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The Effects of Large Herbivores on Soil Organic Matter Quality in Terrestrial Ecosystems

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The Effects of Large Herbivores on Soil Organic Matter Quality in Terrestrial Ecosystems

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Abstract

Understanding the factors that control the natural fluxes of carbon into and out of terrestrial ecosystems is of paramount importance to forecast and adapt to climate change. Soil respiration – the release of carbon dioxide from roots and soil micro-organisms– is considered to be the largest terrestrial source of carbon dioxide. Microbial respiration, the least understood component of soil respiration, is to a great extent determined by soil organic matter quality, reflecting the relative fractions of labile and recalcitrant soil carbon. The goal of this research was to examine how herbivory affects soil organic matter quality across a wide range of terrestrial ecosystems, including Oregon sagebrush steppe, Colorado short grass prairie, Nebraska mixed-grass prairie, Kansas tall grass prairie, and boreal forests in Isle Royale National Park (Michigan) and Acadia National Park (Maine).

Studying the effects of herbivores on soil organic matter quality among such a wide variety of ecosystems has not been previously undertaken. Soil organic matter quality was determined with a long-term, 36-week laboratory incubation experiment on soils collected from paired plots located outside and inside long-term exclosures in each of the ecosystems. For the sagebrush steppe, soils were sampled separately beneath shrubs and interspace because of previous reports of large effects of shrubs on soil properties. Herbivory had varying effects (positive, negative, and neutral) on soil organic matter quality at the sites. Herbivory increased soil organic matter quality at the shortgrass prairie, tallgrass prairie, and Isle Royale boreal forest, and reduced it at one of two boreal forests in Acadia and under shrubs in the sagebrush steppe. Herbivory had no effect on the mixed-grass prairie, one of two boreal forests in Acadia, and under interspace in the sagebrush steppe. The variable effects of herbivores may have been a function of the particular responses of plant species to herbivory among ecosystems and/or potential confounding differences in soil properties between paired plots. Future work should include experiments that investigate how herbivores impact linked plant and soil dynamics of grassland and forest ecosystems. The major implication of these findings is that policy makers will need to develop herbivore management policies on an ecosystem-by-ecosystem basis if they hope to manage soil organic matter quality to maximize soil carbon sequestration.

Executive Summary

There is abundant evidence that climate change is a real phenomenon and human-induced causes, particularly the CO_2 emissions resulting from the burning of fossil fuels, are considered the major culprit. However, the natural fluxes of carbon dwarf human-induced emissions, such as soil respiration – the release of carbon dioxide from roots and soil microbes – which is the largest terrestrial source of carbon. Microbial respiration, the least understood component of soil respiration, is to a great extent determined by soil organic matter quality, reflecting the relative fractions of labile (easily broken down) and recalcitrant (resistant to breaking down) soil carbon. Knowledge of the factors that control natural carbon fluxes into and out of terrestrial ecosystems is of paramount importance if we hope to be able to accurately forecast and successfully adapt to climate change.

Grassland and forest ecosystems dominate the terrestrial surface of the Earth, and large herbivores can have significant impacts on soil carbon processes and plant composition in both those ecosystems. For example, a study in a shortgrass prairie found that herbivory increased soil organic carbon content by increasing the abundance of C4 plant species relative to C3 species. In a study in a boreal forest, herbivory reduced soil organic matter quality by preferentially feeding on deciduous plant species (broad green leaves) over coniferous species (pine needles), and needles decompose more slowly than do broad green leaves.

The goal of this research was to examine how large herbivores affect soil organic matter quality across a wide range of terrestrial ecosystems, including Oregon sagebrush steppe, Colorado short grass prairie, Nebraska mixed-grass prairie, Kansas tall grass prairie, and boreal

forests in Isle Royale National Park (Michigan) and Acadia National Park (Maine). Soil organic matter quality was determined with a long-term, 36-week laboratory incubation experiment on soils collected from paired plots located outside and inside long-term (herbivory) exclosures in each of the ecosystems. For the sagebrush steppe, soils were sampled separately beneath shrubs and interspace (more open areas) as their soil properties have been known to differ.

