

Influence of 90 Years of Protection From Grazing on Plant and Soil Processes in the Subalpine of the Wasatch Plateau, USA

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Abstract

Human communities in the Intermountain West depend heavily on subalpine rangelands because of their importance in providing water for irrigation and forage for wildlife and livestock. In addition, many constituencies are looking to managed ecosystems to sequester carbon in plant biomass and soil C to reduce the impact of anthropogenic CO₂ on climate. This work builds on a 90-year-old grazing experiment in mountain meadows on the Wasatch Plateau in central Utah. The purpose of this study was to evaluate the influence of 90 years of protection from grazing on processes controlling the input, output, and storage of C in subalpine rangelands. Long-term grazing significantly reduced maximum biomass in all years compared with plots within grazing exclosures. For grazed plots, interannual variability in aboveground biomass was correlated with July precipitation and temperature ($R^2 = 0.51$), while there was a weak correlation between July precipitation and biomass in ungrazed plots ($R^2 = 0.24$). Livestock grazing had no statistically significant impacts on total soil C or particulate organic matter (POM), although grazing did increase active soil C and decrease soil moisture. Grazing significantly increased the proportion of total soil C pools that were potentially mineralizable in the laboratory, with soils from grazed plots evolving 4.6% of total soil C in 1 year while ungrazed plots lost 3.3% of total soil C. Volumetric soil moisture was consistently higher in ungrazed plots than grazed plots. The changes in soil C chemistry may have implications for how these ecosystems will respond to forecast climate change. Because grazing has resulted in an accumulation of easily decomposable organic material, if temperatures warm and summer precipitation increases as is anticipated, these soils may become net sources of CO₂ to the atmosphere creating a positive feedback between climate change and atmospheric CO₂.

Resumen

Las comunidades humanas en el oeste intermontañoso dependen fuertemente de los pastizales subalpinos por su importancia en suministrar agua para irrigación y forraje para la fauna silvestre y el ganado. Además, muchos distritos están mirando hacia ecosistemas manejados para la fijación de carbón antropogénico en la biomasa vegetal y el C del suelo para reducir el impacto del CO₂ antropogénico en el clima. Este trabajo se basa en un experimento de apacentamiento de 90 años en las praderas montañas de la Planicie Wasatch en la región central de Utah. El objetivo de este estudio fue evaluar la influencia de 90 años de protección al apacentamiento en los procesos controladores de entrada, salida y almacenamiento de C en los pastizales subalpinos. El apacentamiento a largo plazo, en comparación con las parcelas con exclusión, redujo significativamente la biomasa máxima de todos los años. En las parcelas apacentadas, la variación interanual de la biomasa vegetal se correlacionó con la precipitación de Julio y la temperatura ($R^2 = 0.51$), mientras que la correlación entre la precipitación de Julio y la biomasa de las parcelas sin apacentar fue débil ($R^2 = 0.24$). El apacentamiento del ganado no tuvo un impacto estadísticamente significativo en el C total del suelo o en las partículas de la materia orgánica (POM), aunque el apacentamiento incrementó el C activo del suelo y disminuyó la humedad del mismo. El apacentamiento incrementó significativamente las reservas de carbón del suelo que eran potencialmente mineralizables en el laboratorio, los suelos provenientes de parcelas apacentadas produjeron 4.6% de carbón total del suelo en un año, mientras que las parcelas sin apacentar perdieron 3.3% del C total del suelo. La humedad volumétrica del suelo fue consistentemente mayor en las parcelas sin apacentar que en las apacentadas. Los cambios de la química de C del suelo pueden tener implicaciones de cómo estos ecosistemas responderán al cambio climático pronosticado. Debido a que el apacentamiento ha resultado en una acumulación de material orgánico de fácil descomposición, si la temperatura aumenta y la precipitación de verano también se incrementa, tal como esta anticipado, estos suelos podrán llegar a ser fuentes netas de CO₂ para la atmósfera, creando una retroalimentación positiva entre el cambio climático y el CO₂ atmosférico.

Key Words: subalpine rangeland, soil carbon, grazing exclosure, mineralizable carbon, hydrology

INTRODUCTION

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The mountain lands of the Intermountain West are vital to the wellbeing of human communities in the adjacent valleys, providing these communities with water for domestic and agricultural uses and important summer forage for wildlife and domestic livestock (Sampson and Weyl 1918; Ellison 1954;

Welker et al. 2004). In addition, the substantial increases in atmospheric CO₂ over the past century have prompted policy makers, scientists, and the general public to look to managed ecosystems to sequester anthropogenic carbon in plant biomass and soil C (Follett et al. 2001; Gill et al. 2002; McCulley et al. 2005). Soils in subalpine and alpine meadows are regionally significant terrestrial pools for carbon and the Rocky Mountains are an important carbon sink at a continental scale, likely because of C sequestration in both trees and soils (Welker et al. 2004). However, it is unclear how grazing, with its potential effects on soil carbon chemistry, might influence a suite of important ecological characteristics in these ecosystems that are influenced by soil organic matter dynamics. For example, C fluxes in these ecosystems with forecast climate change may shift from being sinks to sources of C, particularly since subalpine and alpine meadows are likely to see much larger increases in temperature than lower elevation ecosystems (Wagner 2003). In addition, active fractions of soil C are the primary source of nutrients to the vegetation that is so critical for both domestic and native herbivores. Finally, alteration of litter and soil C dynamics has the potential to change water infiltration rates and the hydrology of subalpine watersheds (Kelly 2006).

Herbivores may exert a strong influence on soil C either through modifying the soil microenvironment which alters patterns of decomposition (output control) or through changing patterns and amounts of plant inputs to soil C (input control). Specifically, grazing can influence soil processes by altering soil compaction or erosion rates (Stewart and Forsling 1931; Neff et al. 2005), changing litter amounts or chemistry (Seastedt et al. 1994; Barger et al. 2004), modifying patterns of nutrient cycling (Frank and Evans 1997; Frank et al. 2000), or altering soil temperature or moisture availability (Welker et al. 2004). One of the earliest ecological studies in the Rocky Mountains demonstrated the importance of grazing management in controlling mud-rock floods that plagued communities at canyon mouths along the Wasatch Plateau in central Utah, concluding that much of the soil A horizon in the subalpine zone was lost due to grazing-induced erosion between 1870 and 1905 (Reynolds 1911; Sampson and Weyl 1918; Stewart and Forsling 1931; Klemmedson and Tiedemann 1998). Grazing can also alter C inputs by influencing plant litter chemistry (Milchunas and Lauenroth 1993; Barger et al. 2004), plant biomass allocation patterns (Biondini et al. 1998), litter production, and the spatial distribution of nutrients (Potvin and Harrison 1984; Day and Detling 1990; Frank and Evans 1997). Grazing pressure may potentially modify patterns of litter decomposition by causing a decrease in C/N ratios of plant litter which tends to slow decomposition (Seastedt et al. 1994), or by decreasing standing biomass which increases soil temperatures and may accelerate decomposition (Welker et al. 2004).

One of the key consequences of domestic livestock grazing in subalpine systems was noted by Ellison (1954) as a decrease in plant available water. Overgrazing, with its direct effect on erosion and supposedly the loss of clay and silt from soil surfaces, was thought to increase the distribution of xeric environments and plant species that are adapted to dry conditions. Ellison (1954) suggests that the increase in drier microenvironments is as important as selective grazing or trampling in explaining shifts in plant community composition following overgrazing.

