BIOGEOCHEMICAL AND PLANT FUNCTIONAL GROUP RESPONSE TO LONG-TERM SNOW MANIPULATION IN A SUBALPINE GRASSLAND

by

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ABSTRACT

Snow represents an important control over plant communities in seasonally snow-covered ecosystems. It constrains the growing season and affects the availability of important resources including water, nitrogen (N) and phosphorus (P). Snow depth, distribution and duration have been affected by global climate change making it increasingly important to understand the effects of changing snow regimes on terrestrial ecosystems. Here we leverage a 43-year snow manipulation experiment to examine the effects of long-term changes in snow depth on plant community structure, resource availability and interactions therein in a common grassland type of the northern Rocky Mountains in western North America. Long-term experimental doubling and quadrupling of snowpack was associated with a significant shift in plant functional group distribution to a more forb rich community. Snow addition has resulted in a two to three-fold increase in forb to grass biomass ratios over time. Forbs consistently had greater N and P contents and lower nutrient use efficiencies compared to grasses. Forbs also displayed higher rates of net photosynthesis relative to grasses and sustained positive carbon (C) fixation rates late into the growing season after grasses had ceased. Though there is evidence that water exerts considerable control over ecosystem processes, increased snow depth did not have affect soil water availability through the growing season. However, snow depth was associated with significant differences in plant-available phosphate across the entire growing season with approximate 15% and 31% increases in pools of available P relative to ambient snowpack depth for doubled and quadrupled snowpacks respectively. Estimates of direct P inputs via dust and the ratio of available P to total P in the soil suggest that internal cycling was largely responsible for the observed differences in pools of available P. However, growing season net mineralization rates do not differ across treatments. This may suggest that winter processes make significant contributions to nutrient cycles. It is possible that the increased availability of P favors the shift to a forb-rich community under deeper snow because of their increased productivity under dry conditions and that the increased litter quality of forbs likewise promotes increased litter decomposition and mineralization, especially of P.

CHAPTER 1

INTRODUCTION

Scientific Background

Global climate change has altered precipitation patterns, in many cases increasing precipitation but with a smaller proportion falling as snow, especially across the western United States (Knowles et al. 2006). There has been a marked decline in snowpack distribution and duration reported across the Northern Hemisphere and an unprecedented and synchronous decline in snowpack depths across the Northern Rocky Mountain (NRM) cordillera over the past 50 years due to anthropogenic forcing of the climate system (IPCC 2007, Pederson et al. 2011a, Pederson et al. 2011b). Though the general trend is toward a reduced snowpack, there have also been increases in snowpack depth and duration in some areas (Mote 2006). In either case, it is clear that for seasonally snow-covered landscapes, global climate change signifies alterations to winter snow conditions.

Snow governs multiple ecosystem processes in high altitude and high latitude ecosystems (Chernov 1988, Schmidt and Lipson 2004, Wipf et al. 2009). Changes in snowpack depth, duration and distribution in the Northern Hemisphere, particularly in western North America, due to global climate change (IPCC 2007) portend significant effects on freshwater storage (Pederson et al. 2011a), surface albedo (Bonan 2008), fire (Westerling et al. 2006), and important ecosystem functions like primary productivity. Yet, there remains uncertainty regarding the role of snow in plant community structure,

biogeochemical cycling and resource availability in terrestrial ecosystems. This is particularly true for effects extending into the growing season (Blankinship and Hart 2012).

Changes in seasonal snow cover can structure plant community composition by a number of mechanisms. These include altering growing season length and resource conditions that constrain rates of primary production. Plant community structure and richness have long been known to be a function of snow depth and melt rate (Billings and Bliss 1959, Bjork and Molau 2007). In general, forbs, non-gramminoid herbaceous flowering plants, tend to be the dominant plant functional group in snowbed ecosystems (characterized by deeper snow and later melt dates) while grasses tend to dominate under shallower, earlier melting snow (Bjork and Molau 2007). Floristic differences along snow gradients are thought to be a result of differing tolerances of species to growing season length (Billings and Bliss 1959) and some suggest that the date of snowmelt is the most important factor in explaining differences in species distributions across snow gradients (Ostler et al. 1982).

Snow depth and duration is thought to have profound effects on resource availability and cycling in the plant-soil system. The vast majority of annual nutrient requirements for land plants are supplied through decomposition in the soil (Schlesinger and Bernhardt 2013) and winter processes make an important contribution to annual biogeochemical budgets (Campbell et al. 2005). Deeper snowpacks provide insulation for the soil beneath the snow and lead to increased average winter soil temperatures, protection from frequent and extreme freeze-thaw cycles, and provide more available

liquid water, a limiting factor in winter microbial processes (Brooks et al. 1997, Groffman et al. 2001, Schimel et al. 2004). In general, microbial activity can continue as long as free water is available, typically down to -5 ˚C but perhaps as low as -10 ˚C (Schimel et al. 1996, Schimel et al. 2004, Schmidt and Lipson 2004), temperatures common in late winter under deep snowpacks in the Rocky Mountains (Brooks et al. 1998). Microbial biomass is known to be active under snow (Brooks et al. 1998, Schmidt and Lipson 2004) and the carbon and energy for subniveal microbial proliferation comes from plant litter inputs (Schmidt and Lipson 2004). Litter decomposition has been shown to proceed at fast rates under arctic snowpacks (Hobbie and Chapin 1996). Systems with deeper snowpacks generally exhibit increased winter decomposition rates, soil respiration rates, and spring melt nutrient pulses (Brooks et al. 1997, Brooks et al. 1998, Groffman et al. 2001, Schmidt and Lipson 2004, Monson et al. 2006) particularly for nitrogen (N) and phosphorous (P), two commonly limiting resources in terrestrial systems (Vitousek et al. 2010). Likewise, changes in winter snow cover can exhibit effects into the growing season, influencing processes that are primarily associated with the summer season (Wipf and Rixen 2010).

Here we study the long-term effects of changes in snowpack depth and duration in a subalpine grassland of the Bangtail Range in southwest Montana. Grasslands are useful to study ecosystem responses to global climate change because of the relatively rapid rates of plant-soil processes relative to forests and shrublands (Menge et al. 2009). In particular, high elevation grasslands may be critical indicators of global climate change due to their elevationally-restricted settings (Harte and Shaw 1995).

Study Objectives

Previous research has primarily focused on the effects of snow manipulation on winter and spring processes and shorter-term manipulations, but relatively little has been done concerning the impacts of snowpack change on growing season processes (Wipf and Rixen 2010, Blankinship and Hart 2012). Our goals were as follows:

1. Determine and quantify plant community responses to long-term snow depth manipulation, particularly those of important plant functional groups: grasses and forbs.
2. Determine and quantify soil resource responses to long-term snow manipulation, including water availability, nutrient (N and P) availability and rates of nutrient transformation.
3. Explore the interactions between, and possible mechanisms for, plant community and resource availability changes.

CHAPTER 2

PLANT COMMUNITIES AND RESOURCE AVAILABILITY CHANGE IN RESPONSE TO LONG-TERM SNOW MANIPULATION

Introduction

Plants require light, water and nutrients for growth. However, species differ in their demand for, and ability to procure and utilize, these resources. Because plants rarely occur in monocultures but rather in mixed assemblages of species and functional groups, community composition often depends on the relative availability of resources (Tilman 1985, Huenneke et al. 1990, Davis et al. 2000). In turn, resource availability can be influenced by the composition and resource requirements of the plant community (Tilman and Wedin 1991). The question of how community composition and resource availability interact represents a difficult and enduring challenge in ecology and biogeochemistry.

In semiarid ecosystems like those prevalent throughout the western United States, water is a primary limiting factor for plant growth (Fischer and Turner 1978). Most of the water for plant production derives from snow and seasonal snow cover constitutes an important reservoir of freshwater in high latitude and high elevation systems (Serreze et al. 1999). It has been well documented that snowpack depth, duration and distribution have changed significantly in the Northern Hemisphere, particularly in the northern Rocky Mountains (NRM), due to global climate change (Knowles et al. 2006, Mote

2006, Pederson et al. 2006, IPCC 2007, Pederson et al. 2011a, Pederson et al. 2011b). Such changes portend significant consequences for ecosystems where snow is an important component of the hydrologic cycle.

Snow depth, distribution and duration can influence plant communities and ecosystem biogeochemistry via a number of non-exclusive mechanisms. First, duration of snow cover constrains the length of time for plant growth (Keller et al. 2005). Deeper snowpacks often persist longer and constrict the length of the growing season, effectively limiting access to light. Second, snow can impact ecosystem resources through direct inputs of water and nutrients. Deeper snowpacks deliver more water during spring melt and have been observed to have lasting effects on soil moisture through the growing season (Walker et al. 1999, Chimner and Welker 2005). Similarly, airborne dust and litter is known to accumulate within snow (Fahnestock et al. 2000). Though mineral nutrient inputs from dust are generally small relative to internal cycling within the plant soil system and other sources of atmospheric deposition, they can be important in some terrestrial systems, particularly for phosphorus (P) (Okin et al. 2004). Lastly, snow can affect resource availability through indirect inputs, primarily by altering internal nutrient cycling. Systems with deeper snowpacks generally exhibit increased winter microbial activity and spring nutrient pulses relative to those with shallower snowpacks (Brooks et al. 1997, Brooks et al. 1998, Groffman et al. 2001, Schmidt and Lipson 2004, Monson et al. 2006). Because snow provides insulation for the soil below, deeper snowpacks can result in warmer winter soil temperatures and therefore higher microbial biomass and activity (Brooks et al. 1998, Schmidt and Lipson 2004) as well as higher rates of

decomposition in the soil below (Hobbie and Chapin 1996). Plant communities respond to these changes by individual physiological adaptation, compositional change, or both to compete for resources in this new environment (Tilman 1985).