Herbivory had varying effects (positive, negative, and neutral) on soil organic matter quality at the sites. Herbivory increased soil organic matter quality at the shortgrass prairie, tallgrass prairie, and Isle Royale boreal forest (i.e. herbivory increased the fraction of labile carbon that is more easily broken down), and reduced it at one of two boreal forests in Acadia and under shrubs in the sagebrush steppe. Herbivory had no effect on the mixed-grass prairie, one of two boreal forests in Acadia, and under interspace in the sagebrush steppe. The variable effects of herbivores may have been a function of the particular responses of plant species to herbivory among ecosystems and/or potential confounding differences in soil properties between paired plots. Future work should include experiments that explicitly link differences in soil organic matter quality determined in the laboratory to measured changes in plant abundances.

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1. INTRODUCTION

Climate change poses a major threat to humanity. There is abundant evidence that mean global temperature has increased in recent decades and anthropogenic forcing, particularly the CO_2 emissions resulting from the burning of fossil fuels, is considered the major culprit (Oreskes 2004; Cook et al. 2013; IPCC 2014). Dominating the global carbon (C) cycle, however, are the natural fluxes of C that are still not fully understood. Knowledge of the factors that control natural C fluxes into and out of terrestrial ecosystems is of paramount importance if we hope to be able to accurately forecast and successfully adapt to climate change.

Soil respiration – the release of CO_2 from the soil surface to the atmosphere – represents respiration from roots and soil biota, primarily bacteria and fungi (Rustad et al. 2000; Wang et al. 2009). Soil respiration is considered to be the largest terrestrial flux of CO_2 to the atmosphere and thus is an important contributor to the atmospheric C pool, with estimates ranging from 75 to 80 petagrams C per year (Schlesinger 1977; Raich and Potter 1995; Schlesinger and Andrews 2000; Raich et al. 2002). However, there is currently incomplete knowledge of the factors that control soil respiration, particularly from the soil microbial component, which is the focus of this study.

Grassland and forest habitats dominate the terrestrial surface of the Earth. Grasslands have been estimated to comprise 31 to 43% of the Earth's land surface (Whittaker and Likens 1975; Atjay et al. 1979; Olson et al. 1983; White et al. 2000), with the most recent global dataset placing it at approximately 40.5% (excluding areas of permanent ice cover) (White et al. 2000). Forest ecosystems have been estimated to comprise about 31% of global land area (FAO

2010). Therefore, when considering the great extent of grasslands and forests and the large contribution that soil respiration has on the global C cycle, one should expect these terrestrial ecosystems to greatly influence the global C cycle.

Ungulates can have large impacts on soil C processes and plant composition in grasslands and forests (Milchunas and Lauenroth 1993; Shrestha and Paul 2008; Follett and Reed 2010; McSherry and Ritchie 2013). For example, Derner et al. (2006) found that cattle increased   soil organic C content and the dominance of C4 plants relative to C3 plants. . At a boreal forest site at Isle Royale National Park, moose browsing reduced soil C quality and the abundance of deciduous plants, the preferred forage, over coniferous ones (McInnes et al. 1992; Pastor et al. 1993). Most studies that have looked at herbivore effects on soil C have investigated how the animals change soil C content (Conant et al. 2001; McSherry and Ritchie 2013). Very few have addressed their role in controlling rates of soil C loss. Microbial respiration, the least understood component of soil respiration, is to a great extent driven by soil organic matter quality: reflecting the relative sizes of labile and recalcitrant pools of soil carbon (Yuste et al. 2007; Jagadamma et al. 2014).

The goal of this research was to examine how large herbivores controlled soil organic matter quality across a wide range of terrestrial ecosystems that included Oregon sagebrush steppe, Colorado shortgrass prairie, Nebraska mixed-grass prairie, Kansas tallgrass prairie, and boreal forests at Isle Royale National Park (Michigan) and Acadia National Park (Maine). Studying the effects of herbivores on soil organic matter quality among such a wide variety of ecosystems has not been previously undertaken. To investigate this, I performed a long-term, 36-week laboratory incubation experiment with soils collected from the aforementioned

ecosystems to infer soil organic matter quality. I hypothesized that the response of soil organic

matter quality to herbivores would vary (i.e. increase, reduce, or not change) among

ecosystems, because herbivores have been shown to alter other soil and plant C processes

differently across ecosystems (Milchunas and Lauenroth 1993; Derner and Schuman 2007;

Pineiro et al. 2010; McSherry and Ritchie 2013).