While grazing has a strong potential to alter soil C dynamics in many rangelands, soil and plant processes in the subalpine zone are also strongly controlled by mesoscale environmental conditions (Ellison 1949). At scales of < 1 km differences in topography, aspect, and elevation influence soil temperature, and in a region where most of the summer precipitation comes as convective storms small differences in aspect and topography can influence the formation of these storms and produce substantial differences in precipitation. On the Wasatch Plateau, 2 weather stations that are separated by < 2 km and less than 100 m in elevation differ in annual precipitation by almost 300 mm because of differences in aspect and topography.

The goal of this study was to examine the role of livestock grazing on soil C composition and dynamics within the subalpine zone of the Wasatch Plateau in central Utah. The Wasatch Plateau presents many unique opportunities to evaluate the impacts of grazing on ecological processes. Intensive grazing by domestic livestock began in the subalpine region of the Wasatch Plateau by 1870 and has consistently occurred since then (Ellison 1954; Klemmedson and Tiedemann 1998). By the early 20th century the range was severely degraded when Arthur Sampson initiated pioneering work on the hydrology and ecology of the Wasatch Plateau (Young 2000; Young and Clements 2001). Sampson and others constructed several grazing exclosures that span environmental gradients and plant communities within the subalpine zone (Ellison 1954). This study is unique in a number of respects. This experiment involves perhaps the oldest set of grazing exclosures available in subalpine mountain meadows, allowing for insights into soil processes that might take several decades to recover following disturbance. In addition, while many other studies have used grazing exclosures to identify the effects of grazing on soil processes (Frank and Groffman 1998; Schuman et al. 1999; Welker et al. 2004), often these studies are constrained by difficulties in finding true replicate grazing exclosures. In this study I used 11 grazing exclosures within a 50 km² region of the Wasatch Plateau that span substantial environmental gradients from the windward side to the leeward side of the plateau and 435 m in elevation. I used a 3-year field study to address the following questions 1) Has 80–90 years of protection from livestock grazing altered forage biomass and soil organic matter pools and composition?; 2) What is the relative importance of landscape and grazing effects on soil C fluxes, and composition?; and 3) Is there evidence supporting Ellison's (1954) hypothesis that the impacts of grazing on vegetation and soils is primarily realized through alterations of soil moisture?

METHODS

Site Description

The Great Basin Experimental Range (GBER, 39°17'N; 111°30'W; US Department of Agriculture, US Forest Service) on the Wasatch Plateau in central Utah has sites that have been protected from domestic grazing for 80–90 years (Table 1). This site is currently managed by the Shrub Science Laboratory in Provo, Utah, under the auspices of the USFS, Rocky Mountain Research Station. The original log-and-block exclosures have been maintained by the US Forest Service since they were built. In 2 cases the original exclosures were replaced by

Table 1. Site summaries for 11 grazing exclosures at the Great Basin Experimental Range, Ephraim, Utah.

Site ¹	Treatment	Bulk Density	USDA Texture Categories (%)			Maximum Shoot Biomass (g·m ⁻²)			Soil Organic Matter		Particulate Organic C	1-Year Incubation	Soil Microbial Biomass	Mean <i>In Situ</i> CO ₂ Flux (g CO ₂ ·m ⁻² ·hr ⁻¹)		
			Sand	Silt	Clay	2003	2004	2005	kg C m ⁻²	C/N	kg C m ⁻²	μg g ⁻¹ soil	mg g ⁻¹ soil	2003	2004	2005
AC	Ungrazed-	1.25	29.2	30.0	40.8	165	415	237	5.25	11.0	1.81	13 934	665	0.39	0.56	0.67
	Grazed	1.23	30.4	35.4	34.2	143	303	69	5.66	11.5	1.95	14 101	546	0.12	0.60	0.40
BB	Ungrazed	0.86	49.2	25.8	25.0	376	408	270	6.59	11.8	2.15	14 567	712	0.51	0.72	1.27
	Grazed	0.93	58.0	18.7	23.3	342	376	191	6.52	12.3	1.97	18 295	693	0.35	0.57	0.81
DK	Ungrazed	1.25	62.9	24.6	12.5	224	330	140	3.33	10.8	0.59	5 075	520	0.31	0.43	0.13
	Grazed	1.41	52.9	25.4	21.7	69	213	169	3.46	10.2	1.26	10 531	415	0.10	0.16	0.12
DU	Ungrazed	1.10	45.4	21.3	33.3	— ²	—	—	7.45	10.8	4.02	21 608	729	—	—	—
	Grazed	0.94	56.7	18.3	25.0	—	—	—	6.21	11.0	2.25	30 657	702	—	—	—
EK	Ungrazed	1.07	37.1	27.9	35.0	367	377	205	5.61	11.3	1.93	10 202	657	0.24	0.370	0.26
LH	Ungrazed	1.01	40.8	39.2	20.0	304	408	589	5.20	10.9	1.62	7 752	604	0.14	0.91	0.87
	Grazed	0.95	53.8	27.1	19.2	131	284	254	5.00	10.5	1.85	16 225	651	0.22	0.79	0.54
PF	Ungrazed	1.28	35.8	42.9	21.3	243	301	153	3.31	12.2	0.71	6 089	479	0.24	0.525	0.47
	Grazed	1.22	36.3	42.9	20.8	237	291	180	3.48	12.0	0.80	5 019	490	0.11	0.258	0.51
SS	Ungrazed	0.95	35.8	35.8	28.3	218	338	259	5.80	13.1	1.83	6 101	612	0.59	1.118	0.85
	Grazed	1.10	42.9	29.6	27.5	169	352	107	3.92	11.9	1.65	6 573	544	0.31	1.242	0.73
TR	Ungrazed	1.31	71.3	22.1	6.7	249	332	147	10.47	11.6	3.60	22 787	586	0.53	1.502	0.87
	Grazed	1.06	68.8	22.9	8.3	262	334	113	7.55	11.3	2.60	25 473	745	0.27	1.255	0.90
UH	Ungrazed	1.04	35.0	30.0	35.0	336	369	211	4.57	11.4	1.03	5 991	663	0.44	1.140	0.70
	Grazed	1.03	33.3	31.7	35.0	268	340	99	4.41	11.2	1.15	12 690	727	0.29	0.605	0.36
US	Ungrazed	0.89	41.0	37.4	21.7	116	331	130	3.25	14.4	0.94	10 503	545	0.24	1.010	0.39
	Grazed	1.25	36.8	43.2	20.0	82	249	116	3.45	12.9	0.80	8 539	438	0.12	0.355	0.03

¹The following list includes site, year exclosure established, and elevation (m). AC indicates Alpine Cattle Pasture, 1922, 3 017; BB, Bluebell, 1922, 2 735; DK, Danish Knoll, 1913, 3 048; DU, Dungeon, 1940, 2 800; EK, Elks Ridge Knoll, 1870, 3 048; LH, Lower Horseshoe Flats, 1912, 3 010; PF, Philadelphia Flats, 1913, 3 030; SS, Sampson's Summit, 1922, 3 170; TR, Tom's Ridge, 1922, 2 926; UH, Upper Horseshoe, 1912, 3 018; US, Upper Seeley Creek, 1916, 2 987.

