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Effects of Sheep Grazing on Availability and Leaching of Soil Nitrogen in Low-Alpine Grasslands

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Abstract

Alpine ecosystems are generally nitrogen (N) limited with low rates of N mineralization. Herbivory may affect N cycling and N losses and thus long-term productivity of ecosystems.

Using a controlled grazing experiment in a low-alpine region at Hol, southern Norway, with three density levels of sheep, we determined effects of grazing on *in situ* availability of inorganic N, potential N mineralization, and mobility of dissolved inorganic N (DIN) and dissolved organic N (DON) in soil water of O-horizons in grazing-preferred grassland habitats. In addition, we studied the within-season and spatial variation of these processes.

The low alpine grasslands at Hol were characterized by small rates of N mineralization and relatively large plant demands for N. Significantly greater rates of potential N mineralization were found at sites with high sheep density compared to those with low density or no grazing. Effects of grazing on bioavailable N (as determined by buried PRSTM exchange resins) were greater at low as compared to high altitudes. At low altitudes, low sheep density reduced amounts of bioavailable N. Nitrogen concentration of plants as a proxy of N availability in soils revealed, however, no significant effects of grazing. There was a strong seasonal effect on inorganic N and DIN:DON ratios of the soil water, with decreasing values in the course of the growing season, probably due to increasing nutrient demand of plants and/or microbes.

We conclude that grazing may significantly stimulate N-cycling, but not sufficiently to release the system from its strong N deficiency, as we found no evidence for short-term increased risk in N loss via soil water due to herbivore activity. Nitrogen removal through grazing is small compared to the total soil N pool and at high sheep density is about half of the N deposition. This suggests that grazing in grassland habitats in this low alpine ecosystem is sustainable from a nutrient point of view.

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Introduction

Alpine ecosystems, with their short growing season, low temperatures, and heterogenic vegetation structure (Körner, 2003; Nagy and Grabherr, 2009) differ in several respects from lowland systems. Biogeochemical processes are rate-limited by temperature (Hagedorn et al., 2010; Makarov et al., 2003) and the biomass production is smaller than that of lowland systems (Körner, 2003; Nagy and Grabherr, 2009). Nitrogen (N) is in general the key limiting nutrient for plant growth in terrestrial ecosystems (Vitousek and Howarth, 1991), and particularly alpine and arctic ecosystems are strongly N limited (Bowman et al., 1993; Frank, 2008; Grellmann, 2002; Shaver and Chapin, 1980). Nitrogen mineralization rate is small (Chapin et al., 1988; Fisk et al., 1998), it differs between plant communities (Björk et al., 2007; Makarov et al., 2003), and varies during the growing season (Bardgett et al., 2002; Frank, 2008; Morecroft et al., 1992). Furthermore, absorption of nutrients by plants is related to nutrient concentrations in soil solution (Chapin, 1980). Hobbie and Gough (2002) found positive relationships between foliar N concentration and net N mineralization rates at two tundra sites dominated by moist

tussock tundra in northern Alaska. Thus, factors affecting the form and lability of N (and hence N availability) are likely reflected in the N content of plants.

In addition to direct grazing and plant removal, altering vegetation structure and quality, impacts of grazing include trampling and recycling of nutrients in the form of feces and urea (Hester and Baillie, 1998; van der Wal et al., 2004; van der Wal and Brooker, 2004). This may induce productivity since the ratio of available nutrients per unit of plant biomass will increase. In turn, grazing may affect physical and chemical soil properties [e.g. temperature (Olofsson et al., 2004), bulk density (Steffens et al., 2008) and soil solution chemistry (Haynes and Williams, 1992; Shand and Coutts, 2006)] and thus organic matter (OM) stocks and mineralization rates (Piñeiro et al., 2010; Stark et al., 2002). Ungulates are important agents of ecosystem dynamics (Hobbs, 1996), but the levels of grazing required to influence N mineralization in northern, alpine ecosystems are largely unknown.

Mineralization of OM by heterotrophic microbes produces ammonium (NH₄⁺), which may be oxidized to nitrate (NO₃⁻) (Jackson et al., 2008). Herbivores may enhance (Frank and Groffman, 1998b; Hobbs, 1996; Tracy and Frank, 1998) or retard

(Harrison and Bardgett, 2004; Schoenecker et al., 2004) N mineralization, depending on ecosystem productivity and the nature (i.e. grazing or browsing) of their herbivory (Harrison and Bardgett, 2008; Wardle et al., 2004). Møbbæk et al. (2009) reported herbivore density-dependent selection for productive habitats, associated with a larger proportion of high-quality forage being ingested by sheep at low densities than at high densities (Myrsterud et al., 2011). Christianson and Creel (2009) found a positive relationship between N concentration in feces of elk (*Cervus elaphus*) and the quality of forage grasses. Correspondingly, Kyvsgaard et al. (2000) showed a positive correlation between percentage N in feces (from sheep) and net mineralization of feces N. Thus, impacts of grazing on soil N-mineralization may differ between grazing regimes.

Despite a tight N-cycling due to strong plant and microbial demand for nutrients (Jaeger et al., 1999) associated with little loss of N in alpine areas (Fisk and Schmidt, 1996; Gerzabek et al., 2004), herbivore-induced increase in N-cycling may increase the risk of N-loss from the system (Dahlin et al., 2005; Frank and Groffman, 1998a; Haynes and Williams, 1992). High concentrations of nitrate in soil solutions under urine and feces patches were reported by Haynes and Williams (1992) and Shand and Coutts (2006), respectively. Frank and Groffman (1998a) found a significant herbivore-induced increase in denitrification at mesic sites in grasslands of Yellowstone National Park, with rates about double that of atmospheric N deposition.

Most studies on grazer effects on availability and leaching of N have used grazing enclosures where animals are excluded from a fenced area. By contrast, experimental designs with a density gradient of grazers in enclosures are rare. Here, we use a controlled grazing experiment in a low-alpine region of southern Norway with three levels of grazing intensity. Graminoid-dominated snowbeds and grasslands with a varying cover of willows were selected due to preferential grazing in these habitats (cf. Møbbæk et al., 2009). Our objectives were to determine effects of different sheep densities on *in situ* availability of inorganic N, potential N mineralization rates, and mobility of DIN and DON in soil water of O-horizons as a proxy of runoff export of N. In addition, we studied the within-season and spatial-related variation of these processes. We hypothesize that *in situ* availability of inorganic N (H1), N concentration of plants (% total N) (H2), and potential nitrogen mineralization rates (H3) would be, in order, high sheep density > low sheep density > no sheep. In turn, if availability of N increases with grazing densities, we expect greater ratios of dissolved inorganic to organic N (DIN:DON) in soil water from areas being heavily grazed compared to those with moderate or no grazing (H4). The concentrations of mobile inorganic N (adsorbed on PRSTM-probes or dissolved in soil water) is expected to change throughout the growing season, with lowest values at high primary production and thus high N uptake, even if the effect of grazing (H1 and H4) remains constant (H5).

Material and Methods

SITE DESCRIPTION AND PLOT LOCATIONS

The study site is located in the low alpine region (1050–1320 m a.s.l.; i.e. the area above the forest line up to the upper limit of *Vaccinium myrtillus* cf. Moen (1999)) in Hol municipality, Buskerud county, southern Norway (60°40'–60°45'N, 7°55'–8°00'E). The vegetation is dominated by dwarf shrub heaths (51%), lichen ridges (17%), snowbeds (12%) with graminoids, and alpine meadow communities (9%) dominated by graminoids and herbs (Austrheim et al., 2008; Rekdal, 2001). The latter two are

classified as medium productive and high productive habitats, respectively (Møbbæk et al., 2009). The bedrock consists of meta-arkose and Quaternary deposits of till and colluvium (Kristiansen and Sollid, 1985; Sigmond, 1998). Soils are spatially variable, including peaty deposits in poorly drained pockets and freely drained soils with shallow and acidic organic horizons. Organic horizons (average depth: ~5.5 cm) have a large percentage (~65%) of free particulate organic matter (POM) (Martinsen et al., 2011). Mean annual temperature (MAT) is -1.5 °C and 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 km²) was fenced and divided in three blocks each with three sub-enclosures (approximately 0.3 km²) with no sheep (control), low density (25 sheep km⁻²), and high density (80 sheep km⁻²) of domestic sheep (*Ovis aries*) (Myrsterud and Austrheim, 2005; Myrsterud et al., 2005). The experiment is set up as a randomized block design (Fig. 1). Sheep grazing occurred from the end of June to the beginning of September (approximately 10 weeks) annually, from 2002 to 2009 for a 7 (7–8 for soil water) year treatment time.

Twenty-seven soil plots [each 0.25 m², at 3 different altitudinal levels (mean of 1122, 1172 and 1246 m a.s.l.) in 3 replicates within the 3 enclosures in the eastern block] were established in 2007 ("Location A;" Fig. 1 and Table 1). The plots are located in graminoid-dominated snowbeds and grasslands with a varying cover of willows. They were selected based on criteria of similar altitude and plant community. In addition, 54 soil plots [each 1 m², within all 9 enclosures at 2 different altitudinal levels (mean of 1168 and 1259 m a.s.l.) and in 3 replicates] were established in 2008 ("Location B;" Fig. 1 and Table 1). All location B plots are located in grassland habitats partly covered with willow shrubs. As for location A, the plots were selected based on criteria of similar altitude and plant community. Soil plots of location B, occurring within the grazed enclosures, were fenced in 2008 to prevent damage to the PRSTM-probes and macrorhizons. In a separate study, all plots of location B received a small amount of ¹⁵NH₄Cl (N input about 7% of the annual input in wet deposition) in early July 2008, which did not affect the relative difference in inorganic N between grazing treatments.

