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Long-term snowpack manipulation promotes large loss of bioavailable nitrogen and phosphorus in a subalpine grassland

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Abstract Nutrient retention in ecosystems requires synchrony between the supply of bioavailable nutrients released via mineralization and nutrient uptake by plants. Though disturbance and chronic nutrient loading are known to alter nitrogen (N) and phosphorus (P) dynamics and induce nutrient export, whether long-term shifts in climate affect source-sink synchrony, and ultimately primary productivity, remains uncertain. This is particularly true for snow-dominated ecosystems, which are naturally subject to lags between nutrient inputs and uptake. To address how climate change may affect nutrient source-sink synchrony we examined the impacts of deepened snowpack on N and P losses in a subalpine grassland in the Northern Rocky Mountains, USA, where we have experimentally increased snowpack depths by two- and four-times ambient snow for 45 years. Long-term snow addition resulted in remarkably high levels of bioavailable-N leaching (up to 16 kg ha^{-1} year^{-1}) that were 11–80 times higher than those under ambient snowpack. Estimated bioavailable-P losses also increased with snow addition, but to a lesser degree (up to 0.3 kg ha^{-1} year^{-1}), indicating greater enhancement of N losses over P losses during snowmelt. Because these losses could not be explained by changes in nutrient inputs in snowpack or by changes in plant-soil turnover, our results suggest that high bioavailable-N leaching under deep snowpack originates not from a lack of N limitation of plant productivity, but rather from enhanced subnivean microbial processes followed by snowmelt leaching prior to the growing season. This is supported by reduced soil N pools in the snow treatments. Snow-dominated regions are projected to experience shifts in seasonal snowpack regime. These shifts may ultimately affect the stoichiometric balance between available N and P and future plant productivity.

Keywords Climate change · Grassland · Nitrogen cycle · Nutrient leaching · Phosphorus cycle · Snowmelt · Nutrient stoichiometry

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Abbreviations
BTL   Bangtail study area
DIN   Dissolved inorganic nitrogen
DON   Dissolved organic nitrogen
SWE   Snow-water equivalent
TDN   Total dissolved nitrogen

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Introduction

Nitrogen (N) and phosphorus (P) most commonly limit primary production in temperate and boreal terrestrial ecosystems (Elser et al. 2007; LeBauer and Treseder 2008), but interaction of the two element cycles can be complex. Nitrogen is delivered to ecosystems predominantly from the atmosphere whereas P derives from rock weathering. Furthermore, while both N and P become available through decomposition of organic matter, the availability of P is disproportionately influenced by physical dissolution and sorption compared with that of N, which relies heavily on biological processes and highly susceptible to leaching loss once nitrified. Thus, limitation of plant productivity by N or P depends on the balance between external inputs and losses and the degree to which they remain soluble in the soil.

In many ecosystems, leaching is an important loss pathway for both N and P. However, plant uptake has the capacity to draw down these nutrients to low levels when limited, leaving little for leaching (Gerber and Brookshire 2014). Thus, large nutrient leaching losses are often a good indicator of relaxation of nutrient constraints in the plant-soil system. On the other hand, if the supply of dissolved nutrients and plant uptake are not synchronized, leaching of bioavailable nutrients can occur, at least transiently, despite nutrient limitation of plants (Sickman et al. 2003; Yano et al. 2010; Curtis et al. 2011).

An important example of such dynamics occurs in high latitude and elevation ecosystems in early spring when, before initiation of plant uptake, snowmelt leaches nutrients that accumulated from over-winter mineralization (Buckeridge and Grogan 2010). Snow-driven systems are biogeochemically distinct from other precipitation regimes in that the insulation of soil by snowpack sustains microbial activity over winter (Sturm et al. 2005), but a large loss of nutrients can occur with the snow-melt pulse prior to peak biological uptake (Sickman et al. 2003; Yano et al. 2010). At the same time, snow can be the dominant source of atmospheric N, and in some cases available P (as dust), required for plant production in such ecosystems (Lawrence et al. 2010).

Further, in mountain landscapes variation in topography and vegetation distribution can result in highly heterogeneous distributions of snowpack depth and timing of melt. This means that spatially close areas may experience dramatically different local rates of N and P inputs, internal cycling and loss. For example, in subalpine grasslands of the Northern Rocky Mountains, Weaver (1974) found that soils in areas with deep and long-lasting snowpack had lower concentrations of cations but higher levels of phosphate compared to areas with persistently shallow snowpack. Subsequent experimentation using snow-fences confirmed these results (Weaver and Collins 1977). While a number of snow-fence experiments have since shown that deepened snowpack tends to increase soil microbial activity and nutrient availability (Wipf and Rixen 2010), the long-term (multi-decade) implications of increased snowpack for the balance of available nutrients are uncertain. Moreover, little is understood about the time scales over which plant-soil nutrient cycles would equilibrate to such changes. This is critical given predicted shifts in snowfall and snowpack for many high-latitude areas globally (Stewart 2009; Silverman et al. 2013). Particularly unclear is how long-term changes in snowpack might affect the ratios of N and P in inputs, soil pools, and leaching losses.

To evaluate how multi-decadal change in snowpack may affect N and P dynamics and balance, we initiated new measurements in the snow addition experiment of Weaver and Collins (Collins and Weaver 1978), one of the longest running snow-manipulation experiments globally (45 years; Wipf and Rixen 2010), in which winter snowpack depths have been continuously doubled ($\times 2$) or quadrupled ($\times 4$) using snowfences. The $\times 2$ and $\times 4$ snow-addition treatments prolong the snow-covered period and thus shorten the growing season by up to 2 and 4 weeks relative to the Control with a ~ 13-week growing season. The snow treatments have also significantly altered plant community composition to less drought-tolerant grasses and annual forbs (Brookshire & Weaver, in press). Our objective was to determine how multi-decadal increases in snow affect the pools and ratios of N and P in soils and the magnitude of nutrient losses relative to inputs. In the absence of major disturbance, ecosystems over time approach a steady state in which nutrient inputs equal nutrient outputs. Thus, we were particularly interested in whether leaching losses and available pools of N and P had shifted after 4 decades of sustained snow addition and if there were threshold

responses to different snow addition levels relative to the Control plots. We predicted that sustained asynchrony in nutrient supply and demand magnified by deepened snow would result in enhanced N and P availability in soils and increased leaching losses of bioavailable N and P relative to the Controls but that elevated losses would be balanced directly by external supply from snow.

Methods

Study site description

The study site is a native subalpine grassland-meadow, an ecosystem type common to the North-Central Rocky Mountains. It lies in the Bangtail Study Area (BTL, ~420 ha, 2330 masl, 45°N, 110°W), SW Montana, USA. The soils are Typic Cryoborolls (US Soil Taxonomy) and the vegetation is dominated by *Festuca idahoensis* (Mueggler and Stewart 1974; Weaver and Collins 1977). Mean annual precipitation is ~960 mm, nearly 90 % of which occurs as snow between September and May. Average July and January maximum temperatures are 22 and −5 °C, respectively.

