)		Soil TMN (den DF=168)	
Effect	Num DF	*F* value	*P* value	*F* value	*P* value
Site	2	460.08	**<.0001**	260.16	**<.0001**
Treatment	1	39.29	**<.0001**	26.86	**<.0001**
Site* Treatment	2	21.17	**<.0001**	16.51	**<.0001**
Time	1	30.92	**<.0001**	36.55	**<.0001**
Site*Time	2	0.53	0.5923	78.54	**<.0001**
Treatment* Time	1	37.62	**<.0001**	28.71	**<.0001**
Site* Treatment* Time	2	21.28	**<.0001**	16.25	**<.0001**

NH_4^+ and depleted NO_3^- pool (Table 2). The post-growth non-planted soils demonstrated enriched NO_3^- pools in the WBS and NB soils and depleted NH_4^+ pools in all three soils (p=<0.0001, Tables 2 and 3).

Also as hypothesized, at the time of the final measurement, the height and leaf number of the plants grown in the NB soils was over twice that of those in the WBS and CG soils (Table 4). The plant dry weight was also far greater in the NB soil while the WBS and CG soils exhibited statistically similar dry weights ($p<0.0001$, Tables 4 and 5). The plants from all of these soils had positive isotope signatures when compared to the air standard. Plants from the NB soil had significantly enriched ^{15}N signatures which reflected the enriched soil N pool (Table 4).

The presence of plants reduced the final soil TMN contents, and the sum of soil TMN + plant N was approximately equal to soil mineral N contents in the absence of plants in the CG and WBS soils. In the CG soil, the increase in soil TMN in the absence of plants was slight (<10%) and not statistically significant (Fig. 2). Plant N contents in the WBS and CG treatments were statistically similar but the plant N comprised approximately half of the total pot N in the CG soil but only about one-third of the total pot N in the WBS soils. Our final hypothesis was only supported in the NB soil where post-growth soil TMN + plant N in the planted pots was greater than the TMN in the unplanted pots (Fig. 2). In other words, the planted TMN + plant uptake was greater than the TMN at the end of the incubation period in the unplanted treatment. Plant N in the NB treatment greatly exceeded that found in the WBS and CG treatments ($p<0.0001$, Tables 4 and 5).

Discussion

The high initial concentrations of NO_3^--N in the CG soil are consistent with previous studies that have observed a build-up of NO_3^--N under cheatgrass stands (Blank 2008; Boxell and Drohan 2009; Norton et al. 2004). These soils have a fairly high nitrification potential as indicated by the TMN in the post-growth, unplanted soils. The majority of the TMN in the post-growth unplanted soils was in the form of NO_3^- while

Table 4 Plant growth and nutrient information from the Wyoming big sage (WBS), cheatgrass (CG) and newly burned (NB) soils

	Harvest Plant Height (cm)	Harvest Plant Leaf Number	Harvested Dry Weight (mg)	Plant N Content (mg N/plant)	^{15}N (‰)
WBS	4.8±0.5	3.0±0.3	19.4±4.1	0.24±0.19	2.7±0.1
CG	7.2±0.6	4.5±0.2	32.6±4.5	0.47±0.23	1.5±0.1
NB	18.2±0.7	12.2±0.7	294.2±17.8	3.45±0.80	8.2±0.2

Table 5 Statistical table for ANOVAs examining the plant growth and plant N amounts. Statistically significant values are in bold ($p<0.05$)

Plant statistics

		Plant dry weight				Plant N			
Source	df	Sums of squares	Mean square	*F*-ratio	*P* Value	Sums of squares	Mean square	*F*-ratio	*P* value
Const	1	0.61	0.61	336.02	<.0001	87.88	87.88	356.4	<.0001
Site	2	0.71	0.36	196.52	**<.0001**	95.23	47.61	193.11	**<.0001**
Error	41	0.07	0.002			10.11	0.25		
Total	43	0.79				105.34			

		Plant ^{15}N				Den DF=164		Plant height		Leaf number	
Source	df	Sums of squares	Mean square	*F*-ratio	*P* value	Effect	Num DF	*F* value	*P* value	*F* value	*P* value
Const	1	766.09	766.09	2925.2	<.0001	Date	3	32.41	**<.0001**	204.83	**<.0001**
Site	2	329.31	164.65	628.7	<.0001	Site	2	427.78	**<.0001**	259.19	**<.0001**
Error	30	7.86	0.26			Date*Site	6	20.97	**<.0001**	52.78	**<.0001**
Total	32	337.17									

NH_4^+ was the dominant form in the pre-growth samples (Table 2).