Eighty-nine plots, established in 2001 in grassland habitats, were selected for soil and vegetation sampling in 2008 ("Location C;" Fig. 1 and Table 1). The plots (0.25m²) were selected using a balanced stratified procedure among altitudinal levels and habitats (Austrheim et al., 2005). Soil and vegetation samples from location C were further divided in two different grassland plant communities: snowbed (*n* = 54) and grassland with scattered willow shrub (*n* = 33). In a related study, differences associated with these grassland plant communities were assessed (Martinsen et al., 2011). Willow shrubs were found to be located at lower altitudes than snowbeds, and have thicker O-horizons, lower bulk densities, and higher pH and C:N ratios than snowbeds (Martinsen et al., 2011).

IN SITU AVAILABILITY OF INORGANIC NITROGEN (LOCATION B)

Plant root simulator probes (PRSTM; Western Ag Innovations Inc., Saskatoon, Canada) were used to assess available inorganic nitrogen (NH₄-N and NO₃-N) in soils. Four pairs of cation and anion PRSTM-probes were inserted (~5 cm) in the soil within each of the 54 plots of location B during 3 periods [3–23 July 2008 (*n* = 432); 23 July–11 August 2008 (*n* = 432); 11–31

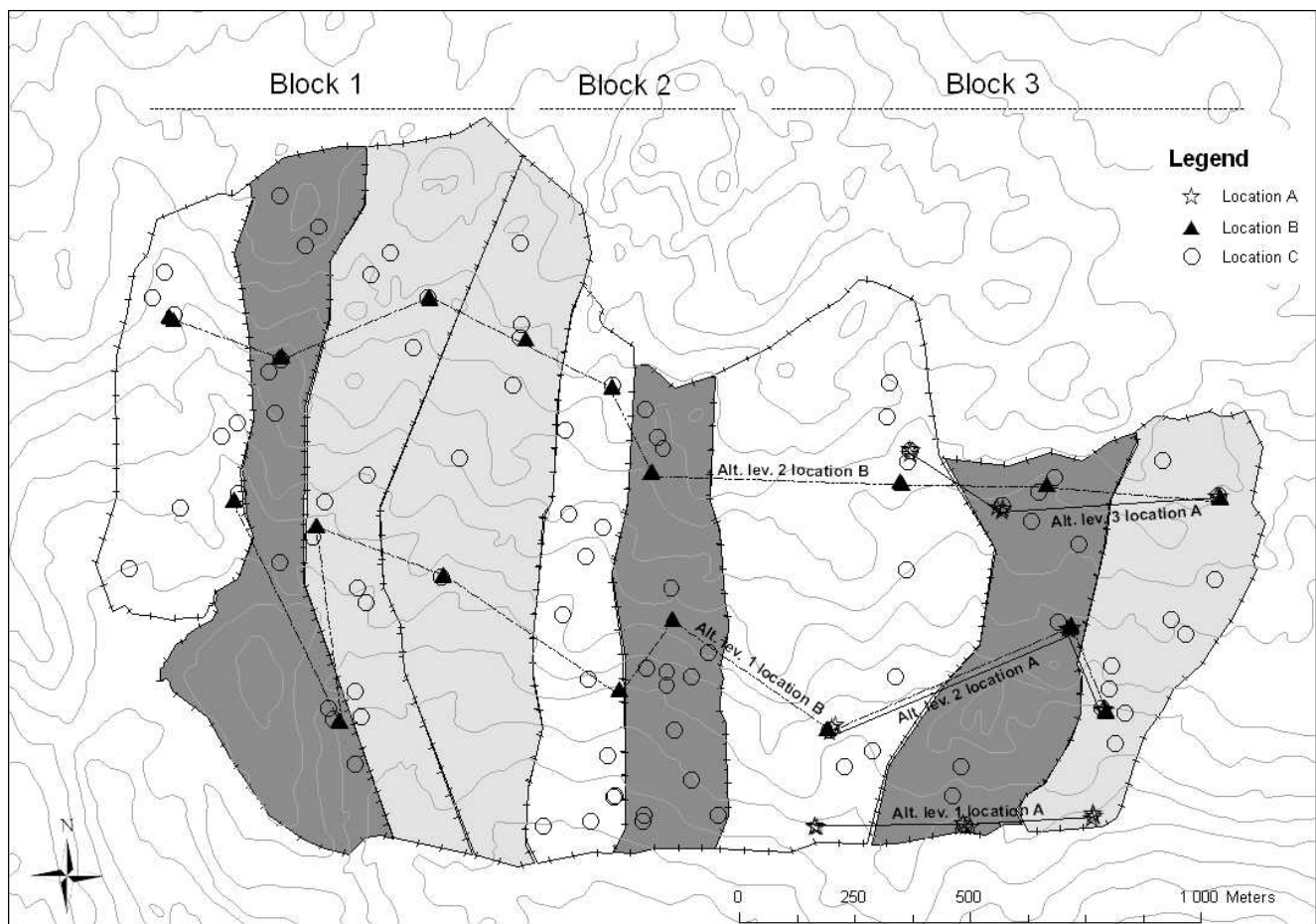


FIGURE 1. Sampling locations and experimental design (3 enclosures with different sheep densities in 3 blocks) Hol, southern Norway. The area of each enclosure is $\sim 0.3 \text{ km}^2$, total area is $\sim 2.7 \text{ km}^2$. White enclosures = no sheep (control), light gray enclosures = low (25 sheep km^{-2}) and dark gray enclosures = high (80 sheep km^{-2}) sheep densities. Points represent three different sampling locations for soil, soil water, and vegetation. At location A (27 soil plots; 3 altitudinal levels), soil and soil water were sampled. At location B (54 soil plots; 2 altitudinal levels) soil and soil water were sampled in addition to determination of *in situ* PRSTM-adsorbed inorganic nitrogen. At location C (89 soil and vegetation plots) soil (subsamples used to determine potential N mineralization) and vegetation were sampled.

August 2008 ($n = 432$]). The four cation and 4 anion probes at each plot and period were bulked prior to analysis ($n_{\text{cation}} = 162$; $n_{\text{anion}} = 162$). After each period, the PRSTM-probes were shipped to Western Ag Innovations for analysis. The PRSTM-probes were eluted using a 0.5N HCl solution for 1 hour and analyzed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ colorimetrically (Western AG Innovations Inc., 2009). As the ion adsorption is not linear in time, we used the

recommended reporting unit “amount adsorbed N cm^{-2} PRS surface time of burial⁻¹” (Western AG Innovations Inc., 2009). The method detection limit was $0.2 \mu\text{g N cm}^{-2} 20 \text{ days of burial}^{-1}$. The PRSTM-probes were inserted directly in the O horizon and the amount of adsorbed N represents nutrient surplus rather than net mineralization (Western AG Innovations Inc., 2009).

TABLE 1
Attributes of sampling locations (A, B, and C) within the fenced experimental site (Fig. 1) at Hol, Norway.

	Location A	Location B	Location C
Establishment of plots	2007	2008	2008
Plant community	Grassland plant communities in snowbeds and grasslands partly covered with willow-shrubs	Grassland plant communities partly covered with willow-shrubs	Grassland plant communities in snowbeds and grasslands partly covered with willow-shrubs
Location within enclosure	Eastern block; no sheep, low and high sheep density	All three blocks; no sheep, low and high sheep density	All three blocks; no sheep, low and high sheep density
Mean altitude (m a.s.l.)	Altitude 1: 1122, altitude 2: 1172, and altitude 3: 1246	Altitude 1: 1168, and altitude 2: 1259	Distributed across the altitudinal gradient of the experimental site
Measurements	DIN:DON ratios of O-horizon water and O-horizon N pool	<i>In situ</i> availability of N (PRS TM -probes) and DIN:DON ratios of O-horizon water	N-content of plants, potential N mineralization, and O-horizon N pool
Sampling period	DIN:DON: from June to August in 2008 and 2009. O-horizon N pool: summer 2007	<i>In situ</i> availability of N: early, mid-, and late growing season 2008. DIN:DON: from June to August in 2008 and 2009	N-content of plants: end of June to the beginning of August 2008. Potential N mineralization and O-horizon N pool: beginning of August 2008