²“—” indicates data not collected.

wire fences in the mid 1980s. Outside the exclosures there has been summer grazing by sheep and cattle for over 130 years (Sampson & Weyl 1918; Ellison 1954). These grazing treatments allow the comparison of long-term ungrazed and long-term grazed ecosystems in a fully replicated design. To be precise, the treatments are long-term grazed, with grazing intensity varying over the past 130 years, and 80–90 years of protection from grazing after a period of intense overgrazing (Ellison 1954). Eleven sites within the GBER have been identified; each site contains a historically grazed area that has been protected from native livestock for 80–90 years and a continuously grazed area (Fig. 1; Table 1). Most exclosures in this study were either 0.1 or 0.2 ha, while 2 of our sites (Elks Knoll and Alpine Pasture) were > 16 ha. The reason for using paired sites is to eliminate potential confounding factors that could explain differences in ecosystem or community properties. At the time the exclosures were constructed, the entire landscape had been impacted by grazing and extensive erosion. Therefore, the conditions inside the exclosures should not be considered typical of what this area would be like prior to the introduction of domestic livestock. There are no reliable estimates of stocking prior to the establishment of the Manti National Forest in 1903, but it has been suggested that there may have been as many as 520 000 sheep on the Wasatch Plateau (Prevedel et al. 2005). Soon after the establishment of the National Forest, stocking rates decreased to 200 000 sheep and 20 000 cattle. By 1950 these rates had decreased to 100 000 sheep and 15 000 cattle (Ellison 1954). Stocking rates

continued to decline and currently permits for 71 000 sheep have been issued for the entire Wasatch Plateau (Prevedel et al. 2005). The Elks Knoll Natural Area is a butte that lacks perennial surface water and whose boundaries are steep enough to preclude domestic livestock from having more than a minor, intermittent impact. It has been used historically as a reference location to infer what the soils and vegetation of the Wasatch Plateau may have been like in the absence of livestock grazing (Ellison 1954).

This work focuses on the subalpine, mountain meadow zone within the GBER. Mean annual precipitation for the windward side of the Wasatch Plateau for the past 75 years was 932 mm, with 85% of precipitation falling between September and May. During the past 70 years there has been a trend of increasing precipitation, although there have been intermittent multi-year droughts, including 1999–2004. In addition there is substantial mesoscale variation in climate. For example, within < 2 km a site at the same elevation as the primary weather station received nearly 300 mm less precipitation (637 mm). Because of elevation differences among grazing exclosures and orographic effects, individual grazing exclosures likely experience different climate means and variability. Mean annual temperature (1987–2004) was 1.3°C and ranged from monthly means of –8.2°C in December to 13.2°C in July.

The subalpine zone lies at the crest of the Wasatch Plateau and lies in an approximately north-south orientation with narrow ridges extending out along an east-west orientation (Ellison 1949). The crest of the plateau tends to be level or

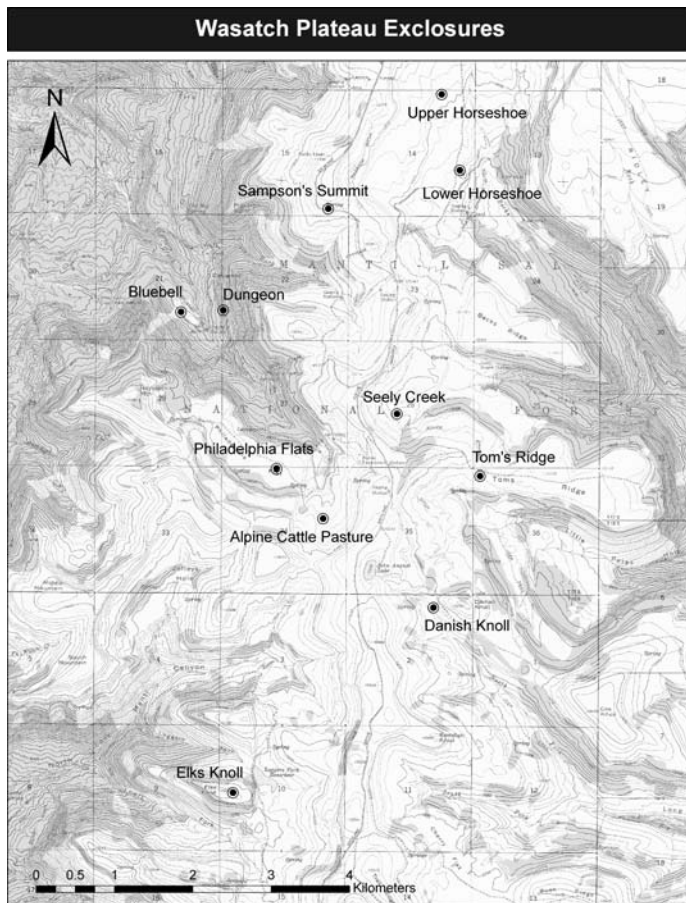


Figure 1. Study site locations at the Great Basin Experimental Range.

rolling with ridge edges sharply defined by cliffs or steep slopes with little soil development. Soils have developed from Eocene limestones and shales and tend to be sandy clay loams (Table 1). Plateau soils are mostly argic Cryoborolls (Klemmenson and Tiedemann 1998). In areas where erosion has been extensive “erosion pavements” form because of the accumulation of limestone fragments at the soil surface (Ellison 1949).

Most of the vegetation in the subalpine zone is herbaceous, although there are small patches of *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt. found across the Plateau. The herbaceous vegetation varies through the growing season and across the plateau, although most of the species are perennials. The herbaceous plant community is dominated by grasses (*Achnatherum lettermanii* [Vasey] Barkworth, *Elymus trachycaulus* [Link] Gould ex Shinnars, *Trisetum spicatum* [L.] Richter) and forbs (*Artemisia michauxiana* Bess., *Taraxacum officinale* G. H. Weber ex Wiggers, *Geranium viscosissimum* Fisch. & C. A. Mey. ex C. A. Mey.) which are found in several combinations. There are well defined communities that often exist in association with specific soil properties, precipitation zones, or grazing pressure (Ellison 1954).

Aboveground Biomass

Aboveground plant biomass was determined using a double sampling approach as a proxy for aboveground biomass, where a regression equation was developed between biomass and the Normalized Difference Vegetation Index (NDVI) (Catchpole

and Wheeler 1992; Paruelo et al. 2000; Sala and Austin 2000). Reflectance in the red and near infrared (NIR) bands of the light spectrum was measured using a handheld radiometer (Skye Instruments, Powys, UK) on 4 dates during the 2003–2004 growing season at four 0.5-m² quadrats at each site (2 dates during 2005). The red and NIR values were used to calculate NDVI, a useful proxy for plant biomass (Paruelo et al. 1997). On each date ten 0.5-m² quadrats were destructively sampled from across the plateau from areas that spanned the range in observed biomass, the biomass was dried to a constant weight at 55°C, and these data were used to develop a regression model correlating green pixels and NDVI to aboveground biomass. The best fit linear regression ($r^2 = 0.91$, $P < 0.001$) between sampled biomass and NDVI was

$$\text{Biomass}(\text{g} \cdot \text{m}^{-2}) = -830.4 + (1411.6 \cdot \text{NDVI}) \quad [1]$$

The data reported here are for maximum biomass at each site. The plots outside of the historical grazing exclosures were protected from grazing in 2003–2005 so they were not grazed during the period that productivity was being determined. As a result, I do not have a measure of compensatory regrowth that may be a factor under grazed conditions (McNaughton 1979). Because nearly all of the aboveground vegetation at these sites is herbaceous, maximum biomass is likely a good proxy for site-level productivity, although this method likely underestimates aboveground net primary production because of species-specific phenological patterns (Sala and Austin 2000).

