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Moisture pulses, trace gas emissions and soil C and N in cheatgrass and native grass-dominated sagebrush-steppe in Wyoming, USA

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Abstract

Effects of large-scale weed invasion on the nature and magnitude of moisture-pulse-driven soil processes in semiarid ecosystems are not clearly understood. The objective of this study was to monitor carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions and changes in soil carbon (C) and nitrogen (N) following the application of a water pulse in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities dominated by the exotic annual grass cheatgrass (*Bromus tectorum*) and by the native perennial grass western wheatgrass (*Pascopyrum smithii*). Sampling locations were established in shrub interspaces dominated by *B. tectorum* and *P. smithi* and beneath shrub canopies adjacent to interspaces dominated by *B. tectorum* and *P. smithi*, where no grass was present. Soils were classified as fine-loamy, mixed, Borollic Haplargids. Soil samples (0–10 cm) and air samples were collected at 0, 4, 8, 24, 49, 72, and 216 h following additions of 25.4 mm of water. Soil samples were analyzed for dissolved organic carbon (DOC), microbial biomass carbon (MBC), extractable ammonia (NH_4^+), extractable nitrate (NO_3^-), and dissolved organic nitrogen (DON). Grass species induced differences in soil nitrification, N_2O and CO_2 emissions, and the quantity and timing of labile C available to microbial populations responding to increased moisture availability. In the first 8-h phase after wetting *P. smithii* soils had the greatest CO_2 emissions compared to other soils but *B. tectorum* soils had the greatest N_2O emissions and the greatest increases in CO_2 emissions relative to before wetting. Microbial biomass C in *B. tectorum* interspace soils increased rapidly but the response was short-lived despite sufficient water availability. After the first 8 h of soil response to wetting, the observed MBC declines in *B. tectorum* interspace coincided with disproportional DOC and DON concentration increases. Similar DOC and DON increases were also observed in *B. tectorum* soils beneath shrub canopy. In contrast, DOC and DON concentrations in *P. smithii* soils remained unaffected by soil wetting and small MBC increases observed during the first 8-h phase did not decline as rapidly as in *B. tectorum* interspace soils. In conclusion, summer drying-wetting cycles that occur frequently in areas invaded by *B. tectorum* can accelerate rates of nitrification and C mineralization, and contribute significantly to trace gas emissions from sagebrush-steppe grasslands. With frequent summer rainfall events, the negative consequences *B. tectorum* presence in the ecosystem can be significant.

Keywords: *Artemisia tridentata*; *Bromus tectorum*; Carbon dioxide (CO_2); Global change; Microbial biomass; Dissolved organic carbon (DOC); Nitrous oxide (N_2O); *Pascopyrum smithii*; Sagebrush-steppe; Trace gas; Wyoming big sagebrush

1. Introduction

Biogeochemical processes in semiarid western rangelands are characterized by strong temporal and spatial variability (Burke, 1989). Precipitation that falls as winter snow and sporadic, short-term summer rains (Matson et al., 1991) is one of the principal drivers of that variability. Minor summer rains that occur after prolonged periods of dry and hot weather are of particular importance to belowground biochemical processes (Austin et al., 2004). They trigger immediate soil microbial activity (Stark and Firestone, 1995), pulses of soil C and N cycling (Cui and Caldwell, 1997) and greenhouse gas (GHG)

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emissions (Matson et al., 1991). Effects of large-scale weed invasion on the nature and magnitude of moisture-pulse-driven soil processes are not clearly understood (Saetre and Stark, 2005).

Much of the original plant community across vast expanses of the semiarid West, which consisted of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and a wide array of native perennial grasses and forbs in shrub interspaces, is now converted to near-monocultures of the exotic annual grass cheatgrass (*Bromus tectorum* L.) with little or no shrub component (Whisenant, 1999; West, 1999; Norton et al., 2004a). It has been estimated that by 1981 cheatgrass was the dominant plant on more than 41 million hectares, and since then, with recent extensive wildfires in the Great Basin, the area under cheatgrass has greatly increased (Ypsilantis, 2003). With this large aerial extent, changes in biogeochemical cycling due to cheatgrass invasion may have notable effects on regional and global C and N fluxes.

Because of different plant life form, phenology and litter decomposition patterns than native vegetation, cheatgrass is well suited to thrive in disturbance-created mineralizing environments where it further exacerbates mineralization-driven nutrient cycles (Chen and Stark, 2000; Booth et al., 2003). Cheatgrass encroachment to diverse sagebrush-steppe plant communities creates a shift in vegetation-soil feedbacks and soil nutrient cycling from very conservative cycles characterized by high plant and microbial uptake to more open, mineralizing cycles with nutrients in excess of plant and microbe acquisition (Haynes and Williams, 1993). Other studies describe changes in soil–plant water relationships (Leffler et al., 2005), increase in carbon (C) and nitrogen (N) availability (D'Antonio and Vitousek, 1992), nutrient losses (Norton et al., 2004b) and soil organic matter (SOM) decline (Sperry et al., 2006). The presence of cheatgrass in sagebrush-steppe also alters soil microbial diversity by reducing species richness, lowering absolute numbers of fungi and invertebrates, and increasing abundance of active bacteria (Belnap and Phillips, 2001).

Existing literature suggests that wetting of a previously dry grassland soil under laboratory conditions generates a pulse of carbon dioxide (CO_2) 4–500% greater than CO_2 measured before wetting and can last 2–6 days (Fierer and Schimel, 2003). In addition, a single summer rainfall event produces a pulse of nitrous oxide (N_2O) amounting to 30% of the total N_2O emitted annually from sagebrush-steppe plant communities (Mummey et al., 1994) and nitrification is the predominant process driving it (Mummey et al., 1994; Mosier and Parton, 1998; Parton et al., 1988).

Several possible sources of C and N that drive pulses upon rewetting of dry soil have been proposed: (1) release from microbes killed by osmotic shock upon rewetting (Kieft et al., 1987); (2) release of highly enriched intracellular solutes by microbes surviving osmotic shock (Fierer and Schimel, 2003; Halverson et al., 2000); (3) disruption of aggregate structure and release of physically protected SOM (Appel, 1998; Denef et al., 2001); and (4) a combination of many sources (Scheu and Parkinson, 1994).

