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Carbon storage in low-alpine grassland soils: effects of different grazing intensities of sheep

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Summary

Grazing in outlying fields has a long history and is important in local communities worldwide. During the last few decades, grazing pressure has both decreased and increased in alpine ecosystems, but little is known about the effects on soil carbon storage. As part of a sheep grazing experiment with three sheep stocking rates of no sheep (control), 25 and 80 sheep km^{-2}, we tested effects of grazing on soil organic carbon storage, the form of soil organic matter (SOM) and its lability (potential carbon mineralization) in organic horizons of low-alpine grasslands in southern Norway. After 7 years of grazing, the greatest sheep density reduced soil organic carbon concentration (% SOC) and carbon stocks at equivalent soil mass as compared with the control. In contrast, the low stocking rate caused no change or a slight increase. The form of SOM, expressed as ratios of particulate organic carbon to soil organic carbon, was only slightly affected by grazing, with a small decrease and moderate increase at the greater and smaller stocking rate, respectively. The lability of SOM was not affected by grazing directly, but was significantly related to the mineral content of the O-horizons. In general, there were large differences between the plant communities of snowbed and willow-shrub for several soil attributes. We concluded that 7 years of grazing had limited impacts on stocks, form and lability of SOM.

Introduction

Land use may be an important factor mitigating climate change, as it may have an impact on soil organic matter (SOM) storage (Schils *et al*., 2008). Organic matter is a crucial fraction of soil affecting attributes and processes known to influence ecosystem functioning and productivity. The amount of organic matter stored in soils is controlled by natural site-specific factors such as parent material, climate, topography, land cover and human-induced factors associated with land use (Schils *et al*., 2008; Piñeiro *et al*., 2010). All these factors may indirectly affect SOM through changes in soil temperature, moisture and acidity (Darmody *et al*., 2004) for example, or cause changes in primary production and decomposition that directly affect SOM (Piñeiro *et al*., 2010). Differences in site-specific factors result in a large variability in SOM quantity and quality and may be pronounced even at small spatial scales (Ostler *et al*., 1982; Stanton *et al*., 1994; Burke *et al*., 1999; Hiller *et al*., 2005).

Grazing may have severe impacts on ecosystem functioning (Wardle *et al*., 2004), thereby potentially modifying soil organic carbon (SOC) storage (Piñeiro *et al*., 2010). According to Piñeiro *et al*. (2010), grazing may alter the content of SOC by influencing (i) the fraction of net primary production (NPP) entering the soil (the net primary production pathway), (ii) soil nitrogen (N) storage (the N pathway) and (iii) the decomposition of soil organic matter (the decomposition pathway) (Piñeiro *et al*., 2010). Grazing has been reported to increase (Manley *et al*., 1995; Leifeld & Fuhrer, 2009), decrease (Steffens *et al*., 2008; He *et al*., 2009) or have little or no effect (Tracy & Frank, 1998) on SOC. A large grazing pressure may decrease the input of above and below-ground (root) biomass (Johnson & Matchett, 2001), thereby reducing the storage of soil carbon (He *et al*., 2008).

Grazing also may affect the form of SOC, including the particulate organic material (POM) fraction. POM, representing uncomplexed organic matter that is neither recognizable as litter nor incorporated into organomineral complexes (Christensen, 2001), consists mainly of root fragments and above-ground plant residues (Golchin *et al*., 1994). As reported by Leifeld *et al*. (2009), this fraction is relatively young, with a mean residence time in the order of years to decades. Leifeld & Fuhrer (2009) found an increased ratio of particulate organic carbon (POC) to SOC in topsoils of a frequently grazed pasture compared with a meadow grazed for short periods in the Swiss Alps.

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It was suggested that this resulted from the incorporation of plant materials by treading (Leifeld & Fuhrer, 2009). In contrast, Steffens *et al*. (2009) observed a larger contribution of free POM C (POC) to the total SOC within grazing exclosures caused by enhanced litter inputs. POM is a potential source of readily available C for decomposers (Christensen, 2001) and is more mineralizable than heavy SOM fractions (Whalen *et al*., 2000). Thus, changes in the POC to SOC ratio resulting from grazing may potentially affect the lability of SOM.

Low-intensity livestock farming produces about half of the world's food (Herrero *et al*., 2010). Norway consists mostly of outlying fields, with a long history of grazing (Austrheim *et al*., 2008a). During the last few decades, sheep densities have both decreased and increased in alpine ranges (Austrheim *et al*., 2011), but little is known about the effects on SOC storage. Here we test effects of different grazing intensities of sheep on SOC storage, form (POC to SOC ratio) and lability in organic horizons of low-alpine grassland soils. The study was carried out as part of a sheep grazing experiment with three stocking rates of sheep (Mysterud & Austrheim, 2005). Previous findings from this grazing experiment indicate a reduction in lamb weight (A. Mysterud, unpublished material) and a smaller vascular plant biomass production (G. Austrheim, unpublished material) with increased grazing pressure. Both factors indicate an overall greater biomass removal at high stocking rate compared with that at a smaller rate and the control. We hypothesized that increasing densities of sheep (i) decreases soil C storage as compared with non-grazed sites and (ii) decreases the ratio of POC to SOC, which is associated with a decline in lability of SOM and reduced potential for carbon mineralization.

Material and methods

Site description

The study site is located in the low alpine region (1050–1320 m above sea level: see Moen, 1999) in the Hol municipality, Buskerud County, southern Norway (7°55′–8°00′E, 60°40′–60°45′N) (Mysterud & Austrheim, 2005). Vegetation is dominated by dwarf shrub heaths with smaller patches of lichen heaths, snow beds and alpine meadow communities in leesides (Rekdal, 2001). The bedrock consists of meta-arkose and quaternary deposits of till and colluvium (Kristiansen & Sollid, 1985; Sigmond, 1998). Soils vary spatially, from peaty deposits in poorly drained pockets to freely drained soils with shallow (restricted by bedrock) and acidic organic horizons. The soils are leptic podsols (snowbeds) and dystric haplic gleysols (willow-shrubs) (IUSS Working Group WRB, 2007). In willow-shrub areas, some soils may be classified as dystric haplic cambisols, depending on topographical position and thus moisture content. Mean annual temperature (MAT) is −1.5°C and the mean annual precipitation (MAP) is about 1000 mm (Evju *et al*., 2009), approximately 75% of which falls as snow.