2. METHODS

2.1. Study Sites

I conducted a laboratory incubation experiment on 0-10 cm soils collected from paired

plots located inside and outside 63 – 98 year old ungulate exclosures in a wide variety of

ecosystems, including boreal forests at Isle Royale National Park (Michigan) and Acadia National

Park (Maine), Kansas tallgrass prairie, Nebraska mixed-grass prairie, Colorado shortgrass prairie,

and Oregon sagebrush steppe (Table 1). At the sagebrush steppe, soils were collected

separately beneath shrubs and interspaces as shrubs have been shown to create "islands of

fertility" with soil properties that differ compared to those of interspaces (Schlesinger et al.

1990).Paired plots were located adjacent to one another on the same aspect and slope to

minimize differences in soil properties at the time the exclosures were established. However,

only one site was sampled per ecosystem type (apart from Acadia National Park), which limited

my ability to infer differences in soil organic matter quality among sites (Hurlbert 1984).

Climatic data were gathered from the nearest weather station to each site that had

complete temperature and precipitation data. The mean 30 year (1984-2014) annual

precipitation among sites ranged from 290 mm at the Oregon sagebrush steppe to 1420 mm at

the boreal forest sites in Acadia National Park (Table 1). The mean annual temperature ranged from 3.5°C at the Isle Royale boreal forest to 12.8°C at the Kansas tallgrass prairie (Table 1).

2.2. Sample Preparation

The soils were sampled in the summer and fall of 2014. After collection, soils from each site were transferred to an oven within 24 hours then dried for >3 days at 100°C. Soils were sieved through a 2mm mesh to remove large roots and rocks. The remaining smaller roots were picked from the soil with forceps. Equal portions of each root-free sample that came from the same site/exclosure treatment were combined to produce a 250-500 g pooled sample. Incubations were performed on three subsamples collected from each of the homogenized pooled soils. Soil C and N concentrations of these subsamples were determined with a CE Instruments NC 2100 Soil Analyzer.

Seventy-five grams of each soil subsample was mixed thoroughly with 25 g sand to facilitate periodic extraction of minerals during the incubation that would have otherwise inhibited microbial activity. Sand was acid-treated and thoroughly rinsed with deionized water to remove minerals before it was combined with soil. Each soil-sand sample was added to a 250 mL Nalgene test funnel (Chuckran and Frank 2013).

2.3. Incubation Experiment: Measuring Microbial Respiration

Soil samples were thoroughly wetted with deionized water four days prior to initial respiration measurements to allow microbial populations to grow. Excess water was removed by fitting funnels to a side-arm flask and drawing excess water out under vacuum. After

removal of excess water, the filter funnels were placed inside quart-size mason jars and capped loosely with a band before being placed inside an incubator set at 25° C.

As soil microbial communities were kept warm, moist, and aerobic throughout the incubation experiment, microbial respiration was used to infer soil organic matter quality, because quality of the organic matter was the only limiting factor of soil respiration. Microbial respiration was measured in week one, two, four, six, nine, twelve, seventeen, twenty-three, twenty-nine, and thirty-six of the experiment. For each of the intervals that respiration was measured, incubation chambers were removed from the incubator and 20 mL glass scintillation vials containing 5 mL of 2N NaOH designed to trap microbe-respired CO_2 were added (Snyder and Trofymow 1984). Incubation chambers were then returned to the incubator.

The titration procedure was as follows: 1 mL of solution from each vial was transferred to a clean vial with a pipette whose tip was replaced with each sample. Excess $BaCl_2$ (2 mL of 1 M $BaCl_2$) was added to the 1 mL of NaOH to stabilize the trapped CO_2 as $BaCO_3$ (Snyder and Trofymow 1984). Approximately 3 drops of 0.6% thymolphthalein was added and the NaOH was titrated with 0.5 N HCl using a microburet accurate to 0.05 mL; the amount of HCl used for each titration was recorded. The calculation of C trapped required subtracting the equivalents of HCl used in titrating a sample from the equivalents used to titrate a blank. I used at least four blanks before each digestion batch and treated the blank digests exactly as the sample digests (Snyder and Trofymow 1984). The amount of C trapped was derived as (modified from Snyder and Trofymow 1984): mg C trapped = (mL blank x 0.5 – mL sample x 0.5) x 12 mg C / 2 meq, which simplified to (mL blank – mL sample) x 3. As each vial originally contained 5 mL of solution in the incubation chamber, this value was multiplied by five.

The amount of time CO_2 traps were left in chambers increased from four to ten days as rates of microbial respiration declined during the experiment. Mason jars were capped loosely between CO_2 trapping periods to allow for ventilation.