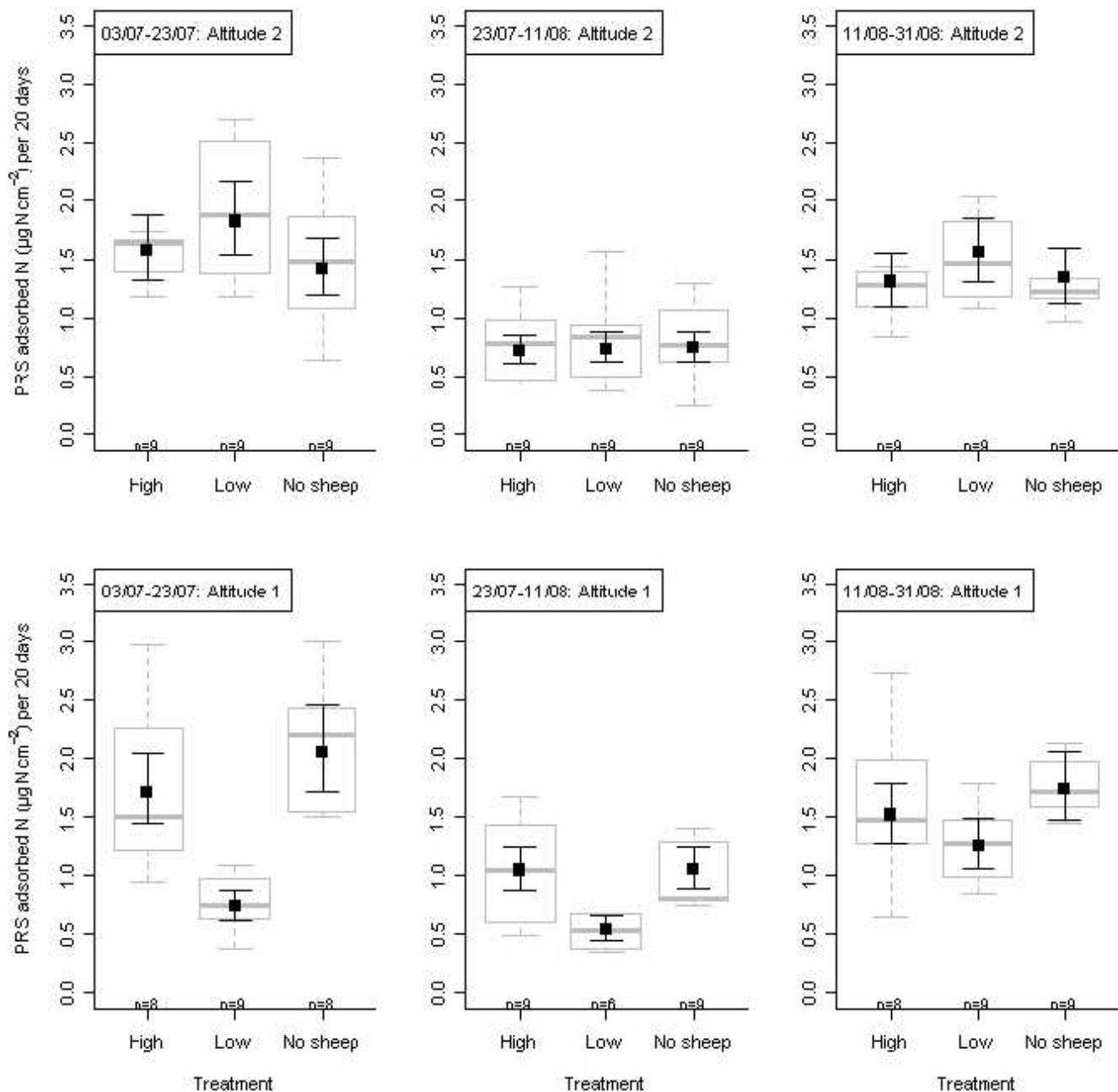


FIGURE 2. *In situ* PRSTM-adsorbed inorganic nitrogen (sum NH₄-N and NO₃-N; µg N cm⁻² 20 days burial⁻¹) in organic soils within grassland habitats (location B, Hol, Norway) at two altitudinal levels (altitude 1, ~1168 m a.s.l.; and altitude 2, ~1259 m a.s.l.), three burial periods (2008: 03.07–23.07, 23.07–11.08, and 11.08–31.08) and three grazing treatments (high, 80 sheep km⁻²; low, 25 sheep km⁻²; and control [= no sheep]). The figure shows PRSTM-adsorbed N (±se) based on fixed effect estimates derived from a linear mixed effect model (Appendix 2, Table A2a) superimposed on box-whisker plots (medians, 25th and 75th quartile, and minimum and maximum values, i.e. whiskers) based on the original data. Six values omitted from the analysis (3 were below the detection limit and 3 considered as outliers [23.5, 7.5, and 6.7 µg N cm⁻² 20 days of burial⁻¹]), n = 156.

PLANT SAMPLING (LOCATION C)

Plant tissue of 6 different plant species representing 3 plant functional groups was sampled: grasses (*Avenella flexuosa* and *Anthoxanthum odoratum*) and herbs (*Alchemilla alpina* and *Rumex acetosa*) and woody species (leaves of *Vaccinium myrtillus* and *Salix lapponum*). All plants were sampled in the period 29 July–7 August 2008 (Mysterud et al., 2011). The plants were milled (1 mm sieve size; Culatti, type DFH48) and dried (60 °C) prior to analysis. Total carbon and nitrogen was determined by combustion in Flash EATM 1112 automatic elemental analyzer (Thermo Finnegan, Milan, Italy).

SOIL SAMPLING AND POTENTIAL NITROGEN MINERALIZATION (LOCATION C)

O-horizons (n = 89) were sampled during the period 5 August–8 August 2008 using a cylinder-shaped auger (diameter 5.2 cm) to a maximum depth of 5 cm. Prior to sampling the O-horizon, the vegetation was cut at the soil surface and the O₁ removed. Four soil samples were taken at most one meter from the vegetation plots. To obtain enough soil material for analysis, more than 4 samples were taken if the O-horizon was <5 cm. The soil samples at each of the 89 plots were bulked per plot prior to analysis. Field moist soil samples (~60% water) were

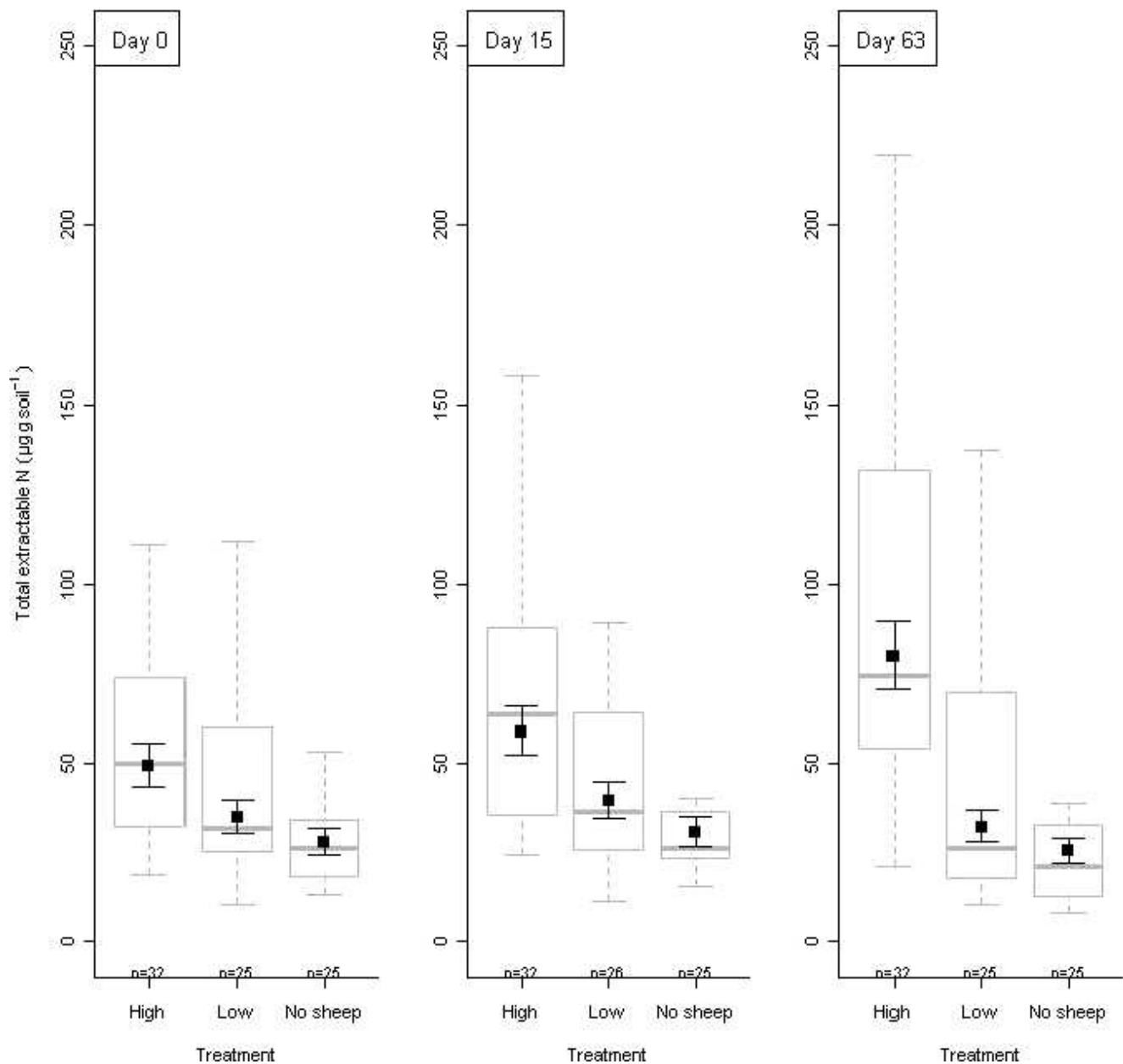


FIGURE 3. Total inorganic nitrogen ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$; $\mu\text{g g}^{-1}$ soil) from O-horizon samples of grassland habitats (location C, Hol, Norway) at three different grazing treatments (high, 80 sheep km^{-2} ; low, 25 sheep km^{-2} ; and control [= no sheep]) during 63 days of incubation (day 0 = start of incubation, initial extractable N; day 15 = extractable N after 15 days of incubation; and day 63 = extractable N after 63 days of incubation). The figure shows total nitrogen (\pm se) based on fixed effect estimates derived from a linear mixed effect model (Appendix 2, Table A2b) superimposed on box-whisker plots (medians, 25th, and 75th quartile and minimum and maximum values, i.e. whiskers) based on the original data. An increase or decrease in extracted N from day 0 indicates net mineralization or immobilization, respectively. Six plots are omitted from the analysis (see Material and Methods). One outlier was removed in addition to one missing value, $n = 247$.

homogenized and divided into two subsamples, one for chemical analysis and one for determination of potential nitrogen mineralization rates. All soil samples were stored dark and cold ($<4^\circ\text{C}$) prior to analysis. A subsample from each plot was air-dried (40°C for 4–5 days), sieved at 2 mm, and the weight of dry roots and gravel (>2 mm) determined. Subsamples of the air-dried fine earth fractions were dried at 60°C to determine dry matter content (DM) and total N. Total N was analyzed by dry combustion (Leco CHN-1000; Leco corporation, Sweden) according to the Dumas method (Bremner and Mulvaney, 1982).