Here, we examine the long-term effects of snow depth change on plant community dynamics and resource availability. In particular we are interested in the interactions between community composition and resource cycling and how snow constrains those interactions. To our knowledge, the Bangtail Research Site (BTL) in southwest Montana represents the longest-running (43-year) snow manipulation experiment worldwide (Wipf and Rixen 2010). Early work at the site demonstrated shifts in plant community composition (away from common species of *Festuca idahoensis* grasslands), phenology (to later flowering dates) and potentially limiting nutrients (increased available P) as well as a constriction in growing season length in response to a doubling and quadrupling of snowpack (Weaver 1974, Weaver and Collins 1977). After 43 years, we aimed to evaluate the strength of these responses, particularly community composition and resource availability shifts, and whether they have changed over time. Similarly, we were interested in physiological differences between communities occupying the different snow treatments, particularly differences in resource use efficiency and rates of primary production, and how those have interacted with resource availability to result in observed community composition and production patterns.

The overarching goals of this study are (1) to examine plant community responses to long-term snowpack manipulation, (2) to determine the ways in which snowpack depth constrains resource availability throughout the growing season and (3) to examine

interactions between plant communities and resource availability. Here we define resources primarily as those that are likely to be altered by snow depth treatments: growing season length, water availability and macronutrient (N and P) availability. We hypothesize that (1) increases in snowpack depth have increased early season water availability as well as increased N and P availability, primarily through indirect inputs (*i.e.* enhanced internal processes) and (2) plant communities have shifted in response to resource availability under the different snowpack treatments.

Methods

Our measures were designed to evaluate plant community and resource dynamics in response to a snow depth gradient. First, we conducted plant-level analyses focusing on responses in individual plant physiology, functional groups of species and the whole community response to long-term snow depth manipulation. Second, we conducted soil analyses to measure soil properties (*e.g.* texture, pH and bulk density) and resource dynamics, particularly of N, P and water to determine which have been impacted by long-term snow manipulation, and ways in which they may interact with changes in plant communities.

Study Location & Characteristics

The BTL is located in a subalpine grassland of the NRM (~2400 m asl) approximately 30 km northeast of Bozeman, Montana (45°46'58" N 110°46'43" W, Fig. A1). It was the representative mountain grassland site (Bridger site) for the International Biological Program studies of the grassland biome from 1968-1974 (Sims and Singh

1978b, a, c, Sims et al. 1978). The BTL lies within a system of rolling Idaho fescue (*Festuca idahoensis*) meadows, a common feature of the NRM. Average annual precipitation is approximately 960 mm of which 87% falls as snow between September and May, on average. Mean July and January maximum temperatures are 22 °C and -5 °C respectively. Soils are classified as Haplocryolls (Weaver and Collins 1977).

Our long-term snow manipulation experiment was established in 1968 and consists of two snow accumulation treatments that approximately double (1.2 m, X2) and quadruple (2.4 m, X4) average ambient snowpack depth (0.6 m), represented in the control treatment (hereafter called "control"). Snowpack manipulation was accomplished by means of snow fences oriented perpendicular to prevailing winds. Each treatment consists of five nested subplots corresponding to the area leeward of the fences (Fig. A2).

Plant-level Measures

We measured late season standing crop (September-October) from 2000-2012 to estimate average annual aboveground net primary production. We used stratified random sampling to select ten 0.5 m^2 plots for each snow depth treatment per year to measure aboveground biomass. Each plot was clipped at ground level, separated by species functional group, dried at 60 °C and weighed. Aboveground plant tissue samples from select years (1987, 1992, 1998, 2003 and 2010) were analyzed by Agvise Laboratories (Northwood, ND) for C and N content using an Elementar CN combustion analyzer (Hanau, Germany) and P content by acid digestion (EPA method 3050) and inductively coupled plasma (ICP) detection.

We measured leaf-level gas exchange for two grasses (*Bromus marginatus* and *Stipa richardsonii*) and two forbs (*Agoseris sp.* and *Hackelia sp.*) throughout the 2012 growing season. These species were selected because they were easily measured, relatively abundant and occur across treatments. Net photosynthesis was measured between 10 AM and 2 PM with a LI-6400 Portable Photosynthesis System (Li-COR, Lincoln, NE). The incident radiation in the measuring chamber was 1500 μE m^{-2} sec^{-1} with a 400 ppm CO_2 reference.

Soil Sampling & Analysis

Surface soils (0-15 cm) were collected to measure growing season nutrient pool dynamics, net mineralization rates and soil moisture using an oakfield sampler (diameter=2.00 cm). For studying subsoils, we collected soil in 10 cm increments to 50 cm for soil physical properties (bulk density, pH) and depth profiles of C, N and P using a king-tube sampler (diameter=2.00 cm). All soil samples were brought back to the laboratory and processed within 24 h of collection. We determined soil moisture gravimetrically by drying a known recorded mass (>20 g) of field moist soil at 50 °C for at least 10 days, reweighing and expressing as a percent of dry weight. Field moist soils were extracted with 1 M potassium chloride (KCl) to determine levels of plant-available N. Dried soils were extracted with a weak Bray's solution to determine available P. We determined soil nitrate (NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^-) by colorimetric flow-injection analysis (Lachat Instruments, Loveland, CO). Soils were analyzed for total C, N and P by Agvise Laboratories (Northwood, ND) as described above for plant tissue samples.

Net transformation rates (N mineralization, nitrification and P mineralization) were measured used the buried bag method (Eno 1960) throughout the 2012 growing season. Three composited samples were mixed and divided into two parts, one to be returned to the laboratory and analyzed immediately and the other to be incubated *in situ* in one quart polypropylene bags (SC Johnson, Racine, WI). Four buried bags were installed within each treatment per incubation, incubated for approximately three weeks and returned to the laboratory for processing and analysis within 24 h of removal. Net transformation rates for NH_4^+, NO_3^- and PO_4^- were calculated as the difference between initial and incubated samples divided by incubation time. All sampling and incubation locations were randomly selected within treatments.

Soil texture was determined by the hydrometer method (Klute 1986). Soils for texturing were collected from 0-50 cm in 10 cm increments using a king-tube sampler. For each treatment, three replicate samples from randomly selected locations were composited for each depth. Dried soils were mixed with a 0.082 M sodium hexametaphosphate solution to dissociate aggregates, transferred to a sedimentation container, shaken and allowed to settle. Hydrometer readings were made at 30 seconds post suspension to calculate percent silt and 270 minutes post suspension for percent clay. Percent sand was calculated by the difference after accounting for silt and clay (*i.e.* % sand = 100 - % silt - % clay).

Statistical Analyses

The following statistical analyses were performed using the R statistical package (R Development Core Team 2011). (1) We used one-way analysis of variance (ANOVA)

to test for differences among treatments for standing crop biomass, forb to grass ratios, forb and grass nutrient content and soil properties including soil pH, bulk density and surface soil pools of total C, N and P. (2) We used two-way ANOVAs to compare net photosynthesis by plant functional group, water availability, and net rates of nitrification, N mineralization and P mineralization using snow treatment and sample time as factors in the analyses. Similarly, comparisons among treatments for total and available N, total and available P and ratios of total to available P were made with two-way ANOVAs using treatment and sampling depth as factors. (3) We modeled nutrient use efficiencies and available P through time using linear regression and models were compared using Extra Sum of Squares F-tests. For all analyses simple linear models were fit to the data to assess normality, equal variance and linearity (where applicable), and the data were transformed when necessary to ensure the correct analyses were being performed. Pairwise comparisons were made following ANOVA tests via the Tukey honestly significant difference (HSD) test. All reported *p* values are two-sided.

Results

Plant-level Measures

Average standing crop biomass in the BTL (2000-2012) did not exhibit large differences across snow depth treatments. There was greater standing crop biomass in the control relative to increased snow treatments (Fig. 1, $p<0.001$ for both X2 and X4 compared to control). Average aboveground biomass production was reduced by 32% and 27% for X2 and X4 relative to the control, respectively (Table 1).