In 2001 a large enclosure (2.7 km^2) was fenced and divided into three blocks, each replicated with three sub-enclosures (each of approximately 0.3 km^2) with three treatments: no sheep (control), and low-density (25 sheep km^{-2}) and high-density (80 sheep km^{-2}) stocking rates of domestic sheep (*Ovis aries* L.) (Mysterud & Austrheim, 2005; Mysterud *et al*., 2005). The study was set up as a randomized block design (Figure 1) with sheep grazing from the end of June to the beginning of September (since 2002).

Twenty plots (0.5 × 0.5 m) were established in each sub-enclosure (a total of 180 plots) in 2001 using a balanced stratified procedure among altitudinal levels and habitats (Austrheim *et al*., 2005). The 180 plots were allocated between grasslands (graminoid-dominated snowbeds (30%) and grassland with a varying cover of willows (21%)) and heathland of dwarf-shrub heath with *Vaccinium* spp. (29%) and ridge vegetation with lichens (20%) (Austrheim *et al*., 2008b). Soil was sampled (summer 2008) at 89 of these plots within the two different grassland plant communities: snowbed ($n = 56$) and willow-shrub ($n = 33$) (Figure 1). The study focused on graminoid-dominated snowbeds and grasslands with a varying cover of willows, caused by preferential grazing in these habitats (Mobæk *et al*., 2009). Willow-shrubs are associated with leeside vegetation, with less snow cover and a longer growing season than snowbeds (Moen, 1999). Further description of experimental design, selection of vegetation plots and plant species composition is given by Austrheim *et al*. (2005).

Soil samples

Soil was sampled with a cylindrical corer of diameter 5.2 cm to a maximum depth of 5 cm within the O-horizon during the period 5–8 August 2008. Four soil samples were taken adjacent to the vegetation plots (one at each of the four sides). To obtain enough soil material for analysis, more than four samples were taken if the O-horizon was <5 cm. The vegetation was cut at the soil surface and the litter (O_i) was removed. Soil samples at each plot were bulked and stored in the dark and at <4°C prior to analysis. The (field moist) soil samples were homogenized and divided into two subsamples, one for chemical analysis (air-dried at 40°C for 4–5 days) and one for determination of potential C mineralization (kept cold and moist). The air-dried samples were sieved (2 mm) and the mass of dry roots and gravels (>2 mm) determined. Subsamples of the air-dried and sieved samples were dried at 60°C to determine dry matter (DM) content and then milled prior to determination of total C and N.

Total C and N were determined by dry combustion (Leco CHN-1000; Leco Corporation, Sollentuna, Sweden) (Nelson & Sommers, 1982) and the Dumas method (Bremmer & Mulvaney, 1982), respectively. The dry matter mass (corrected for amount of roots and gravel) was used to determine bulk density (BD; g cm^{-3}) of the fine earth fraction. pH was determined electrometrically (Orion, model 720, Orion Research Inc., Cambridge, MA, USA) in a soil solution with distilled water (volume soil:volume water ratio of 0.4) (Krogstad, 1992). Soil samples (air-dried and sieved at 2 mm) were extracted with 1 M ammonium acetate (adjusted to pH 7) and base cation concentrations determined

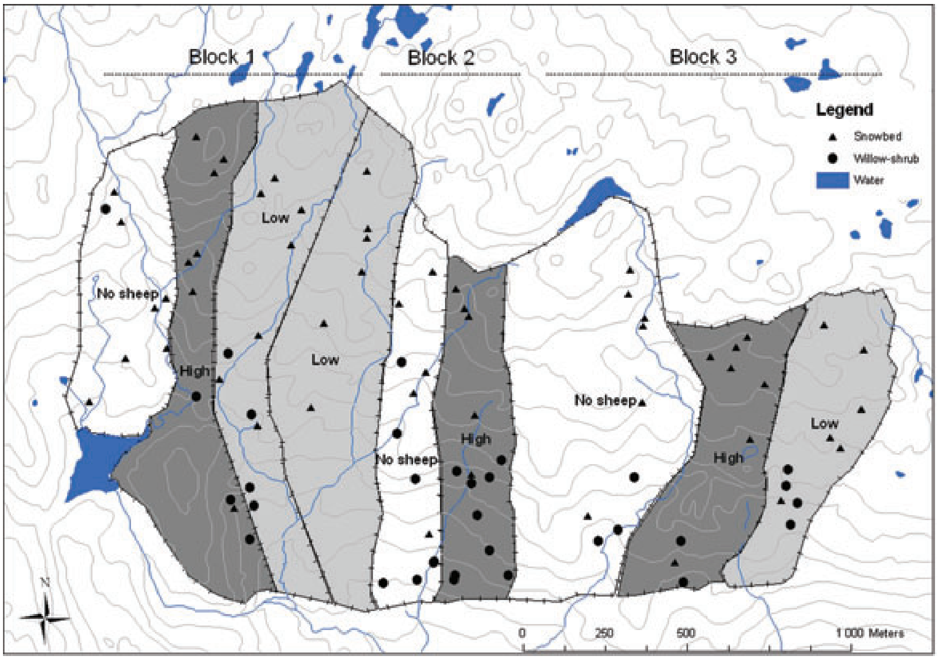

Figure 1 Experimental design (three enclosures with different grazing pressure of sheep in three blocks), Hol, southern Norway. The area of each enclosure is about 0.3 km^{-2}, total area is about 2.7 km^{-2}. White enclosures = no sheep (control), light grey enclosures = low (25 sheep km^{-2}) and dark grey enclosures = high (80 sheep km^{-2}) sheep density. Points represent locations (n = 89) for soil sampling within grassland habitats in two plant communities: snowbed (triangles) and willow-shrub (circles).

in the extracts. Extractable acidity was determined by back-titration with sodium hydroxide to pH 7. The sum of exchangeable base cations and acidity was used to determine cation exchange capacity (CEC) according to Schollenberger & Simon (1945). Exchangeable cation concentrations were determined using ICP-OES (Optima 5300 DV, PerkinElmer Inc., Shelton, CT, USA).

Carbon and nitrogen stock calculations

Volume-based C and N stocks were calculated as:

$$\text{E-stock} = \text{BD (g cm}^{-3}\text{)} \times \text{Depth (cm)} \times \text{E concentration (\%)} \times 0.1, \quad (1)$$

where E-stock is the volume-based elemental stock (density) (kg m^{-2}), BD is bulk density of the fine earth, Depth is the soil depth and E concentration is the elemental concentration of C or N (% by mass).