Beginning in 1968, three snow-treatment areas were established on a flat grassland meadow in which persistent wind renders snowcover to ≤0.6 m depth: an unmanipulated area (Control); and areas in which snow depths were experimentally doubled (×2); and quadrupled (×4) relative to the maximum depth of ambient snowpack (~0.6 m). All treatment plots had similar plant community composition, dominated by *F. idahoensis* prior to the initiation of the snow-addition treatment. Five snowfences (30-m long, plastic mesh or metal wires woven with wooden strips) were built within each of the ×2 and ×4 treatment areas, oriented perpendicular to prevailing westward winds (Fig. 1). These fence arrangements create a massive continuous snowpack over the central section of the treatment areas: the size of continuous snowpack is roughly equivalent to the snowfence height over approximately 25 × 20 m area for the ×2 treatment and 50 × 20 m area for the ×4 treatment, thus allowing evaluation of snowpack effects with minimal edge effects. Persistent strong wind results in stable snow accumulation behind snow fences, achieving more than ~60 % of intended
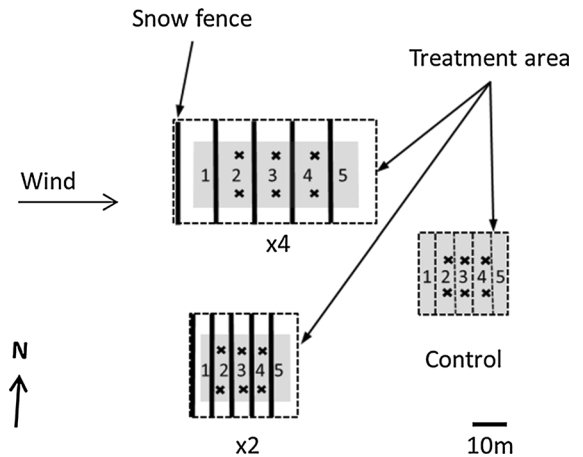

Fig. 1 Experimental design of snow-addition treatments. The *shaded rectangle* within each treatment area (*dotted rectangles*) indicates the area that received the intended snow depth: snow accumulation within the outermost several meters (i.e., white edge just inside the ×2 and ×4 *dotted rectangles*) was less than in the central part (i.e., *shaded areas*). Thus, to avoid edge effects and to sample areas that consistently received the intended snow depth, we collected all samples within these *shaded areas*. The *numbers* indicate five sub-plots for soil samples, and the ×'s indicate approximate locations of lysimeters

snowpack depth even in low-snow years. Within each treatment, the leeward side of each fence was designated as a subplot in the snow-manipulated plots. Five subplots were established within the Control treatment area in the same manner, but without physical fences. The size of each subplot was 11 m × 20 m (×4) and 6 m × 20 m (×2 and Control). Our field measurements were conducted between summers of 2011 and 2013. Snowfall during our study period was normal: peak snow-water equivalent (SWE) in 2012 and 2013 were 95 % of the average for the 2003–2013 period at the nearest snow telemetry monitoring site (SNOTEL) site (Brackett Cr., station ID 365, ~16 km NW of our study site). Average peak snowpack depths were 30 (±3) cm in the Control, 101 (±16) cm in the ×2, and 185 (±25) cm in the ×4 treatments. This translates to a snowpack-depth ratio relative to the Control of 3.3 (×2) and 6.2 (×4). Our measures of SWE (method described below) in spring 2013 (following a winter with a normal snowfall) indicated a factor difference across treatments of 1: 4.4: 8.6 in Control ×2 and ×4 plots, respectively. During winters of 2011–2012 and 2012–2013, the snowpack in the Control treatment nearly completely disappeared in mid-winter at least

once during warm spells. In spring 2012, a snow storm in late May added a new snow cover to all treatment plots, including the Control and ×2 that had been completely snow free.

In the spring of 2012, Campbell Scientific CS650 reflectometers and a solar panel-powered CR1000 data logger (Logan, Utah) were installed at the site. Two time-domain reflectometers (TDR) and temperature sensor (Campbell 107-L) were deployed vertically in each treatment plot to monitor hourly soil moisture and temperature of the top 30-cm soil layer.

Soil leachate sampling

In autumn 2011, six tension lysimeters (Prenart Super Quartz; Prenart Equipment, Denmark) were installed within each treatment at 30 cm below the surface at ~30° angle according to Lajtha et al. (1999) to capture leachate below the primary rooting zone. Within each treatment we installed two lysimeters in each of three central subplots. Lysimeters were installed well under the deepest part of the snowpack to account for tapering of snow pack depth with distance from snowfences. The shortest distances between lysimeters were ~6.5 m in the ×4, ~6 m in the ×2 and ~5 m in Control treatments. Each lysimeter was equipped with 1-L reservoir that was kept in an insulated underground housing.

In early April prior to the onset of snowmelt, narrow snow pits were carefully dug to access the reservoir housings without disturbing the snowpack directly above the lysimeters. Soil water was collected approximately biweekly by applying vacuum pressure (−50 kPa) and later retrieving the water accumulated in the reservoir. We discarded the first collection. At each sampling event the depth of snowpack was recorded by measuring the distance between the bottom of the snow pit and the surface of undisturbed snowpack. We also recorded temperatures at the bottom of the snowpack and soil (0–5 cm). After each access to the reservoir housing, the snow pits were carefully back-filled to ~60 cm with the dugout snow. The access snow pits were often buried or plugged between sampling by new or windblown snow. During our study, no soil water could be collected before April under snowpack or during the mid to late growing season because of lack of mobile water (see *Leachate and snow chemistry* in Results for further information). The soil water was brought back

to Montana State University and stored frozen. The samples were thawed and filtered through acid-washed 0.7 μm glass fiber filters immediately before chemical analysis. One lysimeter in the Control and three in the ×2 treatment (one each from each central subplots) became dysfunctional during 2012 because of disconnected tubing underground.

Snow sampling and SWE measurement

In April 2012, snow samples were collected from the ×2 treatment for chemical analysis. Right before snowmelt started, an undisturbed portion of snowpack was cored to the ground at 20-cm increments (for ease of handling) using an acid-washed PVC corer (diam. = 10 cm) and a plexiglass core cutter (4 cores total). The bottom of each snow core was removed to avoid contamination from the soil, and the snow was transferred to Montana State University in clean plastic bags. Each 20-cm section of all cores was melted in an acid-washed gallon jug that was covered. Ultrapure Milli-Q water was processed along with the snow samples as a laboratory blank. The melted snow and the blank were filtered through acid-washed 0.7 μm glass fiber filters and stored frozen until analysis. SWE (kg/m^2) of the snowpack was determined in late March 2013 by taking four cores from the central part of each plot (Fig. 1, shaded area), using a Federal SWE Tube (Rickly Hydrological Co.) and weighing the snow cores and recording the depth of the holes after cores were removed. Total N and P inputs from snowpack were estimated by adding nutrient contents in all 20-cm sections.