Since cheatgrass alters soil mineralization and microbial activity, we hypothesized that it also changes the magnitude of soil GHG emissions and biogeochemical transformations in response to wetting compared to native perennial grasses. Furthermore, the presence of cheatgrass in shrub interspaces may have significant effects on soil C and N cycling beneath shrub canopies. Therefore, the objective of this study was to monitor CO_2 and N_2O emissions and changes in soil C and N dynamics following the application of a water pulse in two Wyoming big sagebrush communities: one with interspaces dominated by cheatgrass and the other with interspaces dominated by the native perennial grass, western wheatgrass (*Pascopyrum smithii* Rydb.).

2. Materials and methods

2.1. Site description

The study site is located 22 km southeast of Lander in Fremont County, Wyoming (42°42′28″N, 108°36′21″W). Site elevation is 1696 m, mean annual soil temperature (30-year average) is 7.8 °C and mean annual precipitation is 340 mm (Wyoming State Climate Office, measured in Lander). The period of frost-free days ranges between 90 and 120 days. The site is located on a flat valley bottom with a maximum 1% slope. Soils are mapped as very deep and well-drained Diamondville–Forelle association, classified as fine-loamy, mixed, Borollic Haplargids formed on alluvium and material weathered from soft shale (Young, 1981). Average thickness of the surface mineral horizon is 6 cm and depth to calcareous parent material is about 65 cm. Soils are neutral, with calcium carbonate accumulation occurring at about 45 cm. Plot selection was based on extensive soil sampling of the entire site and preliminary soil chemical analyses to ensure equivalent soil properties. Additional soil information specific to our study site is provided in Table 1.

Historically, this area had been under low intensity winter grazing by cattle until 1993 when livestock grazing ceased. Random clusters of sites dominated by sagebrush and either cheatgrass or western wheatgrass in shrub interspaces occur throughout the site. Estimated average shrub canopy cover for the entire site is 37% (data not presented). Grass cover estimated in our study plots is comparable between locations dominated by either cheatgrass (*B. tectorum*) or western wheatgrass (*P. smithii*) species and ranged from 15% to 18% (data not presented).

At the time of the experiment (mid to late August 2003), *A. tridentata* was past the flowering stage and severely drought stressed and *B. tectorum* was dead, its seeds already shattered, and its residue left on the soil surface. On the *P. smithii* sites, perennial grass vegetation was dormant and inflorescences empty.

Table 1
Bulk density, electrical conductivity (EC), cation exchange capacity (CEC), pH, texture, total nitrogen (TN), total organic C (TOC) and inorganic C measured in *B. tectorum* sagebrush sub-canopy (BT shrub canopy) and interspace (BT interspace), and *P. smithii* sagebrush sub-canopy (PS shrub canopy) and interspaces (PS interspace) soils

	BT shrub canopy	BT interspace	PS shrub canopy	PS interspace
Bulk density ($g\,cm^{-3}$)	1.3	1.4	1.2	1.3
EC ($S\,m^{-1}$)	0.02	0.05	0.03	0.02
CEC ($cmol\,kg^{-1}$)	19.4	19.4	20.6	20.7
pH (H_2O)	6.6	7.0	6.6	6.3
Sand (%)	40	40	35	32
Silt (%)	33	34	37	39
Clay (%)	27	26	28	29
TN (%)	0.14 (0.01)^{b*}	0.15 (0.02)^{b}	0.23 (0.02)^{a}	0.20 (0.02)^{a}
TOC (%)	1.44 (0.10)^{b}	1.44 (0.18)^{b}	2.82 (0.35)^{a}	2.13 (0.25)^{a}
Carbonates (%)	0.01 (0.001)^{ns}	0.02 (0.001)^{ns}	0.01(0.001)^{ns}	0.01(0.001)^{ns}

Values in brackets represent mean standard error of $N = 6$ field plots (both wetted and non-wetted before water addition). Different letters indicate significant differences ($P \leqslant 0.05$) using LSD test.

2.2. Treatments

We chose 12 sagebrush plants, six with adjacent *B. tectorum*-dominated interspaces and six with adjacent *P. smithii*-dominated interspaces. Sampling locations with the following designations were established beneath shrub canopies and in interspaces: *B. tectorum*-dominated shrub canopies (BT shrub canopy), *B. tectorum*-dominated interspaces (BT interspace), *P. smithii*-dominated shrub canopies (PS shrub canopy) and *P. smithii*-dominated interspaces (PS interspace). From these 24 locations, three replicates of shrub-interspace pairs in each grass type were randomly selected for water addition (total of 24 sampling plots: 12 plots wetted and 12 not wetted).

To retain water within the plots, 1week before the water pulse experiment, we drove rubber weed barriers approximately 5 cm into the ground, and secured them with metal pins to create circular 1.5-m diameter plots. Inside these plots, we installed PVC rings (25-cm diameter 10-cm high) 10 cm deep in the ground. These rings served as bases for chambers that were periodically installed on plots to monitor trace gas exchange (Mosier et al., 1993) (described below). In each plot we buried one ion exchange resin capsule (approx. 10 cm^3 of mixed bed C-249 and ASB-1P resins enclosed in Nylon mesh) (US Filter, Colorado Springs, CO) at 5-cm depth. The areas within the PVC rings were left undisturbed for the duration of the experiment. No precipitation occurred during the experiment. The last rainfall recorded for the site (0.2 mm) took place 8 days prior to our water pulse application. Mid-day air temperatures averaged 28 °C during the measurement period.

2.3. Field sampling

On August 20, 2003, at 8:30 a.m., we took initial soil samples and GHG measurements from all plots (24 measurements total). Within 10 min following completion of the pre-wetting measurements, we watered (using a watering can) three randomly selected shrub-interspace pairs with an equivalent of 25.4 mm rainfall, approximately the depth of a 2-year, 6-h rainfall event for the Lander area (Miller et al., 1973). After wetting the soil, we took soil samples and GHG measurements at 4, 8, 24, 48, 72, and 216 h (9 days), simultaneously from both wetted and non-wetted plots as described below.

Soil samples were collected from randomly selected locations at each of the 24 plots at each of the six sampling times. Samples from moistened sites were collected from within the rubber barriers but outside the GHG chambers. Collection of soil samples was achieved by driving a 4.8-cm diameter by 10-cm long Lexan tube into the ground and then extracting the soil from the tube. Soil samples from beneath shrub canopy were taken approximately 15 cm away from the stem. Soil cores were homogenized by hand and approximate 10-g sub-samples were drawn for estimates of gravimetric water content and immediate field extraction in 100 cm^3 of 2 M KCl. The remainder of each soil sample was stored in plastic bags. Ion exchange resin capsules were excavated 72 h following water addition and also stored in plastic bags. Field 2 M KCl extracts, bagged soil and bagged resin bags were stored on ice and transported to the lab for immediate analyses.