As grazing and habitat may affect bulk density and depth of the organic horizon, these also may affect elemental stock calculations. Therefore, C and N stocks were also calculated per equivalent soil mass (Ellert & Bettany, 1995):

$$\text{C-stock (eqv. mass)} = \text{Equivalent mass (kg m}^{-2}\text{)} \times \text{C concentration (\%)} \times 10^{-2}, \quad (2)$$

where C-stock eqv. mass is the carbon stock (kg m^{-2}) per equivalent mass of soil.

Density fractionation

Particle size and density fractionation were carried out by a modified method based on Leifeld & Kögel-Knabner (2005) to obtain a free, light (density < 1.8 g cm^{-3}) POM fraction of 20–2000 µm. The samples were not dispersed ultrasonically to retrieve occluded or mineral-associated light fractions. As the free light POM fraction consists of less fragmented plant detritus than occluded POM (Golchin *et al*., 1994) because of the greater mean age of the latter (John *et al*., 2005), it was assumed that effects of grazing within the time frame of our study would most probably be detectable in the free light fraction. The remaining mineral-associated organic material fraction (mOM; of 20 µm and including the occluded fraction to 2000 µm and density > 1.8 g cm^{-3}) was used to calculate percentage recovery, but not further analysed. Ten grams of air-dried and sieved (2 mm) soil was weighed into a 100-cm^3 centrifuge tube. Seventy millilitres of sodium polytungstate, $Na_6(H_2W_{12}O_{40}) \times H_2O$ (Sometu, Berlin, Germany), adjusted to a density of 1.8 g cm^{-3}, was added to the tube and gently turned upside down by hand five times over approximately 10 s. The suspension was left for 10 minutes prior to 10 minutes of centrifugation at 1.5 $\boldsymbol{g}$.

The supernatant with floating particles was poured onto a 20-µm sieve and washed with distilled water (until conductivity was less than 100 µS cm^{-1}; all material <20 µm was discarded) to retrieve the POM fraction. The remaining suspension in the tube was gently stirred (as above) and the steps repeated (with addition of sodium polytungstate) once to retrieve the mOM as sedimentary material with density >1.8 g cm^{-3} in the centrifuge tubes. The POM and mOM fractions were dried (60°C) to determine recovery rate (approximately 95%) and to calculate percentage POM in the samples (w:w). The samples were milled prior to determination of total C and total N. In some cases with a large percentage POM, the calculated ratio of POC:SOC resulted in values >1. As the ratio of POC to SOC cannot be >100%, these values were set to 1. Samples of POM were combusted at 550°C to determine loss on ignition (LOI), and the ash content of the POM fraction.

Potential carbon mineralization

Closed flasks (12 cm^3) with field moist soil (equivalent to 1 g of dry soil) from each sample location (n = 89) were incubated in the dark (15°C; aerated every second day to prevent anoxia) and, after increasing incubation times (11 hours, 4, 8, 15, 20 and 27 days, respectively), placed in a robotized incubation system (Molstad *et al*., 2007) at 15°C to measure CO_2 concentration in head space, using gas chromatography (GL system 7890A, Agilent Technologies, Santa Clara, CA, USA). At each of the six incubation times, the rate of gaseous release was calculated as the difference in headspace CO_2 concentration between the start and the end (approximately 11 hours) of a measuring period. When measuring the rate of CO_2 production, a proportion of the air was removed and transferred to the gas chromatograph from the headspace, thus causing dilution. Dilution of CO_2-C was accounted, and corrected, for by using the difference in headspace N_2 concentration at the start and the end of a measuring period relative to that of the start concentration. Measured CO_2-C concentrations by volume were converted to molar assuming a molar gas volume at 15°C of 23.64 l mol^{-1}. Because there was some uncertainty in the headspace volume and dilution of the individual observations (see footnote, Table S3), we used the average CO_2-C of the six incubation times when testing treatment and plant community effects on CO_2-C production rates. In this way, temporal pseudo-replication of repeated measurements on the same soil sample was also avoided.

Statistical analysis

Statistical analyses were conducted using the libraries lme4, multcomp, ltm and gplots in the statistical package R (version 2.10.1) (R Development Core Team, 2009). We used linear mixed effects models (lmer) with random effects reflecting the block-wise randomization design of enclosure (n = 9) nested within block (n = 3). The categorical explanatory variables (fixed effects) included grazing treatment (three rates: no sheep, high- and low-sheep densities), plant community (snowbed and willow-shrub) and two-way interactions between grazing treatment and plant community. Bulk density and ash content of POM were included as quantitative explanatory variables to account for differences associated with treatment and plant community. We assumed no treatment or plant community-specific differences in the response of the covariates with no difference in slopes. Some variables were transformed (ln or arcsine) prior to analysis to avoid violations of the model assumptions.

Backward selection was used with models fitted by maximum likelihood (ML) and models compared based on AIC ('smaller is better') and likelihood ratio tests (chi-squared) to obtain the minimum adequate model (Table S1). The best model was refitted on the basis of restricted maximum likelihood (REML) and the estimated effects (including standard error) were calculated using general linear hypothesis testing (glht in multcomp; Tables S2 and S3). Means and standard errors are listed in Table 1 and plotted in Figure 2 (Webster, 2007). As pseudo-replication may pose a problem, significant differences between plant communities were also analysed by using means for each community within sub-enclosures (Tables S4 and S5, Figure S2). Residuals and predicted random effects were plotted (histograms and QQ normal plots) to assess normality and potential outliers.

Predictions of different treatment combinations for given extents of the quantitative explanatory variables of BD or ash content of POM were calculated with General Linear hypotheses (glht) in multcomp and reported with standard error (Tables S2 and S3). Multiple correlations between selected soil parameters (including P-values) were calculated with Spearman rank correlation because not all the variables were normally distributed. These are presented in the supporting information (Figure S1). Six soil plots, one from the control snowbed (% SOC = 11.6), three from the control willow-shrub (% SOC = 8.7, 45.8 and 50.8), one from low-density sheep snowbed (% SOC = 11.5) and one from the high-density sheep snowbed (% SOC = 10.4) differed greatly in O-horizon soil attributes compared with the other 83 grassland habitat plots: these plots were excluded from the analysis.