Potential nitrogen mineralization rate was determined in incubation experiments conducted between 17 October and 19 December 2008. At the start of the experiment (day 0), three field-moist subsamples from each of the 89 soil plots were placed in PVC tubes. The amount of soil used was equivalent to 5 g of dry soil for 82 of the soil plots. Due to lack of soil, between 2.5 and 3.6 g dry equivalent soil was placed in PVC tubes from the remaining 7 soil plots. One of the subsamples was immediately frozen (background level), while the remaining two were incubated (dark) in an incubation cabinet (Termaks series 6000) at 15°C . After 15 days and 63 days of incubation, respectively,

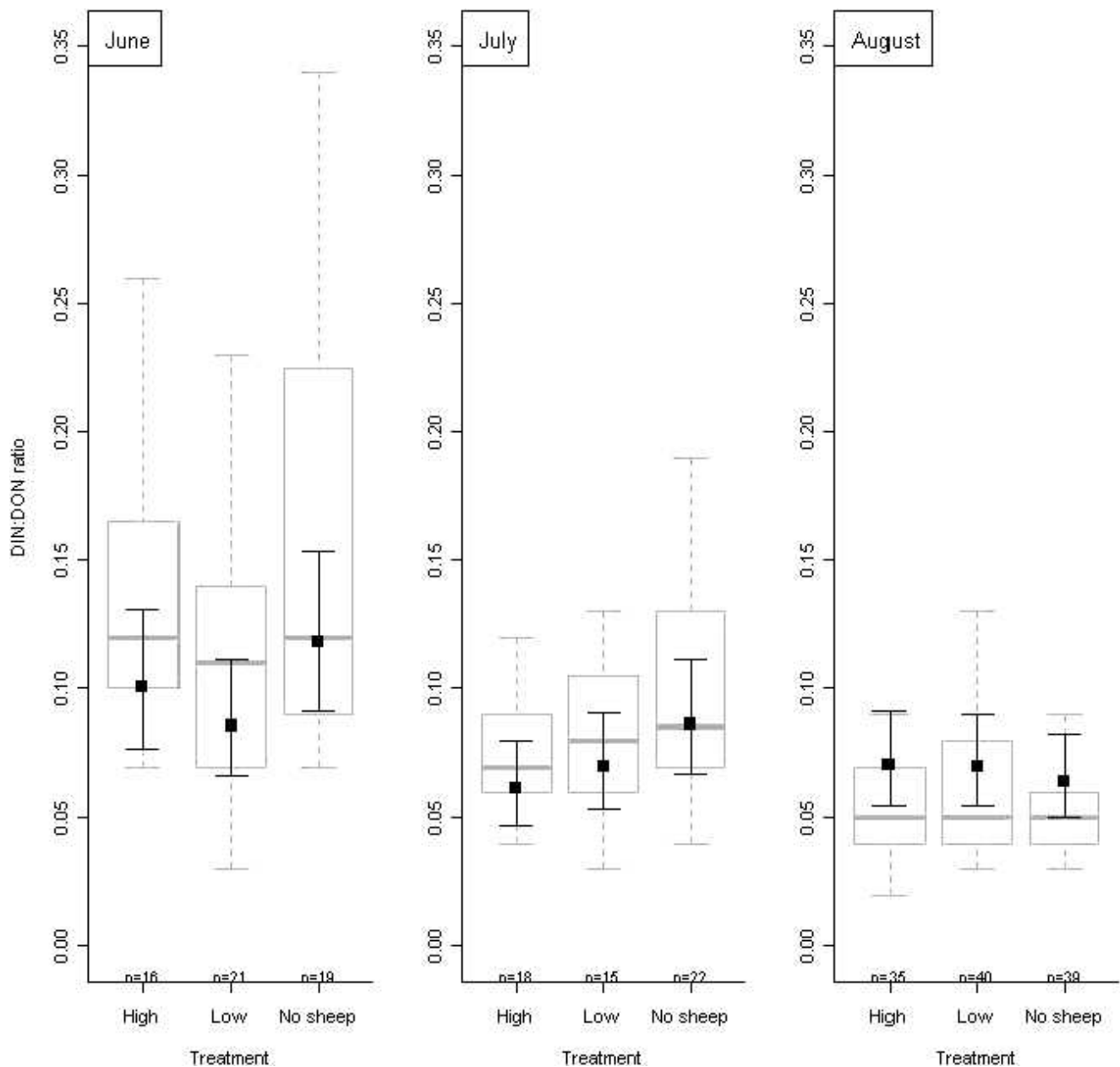


FIGURE 4. Dissolved inorganic nitrogen ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) to organic nitrogen ratio (DIN:DON) in O-horizon soil water from grassland habitats (altitude levels 2 and 3, locations A and B, Hol, Norway) at three different grazing treatments (high, 80 sheep km^{-2} ; low, 25 sheep km^{-2} ; and control [= no sheep]) throughout the growing season. The figure shows estimated DIN:DON ratios (\pm se) derived from a linear mixed effect model (Appendix 2, Table A2c) superimposed on box-whisker plots (medians, 25th, and 75th quartile and minimum and maximum values, i.e. whiskers) based on the original data. One value was deleted prior to analysis (DIN:DON ratio > 0.6), $n = 225$.

the two remaining samples were removed and frozen. To prevent water loss during incubation, a lid was placed on top of the sample tubes and a container with water was placed among the samples.

After thawing, the soils were extracted in 25 mL 2M KCl and filtered prior to analysis. Nitrate-N (sum of NO_3^- and NO_2^-) was determined photometrically (flow injection analysis; FIA star 5020 analyzer, Tecator) according to the Norwegian standard NS 4745 (NSF, 1975a). Ammonium-N was determined photometrically (Photometer, Gilford Instrument) according to NS 4746 (NSF, 1975b). In both cases the detection limit was 0.02 mg L^{-1} . Rates of net ammonification and net nitrification were determined by subtracting initial extractable soil $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ ($\mu\text{g g soil}^{-1}$) from final amounts (after 15 and 63 days, respectively) of extracted $\text{NH}_4\text{-N}$ and

$\text{NO}_3\text{-N}$, respectively. The sum of produced $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ represents net mineralization (Vestgarden and Kj naas, 2003).

SOIL WATER SAMPLING AND ANALYSIS (LOCATIONS A AND B)

Soil water was collected using macrorhizons (type 19.21.35, Eijkelkamp, The Netherlands) installed just below or within the O-horizon (average depth at location A: 4.5 cm and at location B: 3.6 cm). A syringe was used to collect the water. Soil water was collected on 10 occasions from June to August in 2008 (18 June–22 August 2008) and 2009 (9 June–25 August 2009). The samples were stored cold ($<4^\circ\text{C}$) and filtered prior to analysis. $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ were determined as described above. Total N was

TABLE 2

Mean (\pm se) $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and total N of PRSTM-adsorbed N ($\mu\text{N cm}^{-2}$ 20 days burial⁻¹; determined at two altitudinal levels during three burial periods at location B), soil extractable inorganic N ($\mu\text{g g}^{-1}$ soil; determined at three periods of incubation from location C), and soil water concentrations (mg L^{-1} ; locations A and B) from O-horizons of grassland habitats at three density levels of sheep (no sheep = control, low density = 25 sheep km^{-2} , and high density = 80 sheep km^{-2}), Hol, Norway. Number of samples above the detection limit is shown (*n*). Total N represents the mean sum of inorganic N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) for PRSTM-adsorbed N and soil extractable N, and the mean of total inorganic and organic N for the soil water (see material and methods).

Variable	Treatment	$\text{NO}_3\text{-N}$			$\text{NH}_4\text{-N}$			Tot-N		
		Mean	se	n	Mean	se	n	Mean	se	n
PRS adsorbed N ($\mu\text{g N cm}^{-2}$ 20 days burial ⁻¹)	High	0.381	0.017	40	1.126	0.090	49	1.379	0.092	52
	Low	0.410	0.025	32	0.962	0.085	48	1.209	0.091	51
	No sheep	0.419	0.025	41	1.170	0.083	50	1.461	0.088	53
Extractable N ($\mu\text{g N g soil}^{-1}$)	High	13.120	2.910	60	67.884	5.409	96	76.084	5.773	96
	Low	8.969	4.780	24	41.043	3.489	76	43.875	3.768	76
	No sheep	4.840	2.250	21	36.929	5.226	75	38.284	5.332	75
Soil water N (mg L^{-1})	High	0.032	0.004	9	0.105	0.020	69	1.338	0.128	69
	Low	0.061	0.022	5	0.088	0.011	76	1.261	0.098	76
	No sheep	0.026	0.003	5	0.109	0.018	80	1.299	0.114	80

determined photometrically (flow injection analysis; FIA star 5020 analyzer, Tecator) after oxidation by peroxodisulfate according to the Norwegian standard NS 4743 (NSF, 1993). Dissolved organic N (DON) was calculated as total N less the sum of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$. Dissolved organic carbon (DOC) was determined using a total organic carbon analyzer (TOC-V CPN, Shimadzu) according to NS 1484 (NSF, 1997).

STATISTICAL ANALYSIS

Statistical analyses were conducted using the libraries lme4, multcomp, 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. The random effects were not the same for all models, as the sampling strategy (i.e. repeated measurements on the same plots and factors included in the analysis) differed

depending on the data sets (i.e. locations A, B, and/or C) and the dependent variable for which the models were fitted (Appendix 1 and 2).

Backward selection was used [models fitted by maximum likelihood (ML)] and models were compared based on AIC and likelihood ratio tests (Chi-squared) to obtain the minimum adequate model (Appendix 1). The best model was re-fitted based on restricted maximum likelihood (REML) and the estimated effects (including standard error) were calculated using general linear hypothesis testing [glht in multcomp]. Only adjusted *p*-values [single-step method (Hothorn et al., 2008)] are reported (Table 3, Appendix 2). Residuals and predicted random effects were plotted (histograms and QQ normal plots) to assess normality and potential outliers. Six soil plots from location C were excluded from the analysis due to large deviations compared to the rest of the grassland plots (see Martinsen et al., 2011). Missing values and values below the detection limit resulted in non-balanced data sets.