The GHG measurements were taken at each of these six time intervals using a well-established procedure developed by Hutchinson and Mosier (1981). Enclosed chambers equipped with septa were fitted on top of the previously installed PVC bases and sealed with rubber gaskets to form air-tight chambers on the soil. The chambers were monitored for 30 min with air samples taken using a 30-cm^3 syringe at 0, 15 and 30 min after the chamber had been sealed onto the base ring. In all, 25-cm^3 aliquots of these gas samples were injected into previously evacuated 12-cm^3 tubes sealed with butyl rubber septa (Mosier et al., 1993, 2005). The tubes were transported to the laboratory for GHG analysis.

2.4. Laboratory analyses

All soil samples were analyzed for the following indices: water content (Gardner, 1986), dissolved organic carbon (DOC), microbial biomass carbon (MBC), extractable ammonia (NH_4^+), extractable nitrate (NO_3^-), and dissolved organic nitrogen (DON). Soil samples collected before wetting were also analyzed for: bulk density (Blake and Hartge, 1986), pH in H_2O (Thomas, 1996), CEC (Summer and Miller, 1996), EC (Rhoades, 1996), and particle-size distribution (Gee and Bauder, 1986), total organic C (TOC), total N (TN) and carbonates.

Total C and N were determined on a C and N analyzer (NA 2100 Protein, Carlo-Erba Instruments, Italy), after roller-grinding the soils to a fine powder (90% of material passed through a 0.25 mm screen). Carbonates were measured on a separate sub-sample of the finely ground soil using a modified pressure–calcimeter method (Sherrod et al., 2002), and organic C calculated by subtracting carbonates from total C. Soil water content and bulk density estimates were used to calculate % water filled pore space (WFPS). We assumed a particle density of 2.65 g cm^3.

Dissolved organic C, DON, MBC, and microbial biomass N (MBN) were measured in 0.5 M K_2SO_4 soil extracts which were obtained by shaking 10 g of field-moist soil in 100 cm^3 of 0.5 M K_2SO_4 for 30 min and filtering through Whatman # 40 paper. Extracts were analyzed for DOC using a UV-persulfate TOC Analyser (Phoenix 8000, Tekman-Dorhmann, Cincinnati, OH). Microbial biomass C was determined by the fumigation/extraction method as described by Vance et al. (1987). Fumigation was performed on field-moist soils brought to field capacity moisture content within 24 h of sampling. Microbial biomass C was calculated as the difference between 0.5 M K_2SO_4– extractable. DOC in fumigated and un-fumigated samples and divided by a K_{eC} of 0.35 (Horwath and Paul, 1994).

Extractable soil inorganic N was obtained by shaking the 2 M KCl field extractions for 30 min, and filtering through Whatman # 40 paper. Soil remaining in the filters was wet-sieved through 2-mm mesh sieve to estimate gravel content for correction of initial soil sample weights. Inorganic N, sorbed on ion exchange resins in capsules, was extracted by shaking the content of resin bags in 100 cm^3 1 M KCl for 30 min. Extracts were analyzed by Lachat flow injection for NO_3^- using the sodium salicylate based method and NH_4^+ by the cadmium reduction method (Lachat Instruments, Hach Company, Loveland, CO). Dissolved organic N was measured as NO_3^- generated upon N persulfate oxidation of 0.5 M K_2SO_4 extracts obtained from un-fumigated soil samples (Cabrera, 1993).

Gas samples were analyzed for CO_2 and N_2O with an automated gas chromatograph (Varian 38001) equipped with thermoconductivity detector (Mosier et al., 1991). Gas fluxes were estimated based on the rate of change of the gas concentration in the chamber headspace from one sampling time to the next.

2.5. Experimental design and data analyses

For soil and GHG response variables, the experimental layout was a randomized design of triplicate sites located in areas dominated by two grass species (*B. tectorum* and *P. smithii*). Two water addition treatments (wetted and non-wetted) and two life forms present on site (shrub and adjacent interspace) were nested in each *B. tectorum*- and *P. smithii*-dominated site. Grass species and life form were considered fixed variables. Data were initially tested for normality and then analyzed using a repeated measures approach for the seven time intervals. Results indicated significant interactions associated with time, so data were then analyzed separately for each time interval using ANOVA in the MIXED model procedure (SAS Institute, Cary, NC, 1996) with water addition, grass species and life forms as main factors along with interactions. We used two different covariate matrix types: compound symmetry (CS) and first-order autoregressive (AR1), to test for mean treatment differences. Inorganic N adsorbed on ion exchange resin in capsules was analyzed using the MIXED model (SAS, 1996). Least significant differences were compared at $P \leqslant 0.05$ levels.

3. Results

3.1. Non-wetted soil C, N and GHG production

Initial analyses confirm all sites had similar soil bulk density, EC (except for BT interspace) and CEC (Table 1). Surface soil pH ranged from slightly acidic (PS interspace) to neutral (BT interspace) (differences statistically insignificant) and soils were texturally uniform. Total N and organic C content were significantly higher (at $P \leqslant 0.05$) in *P. smithii*-dominated plots compared to *B. tectorum*-dominated plots (Table 1). Carbonates content was low and comparable between sites with levels slightly higher in BT interspace soils (Table 1).

Microbial biomass C concentrations in non-wetted soils were low and differences between treatments were statistically insignificant (Table 2). Concentrations of DOC in BT shrub canopy and BT interspace soils were significantly lower than those measured for PS shrub canopy and PS interspace. Fluxes of CO_2 from BT shrub canopy soils were less than half of fluxes from PS shrub canopy while fluxes from BT interspace soils were one-third of those from PS interspace soils.