Estimation of nutrient flux

Hydrologic losses of dissolved inorganic N (DIN), dissolved organic N (DON), and PO_4–P from the rooting zone were estimated for 2013 snowmelt in three different ways, all of which involved multiplying a snowmelt-water flux during each lysimeter-sampling interval by the lysimeter nutrient concentrations measured at the end of the interval. We then summed all nutrient fluxes over the snowmelt period, which was defined as all sampling intervals in which snow cover was present. We assumed that the lysimeter nutrient concentration at the end of each interval approximates the concentration for the entire interval, but likely yields conservative estimates for N flux due

to the generally decreasing concentrations during snowmelt (Fig. 1). However, this method might over estimate PO_4–P flux, given the slight increases in concentrations over time during snowmelt.

In the first method, the snowmelt-water flux was estimated as a negative change in SWE, which was calculated from snowpack depth measured at each sampling and the initial snowpack density, i.e., snowpack density immediately before the onset of snowmelt (determined on 25 March 2013; Control = 430, $\times 2$ = 526, and $\times 4$ = 559 kg/m^3) to avoid repeated destructive measurement of SWE near the lysimeters. We assumed that overland runoff during snowmelt was negligible, if any, because (1) the ground is essentially flat (and thus predominantly vertical flow is expected) and (2) there was no visible water or saturated snow layer at the bottom of snowpack outside of the treatment plots during the snowmelt period. We also assumed that the initial snow density remained constant throughout the snowmelt period, even though density of snowpack generally increases in spring due to gravitational settling and net condensation (Hood et al. 1999; Mizukami and Perica 2008; Jonas et al. 2009). For example, snow density increased by 150 % at a nearby SNOTEL site at similar elevation (Brackett Cr., station ID 365) during the same snowmelt period. We therefore consider our estimates of hydrologic flux to be highly conservative.

Second, possible lower limits of nutrient fluxes were estimated in the same manner as above, but using minimum initial snowpack density (316 kg/m^3) observed between 2003 and 2013 at the nearby SNOTEL site. We assumed that an initial snowpack density can be approximated by snowpack density at the time of maximum SWE in April.

Third, possible upper limits of nutrient fluxes were estimated by using the maximum possible snowpack density calculated for the depth of the 2013 snowpack as:

$$\rho* = 700 - (20470/h_s)(1 - \exp(-h_s/67.3))$$

where $\rho*$ is the maximum-possible snow density and h_s is the snowpack depth (Brown et al. 2003). This equation has been shown to well describe snow aging during spring in high latitude and alpine ecosystems (Brown et al. 2003). The maximum possible density for the initial snowpack was calculated to be: Control = 459, $\times 2$ = 559, and $\times 4$ = 607 kg/m^3.

We consider our flux estimations to be conservative because (1) we assumed no gain of SWE via settling or condensation and; (2) melt-water flux was calculated to be 'zero' for the second sampling interval when new snowfall resulted in a positive change in snowpack depth and hence a positive change in SWE, even though the collection of leachate and running ephemeral springs indicated that snowpack melted considerably; and (3) we did not estimate leaching fluxes for autumn because we did not estimate water flux (albeit small) during this period.

Soil sampling and analysis

Available N and P in the surface soil were determined during the growing season of 2012. Three soil cores (0–15 cm, diam. = 2.0 cm) per subplot were collected at one- to three-week intervals, with shorter intervals in May and early June when the study site was still not completely snow free. During Jun–Sep sampling, soils were collected from four randomly selected subplots. The cores were brought back to Montana State University, combined by subplot and by depth, weighed, and bulk density was determined. The soils were then manually homogenized, and passed through 2-mm sieve to remove rocks and large roots. Subsamples of the sieved soils were dried at 50 °C to determine moisture content. Available N was determined by extracting the field-moist soil with 1 M KCl (soil: KCl = 1:5) within 48 h of sampling. A weak Bray's extraction (Bray and Kurtz 1945) was used to determine available P; subsamples of the oven-dried soil was extracted in a Bray's solution (0.03 M NH_4F and 0.025 M HCl) at soil: Bray solution = 1:10. Extractants were filtered through Whatman paper filters (No. 5), and stored frozen until analysis.

In the summer of 2011, total soil C, N, and P concentrations were determined for the top 50 cm. Three soil cores (diam. = 2.0 cm) were collected from each subplot at 10-cm depth increments. The soils were processed as described above, dried at 105 °C, and ground.

Soil samples were analyzed by Agvise Laboratories (Northwood, ND, USA) for total C and N contents using an Elementar CN combustion analyzer (Hanau, Germany) and for total P content by acid digestion (EPA method 3050) followed by inductively coupled plasma (ICP) detection.

Aqueous chemical analyses

Water and soil extracts were analyzed for nitrite plus nitrate (here after NO_3) ammonium (NH_4) and phosphate (PO_4) using an automated flowthrough colorimetry. We used SEAL QuAAtro (SEAL Analytical, WI, USA) for the lysimeter and snow samples and Lachat Quikchem (Lachat Instrument, CO, USA) for soil extracts. Dissolved total N (TDN) was determined for lysimeter and snow samples at North Carolina State University, using Shimadzu TOC-V analyzer (Shimadzu Corp.) with a total N detector. Dissolved organic N was determined by subtracting DIN from TDN.

Data analysis

We evaluated the effects of snow addition on bulk soil and plant available nutrient pools and nutrient concentrations in leachate using linear mixed-effect models (LME). We treated subplots as replicates for soils and individual lysimeters within a given treatment as replicates for leaching concentrations. Snow addition was treated as levels corresponding to the factor difference in ambient versus experimental SWE (Control = 1, ×2 = 4.4, ×4 = 8.6). Given the nested nature of the experimental design in which replicate snow fences are clustered in space (Weaver and Collins 1977), we constructed a series of LME models in which we varied fixed effects (treatment versus treatment × time interactions) and random effects (individual snow fences, soil plot and lysimeter locations, and time) to evaluate potentially confounding influences of spatial and temporal variation not controlled by our experimental treatments. We then chose final models with the lowest Akaike's information criterion (AIC). All statistics were performed using the nlme package in R (version 3.0.1; R Core Team 2012).

Results

Leachate and snow chemistry

Experimental snow addition resulted in large increases in N losses and, to a lesser degree, P losses from this subalpine grassland ecosystem. Leaching loss below the rooting zone was restricted to a few months per