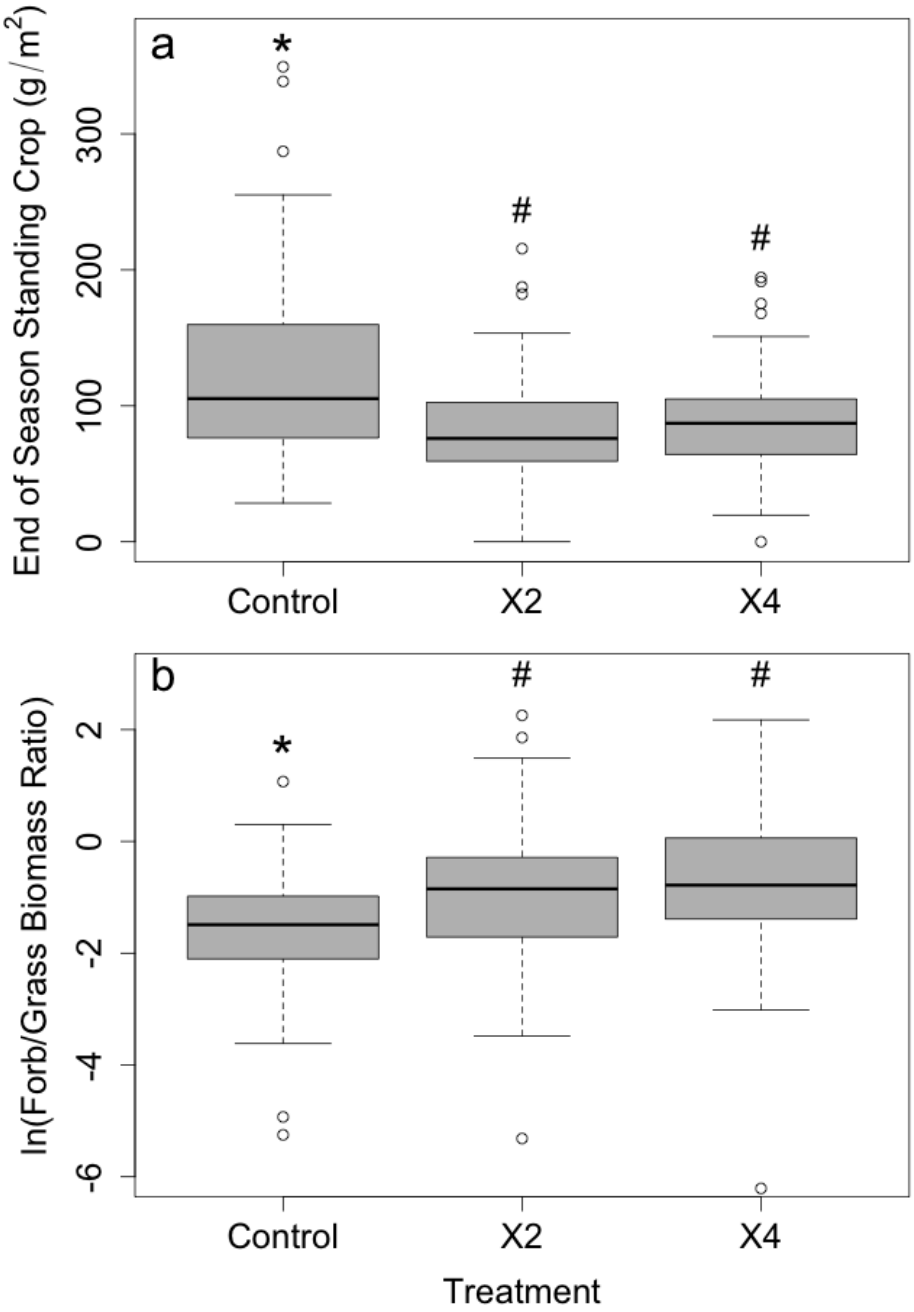

Figure 1. Comparison of end of season biomass (a) and log-transformed forb:grass biomass ratio (b) (2000-2012). Significant differences (p<0.05) between treatments are indicated by differences in symbols (∗ #).

Table 1. Plant community properties at the Bangtail Research Site (BTL) by snow accumulation treatment. Values within parentheses indicate one standard error, *p* values are from one-way ANOVAs for a difference among treatments. Significant differences ($p<0.05$) for within-row pairwise comparisons are indicated by differences in superscripted letters.

	Treatment			
	Control	**X2**	**X4**	***p*-value**
Standing Crop Biomass (g/m^2)	120.8 (4.2)[a]	82.7 (6.1)[b]	88.2 (6.1)[b]	<0.001
Standing Crop N (g/m^2)	1.00 (0.10)	0.88 (0.14)	0.97 (0.14)	0.26
Standing Crop P (mg/m^2)	94 (12)	77 (17)	110 (17)	0.17
Forb:Grass Biomass Ratio	0.32 (0.10)[a]	0.83 (0.15)[b]	0.93 (0.15)[b]	<0.001
Grass N (%)	0.82 (0.02)	0.77 (0.07)	0.83 (0.04)	0.37
Grass P (%)	0.08 (0.003)	0.07 (0.002)	0.09 (0.008)	0.17
Forb N (%)	1.29 (0.16)	1.22 (0.18)	1.30 (0.21)	0.41
Forb P (%)	0.12 (0.005)[a]	0.13 (0.007)[a]	0.16 (0.008)[b]	0.002

Plant functional group distribution has changed under deeper snow as the prevalence of forbs increased with snowpack depth (Fig. 1). There was a higher proportion of forb biomass relative to grass under deeper snow treatments ($p<0.001$ for both X2 and X4 compared to control). Proportions of forbs to grass were 1.98 and 2.60 times greater relative to the control for X2 and X4 treatments respectively. However, the communities occupying all treatments remain grass dominated regardless of snow treatment (grass constituted 79% of the aboveground biomass for the control, 69% for X2, 67% for X4).

Functional groups differed in their nutrient content as well. Forbs were richer in both P and N relative to grasses ($p<0.001$ for all snow treatments) and forb P content increased under deeper snow, though only significantly under the deepest snow treatment ($p=0.003$ and $p=0.01$ for X4 relative to the control and X2 respectively) (Fig. 2).

However, end of year standing crop stocks of N and P did not differ significantly across treatments (Fig. A3, p=0.27 and 0.17 for standing crops of N and P, respectively).

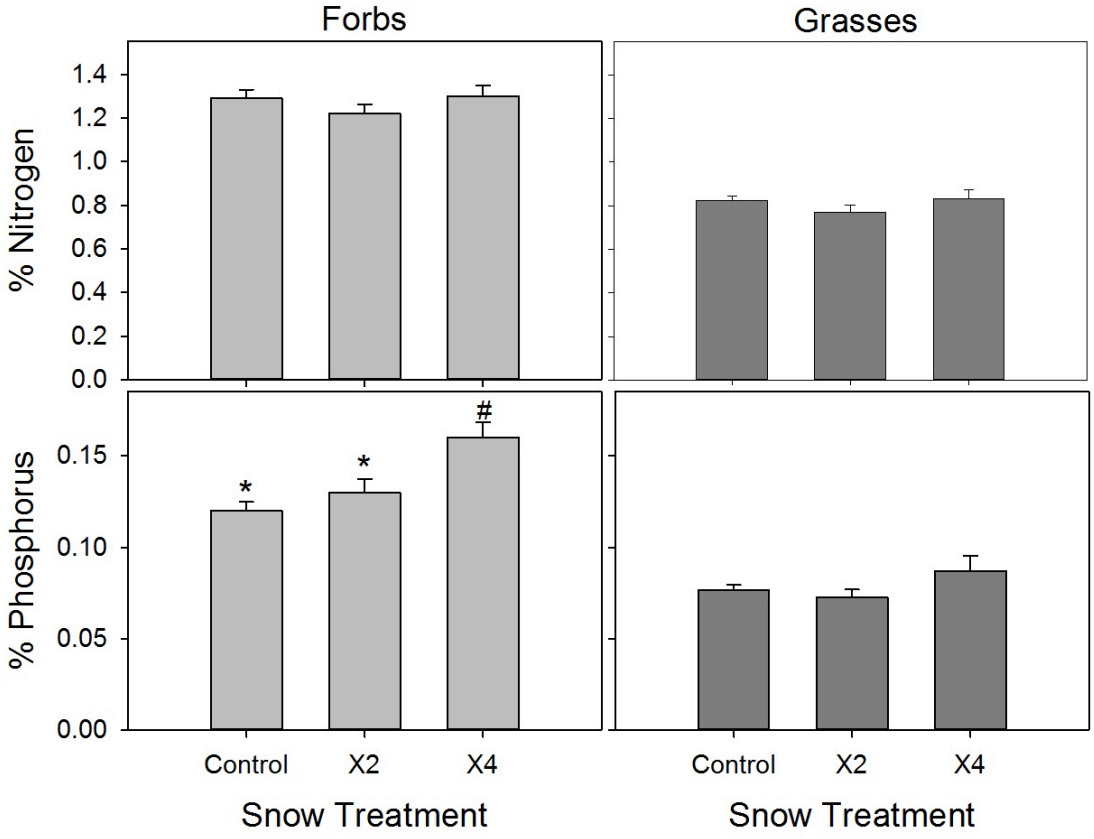

Figure 2. Nitrogen and phosphorus content of plant tissues by functional group and snow treatment. Error bars equal one standard error. Significant differences ($p < 0.05$) within functional group are designated by differences in symbols (∗ #). Absence of symbol indicates no difference.

Grass and forb nutrient use efficiency was markedly different. Grasses had a significantly higher phosphorus use efficiency (PUE), the amount of P required to produce a given amount of biomass, than forbs (Fig. 3, p<0.001) as indicated by the slopes of the PUE curves. On average, for each additional mg of P incorporated in plant tissues, forbs produced an additional 0.74 g/m^2 of biomass and grasses produced an

additional 1.26 g/m^2 of biomass. Similarly, nitrogen use efficiency (NUE) of grasses significantly exceeded that of forbs (p<0.001, Fig. 3). That is, for each additional g of N incorporated in biomass, forbs produced an additional 82 g/m^2 of biomass and grasses produced an additional 125 g/m^2 of biomass on average.

Net photosynthesis of study grass and forb species peaked in June and declined throughout the remainder of the growing season. Though there were slight differences between study species within each functional group, net rates of photosynthesis did not vary significantly across treatments for any species. When averaged across species and treatments, forbs had higher net photosynthetic rates later in the growing season compared to grasses (p<0.05 for all time points after day of year, DOY, 184, Table A2). Grasses reached a minimum on approximately August 13, 2012 (DOY 226) in parallel with declines in soil moisture (Fig. 4, Tables A1 & A2). While early season rates of photosynthesis were similar and net rates also declined with soil moisture, forbs continued to fix carbon late into the growing season when grasses exhibit net respiration (*i.e.* net photosynthesis <0).