2.4. Incubation Experiment: Nitrogen Extracts

For the first seven titration periods, mineralized NH_4^+ and NO_3^- were extracted by leaching soil with a nutrient solution lacking nitrogen (N). The solution was comprised of 4.0 mM $CaCl_2$, 2.0 mM KH_2PO_4, 1.0 mM K_2SO_4, 1.0 mM $MgSO_4$, 25 µM H_3BO_3, 2.0 µM $MnSO_4$, 2.0 µM $ZnSO_4$, 0.5 µM $CuSO_4$, and 0.5 µM Na_2MoO_4 (Pastor et. al. 1993). To each sample, 100 mL of nutrient solution was added, allowed to stand for 10 minutes, and then removed under vacuum. The volume of nutrient solution drained from each sample was recorded, after which a small amount was stored frozen at -20℃ until analysis. These data have yet to be analyzed.

2.5. Statistical analyses

Microbial respiration was represented in two ways: daily CO_2 respired per total soil C content and cumulative CO_2 respired. Total soil C content was determined by multiplying the proportion C in a gram of soil by 75 grams (the amount of soil used per sample). The respiration values for the first week were discarded from analysis because of their very low rates that could have been due to methodological error or insufficient time allowed for the microbial community to reach carrying capacity. As the data from the first titration period was discarded, cumulative respiration for the second titration period was an underestimate and was therefore calculated by multiplying the daily microbial respiration rate for day seventeen by seventeen days. Subsequent cumulative respiration values were calculated by adding the previous value to

the product of days elapsed since the previous titration and the midpoint daily respiration rate between titration periods. For each site and interval, a T-test was performed to compare mean respiration values between the grazed and ungrazed plots ($\alpha = 0.05$).

3. RESULTS

3.1 Soil C and N content

Soil C content ranged from 0.62% at the grazed Nebraska mixed-grass prairie to 4.11% at the grazed Kansas tallgrass prairie (Table 1). Soil N content ranged from 0.05% at the grazed Nebraska mixed-grass prairie to 0.32% at the grazed Kansas tallgrass prairie (Table 1).

Significant differences in soil C content between grazed and ungrazed plots were found at the Colorado short grass prairie (Grazed: 2.06% vs Ungrazed: 3.05%), Nebraska mixed-grass prairie (Grazed: 0.62% vs Ungrazed: 0.82%), and Oregon sagebrush steppe shrub (Grazed: 2.80% vs Ungrazed: 1.69%). Significant differences in soil N content were found at the Colorado short grass prairie (Grazed: 0.19% vs Ungrazed: 0.25%), Oregon sagebrush steppe shrub (Grazed: 0.21% vs Ungrazed: 0.14%), and Kansas tall grass prairie sites (Grazed: 0.32% vs Ungrazed: 0.28%).

3.2. Daily CO_2 respired / total soil C content

Daily CO_2 respiration rates tended to decrease throughout the incubation experiment (Figure 1). In a few instances, respiration rates spiked during a sampling period, especially for the Nebraska and Oregon sites. In those instances, both grazing treatments exhibited similar spikes.

At the Colorado shortgrass prairie, daily CO_2 respiration rates were significantly higher at the grazed plot for all but the second-to-last sampling interval (Figure 1). At the Kansas tallgrass prairie, respiration rates were significantly higher at the grazed plot for all intervals (Figure 1). At the Oregon sagebrush steppe site, respiration rates of soil collected under sagebrush shrubs were significantly higher inside the exclosure for the first five intervals, and not significant beneath interspace soils (Figure 1). Results were nonsignificant at the Nebraska mixed-grass prairie (Figure 1).

At the Acadia boreal forest, respiration rates were significantly higher inside the Murphy Lane exclosure for six out of the nine intervals; the three insignificant values were towards the end of the incubation experiment (Figure 1). At the Breakneck exclosure in Acadia, respiration rates were nonsignificant for all intervals (Figure 1). At the Isle Royale boreal forest, respiration rates were significantly higher at the browsed plot towards the end of the end of the incubation experiment (Figure 1).

3.2 Cumulative CO_2 respired / total soil C content

Cumulative respiration mostly followed the same pattern as daily respiration rates, except that for most sites significant differences between treatments were observable for a longer duration of the experiment (Figure 2). At the end of the 255-day incubation experiment, cumulative CO_2 respired ranged from 9% of the total soil C content at the browsed Acadia boreal forest (Murphy Lane exclosure) to 32% at the Nebraska mixed-grass prairie (Table 2).