Results

Differences in soil characteristics between the plant communities

An overview of selected soil chemical and physical data (means ± SE) is given in Table 1. The mean altitude for the sampling plots in willow-shrubs was lower than that for snowbeds. Willow-shrubs were associated with deeper O-horizons, smaller bulk densities (BDs) and larger base saturations than snowbeds. The organic C concentration in the O-horizon bulk soil (% SOC) differed only slightly between the plant communities. However, C stock per cm soil depth (per unit volume of soil) was larger in snowbeds (0.70 kg m^{-2}) than in willow-shrubs (0.53 kg m^{-2}), because of the greater bulk density in snowbeds (Table 1). The form of organic material (expressed as fraction of particulate organic C to the total amount of bulk soil organic C; POC to SOC ratio) and the percentage POM in the bulk soil, were similar between the plant communities. However, C:N ratios of the bulk

Table 1 Mean O-horizon soil attributes from 83[a] grassland habitats (sampled 2008) within two plant communities (snowbed and willow-shrub) at different grazing densities of sheep (high = 80 sheep km^{-2}, low = 25 sheep km^{-2} and no sheep = control), Hol, Norway

	Snowbed						All treatments		Willow-shrub						All treatments	
	High		Low		No sheep				High		Low		No sheep			
Factor	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Altitude / m.a.s.l.	1248.0	13.0	1251.0	10	1216.0	12.0	1239.0	7.0	1141.0	7.0	1170.0	10.0	1162.0	22.0	1154.0	7.0
Slope / %	14.4	2.1	11.1	1.6	14.4	2.2	13.3	1.1	15.4	1.6	16.9	3.8	13.8	3.1	15.3	1.5
Total O-horizon depth / cm	3.8	0.6	5.3	1.1	4.1	0.6	4.4	0.5	6.8	1.1	6.1	1.8	7.8	1.8	6.9	0.8
Sample depth / cm	2.7	0.3	3.2	0.3	3.3	0.3	3.1	0.2	4.0	0.3	3.4	0.5	3.7	0.5	3.8	0.2
BD / g cm^{-3}	0.35	0.01	0.26	0.01	0.28	0.02	0.30	0.01	0.27	0.03	0.20	0.02	0.23	0.03	0.24	0.02
CEC / $cmol_c$ kg^{-1} soil	40.7	2.1	47.7	2.3	45.8	2.6	44.8	1.4	45.6	3.8	50.6	12.5	43.2	5.3	45.7	3.0
Base saturation / %	33.3	4.0	26.3	5.1	22.9	3.0	27.5	2.4	43.4	3.6	43.9	14.5	37.2	5.2	41.9	3.0
pH	4.6	0.1	4.6	0.1	4.4	0.1	4.5	0.1	4.9	0.1	4.6	0.3	4.8	0.1	4.8	0.1
SOC / % of fine earth	22.0	1.1	25.8	1.3	25.6	1.4	24.4	0.8	20.9	1.7	29.3	2.7	25.1	2.5	24.3	1.4
SON / % of fine earth	1.4	0.1	1.5	0.1	1.4	0.1	1.4	0.0	1.2	0.1	1.4	0.2	1.4	0.2	1.3	0.1
C:N ratio bulk soil	16.1	0.3	17.7	0.5	18.0	0.7	17.3	0.3	17.7	0.6	20.7	1.4	18.5	1.0	18.7	0.6
C stock per cm / kg m^{-2}	0.75	0.02	0.65	0.03	0.69	0.03	0.70	0.02	0.51	0.02	0.56	0.03	0.54	0.04	0.53	0.02
N stock per cm / kg m^{-2}	0.05	0.00	0.04	0.00	0.04	0.00	0.04	0.00	0.03	0.00	0.03	0.00	0.03	0.00	0.03	0.00
POM / % of bulk soil	59.6	3.0	73.0	3.0	67.4	3.7	66.6	2.0	60.1	5.0	73.8	4.2	66.8	6.4	65.6	3.2
POC / % C of POM	28.1	0.7	30.6	0.9	31.6	0.9	30.1	0.5	27.1	1.0	31.4	1.9	29.4	1.5	28.9	0.8
PON / % N of POM	1.7	0.0	1.8	0.1	1.8	0.1	1.8	0.0	1.5	0.1	1.7	0.1	1.6	0.1	1.6	0.1
C:N ratio POM	16.2	0.4	16.8	0.6	18.2	0.6	17.1	0.3	17.9	0.7	19.4	1.3	18.3	1.1	18.4	0.5
POC to SOC ratio	0.8	0.0	0.9	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.8	0.0
PON to SON ratio	0.8	0.0	0.9	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.9	0.0	0.8	0.0	0.8	0.0
Ash content POM / %	45.2	1.4	40.7	1.6	39.4	1.6	41.8	0.9	47.4	1.9	39.9	3.7	42.7	2.8	44.2	1.6

[a]Six soil plots have been removed from this summary table (see Material and methods).

BD = bulk density of the fine earth; C (N) stock per cm = carbon (nitrogen) stock (density) of bulk soil per cm soil depth (i.e. volume based); CEC = cation exchange capacity; POC (PON) = carbon (nitrogen) content in particulate organic matter; POM = particulate organic matter; SE = standard error; SOC = bulk soil organic carbon; SON = bulk soil organic nitrogen.