Non-wetted soil NO_3^- concentrations were significantly greater in BT shrub canopy and BT interspace soils than in PS shrub canopy and PS interspace soils. Soil NH_4^+ concentrations were lowest in BT interspace soils and significantly different than BT shrub canopy, PS interspace, and PS shrub canopy soils (Table 2). Dissolved organic N in non-wetted BT interspace and BT shrub canopy soils was 50% lower than concentrations measured in non-wetted PS interspace and PS shrub canopy soils (Table 2). Resin capsule-accumulated NO_3^-

Table 2
Mean values and significant differences for microbial biomass C (MBC), dissolved organic C (DOC), CO_2, NO_3^-, NH_4^+, N_2O, dissolved organic N (DON), and resin accumulated NO_3^- and NH_4^+ for dry *B. tectorum* sagebrush sub-canopy (BT shrub canopy) and interspace (BT interspace), and *P. smithii* sagebrush sub-canopy (PS shrub canopy) and interspace (PS interspace) soils

	BT shrub canopy	BT interspace	PS shrub canopy	PS interspace
MBC ($\mu g\,g^{-1}$ soil)	23.6 (3.7)	21.1 (5.5)	28.0 (10.7)	23.4 (6.2)
DOC ($\mu g\,g^{-1}$ soil)	65.5 (10.5)^{ab*}	59.6 (5.3)^{b}	91.3 (23.4)^{a}	96.4 (22.6)^{a}
CO_2-C ($mg\,m^{-2}\,h^{-1}$)	11.2 (1.6)^{c}	10.4 (1.8)^{c}	23.2 (2.6)^{b}	30.6 (3.2)^{a}
NO_3^--N ($\mu g\,g^{-1}$ soil)	1.1 (0.3)^{b}	4.1 (0.7)^{a}	0.7 (0.2)^{c}	1.2 (0.3)^{b}
NH_4^+-N ($\mu g\,g^{-1}$ soil)	3.0 (0.6)^{b}	5.7 (0.5)^{a}	4.4 (0.8)^{ab}	5.6 (1.0)^{ab}
DON ($\mu g\,g^{-1}$ soil)	7.4 (0.7)^{b}	6.1 (1.6)^{b}	12.8 (2.4)^{a}	12.6 (1.7)^{a}
N_2O-N ($mg\,m^{-2}\,h^{-1}$)	4.3 (1.2)^{a}	4.2 (1.6)^{a}	0.9 (0.3)^{b}	1.0 (0.3)^{b}
Capsule accumulated NO_3^--N ($\mu g\,capsule^{-1}\,72\,h^{-1}$)	3.3 (0.2)^{c}	5.4 (0.7)^{a}	3.3 (1.2)^{bc}	4.0 (0.4)^{b}
Capsule accumulated NH_4^+-N ($\mu g\,capsule^{-1}\,72\,h^{-1}$)	11.4 (0.1)	11.6 (0.5)	12.5 (1.1)	11.0 (0.3)

Values in brackets represent mean standard error of $N = 21$ (3 field reps per 7 sampling times) for all except $N = 6$ for resin accumulated inorganic N (3 field reps sampled at time 0 and time 72 h). Different letters indicate significant differences ($P \leqslant 0.05$) using LSD test.

Table 3
Changes in water filled pore space measured in *B. tectorum* sagebrush sub-canopy (BT shrub canopy) and interspace (BT interspace) and *P. smithii* sagebrush sub-canopy (PS shrub canopy) and interspace (PS interspace) soils at 0, 4, 8, 24, 48, 72 and 216 h following wetting

Time (h)	BT shrub canopy (%WFPS)	BT interspace (%WFPS)	PS shrub canopy (%WFPS)	PS interspace (%WFPS)
0	8.8 (2.7)	10.4 (1.9)	12.8 (1.0)	13.1 (0.5)
4	44.4 (12.2)	30.5 (1.2)	55.1 (4.9)	29.9 (3.3)
8	40.5 (8.7)	25.8 (1.2)	51.9 (4.9)	35.5 (5.1)
24	26.3 (4.1)	22.7 (2.8)	39.7 (2.5)	41.0 (3.1)
48	31.1 (8.5)	20.4 (2.3)	43.7 (2.7)	24.1 (6.6)
72	26.8 (5.5)	19.2 (0.8)	43.2 (1.5)	23.0 (1.7)
216	9.1 (2.2)	13.0 (1.1)	15.1 (2.9)	15.8 (1.2)

Values in brackets represent mean standard error of $N = 3$ field plots.

from non-wetted soils was the highest in BT interspace soils and the lowest in sub-canopy soils regardless of the vegetation type (Table 2). Resin capsule-accumulated NH_4^+ from non-wetted soils did not show any statistical differences ($P \leqslant 0.05$). Non-wetted BT shrub canopy and BT interspace soils produced on average 80% more N_2O than non-wetted PS shrub canopy and PS interspace soils (Table 2).

3.2. Production of GHG following wetting

The first set of measurements performed four hours after wetting showed increased soil moisture down to 10-cm depth compared with pre-wetted conditions (Table 3). Water filled pore space increased to 30% in both types of grass-dominated interspaces, to 44% in BT shrub canopy soils, and to 55% in PS shrub canopy soils. Differences between BT shrub canopy and PS shrub canopy WFPS were statistically insignificant. All soils sustained increased water content for over 72 h and became similar to pre-wetted conditions by 216 h after wetting. Soils beneath PS shrub canopy sustained elevated WFPS for the longest period of time (over 72 h).

Fluxes of CO_2 measured 4 h following wetting were significantly greater from BT interspace and PS interspace soils than BT shrub canopy and PS shrub canopy soils (Figs. 1a and b). Even though the highest absolute amount of CO_2 produced 4 h following wetting was generated by PS interspace soils, BT interspace soils produced 55 times more CO_2 than the same soils before wetting while PS interspace soils generated 24 times more than the same soils before wetting (Fig. 2a). Carbon dioxide fluxes from BT shrub canopy soils were 26 times greater and fluxes from PS shrub canopy soils were 19 times greater than the fluxes before wetting (Fig. 2a). All soils demonstrated notable decline in CO_2 within 8 h after wetting, but the levels remained higher than before wetting for the entire 216-h monitoring period (Figs. 1a and 1b).