4. DISCUSSION

4.1 Grasslands

My results are consistent with recent reviews that suggest grazing has varying effects on soil organic C in different environments (Milchunas and Lauenroth 1993; Derner and Schuman 2007; Pineiro et al. 2010; McSherry and Ritchie 2013). In my study, grazing improved soil organic matter quality at the Colorado shortgrass prairie site (i.e. grazing increased the fraction of labile carbon). While I could not find other studies that explicitly focused on soil organic matter quality in a shortgrass prairie, two studies found grazing influenced other soil dynamics such as soil carbon content (Derner et al. 1997; Derner et al. 2006). Similar to the shortgrass prairie in those studies, the shortgrass prairie site I examined was also dominated by *Bouteloua gracilis*, a caespitose (bunchgrass) C4 plant. *B. gracilis* is resistant to grazing and under intense grazing increases in abundance relative to other species, especially to C3 grasses (Milchunas et al. 1989, 1990, 1998; Derner et al. 1997, 2006). Under intense grazing, *B. gracilis* also has been shown to increase in basal area and tiller number per plant, and thus maintain soil organic C in a grazed system (Milchunas et al. 1989, 1990, 1998; Derner et al. 1997, 2006). Furthermore, 85% of *B. gracilis*' roots are located in the upper 15 cm of soil profile and via exudation, could contribute labile C in the form of amino acids and sugars (Coupland and Johnson 1965, Dormaar et al. 1995; Derner et. al 2006). As my study focused on 0 – 10 cm soils, changes in C inputs at the upper soil profile would have been recorded. The Colorado shortgrass prairie findings described in this paper could have been caused by similar herbivore-induced changes in *B. gracilis* abundance.

There was no significant difference in soil organic C quality between the grazed and ungrazed plots at the Nebraska mixed-grass prairie. Derner et al. (2006) found that soil organic C content did not differ between grazed and ungrazed plots in a Kansas mixed-grass prairie, which they attributed to cattle grazing having no effect on species composition between treatment types. Studies that have found significant differences in other soil dynamics such as C content in mixed-grass prairies have typically been accompanied with observable increases in *B. gracilis* under heavy grazing (Ganjegunte et al. 2005; Ingram et al. 2008). However, *B. gracilis* was not abundant at the Nebraska mixed-grass prairie site, which was instead was co-dominated by *Agropyron smithii* (C3) and *Andropogon hallii* (C4) As *A. hallii* is structurally similar to *B. gracilis* (i.e. both are C4 bunchgrasses), one may expect it to behave similarly under intense grazing. However, there does not appear to be published studies on how grazing affects this plant species.

Grazing improved soil organic matter quality at the Kansas tallgrass prairie. This finding was unexpected because: (1) tallgrass prairies tend to store a much larger pool of soil organic C compared to shortgrass prairies and so changes in soil C due to grazing could be potentially buffered (Schuman et al. 1999; Derner et al. 2006), (2) C4 plants (*Andropogon gerardii* and *Panicum virgatum*) already dominate this system so changes in species composition would not be expected to change root structure and dynamics. However, my finding that herbivores did not affect soil C content is consistent with previous tallgrass prairie exclosure studies (Derner et al. 1997; Derner et al. 2006).

At the Oregon sagebrush steppe site, herbivores had no effect on soil organic matter quality in interspaces, but decreased it under shrubs. Shrubs have been shown to facilitate the

formation of organic matter and nutrient enriched soils beneath them (Schlesinger et al. 1990).

A study by Manier and Hobbs (2007) on a Colorado sagebrush steppe dominated by mountain

sagebrush found that excluding grazing caused an increase in shrub cover. Thus, if herbivores

reduced shrub size at my sagebrush steppe site similar to the Colorado study, more robust

unbrowsed shrubs may explain why soil organic C quality was greater under shrubs inside

compared to outside the exclosure at my study site

4.2 Boreal forests

Browsing decreased soil organic matter quality at the Murphy Lane site in Acadia

National Park. Results were insignificant at the Breakneck exclosure. The findings at the Murphy

Lane site are consistent with McInnes et al. (1992) and Pastor et al. (1993) who found that

moose browsing at a boreal forest site at Isle Royale National Park reduced soil organic matter

quality by preferentially browsing on saplings of deciduous species over coniferous species. This

has long-term effects on forest structure and soil C processes because needles produced by

coniferous trees and the soil organic matter produced from those needles decompose more

slowly than do deciduous leaves (Raich and Tufekcioglu 2000). A possible explanation for why

herbivores only influenced soil organic matter quality at the Murphy Lane exclosure is that the

site experienced a stand-removing fire some decades ago (Bruce Connery, personal

communication). Fires should intensify browsing effects, as saplings that are colonizing burned

areas are all accessible to herbivores and thus herbivores can have a large effect on the

composition of the developing forest if herbivores selectively browse deciduous species over

coniferous species.