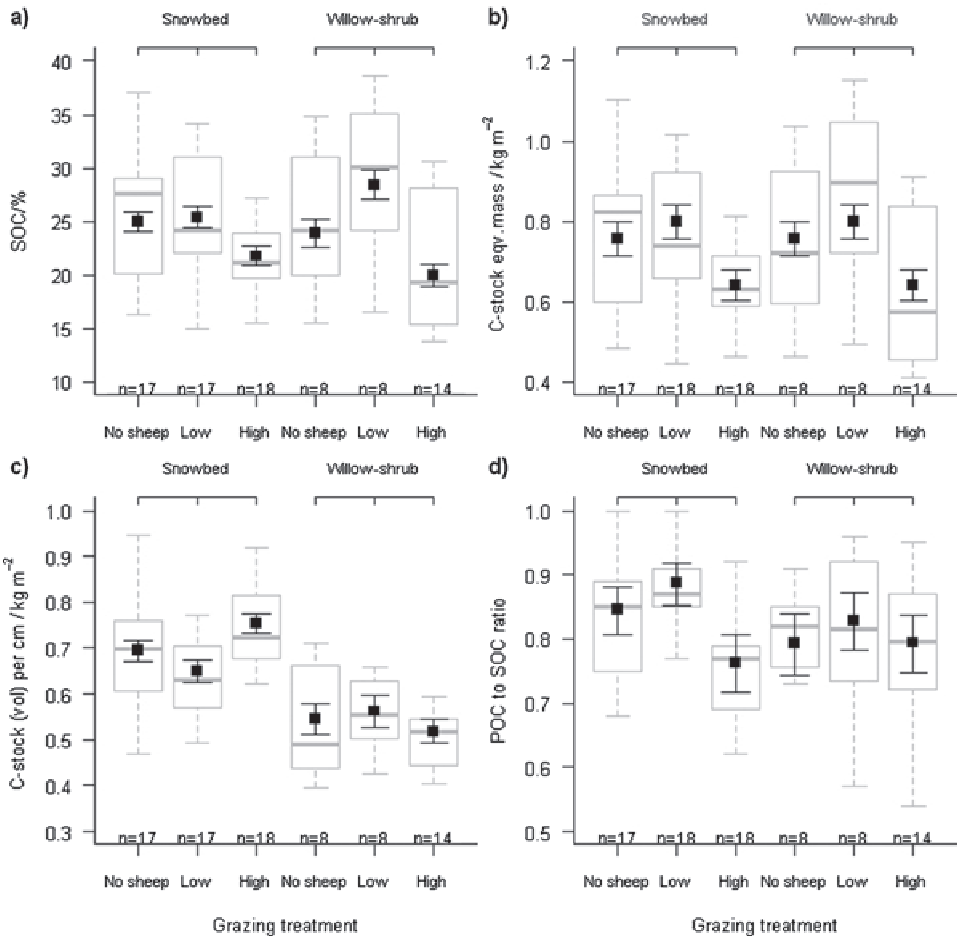

Figure 2 Predicted (±SE) (a) total bulk soil organic carbon content (SOC/% of fine earth; $n = 82$), (b) carbon stock at equivalent soil mass (C-stock eqv. mass as kg m^{-2}; $n = 83$), (c) carbon stock (volume based) per cm soil (C-stock as kg m^{-2}; $n = 82$) and (d) particulate organic carbon to soil organic carbon ratio (POC:SOC; $n = 83$) superimposed on Box-whisker plots (medians, 25th and 75th quartile and minimum and maximum values, shown as whiskers) based on the original data in O-horizon soil samples from grassland habitats within two different plant communities (snowbed and willow-shrub) at three stocking rates (high = 80 sheep km^{-2}, low = 25 sheep km^{-2} and no sheep = control), at Hol, southern Norway. Predictions are based on fixed effect estimates derived from linear mixed effect models (Table S2) at mean bulk density (g cm^{-3}) (Figure 2a,c) and mean ash content (Figure 2d) within each treatment combination (Table 1).

soil and of the POM fraction were greater in willow-shrubs than in snowbeds (Table 1).

Effects of grazing and plant community on quantity, form and lability of SOM

Bulk soil carbon concentration. The fitted linear mixed effect model for bulk soil organic C concentration (% SOC) revealed a significant ($P < 0.05$) interaction between plant communities and treatments and a significant ($P < 0.001$) decrease in percentage SOC per unit increase in BD (Tables S1 and S2). At the mean bulk density within each community and treatment (Table 1), predicted bulk soil organic C concentrations were smaller at high sheep density compared with low sheep density and no sheep, both within snowbeds and willow-shrubs (Figure 2a). The two grazing treatments showed the greatest predicted SOC (at low-grazing pressure; 25.4 ± 0.95 and 28.4 ± 1.35% C) and smallest predicted SOC (at high-grazing pressure; 21.8 ± 0.92 and 19.9 ± 1.05% C) within both plant communities, with SOC at the control sites (24.9 ± 0.95 and 23.9 ± 1.36% C) having intermediate values. The differences between the treatments were more pronounced within willow-shrubs than within snowbeds, with predicted SOC differing as much as around 8.5% between high- and low-sheep stocking rates (Figure 2a). For the high sheep density and the no-sheep treatments, the SOC was less in willow-shrubs than in snowbeds. In contrast, at low sheep density the predicted bulk SOC was greater in willow-shrubs than in snowbeds, illustrating the interaction between habitat and treatment (Figure 2a; Table S2).

Carbon stocks. The fitted model for C stocks based on equivalent mass (C-stock eqv. mass / kg m^{-2}) after model reduction included grazing as the only significant factor (Table S2). Estimated

C-stocks eqv. mass (Figure 2b) were smaller for the high-density treatment (0.64 ± 0.04) compared with the low-density (0.80 ± 0.04) and no-sheep treatments (0.76 ± 0.04), indicating greater loss of soil C and/or less biomass input in areas with high-sheep densities.

The fitted model for C stock per cm soil based on volume of soil (C-stock (volume) / kg m^{-2}) included a significant ($P < 0.05$) interaction effect of treatment and plant community in addition to a significant ($P < 0.001$) increase in C-stock per unit increase in bulk density (Tables S1 and S2). These are the same explanatory variables (fixed effects) as those for SOC. The predicted C-stock at high sheep density in snowbeds was (at the mean bulk density of each treatment; Table 1) greater than at low sheep density and no sheep, and is thus the opposite of that observed for bulk soil C concentration (Figure 2a,c). In contrast, in willow-shrubs (with smaller BD than snowbeds; Table 1), there were only minor differences in predicted volume-based C stocks between the treatments (Figure 2c).

Particulate organic carbon to soil organic carbon ratio (POC to SOC ratio). The fraction of POC (the POC to SOC ratio) was significantly explained by an interaction between grazing and plant community ($P < 0.05$) and ash content of the POM fraction ($P < 0.001$) (Tables S1 and S2), with a reduction in the POC to SOC ratio per unit increase in the ash content of the POM fraction. At the mean POM ash content within each treatment and plant community (Table 1), the predicted POC to SOC ratio in snowbeds was less at high sheep density compared with low density and no sheep, the latter two only differing slightly (Figure 2d). In the willow-shrubs, the predicted POC to SOC ratios revealed only minor differences between the grazing treatments. For all plant community and treatment combinations, the predicted POC to SOC ratios had a similar pattern (although not as pronounced) to bulk SOC (%).

Potential carbon mineralization. Potential carbon mineralization, measured as the mean CO_2-C flux (µg g^{-1} soil $hour^{-1}$) during 27 days of incubation, was not affected by either treatment or plant community (Tables S1 and S3). The overall mean CO_2-C flux at average BD (0.28 g cm^{-3}) was 3.29 (± 0.24) µg g^{-1} soil $hour^{-1}$. Normalizing CO_2-C fluxes on amount of soil particulate organic carbon (µg g POC^{-1} $hour^{-1}$), which is believed to be the most labile soil C fraction, revealed greater CO_2-C fluxes from soils in willow-shrub (approximately 19.8 µg g^{-1} POC $hour^{-1}$) than snowbeds (approximately 15.4 µg g^{-1} POC $hour^{-1}$). However, no effect of grazing treatment was found (Tables S1 and S3).