Soil wetting resulted in significantly greater N_2O fluxes from BT soils compared to PS soils (Figs. 1c and 1d). In addition, BT interspace and PS interspace soils generated greater N_2O fluxes compared to BT shrub canopy and PS shrub canopy soils. During the first 4 h, N_2O fluxes increased by $439\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ from BT interspace soils and by $271\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ from PS interspace soils, and by $106\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ from BT shrub canopy soils and by $42\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ from PS shrub

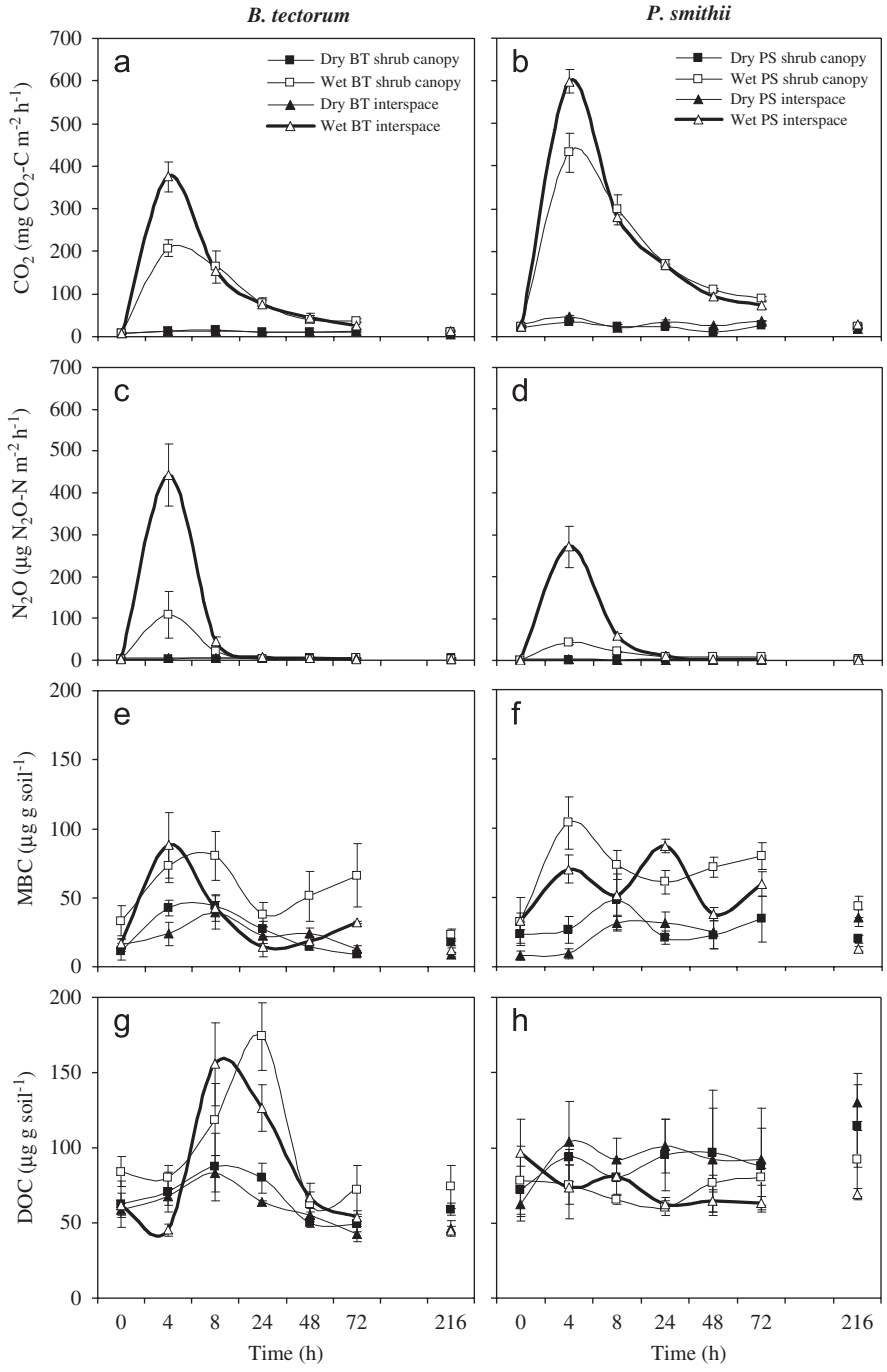

Fig. 1. Fluxes of CO_2 and N_2O, microbial biomass C (MBC) and dissolved organic C (DOC) from dry and wetted *B. tectorum* sagebrush sub-canopy (BT shrub canopy) and interspace (BT interspace) (a, c, e, g) and *P. smithii* sagebrush sub-canopy (PS shrub canopy) and interspace (PS interspace) (b, d, f, h) soils measured at 0, 4, 8, 24, 48, 72, and 216 h following wetting. Bars indicate standard errors of $N = 3$ field plots.

canopy soils. In contrast to CO_2, N_2O production declined to pre-wetted levels within 24 h after wetting (20 h after reaching the maximum levels).

3.3. Soil microbial biomass C and DOC

Microbial biomass C significantly increased (at $P \leqslant 0.01$) in all soils in the first 4 h after wetting with no significant differences between soils (Figs. 1e and f). It increased to five times pre-wetted concentrations in BT interspace soils and to two to three times in other soils (Fig. 2b). High MBC levels observed in all soils at 4 h declined thereafter with the greatest rate of decline observed in BT interspace and BT shrub canopy soils between four and 24 h after wetting. At 24 h after wetting, when the MBC concentrations in BT interspace, BT shrub canopy and PS shrub canopy soils declined, MBC in PS interspace soils experienced another concentration pulse and reached the