At the Isle Royale exclosure, moose increased soil organic matter quality for the later portion of the incubation experiment, which was opposite of what was found at the Acadia Murphy Lane site. A partial explanation for the inconsistency may be due to increased browsing pressure from moose populations following a collapse of their main predator, the wolf, in the past decade (Mlot 2015). To my knowledge, no study that has examined browsing effects on soil C processes has been conducted since the 1990s at Isle Royale (McInnes et al. 1992; Pastor et al. 1993). Therefore, changes in herbivory dynamics due to the recent reduction in predators have not been previously considered. An increase in moose density and a subsequent decrease in browsing selectivity may explain the nonsignificant influence of herbivory early in the incubation experiment, but does not explain why soil organic matter quality increased towards the end of the incubation.

5. CONCLUSION

The effects of large herbivores on soil organic matter quality vary across ecosystems, most likely due to the varying responses in plant composition to herbivory. A major implication of this study is that policy makers will need to develop herbivore management policies on an ecosystem-to-ecosystem, site-by-site basis if they hope to manage soil organic matter quality to maximize soil carbon sequestration and mitigate climate change. Future work should include experiments that investigate how herbivores impact linked plant and soil dynamics of grassland and forest ecosystems.

Table 1: Study site characteristics. Asterisks denote significant differences between treatments (average of three subsamples). Values in parentheses refer to 1 standard deviation.

Ecosystem, State	Exclosure established	Lat.	Long.	Dominant Species	Soil C % (Grazed)	Soil C% (Ungrazed)	Soil N% (Grazed)	Soil N% (Ungrazed)	Annual Temp. (C)	Annual Precip. (mm)
Tallgrass Prairie, KS	1950	39°20'N	96°58'W	*Andropogon gerardii, Panicum virgatum*	4.11 (0.04)	3.99 (0.05)	0.32* (0.006)	0.28* (0.004)	12.8	878.8
Boreal forest, ME (Murphy Lane)	1930	44°20'N	68°11'W	*Acer rubrum, Betula papyrifera, Betula populifolia*	3.06 (0.47)	2.96 (0.18)	0.11 (0.010)	0.09 (0.006)	7.5	1419.9
Boreal forest, ME (Breakneck)	1930	44°23'N	68°15'W	*Acer rubrum, Betula papyrifera, Betula populifolia*	2.73 (0.21)	3.61 (0.45)	0.11 (0.007)	0.14 (0.016)	7.5	1419.9
Central mixed-grass, NE	1951	41°50'N	100°22'W	*Andropogon hallii, Agropyron smithii*	0.62* (0.048)	0.82* (0.046)	0.05 (0.003)	0.06 (0.006)	9.3	561.3
Boreal forest, MI	1947	47°54'N	89°9'W	*Abies balsamea*	3.72 (0.22)	4.00 (0.27)	0.19 (0.010)	0.18 (0.014)	3.5	718
Shortgrass plains, CO	1937	40°50'N	104°45'W	*Bouteloua gracilis*	2.06* (0.02)	3.05* (0.13)	0.19* (0.003)	0.25* (0.010)	8.5	353.1
Sagebrush steppe, OR (Mountain big sagebrush) Interspace	1936	43°5'N	119°4'W	*Artemisia tridentata subsp. vaseyana, Festuca idahoensis*	1.61 (0.05)	1.54 (0.03)	0.14 (0.006)	0.13 (0.003)	8.4	289.6
Sagebrush steppe, OR (Mountain big sagebrush) Shrub	1936	43°5'N	119°4'W	*Artemisia tridentata subsp. vaseyana, Festuca idahoensis*	2.80* (0.06)	1.69* (0.07)	0.21* (0.002)	0.14* (0.008)	8.4	289.6

Table 2: Cumulative %C respired after 255 days. Asterisks denote significant differences between treatments (average of three subsamples). Values in parentheses refer to 1 standard deviation.