Discussion

Grazing lands have a significant potential for short-term mitigation of climate change through C sequestration (Laca *et al*., 2010). Several studies have shown that grazing may strongly affect SOC storage (He *et al*., 2008; Steffens *et al*., 2008; Piñeiro *et al*., 2010). However, grazing-induced effects on SOC concentrations and stocks, the POM fraction and lability of SOM and, in addition, physical characteristics such as BD are expected to depend not only on herbivore densities, but also on plant communities. Our data provide evidence for herbivory-dependent effects interacting with site characteristics such as plant community on SOC storage (expressed either as concentrations or stocks) and POC to SOC ratios of SOM. However, these effects were strongly related to differences in soil physical attributes such as BD and ash content of the POM fraction (as a proxy for the mineral content), which are also associated with grazing and plant community.

Within each of the two plant communities (snowbed and willow-shrub) there was a significant ($P < 0.001$) effect of grazing on O-horizon bulk density (BD: g cm^{-3}). High sheep density caused a greater BD (0.35 and 0.27 g cm^{-3} in snowbed and willow-shrub O horizons, respectively) than no sheep (0.28 and 0.23 g cm^{-3} respectively) and the low sheep density (0.26 and 0.20 g cm^{-3} respectively) treatments (Table 1 and Table S3). Previously, soil compaction caused by grazing has been reported by Steffens *et al*. (2008) and Piñeiro *et al*. (2010). As well as the effects of grazing on BD, we found a significant ($P = 0.05$) effect of grazing on ash content of the POM fraction (which differed only slightly between the plant communities, Table 1). The ash content of the POM fraction was greater in the high-grazing treatment compared with the low-grazing and no-sheep treatments (Table S3 and Table 1). However, analysis of the means for each plant community within each sub-enclosure, which relied on a limited dataset only, suggested no significant ($P = 0.17$) effect of grazing (Tables S4 and S5). Data in Table 1 and Table S3 indicate that there may be two different mechanisms controlling incorporation of mineral matter in the O-horizons, namely compaction caused by either snow cover (BD snowbed > willow-shrub) or by sheep trampling (both BD and ash content of POM at high sheep density were more than at low sheep density or no sheep).

Bulk density and bulk soil organic C concentration were significantly negatively correlated ($\rho = -0.74$, $P < 0.05$; Figure S1), as has been reported by De Vos *et al*. (2005) and Steffens *et al*. (2008). Others have used this relationship to develop pedotransfer functions to predict BD from organic matter content (De Vos *et al*., 2005; Perie & Ouimet, 2008). However, the fitted model for SOC has, in addition to BD, other explanatory variables including site (plant community) and grazing regime (Table S2). In accordance with our hypothesis 1, SOC concentrations were, at the mean bulk density within each plant community and treatment combination, smaller in areas with high sheep density compared with those with low density and no sheep (Figure 2a). This suggests that different pedotransfer functions need to be developed depending on location and management practice. However, if accounting for pseudo-replication, the fitted model for SOC, which is based on a limited number of mean values only, indicated significant effects of BD ($P < 0.001$) and plant community ($P < 0.05$) but not of grazing (Tables S4 and S5, Figure S2).

Calculating C-stocks based on equivalent soil mass (C-stock eqv. mass; kg m^{-2}; see Ellert & Bettany, 1995), revealed smaller C-stock estimates for the high sheep density (H1) compared with low density and no sheep treatments, which differed only slightly (Figure 2b and Table S2). Analysis of differences of the means for each plant community within each sub-enclosure revealed no significant ($P = 0.08$) effect of grazing (Tables S4 and S5, Figure S2). However, this is based on a small number (17) of samples only. Reduced C-stock based on equivalent mass with increasing grazing intensity was reported by Steffens *et al.* (2008) in a semiarid steppe of Inner Mongolia. The difference in C-stock equivalent mass between low sheep density and high sheep density was 0.16 ± 0.06 kg m^{-2}. Although this represents changes in (approximately) the upper 0.9–1.6 cm of O-horizons only (see footnote, Table S2), it implies that the input of C to deeper horizons is significantly altered by grazing regime. As noted by Ellert & Bettany (1995), C-stocks based on soil equivalent mass are more sensitive to management-induced changes in organic C storage than estimates based on soil volume (Table S2, Figure 2b). In contrast to SOC and C-stock equivalent mass, C stocks calculated per soil volume revealed greater predicted C-stocks in snowbeds for the high sheep density compared with the low sheep density and no-sheep treatments (Figure 2a–c, Table S2). However, within willow-shrubs, there were only minor differences in predicted volume-based C-stocks between the treatments (Figure 2c). The model based on the mean data for each of the two plant communities within the nine sub-enclosures (Tables S4 and S5), included plant community but not grazing as a significant explanatory variable. For both models, parameter estimates of C-stocks were greater in snowbeds than willow-shrubs (Tables S2 and S5). These findings illustrate the importance of the reporting unit when assessing effects of land use on C storage. Because volume-based C-stocks are based on an unequal mass of soil, we suggest that C concentrations or C-stock equivalent mass should be used for comparisons of organic C stores.

Particulate organic matter (POM) consists mainly of root fragments and above-ground plant residues (Golchin *et al.*, 1994); hence, any reduction in biomass input or increased decomposition would reduce the POC to SOC ratio within the soil. The fitted model (Table S2), predicted that POC to SOC ratio (at mean ash content within each treatment and plant community; Table 1) was smallest at high sheep density in snowbeds but differed only slightly between the grazing treatments in willow-shrubs (Figure 2d). This partly supports hypothesis 2. In contrast, Leifeld & Fuhrer (2009) found significantly greater SOC with a greater fraction of POC (0–4 cm soil depth) in a frequently grazed pasture (dairy cows grazing daily from mid June to mid September) compared with a meadow grazed for short periods in the autumn in the Swiss Alps. They suggest that the greater fraction of POC in the pasture compared with the meadow is caused by incorporation of plant material by treading (Leifeld & Fuhrer, 2009). At the Hol site, the POC to SOC ratio was negatively correlated with ash content of the POM fraction (Figure S1). In addition, there was a greater ash content of the POM fraction at high sheep density (Table S3). Possibly, the somewhat smaller POC to SOC ratios at the high sheep density treatment at Hol were induced by physical disruption of POM (treading) causing increased decomposition. In addition, the sites with high sheep density had smaller inputs of plant biomass (G. Austrheim, unpublished material).