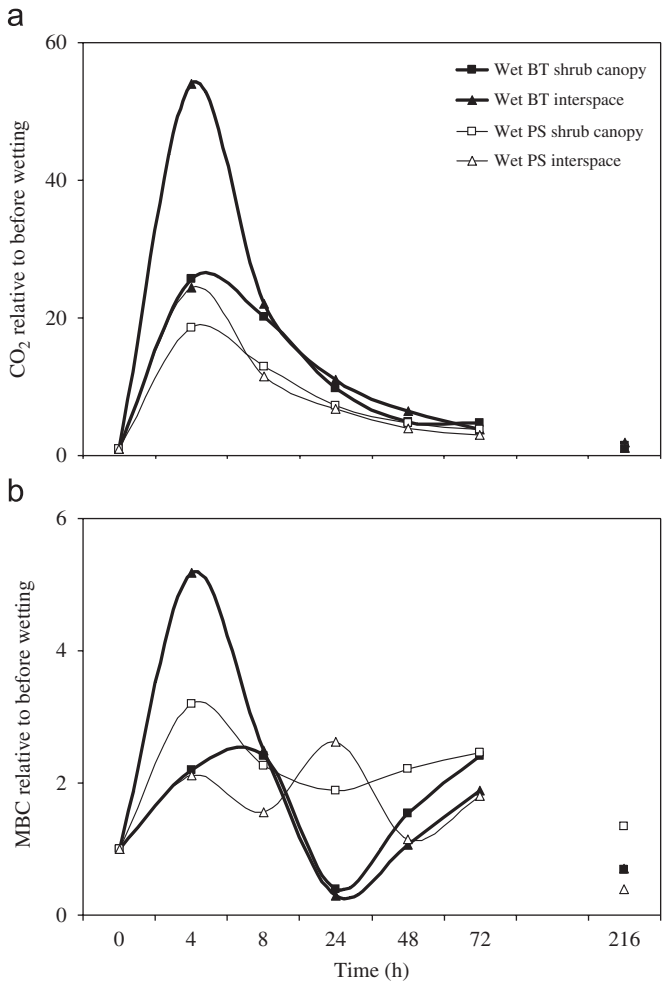

Fig. 2. CO_2 (a) and microbial biomass C (b) relative to before wetting calculated for wetted soil from sagebrush sub canopy and interspace of *B. tectorum* and *P. smithii* soils at 4, 8, 24, 48, 72, and 216 h following wetting.

highest level recorded. Differences between MBC concentrations in PS interspace soils and BT interspace soils measured 24 h after wetting was statistically significant at $P \leqslant 0.01$. By 216 h after wetting, all soils had MBC concentrations similar to pre-wetted levels.

Dissolved organic C increased only in BT interspace and BT shrub canopy soils (Figs. 1g and h). Concentrations increased to over two times pre-wetted levels by 8 h after wetting in BT interspace soils and by 24 h after wetting in BT shrub canopy soils. By 48 h after wetting, DOC levels in BT interspace and BT shrub canopy soils declined to pre-wetted levels. In contrast, DOC concentrations in PS interspace and PS shrub canopy soils gradually declined to reach their lowest levels 24 h after wetting with a significant concentration change between pre-wet and 24 h after wetting at $P \leqslant 0.05$ (Fig. 1h).

3.4. Soil N

All soils experienced short-lived increases in NO_3^- concentrations following soil wetting (Table 4). The earliest concentration spike was observed in BT interspace soils (4 h after wetting), followed by BT shrub canopy soils (8 h after wetting), PS interspace soils (24 h after wetting) and PS shrub canopy soils (72 h after wetting). Nitrate concentrations in BT interspace and PS interspace soils nearly doubled in 216 h, with the greatest concentrations in BT interspace soils.

There was a significant NH_4^+ increase only in BT interspace soils measured 4 h after wetting followed by declining concentrations that returned to pre-wetted levels by 216 h (Table 4). Remaining soils showed significant declines in NH_4^+ concentrations 216 h after wetting compared to before wetting.

Soils beneath BT shrub canopy had the highest resin capsule-accumulated NO_3^- of all soils measured 72 h after wetting (Table 4). Resin capsule-accumulated NO_3^- was significantly higher in BT interspace soils than in PS interspace soils ($P \leqslant 0.05$). No significant differences were found between BT shrub canopy and PS shrub canopy soils. Net NH_4^+ accumulation in resin capsules was significantly greater (at $P \leqslant 0.05$) in BT shrub canopy and PS shrub canopy soils compared to BT interspace and PS interspace soils.

Concentrations of DON in BT interspace and BT shrub canopy soils increased three to four times during the first 8 h after wetting (Table 4). During the next 40 h, DON concentrations declined to levels comparable to or lower than before wetting. In contrast, DON concentrations in PS interspace and PS shrub canopy soils declined significantly shortly after wetting.

4. Discussion

4.1. Overview

Soil responses after wetting beneath all vegetation types fell into two phases: (1) 0–8 h after wetting; and, (2) more than 8 h after wetting. During the first phase, all soils demonstrated dramatic CO_2, N_2O and MBC releases. Saetre and Stark (2005) propose that, initially, the magnitude of microbial activity increase in response to wetting is greater than the magnitude of microbial biomass growth. This is consistent with our observations of proportionally greater increases in CO_2 and N_2O emissions following wetting relative to increases in MBC concentrations. Saetre and Stark (2005) also suggest that the quality and quantity of substrates used by microbes shift with time following wetting and that microbes start utilizing substrates made available due to increased water during the latter stage of the response. Since all soils demonstrated chemical, textural and physical similarities across all sites, the differential magnitude of the responses following wetting is thought to be highly dependent on grass species and interaction between grass species and sagebrush shrub plants present on the site. Below we discuss the response of soil C and N dynamics and GHG emissions in each plant community within the 2-phase time framework.

Table 4
Soil NO_3^-, NH_4^+, dissolved organic N (DON), and resin accumulated NO_3^- and NH_4^+ for *B. tectorum* sagebrush sub-canopy (BT shrub canopy) and interspace (BT interspace) and *P. smithii,* sagebrush sub-canopy (PS shrub canopy) and interspace (PS interspace) soils at 0, 4, 8, 24, 48, 72 and 216 h after wetting