TABLE 3

Parameter estimates of (sqrt) total nitrogen (%) of plants [three plant functional groups (PFG): Grasses (*A. flexuosa* and *A. odoratum*), herbs (*A. alpina* and *R. acetosa*), and woody species (*V. myrtillus* and *S. lapponum*)] within grassland plots at two different plant communities (snowbed and willow-shrub) location C, Hol, Norway. The estimates derive from a linear mixed effect model (REML-estimation) with plot, enclosure, block, and plant species as random factors. The table shows estimated differences between factor levels (i.e. “treatment contrasts”; see Appendix 2), se and adjusted *p*-values. Values in bold indicate significant differences. Estimated parameters for each combination of plant functional group and habitat (\pm se) are shown.

Parameter estimates based on treatment contrasts					Estimates for each factor level		
Parameter (fixed effects)	Estimate	se	z	P	Parameter	Estimate	se
Intercept	1.0542	0.1432	7.3630	<0.001	Snowbed-grasses	1.0542	0.1432
Pl.comm (willow-shrub vs. snowbed)	-0.1039	0.0200	-5.1810	<0.001	Willow-shrub-grasses	0.9504	0.1437
PFG (herbs vs. grasses)	0.4662	0.1915	2.4350	0.0511	Snowbed-herbs	1.5204	0.1432
					Willow-shrub-herbs	1.4166	0.1437
PFG (woody species vs. grasses)	0.3435	0.1915	1.7940	0.2247	Snowbed-woody species	1.3977	0.1432
					Willow-shrub-woody species	1.2939	0.1436
Random effects:							
Groups	Name	Variance	% of Var				
Plot	Intercept	0.0051	8.04	Number of observations: 505.			
Enclosure	Intercept	0.0053	8.37	Groups: Plot, 89; Enclosure, 9;			
Block	Intercept	0.0045	7.06	Block, 3; Plant species, 6.			
Plant species	Intercept	0.0365	57.80				
Residual		0.0118	18.73				

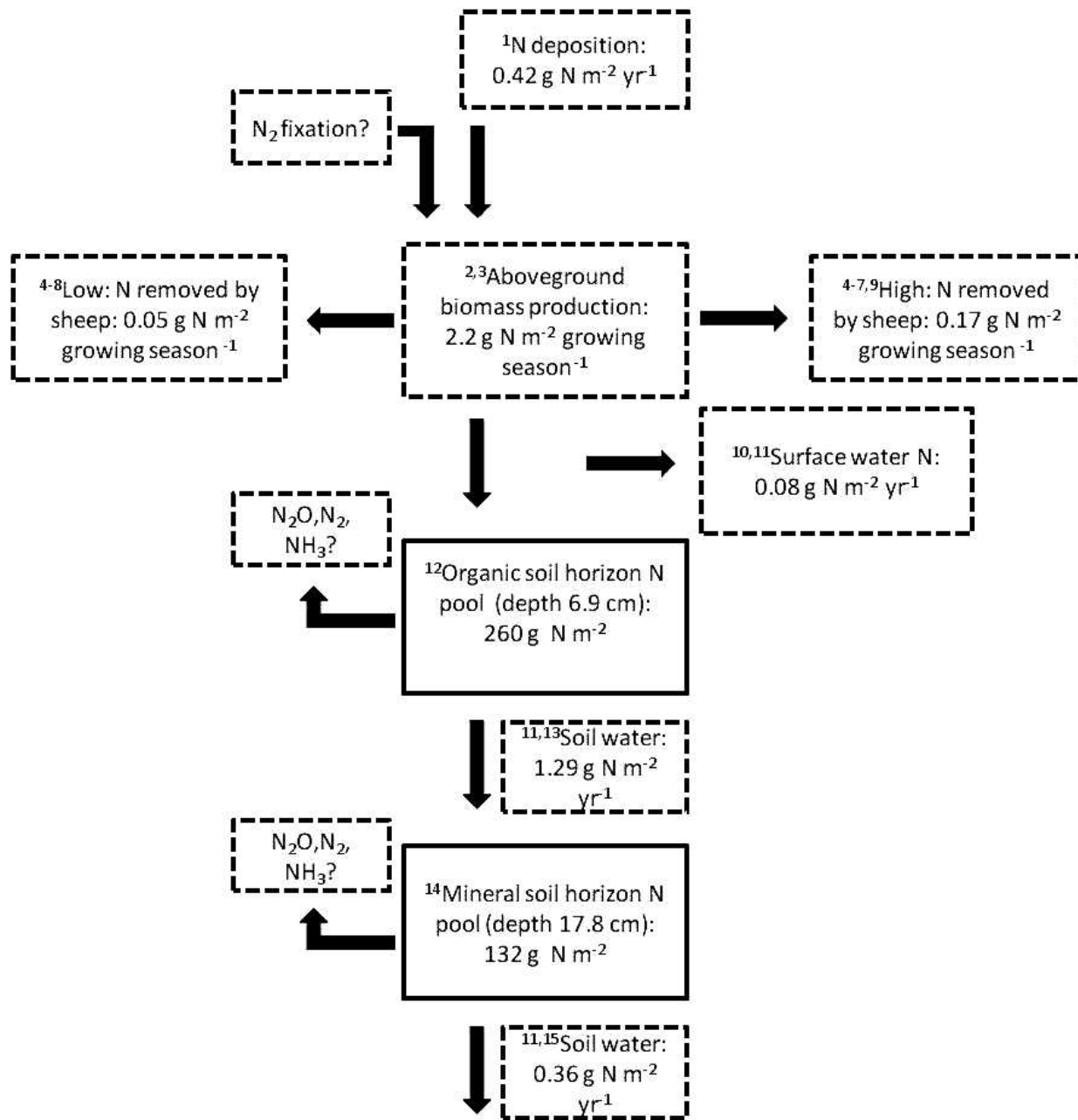


FIGURE 5. Nitrogen budget for grassland habitats at Hol, Norway. The figure shows average pools (closed boxes) and fluxes (dashed boxes) of nitrogen. Input data and assumptions for the N budget are listed below. We have no data on N_2O , N_2 , or NH_3 emissions or N_2 fixation. Input data and assumptions: 1. Average N deposition is $0.416 \text{ g m}^{-2} \text{ year}^{-1}$ (Aas et al., 2008). 2. Aboveground biomass is based on average biomass production in 2008 on grassland plots ($n = 44$) close to “location C plots” (G. Austrheim, unpublished material). 3. N-content of plants (% by weight) is based on average values from location C (graminoids, 1.1%; herbs, 2.3%; and woody species, 1.8%) and unpublished material for cryptogams sampled in 2009 (1.1%). 4. 21% of the net (i.e. excluding impediment) area (Fig. 1) consists of snowbeds (12%) with graminoids and alpine meadow communities (9%) dominated by graminoids and herbs. 5. Lambs gain weight and feed in grassland habitats only (corresponding to an average net lamb density of $3.7 \text{ lambs}/0.052 \text{ km}^2 = 71 \text{ lambs km}^{-2}$; and $11 \text{ lambs}/0.044 \text{ km}^2 = 250 \text{ lambs km}^{-2}$ grassland for the low and high grazing densities, respectively). 6. Lambs gain 22.87 kg (low density) and 20.15 kg (high density) weight during the growing season (Myserud, unpublished material). 7. All weight gain of the lambs is in form of meat, with an average protein content of $212.8 \text{ g kg meat}^{-1}$ (Ådnøy et al., 2005) corresponding to $212.8/6.25 = 34 \text{ g N kg meat}^{-1}$ (i.e. 3.4%). 8. Removal of N in form of weight gain at low grazing density: ($71 \text{ lambs km}^{-2} = 70 \times 10^6 \text{ lambs m}^{-2} \times 22.87 \text{ kg lamb}^{-1} \times 0.034 [\text{N-content}] \times 1000 = 0.05 \text{ g N m}^{-2}$). 9. Removal of N in form of weight gain at high grazing density: ($250 \text{ lambs km}^{-2} = 250 \times 10^6 \text{ lambs m}^{-2} \times 20.15 \text{ kg lamb}^{-1} \times 0.034 [\text{N-content}] \times 1000 = 0.17 \text{ g N m}^{-2}$). 10. Surface water fluxes are based on the mean N-concentration of water samples collected 2006–2009 in Hol (mean 0.08 mg L^{-1} ; Martinsen, unpublished material). 11. Yearly precipitation; 1000 mm (Evju et al., 2009). 12. O-horizon N-pool is based on average values of the data sets from location A (sampled 18 June–11 August 2007 using 100 cm^3 steel rings; $n = 27$; Martinsen, unpublished material) and C ($n = 88$; see Material and Methods). 13. Soil water fluxes from the O-horizon are based on locations A (altitude levels 2 and 3) and B (see Material and Methods). 14. Mineral soil N-pool is based on average values from location A (sampled 18 June–11 August 2007 using 100 cm^3 steel rings; $n = 27$; Martinsen, unpublished material) 15. Soil water fluxes from the mineral-horizon are based on location A (altitude levels 2 and 3) (soil water samples from the mineral horizon were in addition to O-horizon water samples [see Material and Methods] sampled in 2008–2009; Martinsen, unpublished material).

The full models always included grazing treatment (3 levels: no sheep, high and low density) as a fixed factor (Appendix 1). In addition, altitude level (2 levels: 1168 or 1259 m a.s.l., respectively) and period (3 levels: early, middle, or late summer) were included as fixed effects for the PRSTM-adsorbed N model (minimum adequate model, Table A2a; plotted estimates, Fig. 2). Plant community (two levels: grassland in snowbed or grassland partly covered with willow-shrub) and plant functional group (3 levels: grasses, herbs, or woody species) were included for the plant N-concentration model (minimum adequate model, Table 3). Day of incubation (3 levels: day 0, day 15, and day 63) and plant community (two levels) were included for the total extractable N model (minimum adequate model, Table A2b; plotted estimates, Fig. 3). Finally, month (3 levels: June, July, and August) and altitude (2 levels: 1169 or 1255 m a.s.l., respectively) were included as fixed effects for the DIN:DON ratio model (minimum adequate model, Table A2c; plotted estimates, Fig. 4). All full models were fitted with relevant interactions (Appendix 1). Some variables were transformed (ln or sqrt) prior to analysis to avoid violations of the model assumptions. Estimated parameters were back-transformed to the original scale before inclusion in the figures.