The NB soil exhibited elevated levels of both TMN and ^{15}N which supports our first hypothesis. The increase in TMN, particularly in the form of NH_4^+, during the combustion of organic matter immediately following fire is well documented (Certini 2005; Johnson et al. 2007). The NB soil also had significantly enriched ^{15}N in both NH_4^+ and NO_3^- compared to the other two soils, consistent with the hypothesis that fire mobilizes organic N from soils that has an enriched ^{15}N signature.

While the WBS and CG soils exhibited similar growth rates and plant sizes, the response of the plant growth in the NB soil indicate that the primary driver of plant growth in these soils was the influence of the burn event releasing higher levels of plant available N. Subsequently, the plants in the NB soil were more enriched in ^{15}N than the WBS or CG soils. However, the plants from all of these soils had positive isotope signatures (enriched) which suggests that cheatgrass is preferentially assimilating the NH_4^+ pool. Previous studies have observed increased growth and leaf production when the primary N source is in the form of NO_3^- (Monaco et al. 2003). However, our observations are supported by Grogan et al. (2000) who also found that the plants preferentially took up the available NH_4^+ after a fire event.

In the WBS and CG soils, the presence of plants reduced the final soil TMN contents, but the sum of soil TMN + plant N was approximately equal to soil mineral N contents in the absence of plants, indicating that cheatgrass simply took up TMN plus N that was mineralized from soil organic matter without assimilating any additional native soil organic N (Fig. 2). However, the sum of soil TMN + plant N at the end of the growth period in the NB soil was significantly greater than soil TMN in the unplanted NB soil, indicating significant plant assimilation of more recalcitrant soil N pools, more efficient plant capture of TMN that would have been leached, greater microbial biomass turnover, or some combination of these. Assuming that the net loss of TMN in the unplanted NB soil was exclusively due to leaching, this amount (approximately 0.6 mg pot^{-1}) could only account for 21% of plant N uptake in the planted NB treatment (2.9 mg pot^{-1}). The change in TMN in the planted NB soil (2.0 mg) could account for only 58% of the plant N pool, suggesting that 42% (1.4 mg) of the N in these plants was from these more recalcitrant pools of soil N.

Conclusions

Cheatgrass seedlings grew larger (more leaves and were taller and heavier) in the newly burned soil. The growth patterns responded more clearly to the burn event than to differences in overstory vegetation. Nitrogen in the form of NH_4^+ was mobilized by fire and mobilized NH_4^+ had significantly enriched ^{15}N than in soils from earlier burns or from unburned soils.

Hypothesis 1, which stated that the burned soil will have higher levels of TMN and an isotopically enriched extractable N pool than unburned soil, was supported by these data. Hypothesis 2, which stated that the plants grown in the burned soil will have higher growth rates, N uptake and more enriched N was also corroborated. The final hypothesis, which stated that nitrogen in the plant tissue will exceed soil N mineralization in the absence of plants in all three soils due to the ability of cheatgrass to access native soil organic N, was only supported in the NB soil where fire-mobilized TMN accounted for only 58% of plant N. Although the source of the remaining 42% of the plant N is unclear, future work could address this issue using a nitrogen balance approach and attempt to analyze each soil pool.