	Time (h)	BT shrub canopy	BT interspace	PS shrub canopy	PS interspace
NO_3^--N ($\mu g\,g^{-1}$ soil)	0	2.3 (0.8)	3.9 (0.1)	1.3 (0.4)	2.2 (0.0)
	4	2.8 (0.1)	5.8 (0.6)**	2.5 (0.7)	2.1 (0.9)
	8	4.5 (0.6)**	4.8 (0.6)**	3.8 (0.5)	2.6 (0.1)
	24	3.5 (1.0)	3.1 (0.0)	2.8 (1.0)	5.2 (1.4)**
	48	2.2 (0.4)	4.6 (1.2)**	2.9 (0.5)	3.1 (0.9)
	72	4.1 (1.0)*	4.4 (0.1)**	5.5 (1.6)**	2.4 (0.4)
	216	3.3 (0.6)	6.2 (1.4)**	3.7 (1.4)	4.6 (1.5)**
NH_4^+-N ($\mu g\,g^{-1}$ soil)	0	7.1 (0.7)	2.6 (0.0)	7.5 (1.7)	7.8 (0.4)
	4	7.3 (0.2)	7.1 (0.0)**	5.3 (1.1)	5.8 (1.7)
	8	4.0 (1.2)**	4.7 (1.6)**	4.9 (1.3)**	6.8 (1.7)
	24	4.0 (1.0)**	4.4 (0.1)**	4.8 (1.1)**	6.9 (1.5)
	48	2.2 (0.7)**	2.0 (0.1)	4.4 (0.8)**	3.6 (0.5)**
	72	2.2 (0.7)**	2.6 (0.1)	3.3 (0.8)**	3.0 (0.3)**
	216	1.0 (0.2)**	2.0 (0.2)	3.7 (0.8)**	2.2 (1.1)**
DON ($\mu g\,g^{-1}$ soil)	0	8.4 (1.1)	6.5 (1.8)	13.0 (3.4)	12.8 (1.6)
	4	15.1 (1.6)**	11.6 (0.4)**	18.3 (4.7)	11.4 (2.1)
	8	39.7 (3.9)**	17.8 (1.3)**	4.1 (1.2)**	9.4 (8.8)
	24	24.3 (7.5)**	13.0 (3.6)**	3.4 (1.1)**	11.4 (10.9)
	48	2.9 (1.1)**	8.4 (2.4)	7.7 (3.7)*	4.2 (1.4)**
	72	10.8 (4.9)	4.8 (4.0)	11.4 (4.9)	4.2 (1.3)**
Capsule accumulated NO_3^--N (μg capsule^{-1} 72 h^{-1})	72	71.5 (1.1)[a]*	58.3 (9.2)[a]	65.6 (19.8)[a]	33.9 (23.1)[b]
Capsule accumulated NH_4^+-N (μg capsule^{-1} 72 h^{-1})	72	21.1 (3.2)[a]	14.8 (0.7)[b]	18.8 (3.2)[a]	12.2 (0.6)[b]

Values in brackets represent mean standard error of $N = 3$ field plots. Different letters indicate significant differences ($P \leqslant 0.05$) using LSD test. **significantly different ($P \leqslant 0.01$) and *significantly different ($P \leqslant 0.05$) when compared concentrations within each vegetation type against time 0.

4.2. *Bromus tectorum* interspace

Wetting induced the greatest N_2O flux from BT interspace soils compared to other soils. Large amounts of N_2O recorded four hours after wetting, in conjunction with significant increases in soil NO_3^- concentrations during the same period and high capsule NO_3^- accumulation (determined at 72 h) in BT interspace soils compared to other soils, suggest the highest soil nitrification potential after wetting. In addition, significant quantities of nitrification-derived N are likely released to the atmosphere as nitric oxide (NO) after soil wetting (not measured during this experiment). According to Martin et al. (1998) and Mosier and Parton (1998), NO fluxes are typically 10–20 times greater than N_2O fluxes. Deposition of highly decomposable aboveground and belowground *B. tectorum* plant litter and rhizosphere-associated microbial biomass following annual plant senescence in early summer (Booth et al., 2003; Norton et al., 2004a) ensures sufficient supplies of N-rich substrate available to nitrifying bacteria that are ubiquitous in semi arid and arid soils (Booth et al., 2003). However, low soil DON levels beneath BT interspace non-wetted soils by the late summer suggest already diminished pools of labile N. This, in conjunction with low microbial N immobilization (low microbial biomass), significant build up of soil NO_3^- (also observed by Evans and Belnap, 1999; Evans et al., 2001), low soil NH_4^+ concentrations, and high N_2O fluxes from dry soils, suggests high nitrification potentials in BT interspace soils despite low moisture availability, also observed by Booth et al. (2003). Not only was nitrification potential high in BT interspaces when the soils were dry, but with sporadic summer rainfall events these soils mineralized greater amounts of labile N and lost proportionally more N to trace gas emissions in the first 8 h after wetting compared to other soils. This process may ultimately result in smaller retention of plant-derived N in long-term soil pools and subsequent declines in quality and quantity of SOM beneath BT interspaces.

Soil CO_2 emissions and MBC concentrations from BT interspace soils increased proportionally more than other soils following wetting. The CO_2 flux increased 55 times the flux before wetting and MBC increased five times the concentrations before wetting. However, despite nearly identical low MBC concentrations when all soils were dry, BT interspace soils showed the smallest CO_2 flux and the lowest DOC concentrations prior to soil wetting. Moreover, the absolute amount of CO_2 produced after wetting was significantly lower when compared to PS interspace soils. Therefore we propose that microbial populations present in BT interspace soils differ from the populations in the other soils. Microbial activity that depends on C as its energy source was low; likely limited by low C supplies we measured when BT interspace soils were dry. However, the

same microbial populations responded more rapidly and opportunistically to short-lived conditions of improved nutrient availability triggered by soil wetting compared to other soils. Abrupt microbial mortality shortly after the maximum microbial biomass was reached suggests inability of microbes to respond to emergent resource limitations when supplies of available C and N changed rapidly in the hours following soil wetting, or inability to cope with drastic osmotic shock upon soil wetting (as proposed by Kieft et al., 1987).

In summary, our data suggest that in the first 8-h phase after wetting of BT interspace soils, enhanced mineralization and high nitrification rates lead to the most significant N losses to trace gas emissions and to the greatest proportional increases in CO_2 emissions compared to other soils. But rapidly responding microbial growth and activity could not be sustained by the short-lived pulse of C and N resources, which were not available in sufficient quantities to support long-term microbial functioning.

In the second phase, low soil MBC concentrations coincided with very high soil DOC levels in BT interspace soils. Declines in MBC and, within four hours, increases in DOC concentrations suggest a direct relationship between dead microbial biomass and the recharge of the labile C pool. However, DOC concentrations 8-h after wetting were approximately twice as high as maximum MBC concentrations, which occurred four hours after wetting. Therefore, we propose that rapid increases in DOC and DON concentrations may have originated from other, predominantly non-microbial C and N mobilized during the first phase by wetting of *B. tectorum* plant residues, and that only some DOC and DON measured in the second phase originated from labile C and N released upon microbial mortality. This assumption is consistent with findings of a laboratory soil wetting experiment by Saetre and Stark (2005). The non-microbial labile C and N may include solubilized simple organic compounds derived from senesced roots and plant residues transported downward with soil wetting. Horwath and Elliott (1996) demonstrated such movement of organic compounds with the wetting front in a dry soil. In addition, rapid wetting may have disrupted soil aggregate structure and released physically protected soil organic C, as shown by Appel (1998) and Denef et al. (2001).