Results

IN SITU AVAILABILITY OF INORGANIC NITROGEN

The availability of inorganic nitrogen (expressed as PRSTM-adsorbed surplus N; NH₄-N + NO₃-N) was in general low and significantly affected by grazing treatment, altitude, and time of the growing season (Fig. 2, Table A2a). At both altitudes PRSTM-adsorbed N was significantly lower in the middle of the growing season as compared to the start and end, indicating a high plant and microbial demand for N in the middle of the growing season (Fig. 2). At the lower altitude in the early period of the growing season, low sheep density sites had significantly reduced surplus N compared to high sheep density and control. However, this difference diminished throughout the growing season due to an increase and decrease in PRSTM-adsorbed N at the low sheep density and no sheep treatment, respectively. At altitude 2, values for PRSTM-adsorbed N were similar in size as at altitude level 1, but there was no significant difference in surplus N between the grazing treatments (Fig. 2, Table A2a). The average of PRSTM-adsorbed N during the growing season and the two altitudes was dominated by NH₄-N (Table 2).

N-CONCENTRATION OF PLANTS

The N-concentration of the functional plant groups was not significantly affected by grazing (Table A1) but differed between the plant functional groups and was significantly smaller in grassland with willow-shrubs than grassland in snowbeds (Table 3). Grasses had a smaller N-concentration as compared to herbs and woody species, with the latter two only slightly differing (Table 3).

POTENTIAL NITROGEN MINERALIZATION

The amount of soil extractable inorganic nitrogen (NH₄-N + NO₃-N; µg g⁻¹ soil) was highly variable within the treatments with a large variability between the repeated extractions in each soil sample (Fig. 3, Table A2b). Soils from the enclosures with high sheep density had significantly greater amounts of initial extractable N (reflecting the amount of exchangeable N at the time of sampling) compared to the O horizons from the low sheep

density and control after 7 years of grazing treatment. There was a significant net mineralization throughout the incubation experiment at high sheep density (Table A2b). By contrast, soils originating from the low sheep density and no sheep treatments showed immobilization even after 63 days of incubation (Fig. 3). About 85% of the total extractable inorganic N was in the form of NH₄-N (Table 2).

INORGANIC NITROGEN IN SOIL WATER

The concentrations of inorganic N in O-horizon soil water were small compared to the total N, with a greater fraction of NH₄-N than NO₃-N (Table 2). Thus, the dissolved inorganic nitrogen to organic nitrogen ratios (DIN:DON) in the O-horizon soil water were in general small, illustrating the predominance of organic nitrogen in this system (Fig. 4, Table A2c). The fitted model for the DIN:DON ratios included an interaction between sheep density and growing season (i.e. month). DIN:DON ratios declined significantly from June to August. However, the decline was less pronounced at low and high sheep density as compared to the non-grazed sites (Fig. 4, Table A2c).

NITROGEN REMOVAL ASSOCIATED WITH WEIGHT GAIN OF SHEEP

The estimated N removal associated with weight gain of sheep feeding in grazing-preferred habitats (i.e. ~21% of the net study area) were greater and about the same as N lost from the system through runoff for the high and low sheep density treatments, respectively (Fig. 5). Nitrogen removal by sheep was about half of the N input in deposition and very small as compared to the total N-pool of the system (Fig. 5).

Discussion

It is well documented that herbivory by ungulates may affect N cycling (Hobbs, 1996). The type and magnitude of these effects may vary substantially with type of ecosystem, type of grazer, grazer density, season, and climate. The effect of herbivore density on N cycling in alpine areas is scarcely known, despite the importance of these areas for livestock grazing (Austrheim et al., 2011) as for native migratory ungulates during summer (Zeigenfuss et al., 2011). In this study we found clear effects of grazing on rates of PRSTM-adsorbed N (a measure of surplus N; H1) and potential N mineralization (H3); however, the N concentration of plants was not (as predicted; H2) affected by grazing in our study (Table A1). However, dissolved inorganic to dissolved organic N ratios (DIN:DON) in soil water were significantly affected by sheep density (H4). The effects of sheep grazing on rates of PRSTM-adsorbed N and DIN:DON ratios in soil water interacted with temporal and spatial variations in nutrient supply. The smaller amount of PRSTM-adsorbed N at low sheep density as compared to high sheep density and no sheep treatment at the lower altitude is probably caused by enhanced vascular plant biomass production at low sheep density (G. Austrheim, unpublished material), which may have increased plant uptake and thus reduced surplus N.

Net nitrogen mineralization rates in alpine and arctic soils are small and even negative due to high rates of N immobilization (Chapin et al., 1988; Fisk et al., 1998; Olofsson et al., 2004). However, as reported by Fisk and Schmidt (1996), N fertilization may significantly enhance net N mineralization. At our study site the average amounts of net mineralized N (after 9 weeks of

incubation) were 5.0 (± 5.9), 4.8 (± 7.8), and 42 (± 9.5) $\mu\text{g N g soil}^{-1}$ for the non-grazed sites, low density, and high density sites, respectively (Fig. 3). Normalized on amount of soil organic matter (SOM; Martinsen et al., 2011), this represent 7.5 (± 12), 13 (± 16), and 101 (± 19.7) $\mu\text{g N g SOM}^{-1}$, corresponding to rates of 0.1 (± 0.2), ~ 0.2 (± 0.3), and ~ 1.6 (± 0.3) $\mu\text{g N g SOM}^{-1} \text{ day}^{-1}$. A comparable range of mineralized N is reported by Nadelhoffer et al. (1991) in Alaska. Across 6 arctic ecosystems, Nadelhoffer et al. (1991) found a strong variability in amount of mineralized N (13 weeks of incubation) with average values ranging from 6 to 129 $\mu\text{g N g SOM}^{-1}$. By comparing net N mineralization rates of O-horizons from five plant communities in a tundra landscape of northern Sweden, Björk et al. (2007) reported significantly greater N mineralization rates from meadow ecosystems (0.6–0.7 $\mu\text{g N g SOM}^{-1} \text{ day}^{-1}$) as compared to heath ecosystems (0.1–0.2 $\mu\text{g N g SOM}^{-1} \text{ day}^{-1}$) during a 40 day incubation study at 12 °C. Net N mineralization rates from the alpine meadow ecosystems thus correspond well with our findings from enclosures with no sheep and low sheep density, but are somewhat smaller than the rates from enclosures with high sheep density.

Nitrogen mineralization may increase in grazed areas due to trampling and input of nutrients in the form of feces and urea (van der Wal and Brooker, 2004; van der Wal et al., 2001) and/or by herbivore-induced effects on quality and quantity of litter and SOM (Frank and Groffman, 1998b; Harrison and Bardgett, 2008). In a parallel study at Hol, Martinsen et al. (2011) found evidence for reduced amounts of carbon and smaller amounts of particulate organic matter (determined by the fraction of particulate organic matter to the total soil organic matter) at high sheep density as compared to no sheep treatments. Authors reported the opposite at low sheep density; however, there was no difference in the total N pool between grazing treatments, suggesting a density dependent effect of grazing on the form of N in the system, with high sheep density increasing the fraction of inorganic N (Fig. 3). These results correspond with density-dependent effects on fluxes and pools of N found as an effect of reindeer grazing, although total N pools did not differ between grazing treatments (Olofsson et al., 2004). Furthermore, net mineralization and net immobilization occur when microbes are predominately limited by C and N, respectively (Bardgett, 2005). As decomposition of uncomplexed SOM (i.e. SOM that is neither recognizable as litter nor associated with organomineral complexes) may be coupled with immobilization of N (Christensen, 2001; Whalen et al., 2000), the grazing-induced effects on N mineralization in our study suggest that microbes at high sheep density are limited by C (hence net mobilization of N), whereas microbes at low sheep density and non-grazed sites are somewhat more limited by N (hence net immobilization of N).

Despite grazing-induced differences in potential N mineralization and surplus N, the N concentration of plants was strongly related to plant community (Table 3) but not affected by grazing (H2 not supported; Table A1). The greater N concentration of plants in snowbeds as compared to plants in grasslands with willow-shrub is most likely related to the phenological stage of the plants. The carbon to nitrogen (C:N) ratio of plants increases during the growing season (Beck et al., 2005; van der Wal et al., 2000). Plants growing in snowbeds (heavy snowpack, late melting) are in a younger phenological stage (hence greater N concentration) than plants in grasslands with willow-shrub. We found no correlation between net N mineralization or amount of initial extractable N and N concentration of the plants (results not shown). Olofsson et al. (2004) found a significant correlation between soil $\text{NH}_4\text{-N}$ concentration and N content in new growth of plants, but did not find any correlation between N content and

net N mineralization. As discussed by Fisk et al. (1998), *in situ* net N mineralization appears inadequate for estimating plant available N because plants also may utilize other sources of N not accounted for when measuring net N mineralization.