Soil Resources

General soil properties for the BTL are summarized in Table 2. Under deeper snow, soils were more acid (p<0.05). In the top 20 cm of the soil profile, neither bulk density nor pools of soil total C and total N differed significantly between treatments. However, there was evidence for differences among treatments in total P (p<0.05), with 23% greater pools total P in the top of the soil profile in the X4 treatment relative to the

control (Table 2). Soil texture did not vary considerably among snow treatments, but due to a lack of replication any differences could not be statistically analyzed.

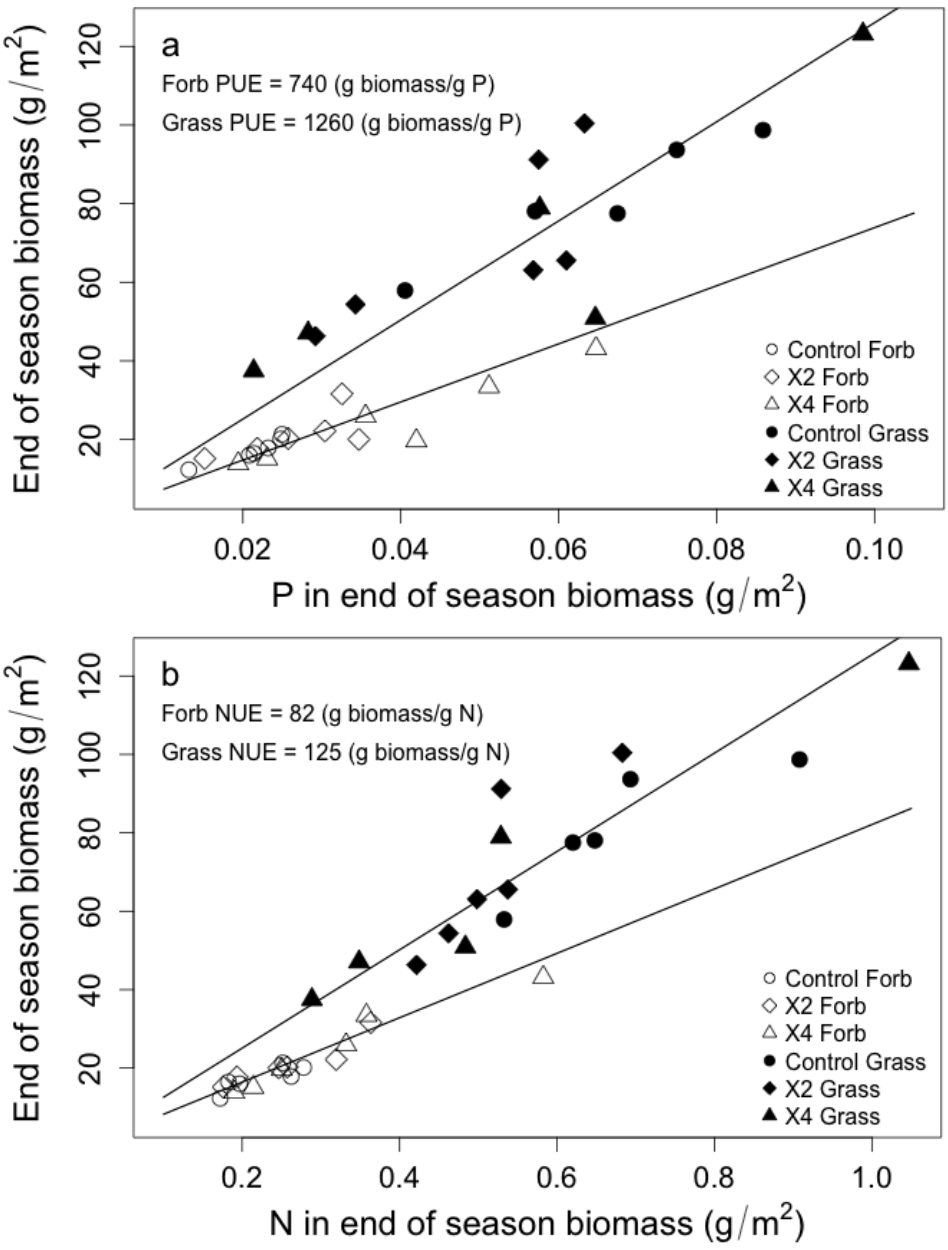

Figure **3.** Grass and forb phosphorus use efficiency (a) and nitrogen use efficiency (b) curves. Grass and forb slopes are different for both phosphorus (p<0.001, multiple r^2=0.98) and nitrogen use efficiencies (p<0.001, multiple r^2=0.98).

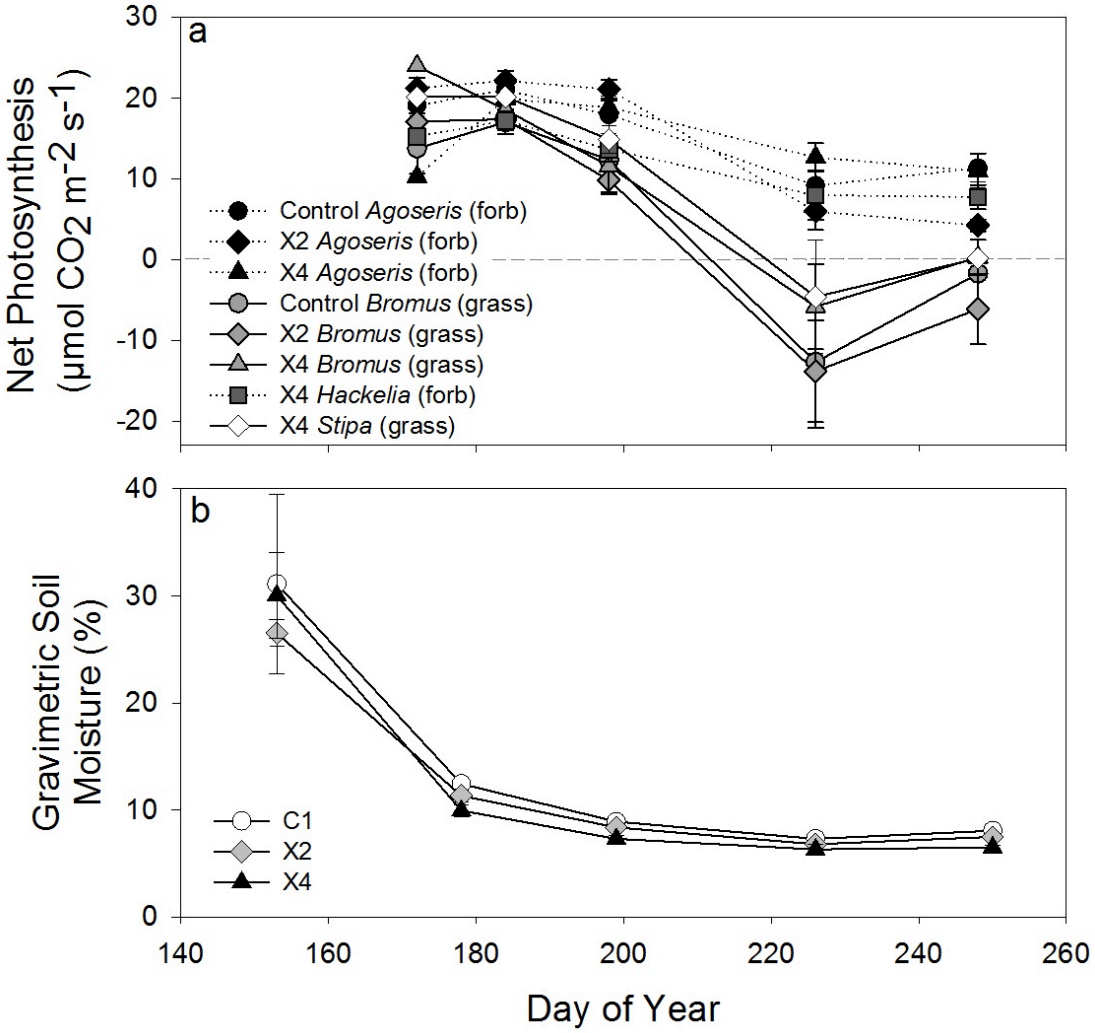

Figure 4**.** Net photosynthesis (a) and gravimetric soil moisture (0-15 cm) (b) across snow accumulation treatments and plant species during the 2012 growing season. Photosynthesis declines simultaneously across all species reaching a minimum at approximately day 226, but forb photosynthesis (dotted lines) is greater for all time points after day 184 (p<0.05 for all) relative to grasses (solid lines). Soil moisture declines synchronously across all snow accumulation also reaching a minimum at approximately day 226. Error bars equal ±1 standard error.

Table 2. Surface soil (0-20 cm) properties at the Bangtail Research Site (BTL) by snow accumulation treatment. Values within parentheses indicate one standard error, *p* values are from one-way ANOVAs (N/A is not applicable) for a difference among treatments. Significant differences ($p<0.05$) for within-row pairwise comparisons are indicated by differences in superscripted letters.