| Ecosystem, State	%C respired (Grazed)	%C respired (Ungrazed)
Tallgrass Prairie, KS	**19.01 (0.30)***	**13.18 (0.33)***
Boreal forest, ME (Murphy Lane)	**9.07 (0.33)***	**12.29 (0.74)***
Boreal forest, ME (Breakneck)	11.10 (0.56)	11.08 (0.73)
Central mixed-grass, NE	32.08 (1.98)	31.27 (1.59)
Boreal forest, MI	12.57 (0.54)	10.87 (0.48)
Shortgrass plains, CO	**26.78 (1.64)***	**15.74 (1.31)***
Sagebrush steppe, OR (Mountain big sagebrush) Interspace	17.67 (0.69)	18.19 (0.85)
Sagebrush steppe, OR (Mountain big sagebrush) Shrub	16.88 (1.43)	19.38 (1.25)
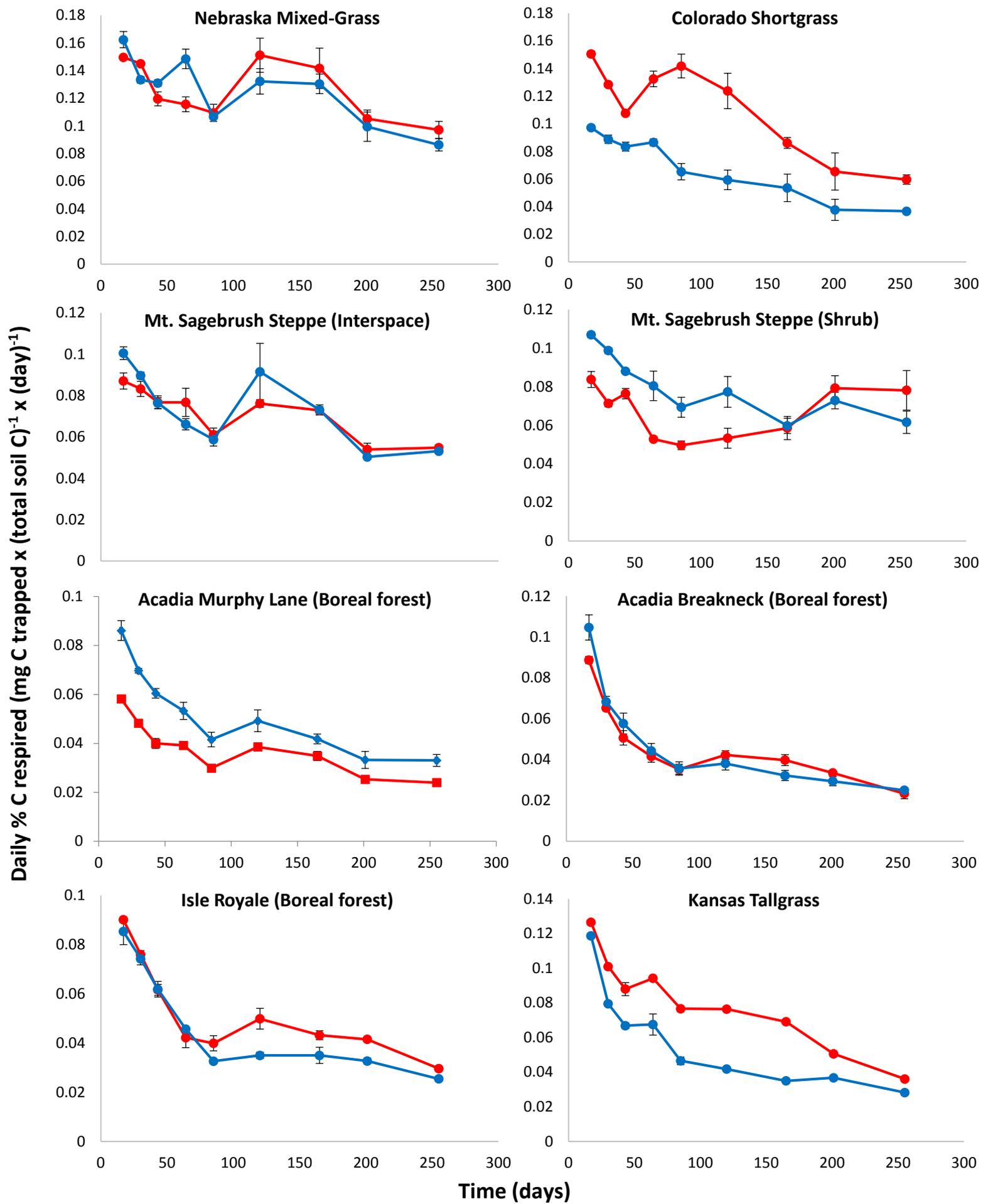