Soil Collection and Characterization

To avoid pseudoreplication, a single value for each soil parameter is reported for inside and outside of each treatment block (grazed and ungrazed plots at a single site). Each value used in the statistical analysis is a mean of 4 soil samples per site within a grazing treatment that are each composites of 2 soil cores (5 cm in diameter × 15 cm). Soil composites were collected within 0.5 m of each other at 4 randomly located areas within the exclosure or outside areas. While there are differences in community composition inside and outside of grazing exclosures (Ellison 1954; Johnson 1964), within each grazing treatment there is relative homogeneity of vegetation so this sampling intensity is likely sufficient to approximate the true mean value for most soil parameters. With few exceptions, exclosures were constructed on level portions of the Plateau allowing cores at each site to be collected from similar topographic positions and aspect. When the exclosures were found on slopes, sites with similar aspect and slope were found as paired sites. Soils were refrigerated and shipped to Washington State University for analysis. Soil texture was determined using a hydrometer technique. Bulk density was determined using the core dry mass and the core volume. Dried samples were combusted using a Eurovector Elemental Analyzer to determine %C and %N. These soils were prewashed with 1 N H₂PO₄ to remove CaCO₃ prior to analysis for organic C, with mass loss due to acidification accounted for in reported values.

Soil C Composition

Coarse (> 250 μm) and fine (250–53 μm) particulate organic matter (POM) were assessed because several authors have shown that POM has kinetic characteristics similar to the

“intermediate” or “slow” pools in many simulation models, with a residence time of between a decade and a century (Cambardella and Elliot 1992; Kelly and Burke 1997; Gill et al. 1999). Furthermore, these fractions are important in determining soil structure and nutrient dynamics (Elliot et al. 1996). A number of approaches have been used to characterize POM, including both physical (Kelly and Burke 1997; Gill et al. 1999) and a combination of density and physical separations (Gale et al. 2000; Gill et al. 2002; Six et al. 2002) leading to potential confusion over the definition of POM. In this work I define POM as any organic material < 2 mm, but > 53 μm without further consideration of whether it was free or found within aggregates (Six et al. 2002). After sieving whole soils through a 2-mm sieve to remove root biomass, 30-g subsamples were dispersed with 0.5 M sodium hexametaphosphate for 18 hours. The resulting soil slurry was washed through 250 μm and 53 μm sieves, and the organic material remaining on each sieve was considered coarse (> 250 μm) and fine (250–53 μm) POM. There may be a small fraction of organic material that is not particulate that remains associated with sand minerals using these fractionation methods, but our approach is consistent with a number of previously reported methods of characterizing POM (Kelly and Burke 1997; Gill and Burke 1999; Six et al. 2000; Gill et al. 2002).

Active soil microbial biomass (SMB) was determined using a substrate-induced respiration (SIR) technique (Anderson and Domsch 1978). For each combination of site and grazing treatment, we analyzed 2 of the composite soils used above. The SIR method uses the response of SMB to a readily consumable substrate to indicate the size of the active SMB, but differs somewhat from the commonly used chloroform fumigation procedure in that it is a measure of active rather than total SMB (Bailey et al. 2002). Two soil cores (0–15 cm depth) were collected from grazed and ungrazed plots, sieved to remove roots and litter, and air dried. Fifty grams of each soil was rewetted to 50% field capacity and preincubated in a 946-ml canning jar at 22°C for 4 days before adding sucrose as a substrate. The jar was capped and CO₂ was allowed to accumulate in the headspace during a 30-minute interval. A 50 mL sample of the headspace air was sampled and atmospheric CO₂ concentration was determined using an infrared gas analyzer (Environmental Gas Monitor version 1; PP Systems, Haverhill, MA, USA). The jars were uncapped and the headspace was allowed to equilibrate with the atmosphere. A sucrose solution was added to each jar sufficient to provide 4 mg sucrose $\cdot\text{g}^{-1}$ soil and to bring the soils to field capacity. The soils were placed on an orbital shaker for 30 minutes. Respiration rates at 1, 2, 4, 12, and 24 hours were measured by capping the jars for 30 minutes and measuring the change in headspace atmospheric CO₂ concentration. The substrate-induced respiration was calculated as the difference between the initial and maximum respiration rates in $\mu\text{L CO}_2 \cdot \text{g soil}^{-1} \cdot \text{sec}^{-1}$. Microbial biomass was determined using the equation

$$\text{SMBC}(\mu\text{g} \cdot \text{g}^{-1}\text{soil}) = (40.04 \times \Delta\text{CO}_2) + 0.37 \quad [2]$$

(Bailey et al. 2002)

where ΔCO_2 is the change in respiration rates in units of $\mu\text{L CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ caused by the addition of the sucrose solution.

Laboratory incubations were conducted on two 100-g subsamples from each grazing treatment at each site using soils sieved to 2 mm and adjusted to 50% water holding capacity (Paul et al. 1999). Soils were placed in 946-ml canning jars and incubated at 25°C in the dark. Control jars contained 100 g of acid washed sand. At day 1, 3, 7, 14, 28, 56, 84, 112, 154, 175, 232, and 365, soils were uncapped and headspace air was allowed to equilibrate. The jars were then recapped and after 1 hour the concentration of CO₂ in the headspace was determined using an infrared gas analyzer (Environmental Gas Monitor). CO₂ fluxes were converted to $\mu\text{g CO}_2 \cdot \text{g-soil}^{-1} \cdot \text{h}^{-1}$. These 1-year incubations were used to determine soil pool sizes and turnover using a method modified from Paul et al. (1999). The analysis was based on a 2-pool model of soil organic matter (SOM) making a simplifying assumption that the resistant pool of SOM contributed little to C mineralization. With this simplification I used a 2-pool, first-order decomposition model that assumed that C mineralized came from an active pool and a slow pool of SOM using the equation

$$C_{\text{min}} = C_a e^{-k_a t} + C_s e^{-k_s t} \quad [3]$$

where C_{min} is the carbon mineralized, C_a and k_a are the size and decomposition rate constant of the rapidly mineralized pool and C_s and k_s are the size and decomposition rate constant for the slowly mineralized pool. These parameters were estimated using the regression analyst in SigmaPlot v. 8 (SPSS 2002). Mean residence time for each soil C fraction was determined as the reciprocal of the decomposition rate constant. Following Paul et al. (1999) we converted laboratory residence times to field residence times using a Q_{10} of 2. This is done as an acknowledgement that decomposition rates are much more rapid in the laboratory than in the field because of higher temperatures. The laboratory to field conversions provide an approximation for what field residence time may be provided that temperature is the primary control over active soil C decomposition rates.

***In Situ* Soil CO₂ Flux**

Soil CO₂ flux was measured at permanently installed collars using a continuous flow infrared gas analyzer (Environmental Gas Monitor) twice in 2003 (July 12–13 and July 28–29) and 3 times in 2004, (July 12–13, 19–20, and 28–29), and twice in 2005 (July 13–14, 21–22). Because of the large number of sites, measurements were taken once daily between 1 000 hours and 1 500 hours and reported values are means of 2 measurements for each treatment at every site. Soil temperature at 5-cm depth was taken at the time that the measurements were made and CO₂ flux values were standardized to 20°C assuming a Q_{10} value of 2 ($2^{(20-\text{Temp})/10}$) (Atkin et al. 2000). The soil collars were placed in plant interspaces.