In a parallel study at Hol, the ^{14}C content of POM suggested that the POM fraction has a relatively small mean residence time (V. Martinsen, unpublished material). Recently, similar observations were reported by Leifeld & Fuhrer (2009) and Leifeld *et al.* (2009). Therefore we expected samples with a large POC to SOC ratio to have greater potential C mineralization rates (CO_2-C fluxes: µg g^{-1} soil hour^{-1}). However, our results revealed no effects of treatment or plant community (Table S3), despite differences in the POC to SOC ratios (Figure 2d). The only significant ($P < 0.001$) factor decreasing the decomposability of SOM was BD (Tables S1 and S3). This may be an effect of less available substrate for microbial decomposition at greater BD.

The fitted model for CO_2-C fluxes normalized to POC (µg CO_2-C g^{-1} POC hour^{-1}), revealed greater flux estimates from willow-shrub areas than from the snowbed areas, with a significant ($P < 0.05$) increase in CO_2-C flux with increased ash content of POM (Tables S1 and S3). The positive response in C mineralization per g POC to increased ash content of POM is indicative of sites exposed to greater disturbances and POM disruption and mixing of mineral and organic matter. Assuming that the mean estimated CO_2-C fluxes (willow-shrub, 19.8 µg g^{-1} POC hour^{-1}; snowbed 15.4 µg g^{-1} POC hour^{-1}) were constant throughout the incubation period of 27 days, the cumulative percentage C loss of POC represents approximately 1.3 and 1% in the incubated samples from willow-shrub and snowbed areas, respectively. As the quality of SOM may be distinguished from quantity by identifying the fraction of SOC found in the mineralizable fraction (Gregorich *et al.*, 1994), these findings suggest that there might be minor differences in the quality of the soil organic matter between the habitats. However, 7 years of grazing at the densities in the Hol soils, may not be sufficient to affect the decomposability of SOM.

As described by Piñeiro *et al.* (2010), grazing may alter the content of SOC through the NPP pathway, the N pathway and/or the decomposition pathway. Forage consumption by herbivores and soil compaction may reduce NPP and thus the C input to the system (Piñeiro *et al.*, 2010). At Hol, the NPP pathway may be a plausible mechanism for the somewhat reduced C storage at high sheep density (see above). Interestingly, N-stocks based on equivalent soil mass (kg m^{-2}; Table S1) revealed no effects of grazing, despite a reduced C-stock equivalent at the high sheep density (Figure 2b). Also, the soil N concentrations were only slightly altered by grazing (Table 1). This is in accordance with previous findings at our study site, indicating small effects of grazing on turnover and loss of N (V. Martinsen, unpublished material). Thus, SOC contents are probably not controlled by N, with no grazing-induced changes in SON stocks at our study site. Furthermore, herbivory may reduce SOC storage by increasing decomposition (Piñeiro *et al*., 2010). Our data on potential C mineralization rates do not indicate significant differences between the grazing treatments in terms of lability of SOM (Table S3).

Plant community and soil properties affecting C storage

Previous studies suggest that the mineral content in surface soils (organic horizons) of snowbeds is large (Hiller *et al*., 2005; Virtanen *et al*., 2008). Our results are partly in accordance with these findings, as bulk density (BD) was greater in snowbeds than in willow-shrubs due to the increased bulk density with increased amount of mineral matter (Table 1).

The contribution of POC to bulk SOC in the O-horizons was large both in snowbed and willow-shrub areas, with only minor differences between the two (82 and 79%, respectively; Table 1). The large POC to SOC ratio found at Hol is similar to that found by Leifeld *et al*. (2009) in the Swiss Alps (>80% in 0–5-cm deep soils at the highest elevations at 2200 m above sea level).

O-horizons were deeper and pH and base saturation greater in willow-shrub areas that have intermediate snow cover than in snowbeds with heavy snow cover (Table 1). Ostler *et al*. (1982) reported a decrease in total soil depth with increasing snow cover on a subalpine meadow in the Uinta Mountains (USA). Snow cover may also affect other soil attributes and a decrease in snow cover has been correlated with greater SOM content (Ostler *et al*., 1982; Stanton *et al*., 1994), nutrient levels and acidity (Stanton *et al*., 1994). Our results revealed no difference in SOC concentrations between the two plant communities and, in contrast to Stanton *et al*. (1994), less acidity and greater base saturation in willow-shrub areas (early melting) than under snowbeds (late melting). The reduced acidity and greater base saturation combined with the deeper O-horizon soils in the willow-shrub areas in the Hol system may be a result of return-flow of ground water rich in base cations.

Supporting Information

The following supporting information is available in the online version of this article:

Figure S1. Spearman rank correlation coefficients (abs.) and smoothing lines between altitude, sampling depth (Depth), bulk density of fine earth (BD Fine), bulk soil organic carbon (SOC), bulk soil organic nitrogen (SON), carbon to nitrogen ratio of the bulk soil (Bulk soil CN), bulk soil carbon stock per cm soil (C stock), carbon in particulate organic matter (POC), nitrogen in particulate organic matter (PON), CN ratio of the particulate organic matter fraction (POM CN), particulate organic carbon to bulk soil organic carbon ratio (POC to SOC ratio) and ash content of POM from O horizon soil samples within 82[a] grassland habitats, Hol, Noway. Units of factors are listed in Table 1. All correlation coefficients (ρ) are significant at $P < 0.05$. Empty cells in the upper panel indicate no significant correlation. [a]One soil plot is not included because of missing data on bulk density data.

Figure S2. Predicted (±SE) (a) total bulk soil organic carbon content (SOC / % of fine earth; $n = 17$), (b) carbon stock at equivalent soil mass (C-stock eqv. mass / kg m^{-2}; $n = 17$), (c) carbon stock (volume based) per cm soil (C-stock / kg m^{-2}; $n = 17$) and (d) particulate organic carbon to soil organic carbon ratio (POC:SOC; $n = 17$) superimposed on box-whisker plots (medians, 25th and 75th quartile and minimum and maximum values, shown as whiskers) based on the the mean data from each plant community within each sub-enclosure in O-horizon soil samples from grassland habitats within two different plant communities (snowbed and willow-shrub) at three levels of grazing: high = 80 sheep km^{-2}, low = 25 sheep km^{-2}, and no sheep (control), Hol, southern Norway. Predictions are based on fixed effect estimates derived from linear mixed effect models (Table S5) at mean bulk density (g cm^{-3}) (Figure S2a) and mean ash content (Figure S2d) within each treatment combination.