year: during spring snowmelt and a short period in late autumn (Fig. 2a–c). Minimum daily soil temperatures of Control plots, which are subject to shallow and
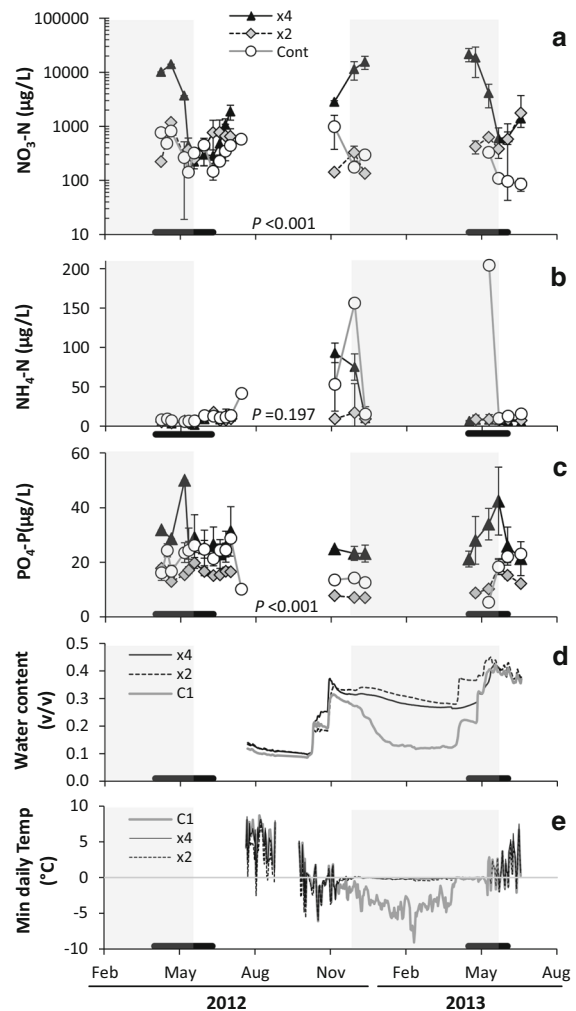

Fig. 2 Effects of snow-input manipulation on N and P leached below rooting zone, soil temperature and moisture. Volume-weighted mean (±1 SE) NO_3–N in log scale (a), NH_4–N (b), and PO_4–P (c) in un-manipulated Control (Cont), doubled (×2), and quadrupled (×4) snowpack-depth treatments. Water could be collected only during spring snowmelt and autumn wet-up periods. (d) Daily means of soil water content and, (e) minimum daily soil temperature for 0–30 cm. The P values shown in the graphs indicate significance of snow treatment effect. The *grey areas* indicate durations during which snow was present continuously on the ×2 treatment plots. Control plots were completely snow free about 2 weeks earlier in both years, and ×4 treatment plots became snow free about one (2013) to two (2012) weeks later than ×2 plot. The *black bars* on the X-axis indicate durations in which ephemeral springs near the study site were running

discontinuous snowpack, were sub-freezing throughout winter (Fig. 2e). This resulted in lower liquid water content during winter (i.e., most water was frozen) compared to soils in the snow-addition treatments (Fig. 2d). Soil conditions under the snow-addition treatments remained isothermal (near 0 °C) throughout winter.

As soon as sufficient soil water became mobile, the water collected in lysimeters consistently displayed NO_3–N concentrations above 10 mg/L in the ×4 treatment and as much as ∼1 mg/L in the Control and ×2 treatments. Treatment differences for NO_3–N remained highly significant after accounting for sub-plot and lysimeter location effects (Fig. 2a). Ammonium concentrations were generally low in spring and rose only moderately in autumn but did not differ systematically across treatments (Fig. 2b). Thus, NO_3–N dominated DIN leaching losses: NO_3–N accounted for ≥79 % (average >93 %) of DIN under the snow-addition treatments and ≥64 % (average 87 %) in the Control in both spring and autumn. Phosphate concentrations were also influenced significantly by the snow-input treatment, showing generally higher concentrations under the ×4 than other treatments across all seasons (Fig. 2c). The snow-addition treatments strongly influenced seasonal nutrient concentrations in the spring and less so in the autumn; mean spring NO_3–N and PO_4–P concentrations were consistently higher under the ×4 treatment than the Control, with NO_3–N concentrations under the ×4 treatment being 8–14 times higher than the ×2 treatment and Control (Table 1).

The snow-addition treatments significantly altered the DIN:PO_4–P ratio of leachate. In spring,

approximately two- to nine-times more N per P was lost from the ×2 and ×4 plots, respectively, compared with the Control (Table 1). The DIN:PO_4–P ratios of the leaching water from the ×4 plots (485, Table 1) were well above the ratio of snowpack water (68, Table 2).

The mean NO_3–N and NH_4–N concentrations of snowpack at our site were similar to the regional average estimated from three US Geological Survey (USGS) snowpack chemistry monitoring (1993–2011) sites located ≤100 km from BTL (Table 2). The range of SWE created by the snowfences at BTL overlapped with the regional range of minimum and maximum means observed during this period (Table 2). In spite of the large differences in SWE at the beginning of snowmelt (Table 2), soil moisture converged to similar levels across treatments soon after the disappearance of snowpack and remained <10 % (w/w) in the mid to late growing season (Figs. 2d, 3).

Estimated nutrient fluxes

Estimated DIN losses were strikingly high under the snow-addition treatments: 16.0 kg-N ha^{-1} year^{-1} of plant-available N was lost from the ×4 and 2.3 kg-N ha^{-1} year^{-1} from the ×2 treatments, while only 0.2 kg-N ha^{-1} year^{-1} was leached from the Control, approximately balancing inputs from snow (Fig. 4a; Table 2). The loss of DIN from the snow-addition treatments greatly exceeded N inputs from snowpack (Table 2; Fig. 4a). Conservatively estimated likely ranges of leaching losses indicate that even when we apply the lowest snowpack density in the last two decades at the nearby SNOTEL site (52–57 % of

Table 1 Seasonal mean DIN and PO_4–P concentrations, and DIN:PO_4–P ratios of leaching water

| | Spring (2012 + 2013) | | | Autumn (2012) | | | P value |
| | (Apr–Jul) | | | (Nov–Dec) | | | |
	Control	×2	×4	Control	×2	×4	
NO_3–N (µg/L)	351.2 (57.2)	621.4 (105)	4970 (1775)	486.7 (253)	202.1 (63.5)	9925 (3739)	<0.001
NH_4–N (µg/L)	24.4 (12.2)	7.9 (0.9)	7.7 (0.9)	74.9 (42.2)	11.8 (2.6)	59.3 (25.2)	0.197
PO_4–P (µg/L)	20.9 (1.5)	15.2 (0.8)	29.1 (1.9)	13.5 (0.5)	7.3 (0.2)	23.8 (1.0)	<0.001
DIN:PO_4–P (molar)	56.0 (15.0)	99.8 (21.2)	484.7 (200)	97.1 (43.9)	66.4 (22.2)	1096 (424)	0.025

Means (±1 SE) are shown

The P values indicate significance of snow treatment effect

Table 2 Average snowpack chemistry and peak SWE for BTL and the region

	Regional[a]		BTL[b]	
Snowpack chemistry (µg/L)				
NO₃–N	83.3	(3.4)	74.2	*(4.7)*
NH₄–N	73.7	(3.4)	79.6	(8.8)
DON	–	–	41.2	(6.4)
PO₄–P	–	–	5.0	(0.3)
DIN:PO₄–P (molar)	–	–	68.1	(8.4)
SWE (cm)				
Average min	22	(16)	Control 14	(3)
Average	47	(4)	×2 62	(5)
Average max	75	(4)	×4 120	(22)
DIN input from snowpack (kg ha⁻¹ year⁻¹)				
Average min	0.3		Control 0.2	
Average	0.7		×2 0.9	
Average max	1.2		×4 1.8	