Soil Water

Analyses of ecosystem water dynamics focused on soil water content at 4 sites. These sites were instrumented with data-loggers that continuously monitor soil moisture content in the upper 20 cm using Echo Probes (Decagon, Inc, Pullman, WA). Because of damage caused by pocket gophers continuous data are only available from the Bluebell Exclosure and the Philadelphia Flats Exclosure.

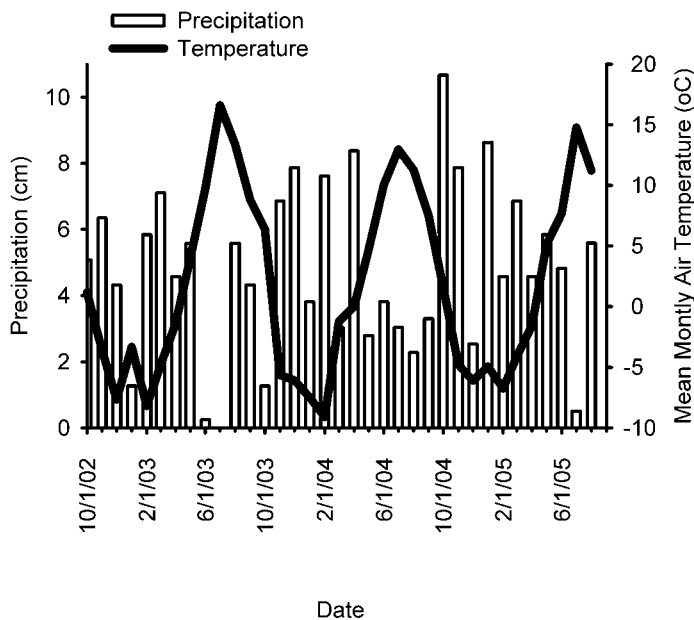


Figure 2. Monthly precipitation total (bars, cm) and mean monthly air temperature (line, °C) for the Upper Seeley Creek SNOTEL site administered by the Natural Resource Conservation Service for October 2002–August 2005.

Statistical Considerations

Paired *t*-tests were used to evaluate the effects of grazing on aboveground biomass, soil carbon pools and composition, and nutrient availability (*df* = 10). A stepwise regression procedure was used to assess the role of summer weather on aboveground biomass, where aboveground biomass was the dependent variable and July precipitation, July temperature, June–August precipitation, and mean June–August temperature were potential explanatory variables. Parameters had to be significant at $\alpha = 0.05$ to be included in the model. I used a mixed model analysis of variance to analyze the influences of grazing and physical characteristics on *in situ* soil respiration. The fixed effects in the model were *site*, *grazing* (grazed, ungrazed) and *year* (2003, 2004, 2005). This statistical approach incorporates a repeated-measure component, allowing for sequential sampling from a single plot over multiple years (McCulley et al. 2005). A stepwise linear regression was used to address the second objective of distinguishing the relative importance of physical environment versus grazing treatments on plant and soil processes (PROC REG). All statistical tests were performed with SAS (SAS Institute 2002). For all analyses, $\alpha = 0.05$ is used for statistical significance.

RESULTS

Data from the NRCS Snotel site at the Seeley Creek enclosure showed that the 3 years of this study demonstrate some of the idiosyncrasies of summer weather on the Wasatch Plateau (Fig. 2). The hottest and driest year was 2003 with an average June–August temperature of 13.2°C, and July air temperatures averaging 16.6°C, with no appreciable precipitation in July and a June–August total precipitation of 58 mm. The second year of the study (2004) was much cooler and wetter with

temperatures and precipitation in July totaling 12.9°C and 32 mm and June–August temperatures and precipitation of 11.4°C and 91 mm. In 2005, July was warm and dry, with precipitation totaling 5 mm and temperatures averaging 14.7°C, with a June–August precipitation of 109 mm and mean temperatures of 11.2°C.

There was substantial variation in soil physical properties and in vegetation among sites, likely due to differences in grazing history, topography, and microclimate (Table 1). Soil texture ranged from clay loam at the Alpine Cattle Pasture to sandy loam on Tom’s Ridge. There was no support for the hypothesis that grazing causes a loss of soil fines or an increased compaction because there was no significant influence of grazing on clay ($P < 0.65$) or bulk density ($P < 0.37$).

Long-term grazing significantly reduced aboveground biomass in all years compared with plots within grazing enclosures even though these plots were not grazed during the study period (Fig. 3, 2003, $P < 0.026$; 2004, $P < 0.017$; 2005, $P < 0.04$). Aboveground biomass was not significantly correlated with any of the measured landscape characteristics, including aspect, elevation, orientation relative to plateau divide, or soil texture. Forage production varied between sites, with maximum biomass ranging from 99–367 $\text{g}\cdot\text{m}^{-2}$ in 2003; 290–392 $\text{g}\cdot\text{m}^{-2}$ in the much cooler and wetter 2004; and 123–421 $\text{g}\cdot\text{m}^{-2}$ in 2005 (Table 1). For grazed plots, 51% of the interannual variability in aboveground biomass can be explained by July climate variables, with most of the variability being explained by precipitation ($P < 0.001$, $R^2 = 0.51$). Much less of the interannual variability in maximum biomass is explained by climate variables for ungrazed plots, with the only significant variable in the model being July precipitation ($P < 0.001$, $R^2 = 0.24$).

Grazing had no significant effect on bulk soil C (Fig. 4, $P < 0.14$), in part because the variability among sites was much greater than the variability within a site. Total C in the upper 15-cm of the soil profile was 5.5 $\text{kg}\cdot\text{m}^{-2}$ for soils from ungrazed plots and 4.9 $\text{kg}\cdot\text{m}^{-2}$ for grazed plots. Soil C varies substantially across the subalpine portion of the Wasatch Plateau (Table 1). A weak correlation exists between elevation and soil C ($R^2 = 0.26$, $P < 0.01$), with soil C tending to decline with increases in elevation across the 435-m elevation gradient from our lowest to highest sites. Tom’s Ridge is somewhat of an outlier and has the highest soil C of any of the sites. Tom’s Ridge lies on a terrace that was likely part of an intermittent fluvial swamp during the end of the last glaciation in this area and has anomalously low clay content compared to the other soils on the plateau (Prevedel et al. 2005).

Grazing had no significant influence on active soil microbial biomass C (SMBC, Table 1). Like soil C, there was a high degree of variation in SMBC across the plateau ranging from a minimum of 415 $\text{mg}\cdot\text{g}^{-1}$ soil at the grazed Danish Knoll site to 745 $\text{mg}\cdot\text{g}^{-1}$ soil at the Tom’s Ridge site. In spite of grazing not being a determinant of SMBC, it was possible to explain 77% of the variability in SMBC using soil parameters. Bulk density was the first parameter added to the regression model and was negatively correlated with SMBC, as was soil C/N, while SMBC was positively correlated with total soil C ($P < 0.001$, $R^2 = 0.77$).