	Treatment			
	Control	**X2**	**X4**	***p*-value**
Bulk Density (g/m^3)	0.98 (0.09)	1.17 (0.08)	1.26 (0.09)	0.07
pH	5.89 (0.01)^{a}	5.76 (0.03)^{ab}	5.68 (0.07)^{b}	0.01
Total C (kg/m^2)	14.3 (1.0)	12.9 (0.4)	13.4 (0.5)	0.39
Total N (kg/m^2)	1.3 (0.07)	1.1 (0.04)	1.2 (0.05)	0.08
Total P (g/m^2)	230 (15)^{a}	249 (9)^{ab}	283 (11)^{b}	0.03
% Clay	19	22	21	N/A
% Silt	26	29	30	N/A
% Sand	55	49	49	N/A

Growing season water availability was not greater under deeper snow treatments despite an approximately four-fold difference in snow water equivalent (SWE) delivered during spring melt (Fig. 4, Table A1). Gravimetric soil moisture declined in concert through time across all treatments, reaching a minimum by approximately August 13, 2012 (DOY 226). Where there were significant differences in soil moisture ($p<0.05$), the control was always greater than either X2 or X4, though only by a small amount (Table A1).

Total and available pools of P were altered by deepened snow. Though pools of total P did not exhibit consistent treatment effects through the entire soil profile (Fig. 5), there were larger pools of total P under deeper snow treatments in the top 20 cm ($p<0.05$, Table 2). In contrast, the proportion of total P in available form (the ratio of PO_4^--P to total P) increased significantly with increasing snow levels in the top 40 cm of the soil profile in both X2 and X4 treatments (Fig. 5, Table A3).

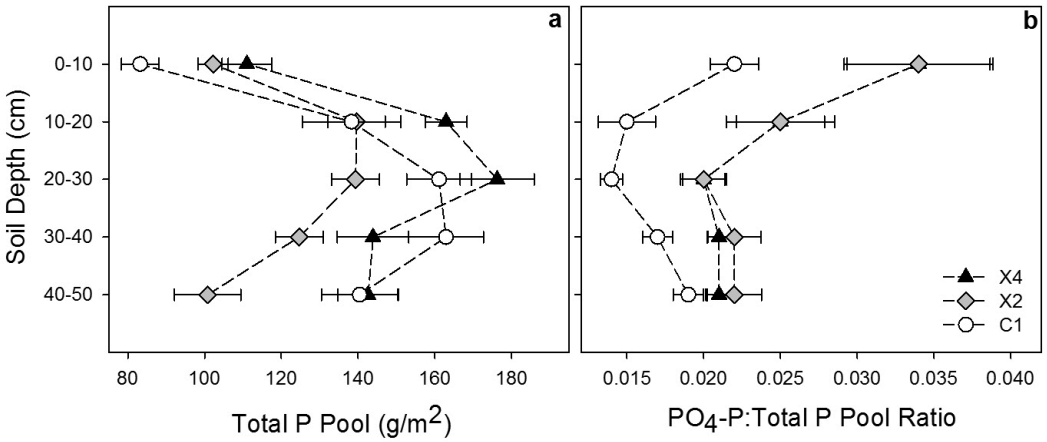

Figure 5. Depth profiles of soil total P pools (a) and portion of total P as available soil phosphate (PO_4^-:Total P ratio) (b) by snow accumulation treatment. Error bars equal ±1 standard error.

Bioavailable P in surface soils declined over the course of the growing season (Fig. 6). Available P pools (Bray's-extractable PO_4^-) of surface soils (0-15 cm) declined across all snow treatments, and both X2 and X4 had greater pools of PO_4^- than the control (Fig. 6, $p<0.001$ for both X2 and X4 compared to the control and X2 compared to X4). There was insufficient evidence that the slope of the change in PO_4^-pools over time depended on snow treatment ($p=0.09$) so a parallel lines regression model was used to describe the decline through time across treatments (Fig. 6, multiple $r^2=0.78$). The step-wise relationship of PO_4^- pools between treatments persisted after accounting for soil texture. Relative to the control, PO_4^-availability increased by 1.0 g/m^2 and 1.9 g/m^2 in the X2 and X4 treatments respectively.

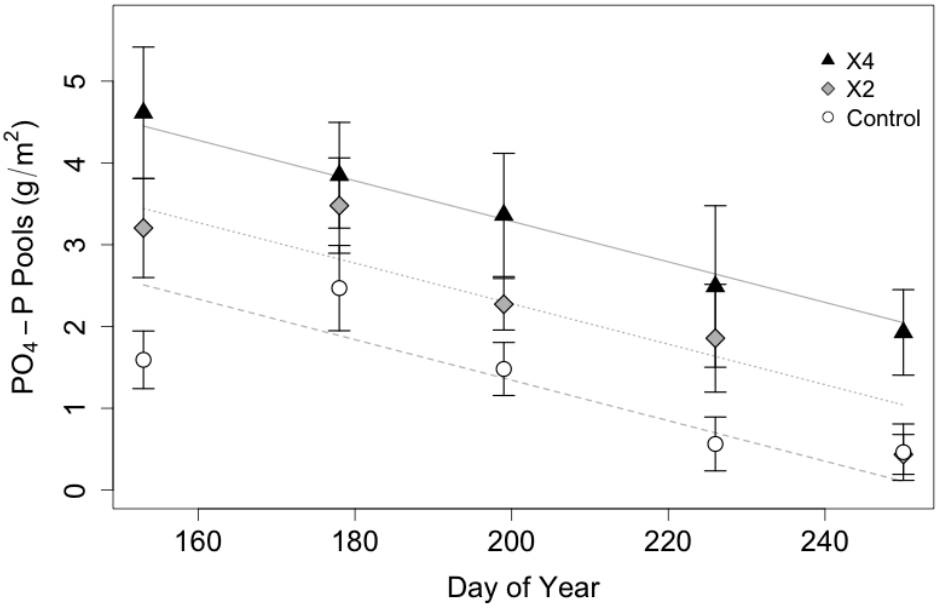

Figure 6. Surface soil (0-15 cm) phosphate pools during the 2012 growing season. Intercepts for a parallel lines regression model (multiple r^2=0.78) were significantly different (p<0.05) for all snow accumulation treatments. The dashed, dotted and solid lines indicate linear regressions for the control, X2 and X4 respectively. Error bars equal ±1 standard error.

Inorganic soil N also showed distinct seasonal patterns of availability, but lacked the consistent step-wise treatment effects observed with P (Fig. 7). Ammonium was the dominant form of available dissolved inorganic nitrogen and, while it declined across all treatments through the growing season, it exhibited no consistent or significant treatment effects. Pools of NO_3^- increased across all treatments through the growing season and tended to be lower in the control, though not significantly. Total N also showed no consistent treatment effects with depth (Fig. A4).

Despite some differences in availability, neither net nitrification nor net P mineralization exhibited consistent treatment effects throughout the growing season (Fig. 7). In contrast, net N mineralization showed consistently higher rates of NH_4^+

immobilization under the control treatment relative to the snow accumulation treatments (X2 and X4) for the majority of the growing season (Fig. 7, Table A4).

All measures of net transformation, however, showed consistent temporal patterns across treatments and appeared to be closely tied to soil moisture (Fig. A5). Net nitrification increased early in the growing season, then declined across all treatments to near zero shortly after soil moisture reached its minimum. Likewise, both N and P mineralization exhibited temporal patterns across all treatments and transition from net immobilization to net mineralization around the time of minimum water availability.

Discussion

Long-term snow addition resulted in significant changes to plant community structure and function as well as resource availability. Increased winter snow depth corresponded to increased relative abundance of forbs and greater PO_4^- availability. In contrast, deeper snow did not result in greater water availability. Increased forb productivity is likely in response to changes in resource availability that favor forb growth: increased nutrient availability, constricted growing season length or earlier onset of water limitation in surface soils during the growing season. Enhanced internal nutrient cycling is likely the primary cause of increased PO_4^- availability to which both deeper snow and higher litter quality of forbs may contribute. Biogeochemical processes in this grassland ecosystem appear to be strongly linked to water availability which may ultimately drive observed changes under different snow treatments.