NO_3–N, NH_4–N, PO_4–P, DIN:PO_4–P (molar), kg ha^{-1} year^{-1}

Regional average is determined for a 1993–2011 period

Mean (±1 SE) are shown

[a] Data from USGS Rocky Mountain regional snowpack chemistry monitoring sites for Big Sky, Daisy Pass, and Twenty-Mile. Regional SWE data were not available between 1994 and 2001. Average min (max) is the average of the lowest (highest) annual SWE observed across the three sites over the monitoring period ($n = 3$); average is the average of all SWE data points across all three sites ($n = 33$)

[b] Snow chemistry determined for 2012 snowpack and SWE for 2013 snowpack ($n = 4$). Ambient snow input (Control); doubled (×2) and quadrupled (×4) snowpack depth

[c] Snowpack DIN concentrations were multiplied by SWE

snowpack density observed in 2013 for the ×2 and ×4 treatments) to our snow-addition treatments, ∼2 and ∼9 kg ha⁻¹ year⁻¹ would still have been lost from the ×2 and ×4 treatments, respectively. Similarly, loss of PO₄–P from the snow-addition treatments exceeded input from snowpack by about two to fivefold (Fig. 4b).

Soil N and P pools

The large hydrologic losses of N under deeper snowpack were reflected in differences in bulk soil-N pools and N:P ratios. Bulk N concentration declined under the snow-addition treatments relative to the Control throughout the soil profile (0–50 cm), with the greatest differences in the rooting zone (0–30 cm,
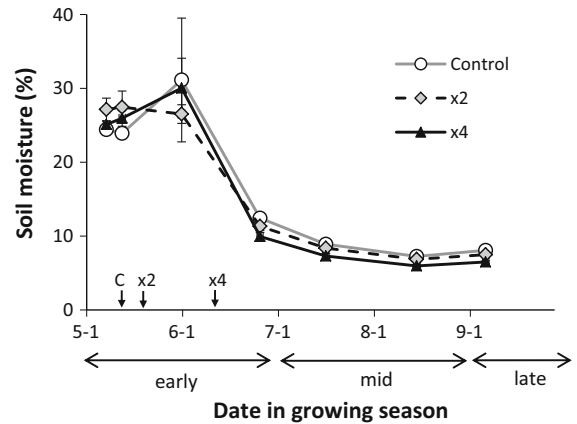

Fig. 3 Gravimetric soil moisture (0-15 cm) during 2012 growing season across snow-manipulation treatments. The growing season was divided into three stages; early (May–Jun), mid (Jul–Aug), and late (Sep) growing seasons. *Error bars* are ±1 SE ($n = 5$ in May; 4 for the rest). The *arrows* indicate the timing when Control (C), doubled (×2), and quadrupled (×4) snowpack-depth treatment plots became completely snow free for the first time after April. All treatment plots become completely under a snow cover once again due to a snow storm in late May

Fig. 5a). This pattern was accompanied by parallel changes in bulk soil C but not by P, which did not differ systematically across the snow-addition treatments or with depth (Fig. 5b, c). Soil N:P ratios followed the profile of N, varied roughly from 3 to 6, with ratios being generally lower in the ×4 relative to Control within the rooting zone (Fig. 5d). The bulk density within the top 30-cm soil was significantly higher under the snow-addition treatments relative to the Control soil (Fig. 5e). This increase in bulk density offset lower soil C and N concentrations, resulting in a lack of significant differences in area-based soil C, N, and P pools across the snow-addition treatments (Table 3). Soil pH was also significantly lower under the snow treatments, especially within the surface horizons (Fig. 5f).

Following the large increases in NO₃–N exports under deepened snowpack, we observed low extractable NO₃–N throughout the entire growing season with no difference among the snow-addition treatments (Fig. 6a). In contrast, extractable NH₄–N concentrations were roughly twice that of NO₃–N throughout the year (Fig. 6b). The snow-addition treatment significantly lowered NH₄–N concentrations, with concentrations in the Control generally
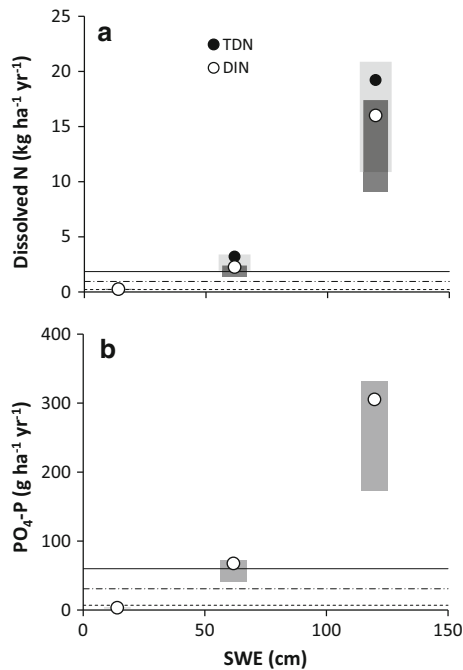
Fig. 4 Relationship between snow-water equivalent (SWE) and leaching loss of DIN, TDN (**a**) and PO$_4$–P (**b**) below rooting zone (30 cm) during 2013 snowmelt. The lowest SWE (14 cm) corresponds to the Control; medium SWE (62 cm) to ×2 treatment; highest SWE (120 cm) to ×4 treatment. Note that NO$_3$–N accounts for ≥87 % (Control) and ≥93 % (×2, ×4) of DIN. The *black* and *white circles* are estimated fluxes for DIN, TDN, and PO$_4$–P during 2013 snowmelt. The *light grey boxes* indicate likely ranges of TDN flux and darker grey boxes DIN (**a**) or PO$_4$–P (**b**). The ranges of flux were estimated from likely ranges of snowpack density at our site (for details, see Methods). Note that the *grey boxes* are too small to be seen for the Control. The *horizontal lines* indicate estimated DIN and PO$_4$–P inputs from the snowpack in 2013: the Control (*dotted line*), ×2 (*dot-dash line*), and ×4 (*solid line*) treatment plots

higher than the other two treatments. The strongest treatment effect was observed in the availability of P: extractable PO$_4$–P was generally higher under deeper snowpack throughout growing season. Unlike available N, the extractable PO$_4$–P pool declined steadily by 50 % or more over the three-month growing season in all treatments (Fig. 6c). The ratio of available N to P was extremely low under the snow-addition treatments throughout the growing season (≤1) relative to the Control, largely driven by higher extractable P and lower NH$_4^+$ (Fig. 6d).