Grazing was not a significant predictor of total particulate organic matter C (POM C, $P < 0.38$) and the proportion of C

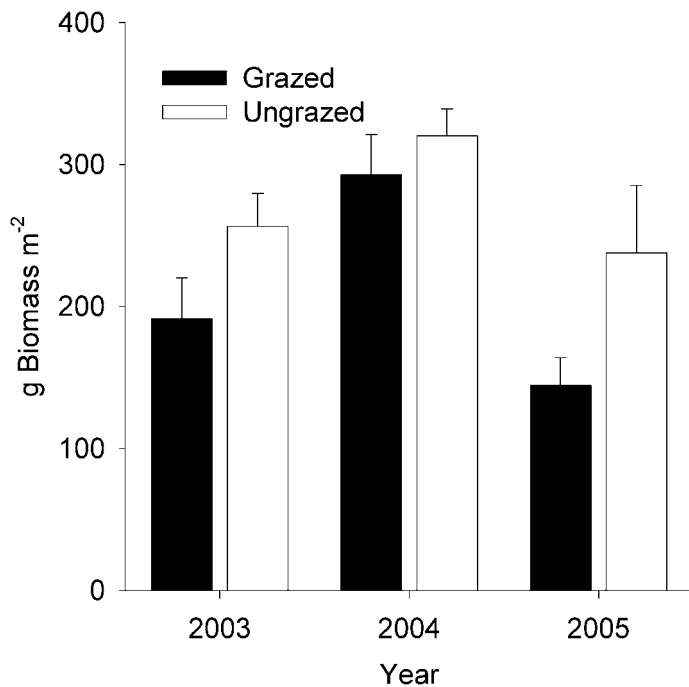


Figure 3. Maximum aboveground biomass for grazed (solid bars) and ungrazed (open bars) plots for 3 years. Bars are +1 standard error. In all years, maximum aboveground biomass was greater in ungrazed plots than in grazed plots.

in POM (% POM, $P < 0.65$) in the upper 15 cm of the soil profile (Fig. 4B, Table 1). Mean values for ungrazed plots were $1.83 \text{ kg POM C} \cdot \text{m}^{-2}$, which represents 30.9% of total soil C, while grazed plots had $1.63 \text{ kg POM C} \cdot \text{m}^{-2}$ which comprises 32.3% of total soil C. However, grazing significantly increased the proportion of total soil C that were potentially mineralizable ($P < 0.016$). For soils from grazed plots, 4.6% of total soil C was evolved in 1 year, while ungrazed plots lost 3.3%. The 2-pool, first-order decomposition model for soil C produced high regression coefficients and was consistently significant. Approximately 30% of the C mineralized in the lab was lost in the first week of the incubation, which after correcting for lab versus field temperatures, corresponds to a MRT of 20 to 30 days in the field (Fig. 5, Table 2). The proportion of C in this most active pool was not significantly affected by grazing, but the absolute amount was greater for grazed soils than ungrazed soils (Fig. 5, $P < 0.01$). Six of the 9 sites showed much higher C loss from grazed treatments than ungrazed treatments in laboratory incubations, with the other 3 sites showing no differences between sites. This contrasts strongly with the pattern that was observed in the field. Rates of *in situ* soil respiration were consistently higher under ungrazed conditions than in grazed areas (Fig. 6, $P > 0.001$). There were significant time and treatment effects ($P > 0.001$), with respiration lower in 2003 than in 2004–2005 corresponding to the much wetter winters and early summer of 2004 and 2005. Mean July respiration rates over the 3 years were $0.71 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ for ungrazed plots and $0.46 \text{ g CO}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ for grazed plots. The declines in soil respiration that were observed in July 2004 closely corresponded to seasonal declines in soil moisture.

Continuous monitoring of soil moisture at Bluebell and Philadelphia Flat demonstrated that during the 2003 growing

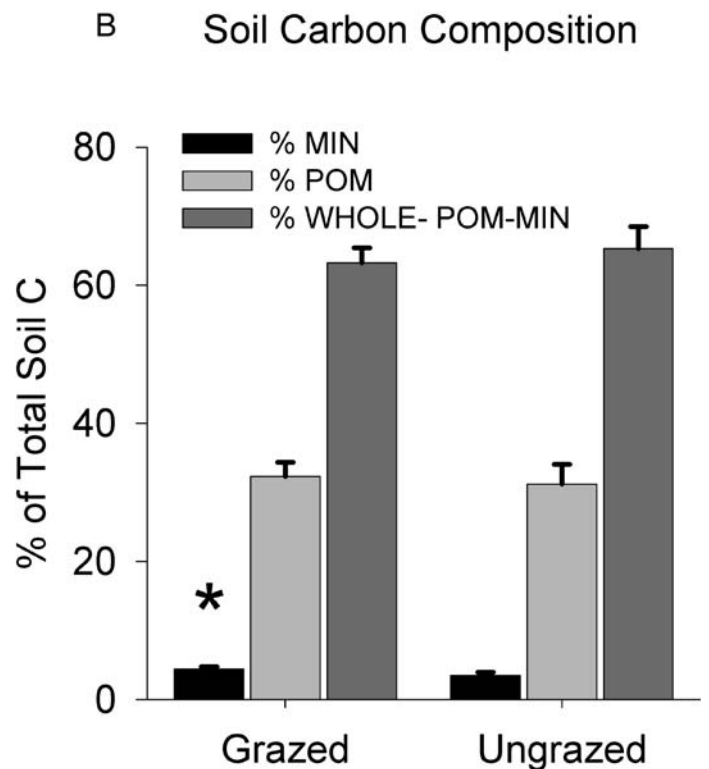
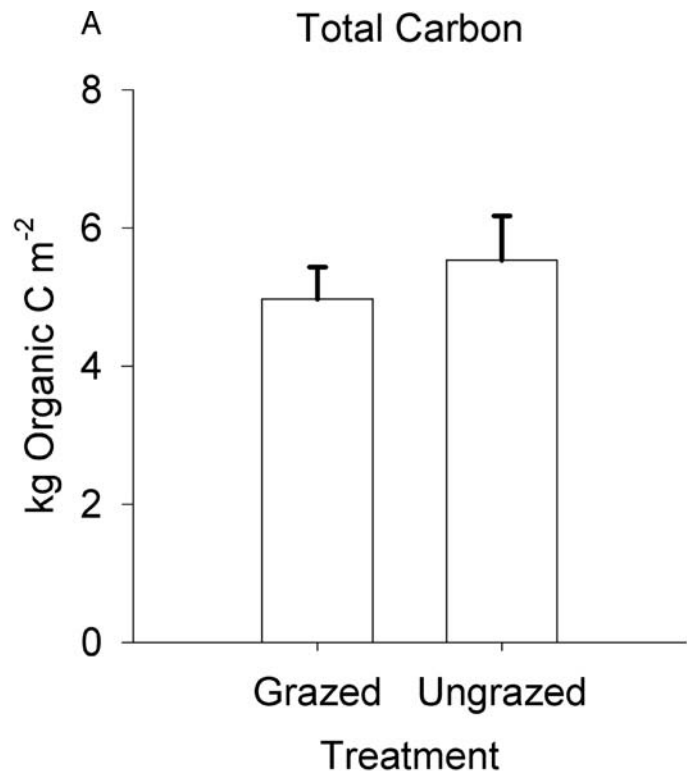


Figure 4. A. Mean (± 1 standard error) soil organic matter for grazed and ungrazed sites on the Wasatch Plateau. B. Relative contribution of mineralizable (open bars), particulate organic matter (light gray bars), and mineral associated C (dark gray bars). There was significantly more mineralizable C in grazed soils than in ungrazed soils.