Management implications of this study are that the fire can encourage cheatgrass invasion in two ways via soil N. First, cheatgrass clearly takes up fire-mobilized NH_4^+, as has been well known for quite some time (Grogan et al. 2000). Secondly, it appears that fire also enhances the ability of cheatgrass to assimilate recalcitrant native soil N not mobilized by the fire. Whether the latter is due to enhanced rhizosphere activity or fire-induced partial mobilization of native soil N is unknown and would also be worthwhile topic for further research.

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References

Blank RR (2008) Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*). Invasive Plant Sci Manag 1:226–238

Blank RR, Young JA (2004) Influence of three weed species on soil nutrient dynamics. Soil Sci 169(5):385–397

Boxell J, Drohan PJ (2009) Surface soil physical and hydrological characteristics in *Bromus tectorum* L. (Cheatgrass) versus *Artemesia tridentata* Nutt. (Big Sagebrush) habitat. Geoderma 149:305–311

Brooks PD, Stark JM, MacInteer BB, Preston T (1989) Diffusion method to prepare soil extracts for automated nitrogen-15 analysis. Soil Sci Soc Am J 53:1707–1711

Certini G (2005) Effects of fire on properties of forest soils. Oecologica 143:1–10

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes great basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol Monogr 77(1):117–145

Denny DW (2002) Soil survey of humboldt county, Nevada, East Part, Part 1. Reno, NV, USA: US Department of Agriculture, Natural Resources Conservation Service 521 p

Grogan P, Bruns TD, Chapin FS III (2000) Fire effects on ecosystem nitrogen cycling in a California Bishop Pine Forest. Oecologia 122:537–544

Högberg P (1997) 15N natural abundance in soil–plant systems. New Phytol 137:179–203

Hooker TD, Stark JM, Norton U, Leffler AJ, Peek M, Ryel R (2008) Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry 90:291–308

Johnson DW, Murphy JD, Susfalk RB, Caldwell TG, Miller WW, Walker RF, Powers RF (2005) The effects of wildfire, salvage logging, and post-fire N fixation on the nutrient budgets of a Sierran forest. For Ecol Manag 220:155–165

Johnson DW, Murphy JD, Walker RF, Glass DW, Miller WW (2007) Wildfire effects on forest carbon and nutrient budgets. Ecol Eng 31:183–192

Knapp PA (1996) Cheatgrass (*Bromus Tectorum* L) Dominance in the Great Basin Desert. Glob Environ Change 6(1):37–52

Korb JE, Johnson NC, Covington WW (2004) Slash pile burning effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. Restor Ecol 12(1):52–62

MacKown CT, Jones TA, Johnson DA, Monaco TA, Redinbaugh MG (2009) Nutrient uptake by perennial and invasive annual grass seedlings: nitrogen form effect. Soil Sci Soc Am J 73(6):1864–1870

Miller WW, Johnson DW, Loupe TM, Sedinger JS, Carroll EM, Murphy JD, Walker RF, Glass DS (2006) Nutrients flow from runoff at burned forest site in Lake Tahoe Basin. Calif Agric 60(2):65–71

Monaco TA, Johnson DA, Norton JM, Jones TA, Connors KJ, Norton JB, Redinbaugh MB (2003) Contrasting responses of intermountain west grasses to soil nitrogen. J Range Manag 56:282–290

Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA (2004) Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. J Arid Environ 57:445–466

Norton U, Mosier AR, Morgan JA, Derner JD, Ingram LJ, Stahl PD (2008) Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush—steppe in Wyoming, USA. Soil Biol. Biochem 40:1421–1431

Rimer RL, Evans RD (2006) Invasion of Downy Brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. Amer Midl Nat 156(2):252–258

Roundy BA, Hardegree SP, Chambers JC, Whittaker A (2007) Prediction of cheatgrass field germination potential using wet thermal accumulation. Rangeland Ecol Manag 60 (6):613–623

Saito L, Miller WW, Johnson DW, Qualls RG, Provencher L, Carroll E, Szameitat P (2007) Fire effects on stable isotopes in a Sierran Forested Watershed. J Environ Qual 36:91–100

Sperry LJ, Belnap J, Evans RD (2006) *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland ecosystem. Ecology 87(3):603–615