In summary, during the second phase of BT interspace soil responses to wetting, rapid MBC declines coincided with disproportional DOC concentration increases. Significant amounts of labile C and N in the DOC and DON pools may originate from non-microbial sources mobilized by direct exposure of dry plant detritus or soil aggregates to sudden wetting. Mobilization of residue-derived labile C and N upon soil wetting may have lead to diminished plant litter contributions to stable C and N pools and, ultimately, to the lower overall concentrations soil organic C and total N in BT interspace soils compared to other soils we analyzed in this experiment.

4.3. *Pascopyrum smithii* interspace

During the first phase of PS interspace soils response to wetting, the N_2O flux was significantly lower than the flux from BT interspace soils. Lower N_2O flux, lower capsule NO_3^- accumulation compared to BT interspace soils, and lack of soil NO_3^- concentration changes after wetting suggest reduced nitrification potential of PS interspace soils compared to BT interspace soils when soils were wet. Moreover, the same soils had low nitrification potential when dry (also reported by Booth et al., 2003), as demonstrated by very low N_2O flux and soil NO_3^- concentrations but high soil DON concentrations.

However, PS interspace soils produced the greatest total amount of CO_2 of all soils both after wetting and when soils were dry. The relatively high CO_2 production is consistent with relatively high dry soil DOC concentrations, which would supply sufficient labile C for high CO_2 flux. Morgan et al. (1998) observed increased concentrations of water soluble organic compounds transported from *P. smithii* stems to roots during the onset of a simulated dry season. They concluded that some of these organic compounds function as osmoregulators to alleviate plant water stress and are exuded by plant roots to the rhizosphere where they may become microbial substrates. However, due to the fact that microbial activity is suppressed by limited water (demonstrated in this experiment by relatively low soil MBC concentrations), labile C accumulates in PS interspace soils until more desirable conditions for microbial activity occur.

With the onset of soil wetting, *P. smithii* roots excrete even more organic compounds to balance for osmotic pressure differences and ensure correct mass flow of nutrients between soil and roots (Morgan et al., 1998). Interestingly, during the first phase of PS interspace soil response to wetting, soil DOC concentrations did not significantly change and MBC concentrations only doubled, but CO_2 production was very high relative to other soils. This suggests that a significant amount of accumulated labile C was utilized for increased microbial respiration after wetting.

In summary, during the first phase of soil PS interspace response to wetting, N_2O production and soil NO_3^- production were lower compared to BT interspace soils. The relatively high rate of CO_2 production suggests that microbial respiration was supported by sufficient supplies of labile C.

During the second phase of PS interspace soil response to wetting, soil MBC concentrations reached their maxima (second peak), on average less than three times greater than soil MBC concentrations before wetting and much less in magnitude than those in BT interspace soils. This coincided with the lowest soil DOC concentrations after wetting that we measured. Both MBC concentration peaks (during the first and the second phase of PS interspace soil response to wetting) were relatively small and were followed by gradual declines in soil DOC and DON concentrations while

microbial activity was more steady and microbial mortality was lower compared to BT interspace soils. Therefore we postulate that continuous supplies of available C and N in PS interspace soils better sustained the microbial population than in BT interspace soils. This may have led to more efficient microbial N immobilization in PS interspace soils (as observed by Booth et al., 2003) and to less loss of soil N to mineralization.

Overall, steady supplies of labile C and N continued to support gradual microbial recovery in the second phase of soil PS interspace response to wetting. Root exudation of dormant *P. smithii* vegetation is likely to be one of the important sources contributing to labile C and N pools.

4.4. *Bromus tectorum* shrub canopy and *Pascopyrum smithii* shrub canopy

In the first phase of the response to wetting, shrub canopy soils generated significantly smaller CO_2 and N_2O pulses compared to interspace soils. Our results differed from estimates obtained in laboratory water pulse experiments (Fierer and Schimel, 2003; Saetre and Stark, 2005) where the opposite pattern of CO_2 production was observed. Soil homogenization (sieving and removing coarse fragments) and laboratory pre-incubation before wetting can lead to soil aggregate destruction and priming of plant residue-derived organic compounds not readily available in field conditions. The high NO_3^- and NH_4^+ accumulation in ion exchange capsules and high soil MBC concentrations during the second phase of the response to wetting in BT shrub canopy and PS shrub canopy soils are consistent with the laboratory work by Saetre and Stark (2005). They linked these soil wetting responses to lower gross nitrification, but higher microbial immobilization of inorganic N in shrub canopy soils than grass-dominated interspace soils.

Grass species in shrub interspaces significantly influence shrub canopy soil responses to wetting. This was demonstrated by significantly higher N_2O and significantly lower CO_2 production in BT shrub canopy soils compared to PS shrub canopy soils in the first phase of response to wetting. Differences between the two shrub canopy soils were similar to differences between BT interspace and PS interspace soils. High N_2O flux, high NO_3^- concentrations, and low DON concentrations from dry soils also suggested greater nitrification potential in BT shrub canopy soils compared to PS shrub canopy soils.

Soils beneath BT shrub canopy also had MBC, DOC and DON responses comparable to BT interspace soils in the first and the second phase after wetting which lead us to believe that these soils had similar microbial populations. A large DOC concentration increase in the second phase in BT shrub canopy soils, similar to the DOC increase in BT interspace soils is strongly connected with similar sources of labile C mobilized during the first phase of soil response to wetting.

In summary, the type of grass in shrub interspaces had significant impacts on how soils beneath shrub canopies responded to wetting. Grass-type-induced differences in soil nitrification, N losses to trace gas emissions, and the quality, quantity, and timing of labile C available to microbial populations responding to increased moisture availability.

Based on our results, we conclude that summer drying-wetting cycles that occur frequently in areas invaded by *B. tectorum* can accelerate rates of nitrification and C mineralization, which contributes significantly to C and N losses to GHG emissions from sagebrush-steppe grasslands. Wetting-induced mobilization of labile C and N likely originates from freshly deposited *B. tectorum* plant material and leads to diminishing supplies of residue-derived organic compounds. With the estimates of total land area under *B. tectorum* invasion continuously on the rise and threatening the healthy functioning of sagebrush-steppe grasslands, processes we measured could lead to gradual ecosystem impoverishment. Moreover, with the possibility of increasing frequency of summer rainfall events, as predicted with climate change, the negative consequences *B. tectorum* presence in the ecosystem can increase disproportionately.

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