Figure 1: Daily microbial respiration rate for the 255-day laboratory incubation. Error bars represent one standard error of the mean (average of three subsamples). **Red lines: Grazed/Browsed**. **Blue lines: Ungrazed/unbrowsed.**
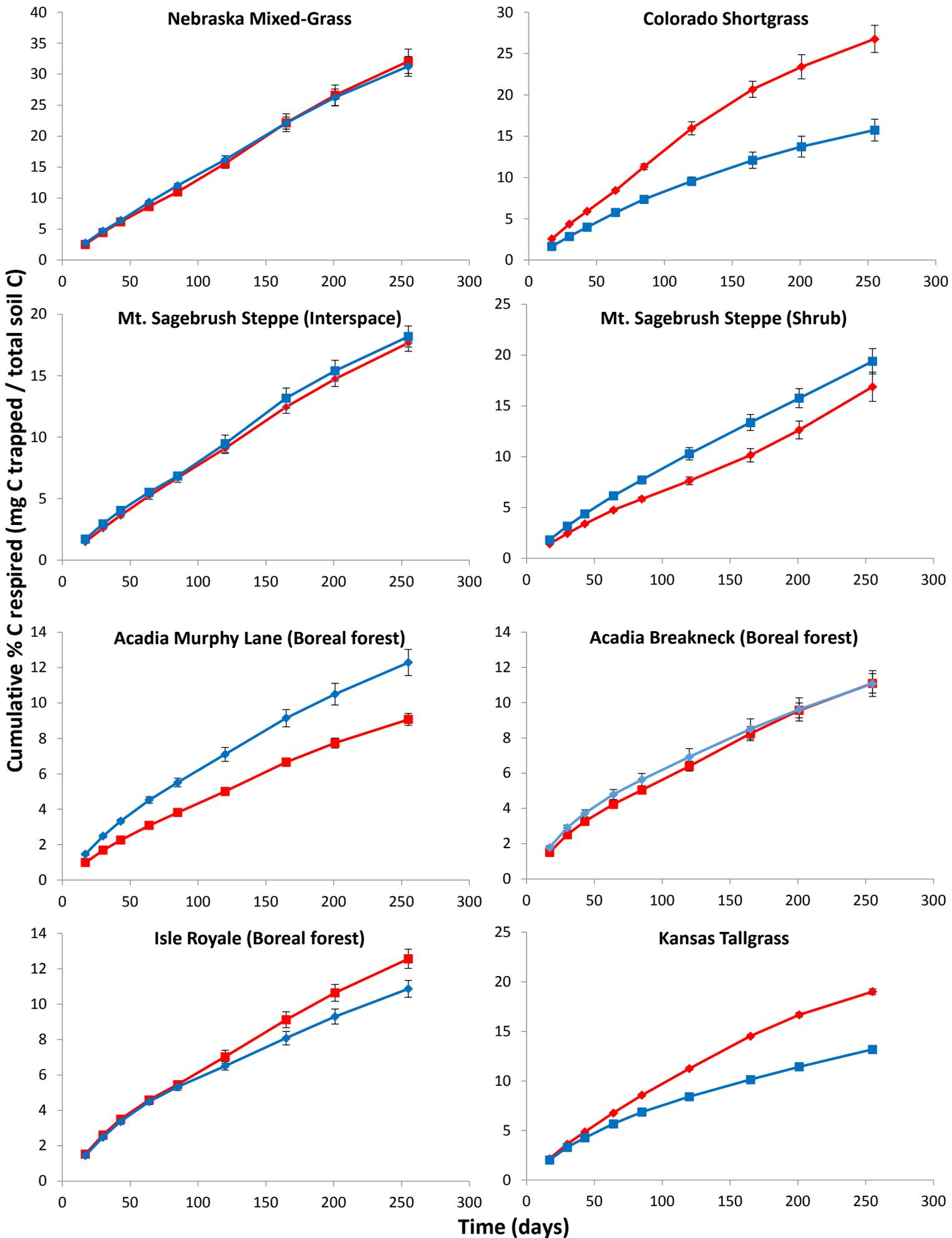
Figure 2: Cumulative microbial respiration rate for the 255-day laboratory incubation. Error bars represent one standard error of the mean (average of three subsamples). **Red lines: Grazed/Browsed**. **Blue lines: Ungrazed/unbrowsed.**

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