Many of the PRSTM-adsorbed N values and inorganic N concentrations in soil water (DIN) were at or below the detection limit (Table 2), which were 0.2 $\mu\text{g N cm}^{-2}$ and 0.02 mg L^{-1} for PRSTM-adsorbed N and DIN, respectively. Dissolved nitrogen in the O-horizon soil water was dominated by DON ($\sim 90\%$), as has been reported by Makarov et al. (2003) in alpine ecosystems of the northern Caucasus. By reinvestigating a ^{15}N -tracer experiment in an alpine grassland in Austria (^{15}N introduced by single pulse labeling in 1974/1975), Gerzabek et al. (2004) reported an N loss of only 55% during 27–28 years. The low rates of PRSTM-adsorbed N (Fig. 2), low concentrations of DIN, and low DIN:DON ratios in soil water (Fig. 4, Table 2) at our study site support that N in alpine ecosystems is effectively recycled and remains in the plant-soil system (Gerzabek et al., 2004). Furthermore, we found a strong seasonal variation in PRSTM-adsorbed N and DIN:DON ratios of the soil water with a decline in the middle of the growing season. Changes in availability of soil N throughout the growing season due to seasonal changes in microbial and plant demand has been reported by e.g. Lipson et al. (1999), Weintraub and Schimel (2005), and Morecroft et al. (1992). Factors like N deposition and catchment productivity may also affect DIN:DON ratios, as reported by Hessen et al. (2009). They found a significant positive relationship between $\text{NO}_3\text{-N}$ to organic N ratios and N deposition. However, N deposition is likely the same within the experimental area at Hol, and should therefore not affect the relative differences in soil water DIN:DON ratios between grazing treatments.

Grazing may also promote nitrification. Frank et al. (2000) found a grazing-induced increase in nitrification rate of 68% in the Yellowstone National Park, and Gao et al. (2009) reported significantly greater gross nitrification and denitrification rates at high grazing intensity as compared to low grazing intensity in the Tibetan Plateau, China. We found evidence for increased net N mineralization at the sites with high sheep density compared to low density and controls (Fig. 3). However, the fraction of $\text{NO}_3\text{-N}$ to the sum of inorganic N ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) was in general very low irrespective of grazing (Table 2). The fraction $\text{NH}_4\text{-N}$ of the total initial extractable inorganic N ranged from about 80% to 100% in our study. $\text{NH}_4\text{-N}$ was also the dominant form of inorganic N in mountain areas in northern Sweden and in the Colorado Front Range (Björk et al., 2007; Mullen et al., 1998). Furthermore, inorganic N adsorbed on the PRSTM-probes was dominated by $\text{NH}_4\text{-N}$ contributing about 70% to 75% of the sum of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ (Table 2). In addition, we found $\text{NH}_4\text{-N}$ to be the dominant form of inorganic N in soil water. Only 8% of the 225 water samples (Table 2) had $\text{NO}_3\text{-N}$ values above the detection limit. Together, these findings clearly indicate low nitrification potentials in this system, and thus small risk of N loss through leaching.

Ungulates may strongly impact C and N storage (Piñeiro et al., 2010). However, impacts of grazing depend on herbivore density and the productivity of the system (Wardle et al., 2004). Grazing clearly affected N cycling in grazing-preferred grassland habitats in our study. Estimates of N loss associated with grazing revealed greater and about the same loss of N from the system as N lost through runoff for the high and low sheep density sites, respectively (Fig. 5). At high sheep density, the estimated N removal associated with weight gain of sheep is about half of the N input in deposition and is very small compared to the total N-pool of the system (Fig. 5). Furthermore, removal of N by the sheep as compared to the total input of N is probably even smaller, as N-fixation was not included and has been found to be significant in

high-elevation systems (Hobara et al., 2006). Losses of N associated with denitrification (Frank and Groffman, 1998a) and volatilization of NH_3 from feces and urea may be significant (Dahlin et al., 2005), but were not assessed in our study. However, denitrification rates are likely to be small due to the small concentration of $\text{NO}_3\text{-N}$ we found in our study. Also NH_3 emissions are expected to be minor from the acidic soils at Hol. Since the amount of N removed by sheep (both densities) and the amount lost in surface runoff do not exceed the N input in N deposition, the system will likely accumulate N, even at high sheep density.

Herbivores may transport nutrients from grazing-preferred habitats where they consume biomass to areas where they rest and defecate (Schoenecker et al., 2004; Van Uytvanck et al., 2010). In turn, this may affect the spatial distribution of N as ruminants return a great share of ingested N in form of urea and feces (Dahlin et al., 2005; Van Uytvanck et al., 2010; Whitehead, 2000). Typically, sheep retain between 5 and 15% of ingested N (Whitehead, 2000). Assuming a retention of ingested N of $\sim 10\%$, an estimated removal of $0.17 \text{ g N m}^{-2} \text{ growing season}^{-1}$ at high sheep density implies a biomass removal of $\sim 1.7 \text{ g N m}^{-2} \text{ growing season}^{-1}$. This is about two-thirds of the biomass production (2.2 g N m^{-2}) in grasslands (Fig. 5). Depending on location of excretal return, this may locally enhance substrate quality, stimulating microbial activity and nutrient cycling (Hobbs, 1996). At our study site, where grazing-preferred grasslands cover about 20% of the area, the sheep may have a significant influence on N availability in the surrounding vegetation (e.g. dwarf shrub heath), affecting the competition between plant species in the long term.

We conclude that grazing significantly affects N mineralization rates and the bioavailability of N in grazing-preferred grasslands. However, despite grazing-induced effects on N cycling, we found no evidence for increased risk of N loss in soil water. Losses associated with weight gain of the sheep are relatively small compared to the total N-pool in the system. Thus, the sheep densities used in this experiment are likely to have minor impacts on the system in terms of long-term N losses.

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APPENDIX 1.

TABLE A1. Model selection for the fixed effect structure of linear mixed effect models (based on ML-estimation) for $\ln(\text{PRS}^{\text{TM}}\text{-adsorbed N})$ ($\mu\text{g N cm}^{-2}$ 20 days burial $^{-1}$), $\text{sqrt}(\text{N-content plants})$ (%), $\ln(\text{total extractable N})$ ($\mu\text{g N g soil}^{-1}$), and $\ln(\text{DIN:DON})$ ratio of soil water. The minimum adequate models are highlighted in italics and bold. The models always included enclosures ($n = 9$) nested in blocks ($n = 3$) as random effects. In addition, plot and site (each consisting of 3 plots) were included for the $\text{PRS}^{\text{TM}}\text{-adsorbed N}$ model (based on data set B; see Material and Methods); plot and plant species (6 different species) were included for the plant N-content model (based on data set C; see Material and Methods); plot was included for the total extractable N model (based on data set C; see Material and Methods); and plot, site (each consisting of 3 plots) and year were included for the DIN:DON ratio model (based on data sets A and B; see Material and Methods). Step indicates models with a different fixed effect structure for each dependent variable. AIC = Akaike's information criterion. ΔAIC = change in AIC between 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 lower explanatory power. Step comp. indicates the models compared.

Dependent variable	Model (random effects)	Step	Model (fixed effects)	Df	AIC	Δ AIC	P	Step comp.
In(PRS adsorbed N) ($\mu\text{g N Cm}^{-2}$ 20 day s burrial $^{-1}$)	~(1 block) +	1	<i>~treatment*altitude*period</i>	23	162.16			
	(1 enclosure) + (1 site) + (1 + plot)	2	<i>~treatment*altitude+treatment* period+altitude*period</i>	19	164.24	2.08	0.042	1 vs. 2
sqrt(N-content plants) (%)	~(1 block) +	1	~treatment*pl.comm*PFG	23	-619.90			
	(1 enclosure) +	2	~treatment*pl.comm+treatment* PFG+pl.comm*PFG	19	-624.55	-4.65	0.501	1 vs. 2
	(1 plot) + (1 + plant species)	3	~treatment*pl.comm+treatment*PFG	17	-623.39	1.16	0.076	3 vs. 2
		4	~treatment*PFG+pl.comm*PFG	17	-626.72	-2.17	0.399	4 vs. 2
		5	~treatment*pl.comm+pl.comm*PFG	15	-631.91	-7.36	0.958	5 vs. 2
		6	~treatment+pl.comm+PFG	11	-632.62	-8.07	0.440	6 vs. 2
		7	~pl.comm+PFG	9	-633.49	-0.87	0.209	7 vs. 6
		8	~treatment+PFG	10	-611.69	20.93	<0.001	8 vs. 6
		9	~treatment+pl.comm	9	-630.62	2.00	0.038	9 vs. 6
		10	~pl.comm	8	-611.83	21.66	<0.001	10 vs. 7
		11	~PFG	7	-630.94	2.55	0.038	11 vs. 7
In(total extractable N) ($\mu\text{g N g soil}^{-1}$)	~(1 block) +	1	~treatment*day*pl.comm	22	397.46			
	(1 enclosure) + (1 plot)	2	~treatment*day+treatment*pl.comm+ day*pl.comm	18	391.46	-6.00	0.737	1 vs. 2
		3	~treatment*day+treatment*pl.comm	16	389.21	-2.25	0.419	3 vs. 2
		4	~treatment*day+day*pl.comm	16	390.57	-0.89	0.212	4 vs. 2
		5	~treatment*pl.comm+day*pl.comm	14	408.90	17.44	<0.001	5 vs. 2
		6	~treatment*day+pl.comm	14	388.34	-0.87	0.209	6 vs. 3
		7	~treatment*day	13	399.19	-0.15	0.174	7 vs. 6
In(DIN:DON ratio)	~(1 block) +	1	~treatment+day	9	407.44	19.25	<0.001	8 vs. 7
	(1 enclosure) +	2	~treatment*altitude*month	24	292.70			
	(1 site) +	2	~treatment*altitude+treatment*month+ altitude*month	20	290.01	-2.69	0.293	1 vs. 2
	(1 plot) +	3	~treatment*altitude+treatment*month	18	286.31	-3.70	0.825	3 vs. 2
	(1 year)	4	~treatment*month+altitude*month	18	288.41	-1.60	0.324	4 vs. 2
		5	~treatment*altitude+altitude*month	16	293.81	3.80	0.018	5 vs. 2
		6	~treatment*month+altitude	16	284.60	-5.41	0.639	6 vs. 2
		7	~treatment+month+altitude	12	287.90	3.30	0.023	7 vs. 6
		8	~treatment*month	15	284.72	0.12	0.161	8 vs. 6
	9	~treatment+month	11	288.48	3.76	0.019	9 vs. 8	

APPENDIX 2.