Discussion

Increased snowpack resulted in increased nutrient leaching as predicted but we did not expect losses to far exceed external inputs. Losses of bioavailable nutrients are thought to be a good indicator of the nutrient limitation status of terrestrial ecosystems. That is, if nutrient limited, terrestrial biota should efficiently draw down bioavailable nutrients and minimize leaching losses (Aber et al. 1998; Curtis et al. 2011; Gerber and Brookshire 2014). The elevated snow inputs to our subalpine grassland has resulted in extremely high leaching loss of NO$_3$–N from the plant-soil system: estimated NO$_3$–N leaching from the snow-addition treatments (∼2–16 kg/ha) is comparable to or even exceeds annual NO$_3$–N leaching from ecosystems subject to long-term pollution (e.g., Currie et al. 1996; Nohrstedt et al. 1996; Hentschel et al. 2009). Although the large losses of available N could indicate N-saturation (Aber et al. 1998), our results suggest that this is not the case in this grassland judging from lack of change in available N in soils and N in plant biomass (Brookshire & Weaver, in press). Rather, we propose that asynchrony between plant uptake and internal supply resulted in large leaching losses of available N despite possible N limitation.

We first considered the degree to which N in the snowpack could have contributed directly to the large losses of bioavailable N. Estimated DIN losses from our unmanipulated grassland (Control) were similar to or below external N inputs from snow. However, our measures indicate that DIN losses from the snow-addition treatments could not be accounted for by a lack of retention of snowpack-derived DIN (Table 1). We conservatively estimate that DIN losses from the snow-addition treatments were two to nine times greater than N delivered in snowpack. The inference that contemporary atmospheric deposition is insufficient to account for the observed high losses is supported by low annual wet DIN deposition (0.9 kg ha^{-1} year^{-1}) measured at the nearest NADP monitoring sites (Clancy, MT; Yellowstone, WY) between 1985 and 2012 (http://nadp.sws.uiuc.edu/NTN/ntnData.aspx). Even if DIN is assumed to be 46 % of total N deposition, as observed in the Color-
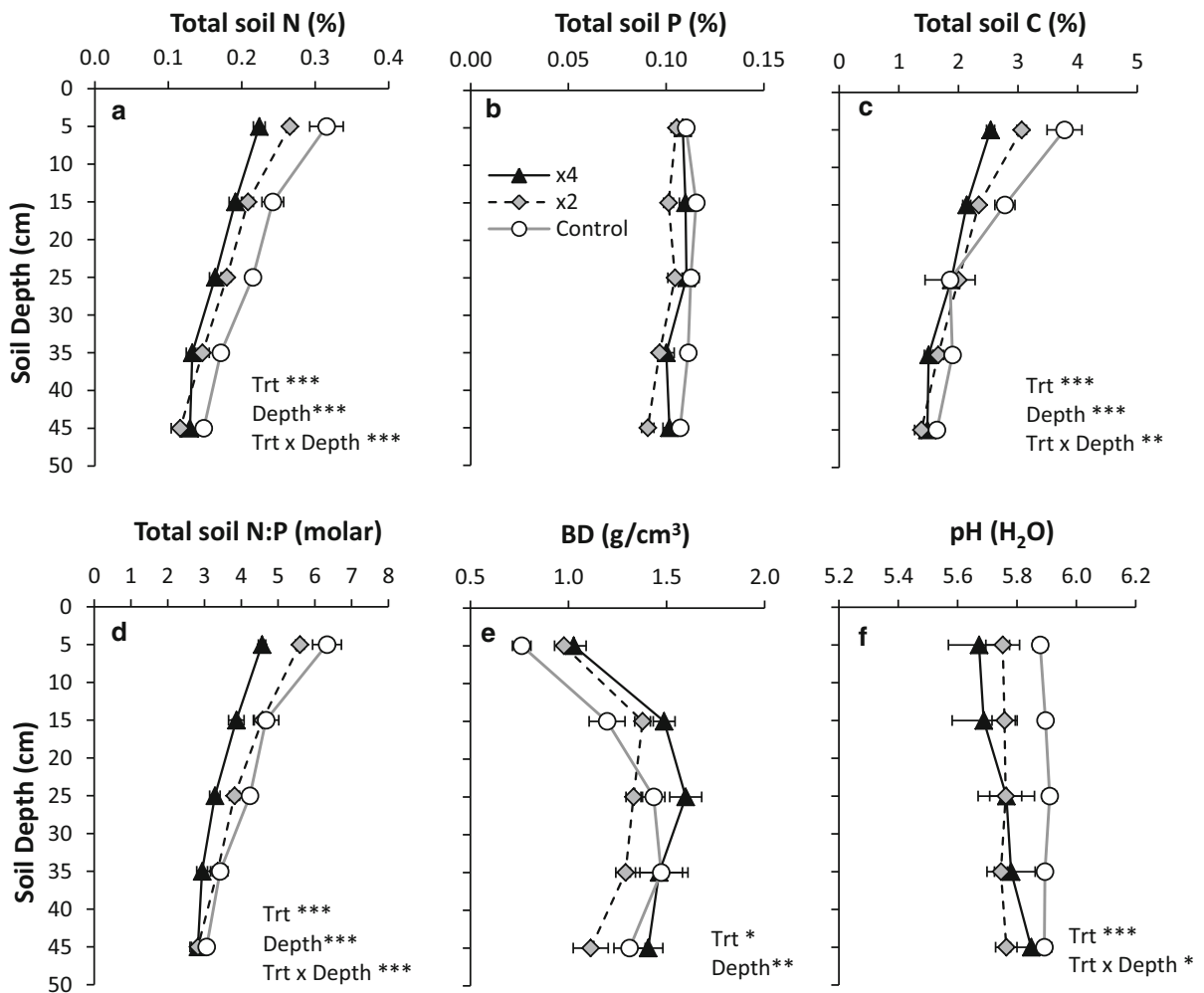
Fig. 5 Effect of snow addition treatments on chemical and physical properties of soil. The depth profiles of total soil N (a); total soil P (b); total soil C (c); molar ratio of soil N:P (d); bulk density (e); and pH (f) are shown for soils collected in 2011 (n = 5). Mean (±1 SE). Statistical significance of snow treatment (Trt), soil depth and the interaction of treatment and depth were shown when the differences are present: *$P < 0.05$; **$P < 0.01$; and ***$P < 0.001$. See Fig. 1 for other abbreviations

Table 3 Bulk soil C, N, P pools and N:P ratio of top 30 cm soil collected in 2011. Mean (±1 SE) are shown (n = 5)

Treatment	(g/m²)							
	Total C		Total N		Total P		N:P (molar)	
Control	8826	(663)	833	(23)	384	(15)	4.8	(0.2)
×2	8867	(193)	785	(20)	382	(15)	4.6	(0.2)
×4	8769	(362)	774	(34)	451	(20)	3.8	(0.1)

ado Front Range in Central Rocky Mountains (Benedict et al. 2013), and all N sources from elevated snowpack are incorporated, maximum total N inputs