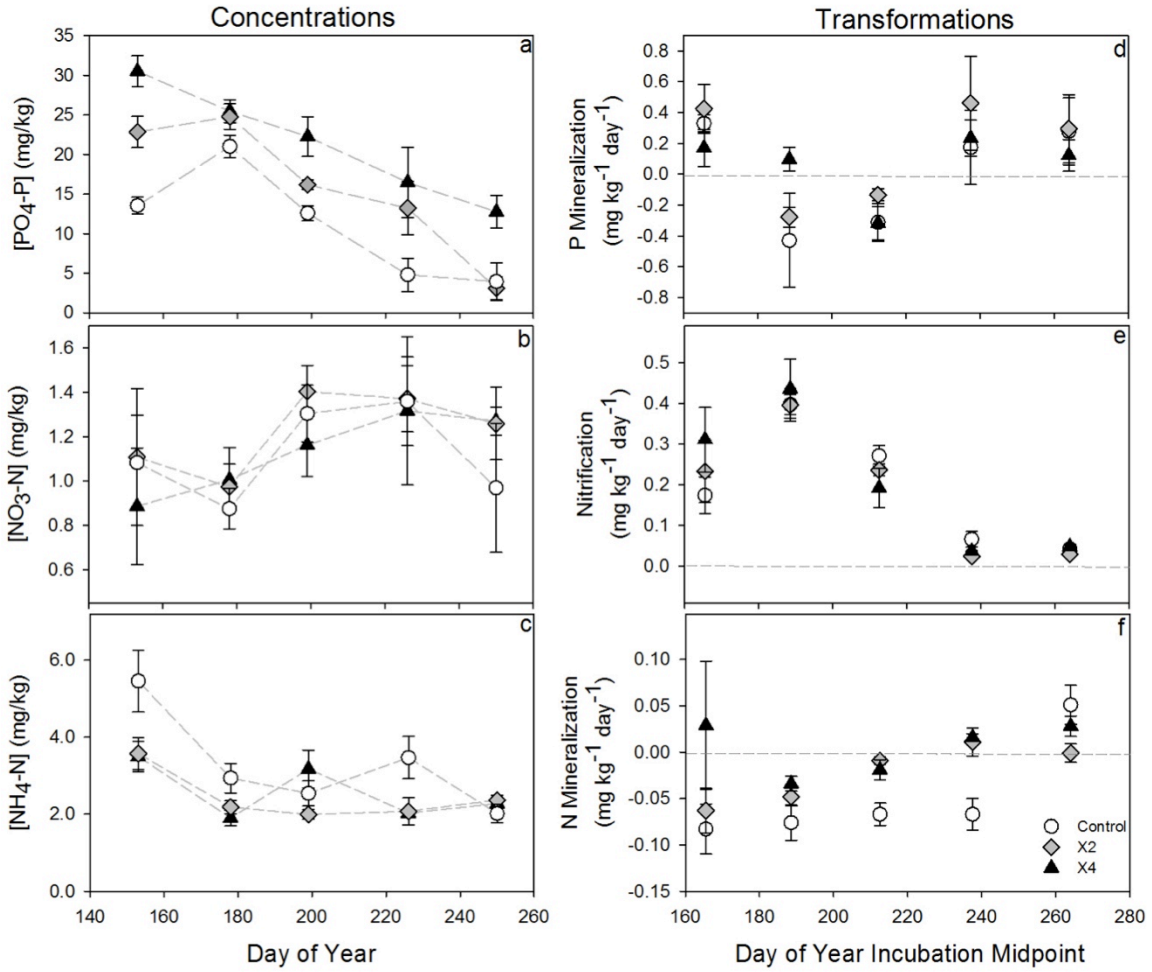

Figure 5. Surface soil (0-15 cm) concentrations of PO_4^--P (a), NO_3^--N (b) and NH_4^+-N (c) as well as net rates of P mineralization (d), nitrification (e) and N mineralization (f) for the 2012 growing season. Error bars equal ±1 standard error.

Despite differences in seasonal snow depth and snow-free season length, differences in plant production in the BTL (estimated by standing crop biomass) were not proportional to differences in either of these factors (Fig. 1). Average aboveground biomass production was only moderately lower under X2 (38.1 g/m^2) and X4 (32.6 g/m^2) snow treatments relative to the control despite an estimated two and four-week shorter snow-free season respectively.

There have, however, been distinct changes in plant community structure. First, there has been a near complete change in community composition under the deepest snow treatment (X4) relative to the control (Weaver in prep.). Most of the common species of the fescue meadows have been replaced by species apparently favored by deeper and more persistent snow cover, a response that began as early as five years after the initiation of the experiment (Weaver 1974, Weaver and Collins 1977). Prior to the installation of the snow fences the plant community was relatively homogeneous, dominated by *Festuca idahoensis.* Vegetation composition was similar to what is still present in the control and has since diverged in plant community structure under deeper snow treatments. Similar deep snow communities have been observed in nearby natural snow drifts (*i.e.* areas of snow accumulation) (Weaver 1974) and globally such compositional changes are projected to be a consequence of deeper snow cover (Wipf and Rixen 2010). Second, the species composition change has been accompanied by a change at the functional group level. There has been a shift to a more abundant forb community relative to grasses under deeper snowpack treatments (Fig. 1). Forbs are commonly found in habitats with long snow cover duration (Galen and Stanton 1995, Bjork and Molau 2007) and previous research has shown that forbs tend to be more flexible in response to changes in snowmelt timing as they generally remain neutral or increase in abundance in response to increased snow depth and duration while grasses generally decrease (Wipf and Rixen 2010).

While biomass was still dominated by grasses across all treatments, the shift to a forb rich community portends significant effects on productivity. Forbs tend to grow

more rapidly than grasses (Weaver 1958), conferring a competitive advantage in the deeper snow treatments (X2 and X4) which have constricted growing seasons due to later snow melt. This is observed in increased rates of net photosynthesis in forbs relative to grasses later in the growing season (Fig. 4). Forbs maintain net photosynthesis during conditions where respiration exceeds photosynthesis in grasses.

Water is an important limiting resource in many terrestrial ecosystems. Altered winter snow cover can affect growing season soil moisture, especially in regions with low summer precipitation (Walker et al. 1999, Chimner and Welker 2005). However, even though spring snowmelt delivered approximately double and quadruple the amount of water to the soil system approximately two and four weeks later (X2 and X4 respectively), soil moisture declined in concert across all snow treatments (Fig. 4). In fact, where differences did exist in soil moisture ($p<0.05$), the control was slightly higher than X2 or X4 treatments (Table A1). This demonstrates that increased spring water loading does not translate to greater moisture availability in surface soils throughout the growing season in this system. Weaver and Collins (1977) showed that soil water stress was delayed in lower horizons of the soil profile relative to surface soils, but that the timing of this stress was nearly simultaneous across treatments. Because neither growing season precipitation patterns or soil texture varied across treatments (Table 2), the similarity in soil moisture was most likely due to soils becoming saturated, draining to field capacity, then drying out simultaneously. Similarly, strong winds and warm temperatures are common throughout the growing season and may drive high rates of evapotranspiration across all treatments.

Temporal patterns of soil moisture and net photosynthesis indicate a strong link between the two. Net photosynthesis had a clear connection to soil moisture and declined simultaneously in both grasses and forbs with grass photosynthesis reaching a minimum at approximately the same time as water availability (Fig. 4). Forb photosynthesis declined in parallel, had not appeared to cease during the time of study. Forb species not only had greater rates of photosynthesis late in the growing season when water availability became scarce, but they were able to maintain net photosynthesis during drier conditions when respiration exceeded photosynthesis in grasses. Coherent relationships between soil moisture and net photosynthesis suggest that water exerts a strong control over primary production and is an important limiting resource across all treatments, especially for grasses (Figs. 4 and A6). The ability for forbs to continue fixing carbon during the driest part of the year effectively extends their growing season and may suggest the ability to access sources of water in deeper parts of the soil profile that are not available to grasses. It has been observed that forbs are generally more deeply rooted and subsist largely on water that penetrates beyond the rooting depth of grasses (Weaver 1958) in part because forbs tend to be more tap-rooted while grass roots are more fibrous (Schenk and Jackson 2002). Access to grass-unavailable sources of water, the ability to fix carbon later into the growing season, and increased rates of productivity may confer competitive advantages to forbs under deeper snow.

Though water appears to be an important limiting resource, it is important to consider other soil resources as well. Though springtime nutrient pulses are generally enhanced under deeper snowpacks (Schmidt and Lipson 2004), relatively little is known

about the lasting effects of snowpack depth on nutrient availability through the growing season. Pools of available N, both NO_3^- and NH_4^+, were not consistently different across treatments, not even early in the growing season (Fig. 7). Ammonium was the dominant bioavailable form of soil N in this grassland ecosystem and microbial demand for NH_4^+, measured as net immobilization, was reduced under deeper snowpacks relative to the control (Fig. 7). This implies the possibility of greater N limitation to plant growth in the control grasslands relative to the snow treatments, even though there was no evidence of consistently larger pools of available N.

Contrary to N, availability of PO_4^- was consistently different across treatments throughout the entirety of the growing season (Fig. 6). The consistent, step-wise differences in pools of PO_4^- tracked differences in winter snow depth. Depth profiles showed slightly greater pools of total P in X2 and X4 in upper soil horizons relative to the control (Fig. 5), but this pattern disappeared deeper in the soil profile. Since atmospheric inputs of P-rich dust are known to be important sources of P in some terrestrial systems (Okin et al. 2004) and snow is known to collect and deposit additional airborne dust and litter (Fahnestock et al. 2000), it is likely that the additional P in surface soils is due to long-term accumulation of aeolian P rather than a difference in parent material. This is supported by a slight increase in the soil silt fraction under deeper snow treatments (Table 2), consistent with loess accumulation. More striking, however, is the pattern of available PO_4^- relative to total P pools (Fig. 5). The proportion of total P in an available form was much higher under deeper snow treatments and persisted throughout

much of the soil profile suggesting increases in PO_4^- availability are likely due to internal processes (*i.e.* nutrient cycling).

Because dust can be an important source of P, the amount of available P deposited in dust was estimated using data from a high dust deposition area of the Colorado Rockies (Lawrence et al. 2010) to determine if aeolian inputs alone could account for the observed differences in PO_4^-. To be conservative, the estimate assumed that all dust was deposited with snow, that dust flux scaled linearly with snow depth and that no leaching losses occured. Despite these simplifications, potential dust inputs could not explain the observed differences in PO_4^- between snow treatments. Estimates of accumulation over the 43-year history of the BTL experiment only account for 47% and 45% of observed differences in available P for X2 and X4 relative to the control, respectively. This is likely an overestimation of deposited PO_4^- since leaching losses are known to be high especially under the snow accumulation treatments (unpublished data). This provides further evidence that the increases in available PO_4^- are largely due to internal processing.