We report differences between fixed effect factor levels based on “treatment contrasts.” Treatment contrasts is the default in R, with factor levels arranged in alphabetical sequence (Crawley, 2007, p. 377). Thus the intercept will be the factor level that comes first in the alphabet. The only exception is the DIN:DON model (Table A2c), where differences between months are based on differences with June (intercept) and not August.

TABLE A2a. Parameter estimates of (ln) PRSTM-adsorbed inorganic nitrogen ($\mu\text{g N cm}^{-2}$ 20 days burial⁻¹) within O-horizons of grassland habitat soils location B, Hol, Norway. The estimates derive from a linear mixed effect model (REML-estimation) with plot, site, enclosure, and block as random factors. The fixed effect factors are treatment (different sheep densities [high = 80 sheep km⁻², low = 25 sheep km⁻², and no sheep = control]), altitude (two altitudinal levels [\sim 1168 and 1259 m a.s.l]), and period (three burial periods [1: 03.07–23.07; 2: 23.07–11.08; and 3: 11.08–31.08]). The table shows estimated differences between factor levels (i.e. “treatment contrasts”), se, and adjusted *p*-values. Values in bold indicate significant differences. Estimated parameters for each factor combination (\pm se) are shown. P1, P2, and P3 = period 1, 2, and 3; A1, A2 = altitude level 1 and 2; C = control (no sheep); H = high sheep density; and L= low sheep density.

<i>Parameter estimates based on treatment contrasts</i>					<i>Estimates for each factor combination</i>		
Parameter (fixed effects)	Estimate	se	z	P	Parameter	Estimate	se
Intercept	0.7215	0.1773	4.0690	<0.01	P1A1_C	0.7215	0.1773
Treatment (high vs. control)	-0.1819	0.2440	-0.7460	0.9982	P1A1_H	0.5396	0.1773
Treatment (low vs. control)	-1.0360	0.2405	-4.3080	<0.01	P1A1_L	-0.3145	0.1725
Altitude (alt 2 vs. alt 1)	-0.3728	0.2405	-1.5500	0.7144	P1A2_C	0.3487	0.1725
Period (period 2 vs. period 1)	-0.6801	0.1520	-4.4730	<0.01	P2A1_C	0.0414	0.1725
Period (period 3 vs. period 1)	-0.1688	0.1520	-1.1100	0.9513	P3A1_C	0.5527	0.1725
Treatment (high vs. control): Altitude (alt 2 vs. alt 1)	0.2882	0.3401	0.8470	0.9941	P1A2_H	0.4551	0.1725
Treatment (low vs. control): Altitude (alt 2 vs. alt 1)	1.2870	0.3377	3.8110	<0.01	P1A2_L	0.5996	0.1725
Treatment (high vs. control): Period (period 2 vs. period 1)	0.1765	0.2150	0.8210	0.9956	P2A1_H	0.0360	0.1725
Treatment (low vs. control): Period (period 2 vs. period 1)	0.3669	0.2266	1.6190	0.6633	P2A1_L	-0.6277	0.1912
Treatment (high vs. control): Period (period 3 vs. period 1)	0.0397	0.2188	0.1810	1.0000	P3A1_H	0.4106	0.1773
Treatment (low vs. control): Period (period 3 vs. period 1)	0.7013	0.2111	3.3220	0.0127	P3A1_L	0.2180	0.1725
Altitude (alt 2 vs. alt 1): Period (period 2 vs. period 1)	0.0309	0.2111	0.1460	1.0000	P2A2_C	-0.3005	0.1725
Altitude (alt 2 vs. alt 1): Period (period 3 vs. period 1)	0.1145	0.2111	0.5420	0.9999	P3A2_C	0.2944	0.1725
Treatment (high vs. control): Altitude (alt 2 vs. alt 1): Period (period 2 vs. period 1)	-0.3100	0.2985	-1.0380	0.9696	P2A2_H	-0.3276	0.1725
Treatment (low vs. control): Altitude (alt 2 vs. alt 1): Period (period 2 vs. period 1)	-0.6250	0.3070	-2.0360	0.3592	P2A2_L	-0.3077	0.1725
Treatment (high vs. control): Altitude (alt 2 vs. alt 1): Period (period 3 vs. period 1)	-0.1717	0.3013	-0.5700	0.9999	P3A2_H	0.2688	0.1725
Treatment (low vs. control): Altitude (alt 2 vs. alt 1): Period (period 3 vs. period 1)	-0.8050	0.2957	-2.7220	0.0773	P3A2_L	0.4417	0.1725
Random Effects:							
Groups	Name	Variance	% of Var				
Plot	Intercept	0.00356	20.1	Number of observations: 156. Groups: Plot, 54; Site, 18; Enclosure, 9, Block, 3.			
Site	Intercept	0.0402	22.7				
Enclosure	Intercept	0.0000	0.0				
Block	Intercept	0.0050	2.8				
Residual		0.00965	54.4				

TABLE A2b. Parameter estimates of (ln) total nitrogen (NH₄-N + NO₃-N; µg g⁻¹ soil) extracted on organic soil samples from grassland habitats (location C, Hol, Norway). The estimates derive from a linear mixed effect model (REML-estimation) with plot, enclosure, and block as random factors. The fixed effect factors are Treatment (different sheep densities [high (H) = 80 sheep km⁻², low (L) = 25 sheep km⁻², and no sheep (C) = control]) and Day (number of incubation days [day 0 (D0) = start of incubation; initial extractable N, day 15 (D15) = extractable N after 15 days of incubation and day 63 (D63) = extractable N after 63 days of incubation]). The table shows estimated differences between factor levels (i.e. “treatment contrasts”), se, and adjusted *p*-values. Values in bold indicate significant differences. Estimated parameters for each factor combination (±se) are shown.

<i>Parameter estimates based on treatment contrasts</i>					<i>Estimates for each factor combination</i>		
Parameter (fixed effects)	Estimate	se	z	P	Parameter	Estimate	se
Intercept	3.3179	0.1358	24.4330	<0.001	DO_C	3.3179	0.1358
Treatment (high vs. control)	0.5737	0.1756	3.2670	0.0085	DO_H	3.8916	0.1211
Treatment (Low vs. control)	0.2253	0.1855	1.2140	0.7768	DO_L	3.5431	0.1344
Day (15 vs. 0)	0.0966	0.1027	0.9410	0.9230	D15_C	3.4145	0.1358
Day (63 vs. 0)	-0.0898	0.1027	-0.8740	0.9463	D63_C	3.2281	0.1358
Treatment (high vs. control): Day (15 vs. 0)	0.0824	0.1371	0.6010	0.9940	D15_H	4.0706	0.1211
Treatment (low vs. control): Day (15 vs. 0)	0.0310	0.1148	0.2140	1.0000	D15_L	3.6707	0.1333
Treatment (high vs. control): Day (63 vs. 0)	0.5745	0.1371	4.1910	<0.001	D63_H	4.3763	0.1211
Treatment (low vs. control): Day (63 vs. 0)	0.0128	0.1459	0.0880	1.0000	D63_L	3.4661	0.1344
Random effects:							
Groups	Name	Variance	% of Var				
Plot	Intercept	0.3009	69.0		Number of observations: 247.		
Enclosure	Intercept	0.0000	0.0		Groups: Plot, 83; Enclosure, 9, Block, 3.		
Block	Intercept	0.0033	20.7				
Residual		0.1319	30.2				

TABLE A2c. Parameter estimates of (ln) dissolved inorganic nitrogen to organic nitrogen ratio (DIN:DON) of O-horizon soil water from grassland habitats at locations A and B, Hol, Norway. The estimates derive from a linear mixed effect model (REML-estimation) with plot, site, enclosure, block, and year as random factors. The fixed effect factors are Treatment (different sheep densities [high (H) = 80 sheep km⁻², low (L) = 25 sheep km⁻², and no sheep (C) = control]) and Month (June, July, and August). The table shows estimated differences between factor levels (i.e. “treatment contrasts”), se, and adjusted *p*-values. Values in bold indicate significant differences. Estimated parameters for each month and treatment combination (±se) are shown.

<i>Parameter estimates based on treatment contrasts</i>					<i>Estimates for each factor level</i>		
Parameter (fixed effects)	Estimate	se	z	P	Parameter	Estimate	se
Intercept	-2.1351	0.2597	-8.2220	<0.001	June_C	-2.1351	0.2597
Treatment (high vs. control)	-0.1637	0.1593	-1.0280	0.8865	June_H	-2.2988	0.2635
Treatment (low vs. control)	-0.3203	0.1496	-2.1410	0.1886	June_L	-2.4554	0.2572
Month (July vs. June)	-0.3139	0.1277	-2.4570	0.0906	July_C	-2.4489	0.2559
Month (August vs. June)	-0.6115	0.1250	-4.8920	<0.001	Aug_C	-2.7465	0.2510
Treatment (high vs. control): Month (July vs. June)	-0.1774	0.1900	-0.9340	0.9273	July_H	-2.7901	0.2628
Treatment (low vs. control): Month (July vs. June)	0.1062	0.1873	0.5670	0.9962	July_L	-2.663	0.2633
Treatment (high vs. control): Month (Aug. vs. June)	0.2607	0.1698	1.5350	0.5460	Aug_H	-2.6496	0.2514
Treatment (low vs. control): Month (Aug. vs. June)	0.4090	0.1585	2.5800	0.0661	Aug_L	-2.6578	0.2502
Random effects:							
Groups	Name	Variance	% of Var				
Plot	Intercept	0.0168	5.56		Number of observations: 225.		
Site	Intercept	0.0161	5.32		Groups: Plot, 69; Site, 24,;		
Enclosure	Intercept	0.0000	0.00		Enclosure, 9, Block, 3; Year, 2.		
Block	Intercept	0.0032	1.07				
Year	Intercept	0.1081	35.81				
Residual		0.1577	52.24				