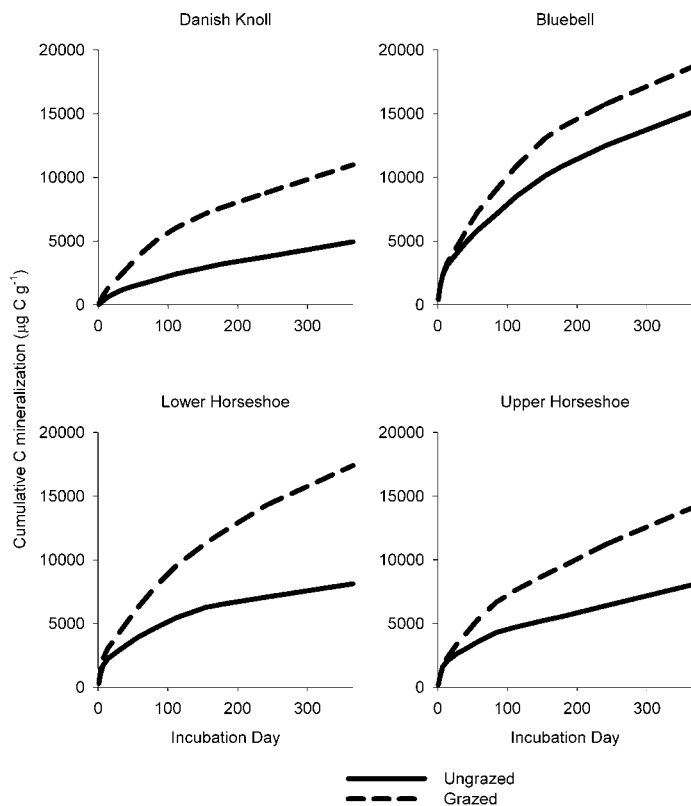


Figure 5. Cumulative C mineralized over 1-year laboratory incubations for the 0–15 cm soil layer from grazed (dashed lines) and ungrazed (solid lines) plots at 4 representative sites on the Wasatch Plateau. Descriptions of the sites are found in Table 1.

season there was higher volumetric soil moisture in ungrazed plots than in grazed plots (Fig. 7). At Bluebell (Fig. 7A), there was a sawtooth pattern of soil moisture with soil moisture increasing following storm events, but with recharge being greater in ungrazed plots than in grazed plots. In the drydown period following a storm event soil moisture declines to nearly the same values between grazing treatments. However, at the Philadelphia Flat site (Fig. 7B), soil moisture is continuously higher in ungrazed than in grazed plots, in spite of very similar aboveground biomass. While both grazed and ungrazed plots experienced declines in soil moisture between storms the ungrazed plots always maintained higher soil moisture contents than the grazed plots.

DISCUSSION

This study showed that the protection of sites from grazing did little to alter total soil C in these ecosystems, although it did change the nature of the soil C and rates of C input and losses. While there are a number of interrelated factors that could account for this, including grazing-mediated alterations in water infiltration rates (Kelly 2006), evaporation rates, and nutrient dynamics (Frank and Evans 1997), I concur with Ellison (1954) who thought that the primary grazing influence was realized through altered soil moisture. The data presented here are consistent with grazing decreasing both C inputs and soil moisture. I hypothesize that the reduced soil moisture is

Table 2. Carbon mineralization and pool sizes for 1-year laboratory incubations.

Treatment	Total C ($\mu\text{g}\cdot\text{g}^{-1}$ soil)	Active C		Slow C			
		%	MRT (Lab) days	%	MRT (Field)		
Grazed	14 810	31.3	7.1	30.4	68.7	293	3.4 years
Ungrazed	11 330	34.2	4.6	19.7	65.8	308	3.6 years

sufficient to decrease rates of decomposition, which leads to an accumulation of active SOM, offsetting the decreases in C inputs in grazed plots.

Over the 3 years of this study, areas protected from grazing had significantly higher maximum aboveground biomass than areas that have been continuously grazed by domestic herbivores for > 130 years. The pattern observed on the Wasatch Plateau is consistent with Milchunas and Lauenroth (1993) where grazing decreased net primary production in most systems with a long-term treatment history that lack a long evolutionary history of grazing.

Given the consistently higher aboveground biomass in ungrazed plots than in grazed plots I hypothesized that if soil C storage is input controlled protection from grazing would increase soil C. Likewise, Parton et al. (1987) used the CENTURY soil organic matter model to predict decreasing soil C levels with grazing. In contrast to these predictions, there was no significant change in bulk soil C due to grazing on the Wasatch Plateau. There are a number of alternative explanations for the absence of a grazing-driven change in soil C with substantial and significant differences in litter inputs. The first explanation involves potential changes in C partitioning within primary producers, either due to physiological changes or plant community shifts. A number of previous studies have shown differences in plant community composition between continuously grazed plots and plots found within grazing exclosures on the Wasatch Plateau (Ellison 1949, 1954; Johnson 1964; Schuman et al. (1999) found that 12 years of grazing in the mixed grass prairie increased soil C in the upper 30 cm of the soil profile, likely due to a shift in plant community composition and the allocation of C belowground by plants. Frank et al. (1995) suggested that species-specific allocation patterns can substantially alter soil C. For example, grazing-induced increases of *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths in the mixed grass prairie increases the net allocation of C belowground and increased C inputs to soil organic matter. Root biomass was not significantly different between grazing treatments on the Wasatch Plateau, although this does not eliminate the possibility that there might be differences in belowground primary production that might compensate for the observed differences in aboveground biomass.

An alternative to the input-control model of soil C is one where the influence of grazing is seen in the control over soil C decomposition dynamics. With an output control model, grazing alters soil physical properties and microenvironment in a way that reduces decomposition rates compared to ungrazed sites. Abundant evidence from soil C composition and dynamics data suggest that on the Wasatch Plateau the most significant influence of grazing on soil C is through

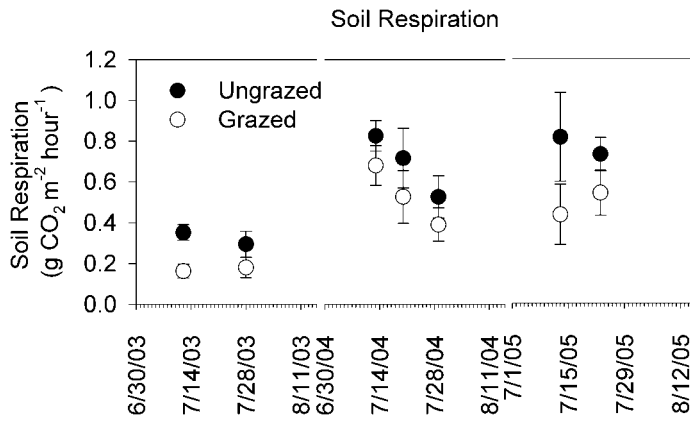


Figure 6. Mean (± 1 standard error) soil respiration rates for grazed (solid circles) and ungrazed (open circles) for sampling dates in July 2003, 2004, and 2005. Repeated measures ANOVA showed that year and grazing treatment were both significant effects ($P < 0.001$).

decreasing decomposition rates. The evidence for a grazing-driven change in microenvironment comes from the markedly different response of C mineralization in the field compared to potential C mineralization measured in lab conditions. As Welker et al. (2004) found, grazing alters CO₂ exchange, and in the case of the Wasatch Plateau there is a significantly lower soil CO₂ flux from grazed plots than ungrazed plots. However, when soils from those same plots are brought into the lab and incubated for 1 year at field capacity and 25°C, grazed soils evolved significantly more CO₂ than ungrazed soils—in many cases double the amount of C. Frank and Groffman (1998) also report an increase in potentially mineralizable C with grazing, although in their study the significant influence of grazing on respiration was lost by the 10th week of the incubation.