Despite evidence suggesting increased nutrient cycling under deeper snow treatments, growing season net mineralization of P did not vary across treatments (Fig. 7). It is possible that the increased P is a result of enhanced decomposition and mineralization during the winter and spring snowmelt periods not represented during the time span of our measures. This is further supported by the considerably lower amounts of litter that were observed under deeper snow treatments (Weaver and Collins 1977), suggesting a greater proportion of the litter produced in previous years was decomposed under deeper snow. Like P mineralization, net nitrification did not exhibit consistent

treatment effects during the growing season but net N mineralization was greater throughout much of the growing season for deeper snow treatments. Microbial demand for NH_4^+ is greater under ambient snow conditions and less under deeper snow conditions and may suggest great N limitation under shallower snow treatments.

Microbial nutrient transformations all showed consistent temporal patterns across treatments and, like net photosynthesis, appeared to be closely tied to water availability (Fig. A5). Net nitrification was highest early in the growing season when water availability was the greatest and declined across all treatments as soils dried. Mineralization of N and P increased as the growing season progressed and soils dried. Ammonium and PO_4^- each showed net immobilization during peak growing season, indicating a strong biotic sink, and transitioned to net mineralization shortly after water availability reached its minimum and the biotic sink strength was likely reduced.

Our results suggest that the shift toward forbs has had significant biogeochemical consequences. The increase in available PO_4^- under deeper snow was reflected in the plant community as forbs have higher N and P contents and forb P increases with increasing snow depth (Fig. 2). Forbs also have lower PUE and NUE than grasses (Fig. 3). That is, forbs require greater amounts of both N and P to produce the same amount of biomass as grasses and are better suited to environments where competition for N and P is less severe. Due to the higher proportion of forbs under deeper snow, lower NUE and PUE (higher percent N and P, Fig. 2) in forbs results in higher litter quality under deeper snow on average. Higher litter quality may promote higher rates of decomposition and

mineralization and in turn lead to increased availability of nutrients, further favoring forbs.

The shifts in resource availability and plant community composition are complimentary. Forbs both require greater nutrient availability and are able to continue growing when conditions become too dry for grasses. The increase in snow depth has led to greater availability of nutrients, particularly PO_4^-, primarily through enhanced internal cycling. Increased snow depth shifts the system away from nutrient limitation and allows forbs, which have lower efficiencies of N and P use, to increase in abundance because they are able to fix more carbon per unit water during the driest part of the growing season. These changes ultimately manifest themselves in the shift to a more forb rich community under deeper snow conditions, which may in turn promote greater internal cycling of nutrients through higher litter quality.

Conclusions

Long-term snow depth manipulation in the BTL has resulted in a significant change in plant community structure. There has been a shift in plant functional groups under deeper snow to a more forb-rich community. However, aboveground biomass production was only moderately different across snow treatments. Forbs had lower nutrient use efficiencies (both NUE and PUE) and required greater availability of N and P to produce as much biomass as grasses. Forbs maintained higher productivity than grasses as water became scarcer, effectively extending the length of their growing season, perhaps because they were able to access sources of water unavailable to grasses.

Snowpack manipulation has also resulted in changes in resource availability. Throughout the growing season there were consistently greater pools of PO_4^- under deeper snow treatments. Estimates of direct inputs of aeolian PO_4^- could not account for the difference and increased ratios of available P to total P under deeper snow treatments suggest increases in PO_4^- pools were primarily due to internal processes and cycling. Yet net measures of growing season PO_4^- mineralization did not exhibit treatment effects, perhaps because the differences in internal cycling occurred primarily during the cold months where plant growth is negligible. The increased cycling may also be enhanced by increased litter quality (higher N and P content) under deeper snow treatments as forbs, which were more prevalent under deeper snow, had higher levels of P and N in their tissues and forb P increased with increasing snow depth.

Nitrogen species did not exhibit the consistent step-wise treatment effects across snow depths as were observed with PO_4^-. This may be due to N limitation across all treatments causing pools to be drawn down to equally low levels. However, increased rates of NH_4^+ immobilization under a shallower snowpack suggest a greater microbial N demand and perhaps more extensive N limitation even if pools of available N do not vary significantly among treatments.

Our work shows the importance of snow depth for community structure and ecosystem resource availability. Changes in snowpack depth altered both plant communities and resource availability, and each in turn helped to shape the other. The constricted snow-free season has likely promoted the shift toward forb-rich communities under deeper snow treatments, as they are able to grow more rapidly and under drier

conditions than grasses. Forbs also required more nutrients (N and P) to grow compared to grasses, and the increased availability of soil nutrient pools with snow depth, particularly PO_4^-, has likely influenced the shift in plant functional group distribution. Similarly, deeper snow likely enhanced internal cycling of nutrients, particularly P, possibly via insulation effects during the winter. The increased litter quality of forbs, more prevalent under deep snow, further promoted higher rates of decomposition and nutrient cycling.

As changes in global climate continue to alter winter precipitation patterns, snow depth and snow distribution, we may see widespread shifts in resource availability in plant-soil systems, particularly changes in the availability of nutrients relative to water. As relative resource availability changes, plant communities will also change to best take advantage of resource availability.

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APPENDIX A

SUPPLEMENTAL TABLES AND FIGURES

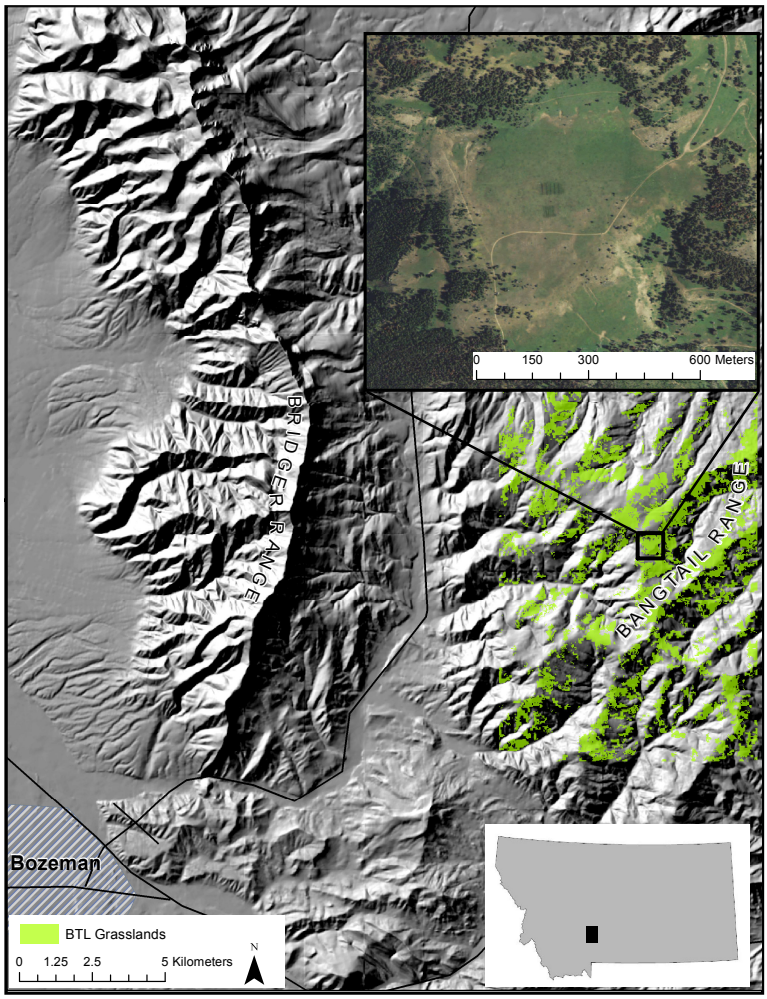

Figure A1. Map of the Bangtail Research Site (BTL) in SW Montana with Bangtail range grasslands shown in green (data from the National Land Cover Database). Inset is an aerial photograph of the BTL.

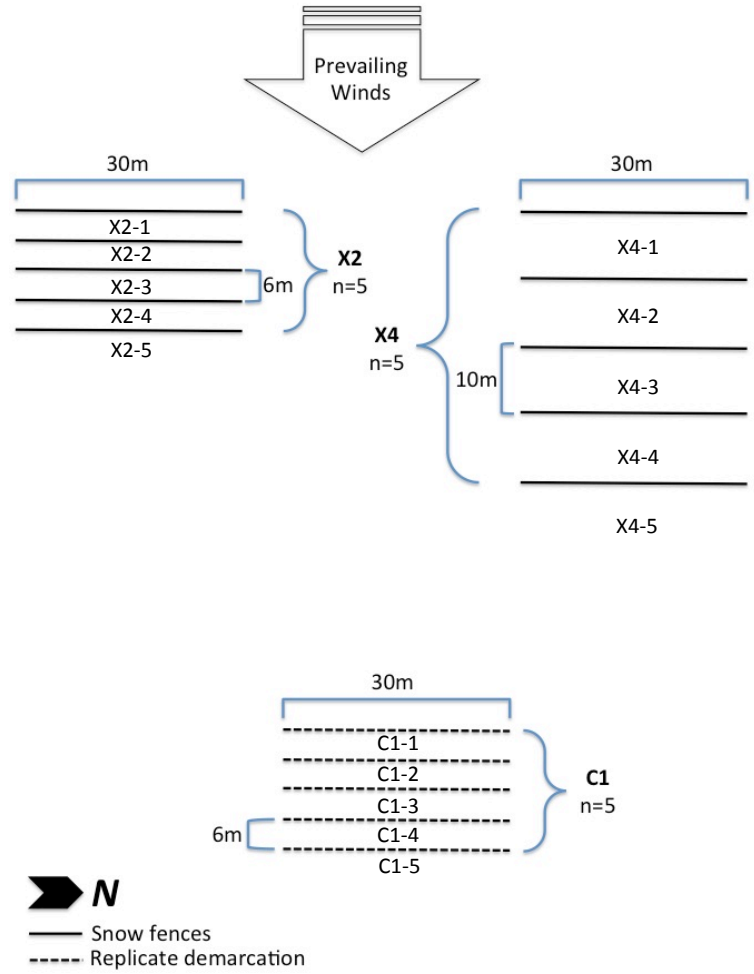

Figure A2. Diagram of the Bangtail Research Site (BTL) snow treatments showing the relative position and orientation of snow manipulation treatments and control (C1) with each treatment consisting of 5 nested subplots (or replicates) on the leeward sides of fences/replicate demarcations.