(×4 treatment) from added snow is calculated to be only 4.0 kg ha⁻¹ year⁻¹. This is still well below DIN losses from the rooting zone, implying that these
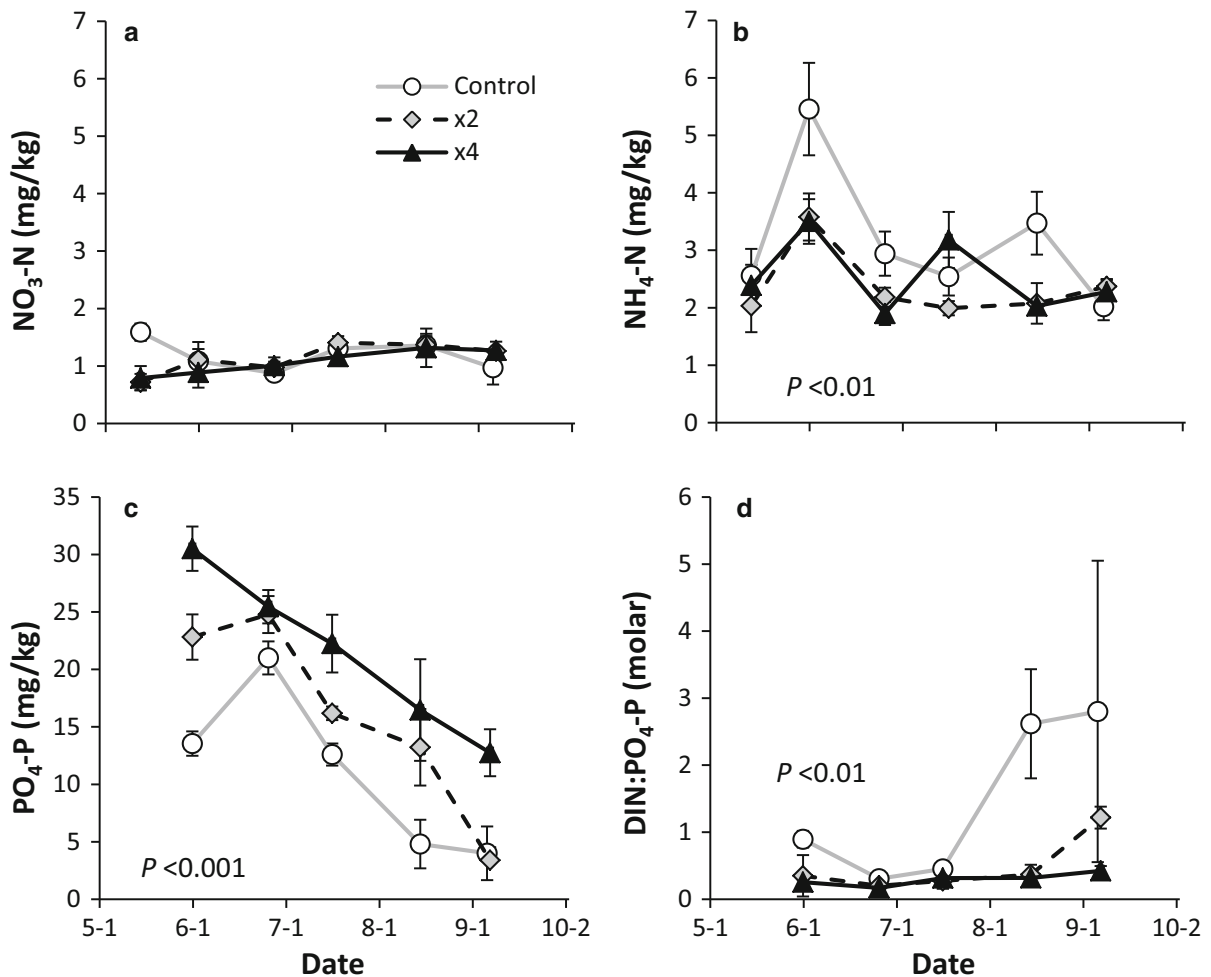
Fig. 6 Effects of snow-input treatments on available soil N and P in 2012 growing season. 1 M KCl-extractable NO_3–N (**a**), and NH_4–N (**b**); extractable (Bray's method) PO_4–P (**c**); and DIN:PO_4–P ratio (**d**). Means ±1 SE are shown ($n = 5$ for May; $n = 3$ for Aug (×4) and DIN:PO_4–P of Sep (Control and ×2); $n = 4$ for the rest). The P values shown in the graphs indicate significant snow-treatment effect at $P < 0.05$

losses originate from mineralization followed by nitrification within the internal plant-soil system.

We did not consider N inputs from biological N_2 fixation which can be a major source of new N in many terrestrial ecosystems. However, our observations suggest that differences in N_2 fixation are unlikely to account for the treatment differences in N losses observed in our study. First, though biological N_2 fixation can increase N contents of plant biomass at the community level we find no long-term treatment differences in the N contents of grasses and forbs (Brookshire and Weaver, in press). Second, rates of asymbiotic N_2 fixation associated with snowpacks appear to be quite low (Larose et al. 2013). Third, the

only symbiotic N_2 fixer in our study area *Lupinus argenteus,* a species capable of high levels of N_2 fixation (Goergen et al. 2009), is less common in our study plots (Weaver and Collins 1977) and has decreased markedly in the snow-addition treatments over time (Weaver, unpublished data).

We attribute the large supply of leachable N under the snow-addition treatments to enhanced microbial mineralization and nitrification of soil organic N. Studies have shown that soil microbial activities can peak in winter under snowpack and that better insulated soils under deeper snowpack supports greater microbial biomass and N mineralization (Schadt et al. 2003; Schimel et al. 2004; Buckeridge

and Grogan [2010]). Snowpack in the Control is susceptible to loss of snowpack during warm spells, as observed in the middle winters during our study. Shallow and discontinuous snowcover in the Control likely constrains over-winter mineralization, potentially supplying much less substrate (NH_4) for nitrification. Observed long-term decreases in bulk soil N in the snow-addition treatments (Fig. 5a) are consistent with the effect of snowpack insulation, supporting greater production of leachable N. The idea that insulation of soil alone can trigger increased N leaching via enhanced microbial activity is supported by a snow-insulation experiment in Norway that showed large hydrologic losses of N after adding insulation to existing snowpack without increasing SWE (Kaste et al. [2008]). However, the large differences in leachate concentrations and estimated losses of NO_3–N between the ×2 and ×4 treatments could not be explained by snowpack's insulation effect alone, given the similar over-winter soil temperature of both treatments (Fig. 2e).

Our observations indicate a strongly non-linear relationship between SWE and nutrient fluxes in this grassland. It is not clear why nearly doubled SWE in the ×4 treatment resulted in ~7 times higher estimated NO_3–N leaching compared to ×2, even though soils of both treatments were well-insulated and maintained similar soil temperature over winter (Fig. 2e). Large losses of NO_3–N during snowmelt resulted not only from high melt-water throughput, as indicated by the presence of active ephemeral springs, but also concurrently high NO_3–N concentrations (Fig. 2a). Indeed, NO_3–N concentrations were elevated rather than diluted by increasing water throughput in the first half of snowmelt period, indicating a large mobile pool available for transport.