The second objective for this study was to evaluate the relative importance of mesoscale landscape differences relative to grazing on soil C content and dynamics. Soil C was only slightly modified by grazing treatments whereas there was a threefold difference in bulk soil C depending on site location. Clearly the processes that affect ecosystem C dynamics are more tightly controlled by the substantial variability in climate that occurs over small spatial scales on the Wasatch Plateau. This is particularly evident in bulk soil C where the lower elevation sites (< 2 950 m) have much greater soil C than high elevation sites where growing season duration is shorter and precipitation is greater.

My third objective in this study was to determine whether there was evidence to support the hypothesis advanced by Ellison (1954) on the effects of grazing on soil moisture. In Yellowstone National Park, Frank and Groffman (1998) found that grazing by native ungulates consistently decreased soil moisture. Grazing by native ungulates lowered soil moisture in a pattern similar to the one that was observed on the Wasatch Plateau (Fig. 7). Both the data presented here and the Frank and Groffman (1998) data are fully consistent with Ellison's (1954) contention that grazing on the Wasatch Plateau increased drier microenvironments and is likely as important as selective grazing or trampling in explaining shifts in plant community composition following overgrazing. It may be that the decreases in soil moisture are responsible for lower aboveground biomass

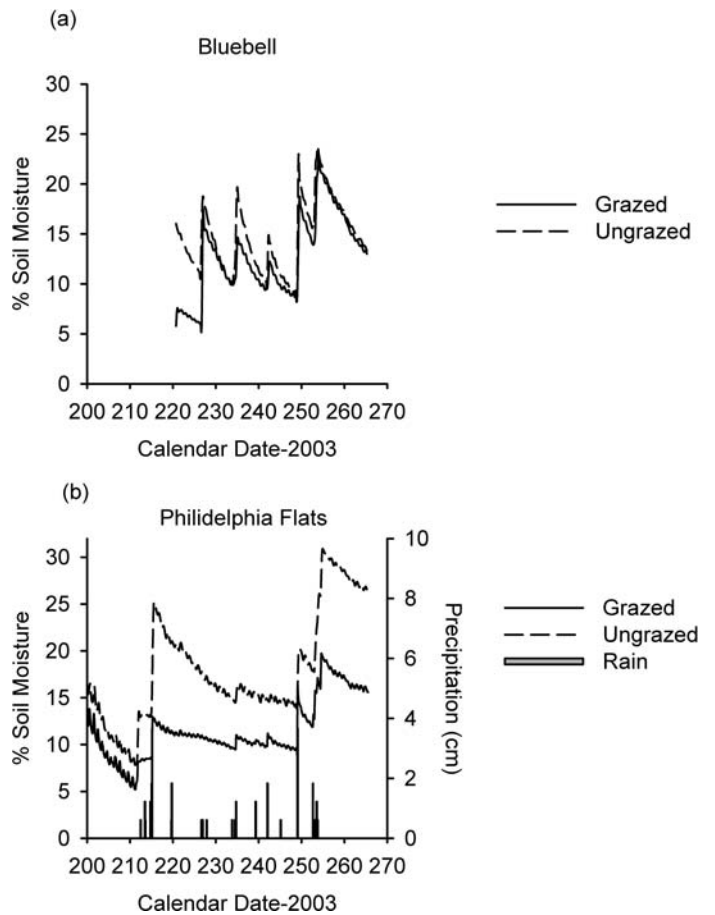


Figure 7. Percent soil water content for (a) Bluebell and (b) Philadelphia Flats sites. Measurements made within the exclosures (ungrazed—dashed line) were consistently greater than in the long-term grazed plots (grazed—solid line).

in grazed plots compared to ungrazed areas, particularly since aboveground biomass in the grazed plots was closely correlated with midsummer precipitation. The mechanism controlling this change in soil moisture is unclear, although Coughenour (1991) and Frank and Groffman (1998) both suggest that grazing might reduce the accumulation of litter and standing dead which might increase evaporation rates from the soil surface.

My findings that grazing increases the size of the potentially mineralizable C pool in subalpine rangelands has implications for regional C responses to forecast climate change (Conant et al. 2003; Wagner 2003; Welker et al. 2004). Climate change is anticipated to 1) increase temperatures, particularly in high-elevation ecosystems, with a lengthening of the growing season; and 2) alter the seasonality, frequency, and amount of precipitation (Houghton et al. 2001; Karl and Trenberth 2003; Wagner 2003). If, as is suggested by the observed grazing-driven differences in soil moisture in this study, the primary physical change caused by grazing involves a decrease in soil moisture, alterations in the timing and amount of precipitation could change the C source-sink relationships in these subalpine systems. Increases in the frequency or total amount of precipitation could offset grazing-caused soil moisture deficits and promote the decomposition of rapidly cycling soil C in grazed systems. There was evidence for this in how *in situ* soil

respiration changed from the very dry 2003 and the wet 2004. Soil respiration increased by a factor of 3 between these years for grazed soils while ungrazed soils only increased by a factor of 2. Welker et al. (2004) clearly show that subalpine rangelands are delicately balanced between being sources and sinks and grazing is one element that can influence whether soils can sequester or release CO₂. As Falkowski et al. (2000) suggest, land use history is tightly linked with C cycle processes and land use may be as important as climate change in controlling C source-sink relationships in high altitude ecosystems (Welker et al. 2004).

To assess whether Ellison (1954) was correct in concluding that soil moisture was the dominant control over grazing responses in this system we can evaluate the relative effects of grazing on both soil moisture and soil organic matter dynamics. Using the ratio of soil organic matter pool size to aboveground biomass as a crude estimate of turnover time, I can assess whether the grazing-induced changes in soil moisture are similar in magnitude to grazing driven changes in organic matter turnover. I found that during the growing season of 2003 (July 1 to September 30), there is a 7%–30% decrease in volumetric soil moisture on grazed relative to ungrazed plots (Fig. 7A and 7B). This is similar in magnitude to the responsiveness of POM turnover (POM C/aboveground biomass decreased by 29% due to grazing) or total organic C turnover (Total SOC/aboveground biomass decreased by 18% due to grazing) (Table 1). These ratios are not a complete estimate of turnover of these SOM pools since there is not an accounting of belowground NPP, but it is indicative of relative turnover rates. Grazing appears to cause approximately a 20%–30% decrease in turnover rates, which correlates reasonably well with the 7%–30% decrease in soil moisture.

IMPLICATIONS

Ninety years of recovery following overgrazing was sufficient time to produce differences in aboveground biomass. The data suggest that both productivity and patterns of soil C decomposition are strongly influenced by the grazing-induced differences in soil water availability. Grazing shifts the interaction between aboveground biomass production and decomposition dynamics. Aboveground biomass was tightly correlated with July precipitation, particularly in grazed plots, showing that grazed plots have greater sensitivity than ungrazed plots to moisture deficits. However, decomposition also appears to be sensitive to grazing-induced changes in soil moisture since soils brought into the lab and incubated at field capacity, and samples from grazed plots consistently mineralized more soil C than samples from ungrazed plots. The net result is that there are no changes in total soil organic matter content in the upper 15 cm of the soil profile, but there are grazing-controlled changes in soil organic matter composition.

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