Table S1. Model selection for the fixed effect structure of linear mixed models (based on ML estimation) for percentage carbon of the bulk soil (% SOC), carbon and nitrogen stock based on equivalent mass of soil (kg m^{-2}), carbon stock per cm soil depth (kg m^{-2}), particulate organic carbon to bulk soil organic carbon ratio (POC to SOC ratio) (arcsine-transformed), carbon flux (CO_2-C g^{-1} soil hour^{-1}), carbon flux (CO_2-C g^{-1} POC hour^{-1}) (ln-transformed), bulk density of the fine earth (g cm^{-3}) (ln transformed) and ash content of the POM fraction (%) within two different plant communities (snowbed and willow-shrub; factor 'pl.comm') at three levels of grazing (high = 80 sheep km^{-2}, low = 25 sheep km^{-2}, and no sheep; factor 'treatment') in grassland habitats (Hol, Norway). Quantitative explanatory variables are BD and ash content of POM. The models always included sub-enclosures ($n = 9$) nested in blocks ($n = 3$) as random effects. Steps indicate models with a different fixed effect structure for each dependent variable. AIC = Akaike's information criterion. ΔAIC = change in AIC betwen the models (negative values indicate improved fit). P is the P-value based on likelihood ratio tests (chi-squared) between two models. P values <-0.05 indicate significantly smaller explanatory power. Step comp. indicates the models compared.

Table S2. Results of linear mixed model analysis (based on REML estimation) for total bulk soil carbon content (SOC / % of fine earth), carbon stock based on equvialent soil mass[a] (C-stock eqv.mass / kg m^{-2}), carbon stock (volume based) per cm soil (C-stock (volume) per cm / kg m^{-2}) and particulate organic carbon to bulk soil organic carbon ratio (POC to SOC ratio) (arcsine transformed) within two different plant communities (snowbed and willow-shrub; denoted 'pl.comm') at three levels of grazing (high = 80 sheep km^{-2}, low = 25 sheep km^{-2}, and control (no sheep); denoted 'treatment') in grassland habitats (Hol, Norway). Logarithm-transformed bulk density (BD) of the fine earth (g cm^{-3}) and ash content of POM (%) are included as quantitative explanatory variables. Random effects are sub-enclosures (n = 9; factor sub-enclosure) nested in blocks (n = 3; factor 'block'). The table shows parameter estimates (±SE) for each factor combination and for BD and ash content of POM (column A) and predicted % SOC, C-stock per cm soil and POC to SOC ratio (arcsine transformed) at mean bulk density and ash content of POM (Table 1) for each combination (column B). The model reduction steps (based on ML estimation) are presented in Table S1. Not relevant is marked as '–'.

Table S3. Results of linear mixed model analysis (based on REML estimation) for carbon flux[a] (μg CO_2-C g^{-1} soil $hour^{-1}$), carbon flux[a] (μg CO_2-C g^{-1} POC $hour^{-1}$) (ln transformed), bulk density of the fine earth (g cm^{-3}) (BD; ln-transformed) and ash content of POM (%) within two different plant communities (snowbed and willow-shrub; denoted 'pl.comm') at three levels of grazing (high = 80 sheep km^{-2}, low = 25 sheep km^{-2}, and control (no sheep); denoted 'treatment') within sub-enclosures ($n = 9$; factor sub-enclosure; random effect) nested in blocks ($n = 3$; factor 'block'; random effect) in grassland habitats (Hol, Norway). The table shows parameter estimates (±SE) for each factor combination and for BD and ash content of POM (column A) and predicted carbon fluxes at mean bulk density and ash content of POM (Table 1) for each combination (column B). The model reduction steps (based on ML estimation) are presented in Table S1. Not relevant is marked as '–'.

Table S4. Model selection for the fixed effect structure of linear mixed models (based on ML estimation) for percentage carbon of the bulk soil (% SOC), carbon and nitrogen stock based on equivalent soil mass (kg m^{-2}), carbon stock per cm soil depth (kg m^{-2}), particulate organic carbon to bulk soil organic carbon ratio (POC to SOC ratio) (arcsine-transformed), carbon flux (CO2-C g^{-1} soil $hour^{-1}$), carbon flux (CO2-C g^{-1} POC $hour^{-1}$) (ln-transformed), bulk density of the fine earth (g cm^{-3}) (ln transformed) and ash content of the POM fraction (%) within two different plant communities (snowbed and willow-shrub; factor 'pl.comm') at three levels of grazing (high = 80 sheep km^{-2}, how = 25 sheep km^{-2}, and no sheep; factor 'treatment') in grassland habitats (Hol, Norway). Quantitative explanatory variables are BD and ash content of POM. The models always included sub-enclosures ($n = 9$) nested in blocks ($n = 3$) as random effects. Steps indicate models with a different fixed effect structure for each dependent variable. AIC = Akaike's information criterion. ΔAIC = change in AIC betwen the models (negative values indicate improved fit). P is the P-value based on likelihood ratio tests (chi-squared) between two models. P-values <-0.05 indicate significantly smaller explanatory power. Step comp. indicates the models compared. Note: Model reductions are based on mean data from each plant community (i.e. snowbed and willow-shrub) within each sub-enclosure.

Table S5. Results of linear mixed model analysis (based on REML estimation) for total bulk soil carbon content (SOC / % of fine earth), carbon stock based on equivalent soil mass (C-stock eqv.mass / kg m^{-2}), carbon stock (volume based) per cm soil (C-stock (volume) per cm / kg m^{-2}), particulate organic carbon to bulk soil organic carbon ratio (POC to SOC ratio) (arcsine transformed), carbon flux (μg CO_2-C g^{-1} soil $hour^{-1}$), carbon flux (μg CO_2-C g^{-1} POC $hour^{-1}$) (ln transfomred), bulk density of the fine earth (g cm^{-3}) (BD; ln-transformed) and ash content of POM (%) within two different plant communities (snowbed and willow-shrub; denoted 'pl.comm') at three levels of grazing (high = 80 sheep km^{-2}, low = 25 sheep km^{-2}, and control (no sheep); denoted 'treatment') in grassland habitats (Hol, Norway). Logarithm-transformed BD of the fine earth and ash content of POM (%) are included as quantitative explanatory variables. Random effects are sub-enclosures ($n = 9$; factor sub-enclosure) nested in blocks ($n = 3$; factor 'block'). The table shows parameter estimates (±SE) for each factor combination and for BD and ash content of POM (column A) and predicted % SOC, POC to SOC ratio (arcsine transformed) and carbon fluxes (μg CO_2-C g^{-1} soil $hour^{-1}$ and μg CO_2-C g^{-1} POC $hour^{-1}$; ln transformed) at mean bulk density and ash content of POM for each combination (column B). The model reduction steps (based on ML estimation) are presented in Table S4. Not relevant is marked as '–'. Note: Analyses are based on mean data from each plant community (i.e. snowbed and willow-shrub) within each sub-enclosure.

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