It is possible that higher water throughput under the ×4 versus the ×2 treatment also promotes higher rates of mineralization, especially at the beginning of snowmelt. The moving meltwater would likely deliver dissolved oxygen and C (substrate) effectively through soil micropores thus promoting N mineralization and substrate (NH_4^+) for nitrification. This mechanism is congruent with increased respiration as suggested by reduced bulk soil C concentration in the snow-addition treatments in the top 30 cm (Fig. 5c). The importance of N mineralization in early snowmelt is supported by our observation that new snowcover formed by a snow storm at the end of snowmelt (late May of 2012) did

not induce N leaching pulse (Fig. 2a). Observations in alpine tundra ecosystem are also consistent with the idea of high microbial activity in early snowmelt: microbial biomass N peaked immediately after the onset of snowmelt (Brooks et al. [1998]).

It is uncertain at which point N leaching began to surge in this long-term snow manipulation experiment and whether this pattern will continue. Based on results from other snowpack manipulation studies (Kaste et al. [2008]) it is quite possible that the shift in N leaching loss started soon after the implementation of the experiment. While uncertainty remains in the range of historical snowpack depths, it is reasonable to assume that N leaching in average years was similar to that reported in current study (average snowfall over a 2003–2013 period), at least in the past decade.

Although not measured in this study, N loss via denitrification could also be considerable during snowmelt. Studies in the Colorado Front Range show that soil denitrification is highest under deeper snowpack (up to 170 cm deep) and peak at the end of snowmelt (Brooks et al. [1997]; Williams et al. [1998]). Thus, it is possible that denitrification is partly responsible for the drop of NO_3–N concentrations right before the disappearance of snowpack (Fig. 2a). However, the contribution of denitrification to total N loss is likely small relative to leaching, based on the fact that the highest denitrification rates observed in these studies are one- to two-orders of magnitude lower (0.1–0.2 kg-N/ha during snow-covered season) than leaching losses estimated in our grassland (2–16 kg-N/ha).

Leaching loss of available P was also higher under the snow treatments relative to the Control (Fig. 4b), although PO_4–P concentrations throughout snowmelt were relatively similar across treatments. It is possible that sustained deeper snowpack over four decades has resulted in greater mineralization as well as weathering rates that in turn increased the 'leachable-P' pool. In alpine landscapes of the Colorado Rockies, for example, Litaor et al. ([2005]) found that topographically-driven variation in snowpack explained much of the variability in P forms and availability in soils. Chemical weathering of minerals in cold regions, such as glaciated environments, has been shown to be significant and that PO_4–P concentrations in water are controlled by the balance between weathering and precipitation with metal hydroxides (Chillrud et al. [1994]). Because insulated soil under deep snowpack

generally supports greater soil respiration and microbial activity compared to soil under shallower snow-pack (Williams et al. 1998; Walker et al. 1999; Schimel et al. 2004) it is possible that greater microbial mineral oxidation (Sharp et al. 1999) and increased soil acidity by respiration contribute to greater mineral weathering rates, and increased 'leachable-P' in soils. The lowered soil pH under the snow-addition treatments relative to Control (Fig. 5f) supports the idea that long-term increases in snowpack accelerates weathering.

Our results further indicate that N:P ratio of leachate increased with increasing snow inputs in this grassland ecosystem (Table 1): $DIN:PO_4–P$ ratios of leaching water (>50) were more than ten times greater than those of bulk soil (4–6, Fig. 5d). This large shift in N:P ratio of leachate was not associated with a change in plant N pools, supporting that over four decades of preferential N leaching resulted in lower soil N:P ratios under the $\times4$ treatment relative to the Control. The preferential loss of N over P is likely influenced by high reactivity of PO_4 with organic and mineral components of soil that immobilize PO_4 (McBride 1994). It is possible that the disproportional loss of N over P, combined with a shorter growing season, has contributed to observed shifts in plant community composition under elevated snow (i.e., increases in annual forbs and shifts in grass species; Brookshire & Weaver, in press).

Despite a considerably shorter growing season and large snow-induced losses of N, however, our results indicate that the long-term shift in snow inputs had little impact on growing season N availability. We suspect that this may result from similar rates of microbial mineralization during the growing season due to similarly low soil moisture content (Fig. 3). Indeed, even the nine-fold higher SWE in the $\times4$ treatment relative to Control did not translate to higher water availability during growing season. The soil's high sand content ($\sim50~\%$ or more) likely results in a relatively low water holding capacity. Alternatively, the lack of a treatment effect in extractable $NO_3–N$, despite the presence of large leachable $NO_3–N$ pool in the snow-addition treatments under snowpack (Figs. 2a, 4a), could arise from near complete flushing of this pool as well as the source of mineralizable N (e.g., proteins) during spring snowmelt. The smaller DON loss during snowmelt (Fig. 4a) followed by larger extractable $NH_4–N$ pool in the early growing season in the Control compared to the other treatments (Fig. 6b) may reflect greater retention of mineralizable N in the soil with smaller melt-water flux.

In contrast to available N, P availability in soils was clearly elevated during the growing season with enhanced snow pack (Fig. 6c). Increased $PO_4–P$ levels under the snow-addition treatments generated low ratios of available N:P pools throughout the growing season; approximately <1 in the $\times2$ and $\times4$ plots compared with 0.5–3 in the Control (Fig. 6d). These ratios are well below the Redfield ratio ($N:P = 16$) as well as those of soil microbial biomass in grasslands (8.3, Cleveland and Liptzin 2007). Generally low ratios of available N:P, and low concentrations of soil N overall, suggests that our grassland meadow ecosystem may be N limited, in which case N limitation would be expected to become more severe with long-term snow-addition. However, there are no data (from fertilization) to indicate what nutrient or combination of nutrients may limit net primary production (NPP) in this ecosystem.

In addition to accelerating losses of N and P from soil, deeper snowpack may directly and indirectly affect the C cycle. We found that soil C concentrations were reduced significantly with increasing snow input (Fig. 5c) consistent with small but significant declines in aboveground plant biomass after in the snow treatments (Brookshire and Weaver, in press). This could result from increased over-winter decomposition of soil organic matter and elevated soil respiration as mentioned above, and perhaps increased leaching loss of dissolved organic C, which often positively related to soil respiration (Godde et al. 1996; Hobbie et al. 2002). Other snow-manipulation studies have shown that deeper winter snowpack stimulates high soil respiration during winter (Williams et al. 1998; Walker et al. 1999; Schimel et al. 2004) and the growing season (Chimner et al. 2010; Nowinski et al. 2010). Net loss of soil C under deep snowpack may also be accelerated if root biomass deposition declines, as observed at our site after the first few years of the experiment (Weaver and Collins 1977).

Although snowpack has generally declined in western North America in recent decades because of rising air temperature (Mote et al. 2005), large uncertainty exists in our understanding of the long-range dynamics of snowpack at high elevations (Silverman et al. 2013). In fact, some of the highest elevation mountains have witnessed increased

snowfall over the past several decades (Williams et al. 2002; Stewart 2009). Our results have implications for understanding the role of heterogeneously distributed snowpack on nutrient exports in complex landscapes. Further, our results suggest that such increases in snow have the potential to non-linearly accelerate leaching losses of available N and exacerbate N limitation in high-elevation ecosystems not subject to high levels of N deposition. Potential shifts in the balance of soil N and P with changing snow regimes have significant implications for future primary productivity and plant community composition in currently snow-dominated high-elevation ecosystems.

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