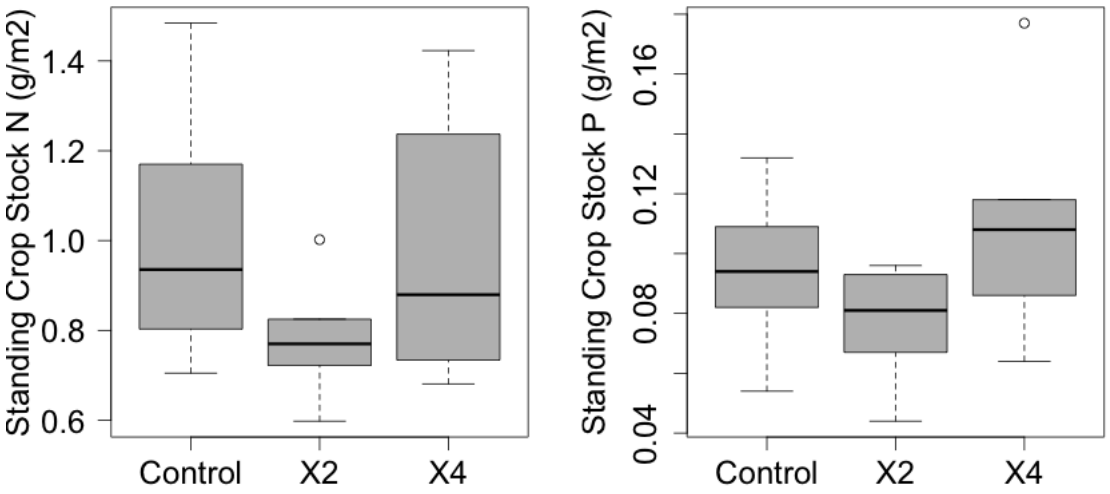

Figure A3. Standing crop stocks of N (a) and P (b) (2000-2012). There is no significant difference in stocks returning to the soil system as litter across snow depth treatments for either N (p=0.27) or P (p=0.17).

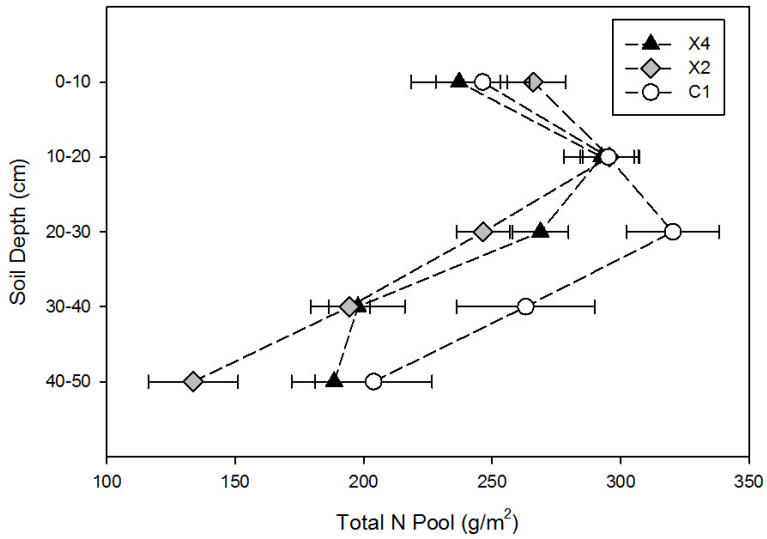

Figure A4. Depth profile of total N pools by snow treatment. Error bars equal ±1 standard error.

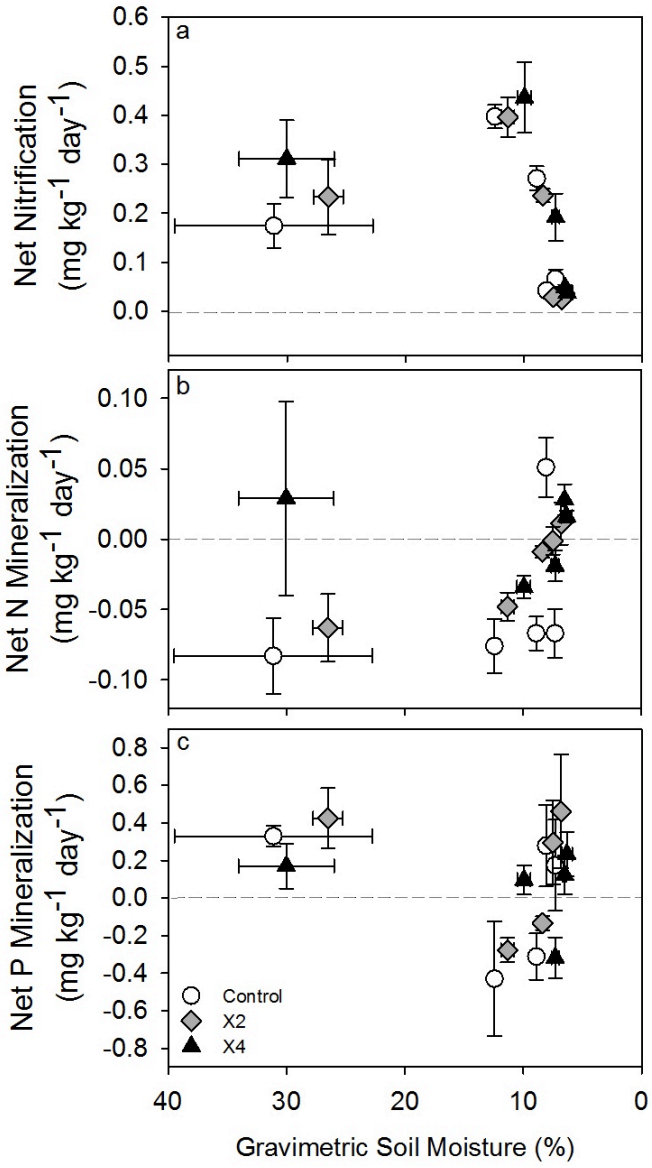

Figure A5. Mean gravimetric soil moisture versus net rates of nitrification (a), N mineralization (b) and P mineralization (c). Error bars equal ±1 standard error.

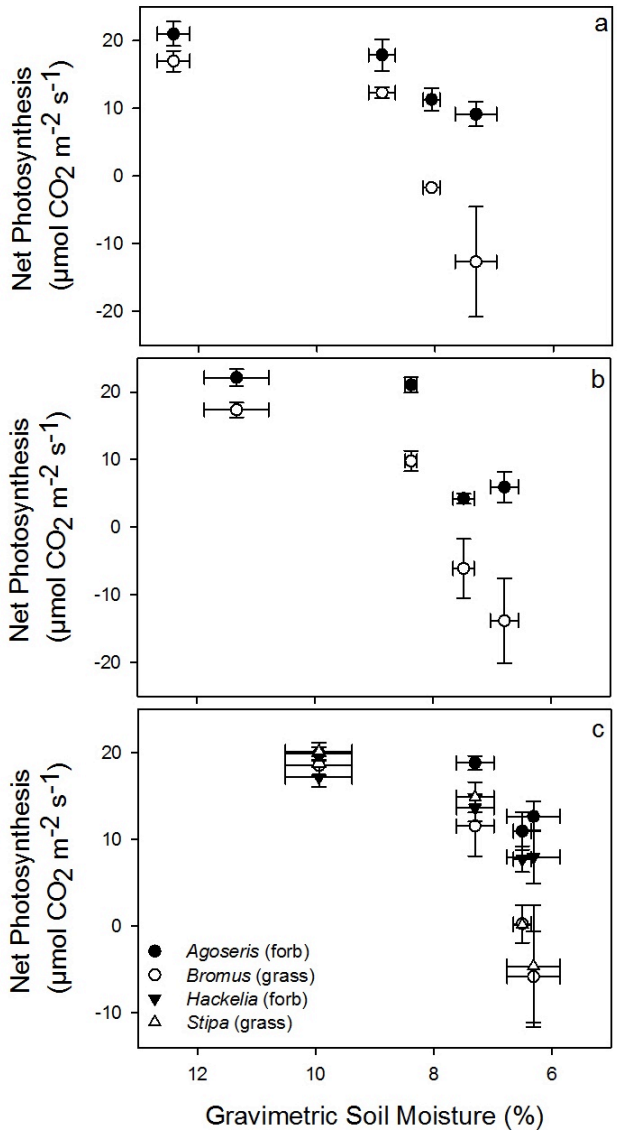

Figure A6. Mean gravimetric soil moisture versus net photosynthesis for study species across snow accumulation treatments for the control (a), X2 (b) and X4 (c). Error bars equal ±1 standard error.

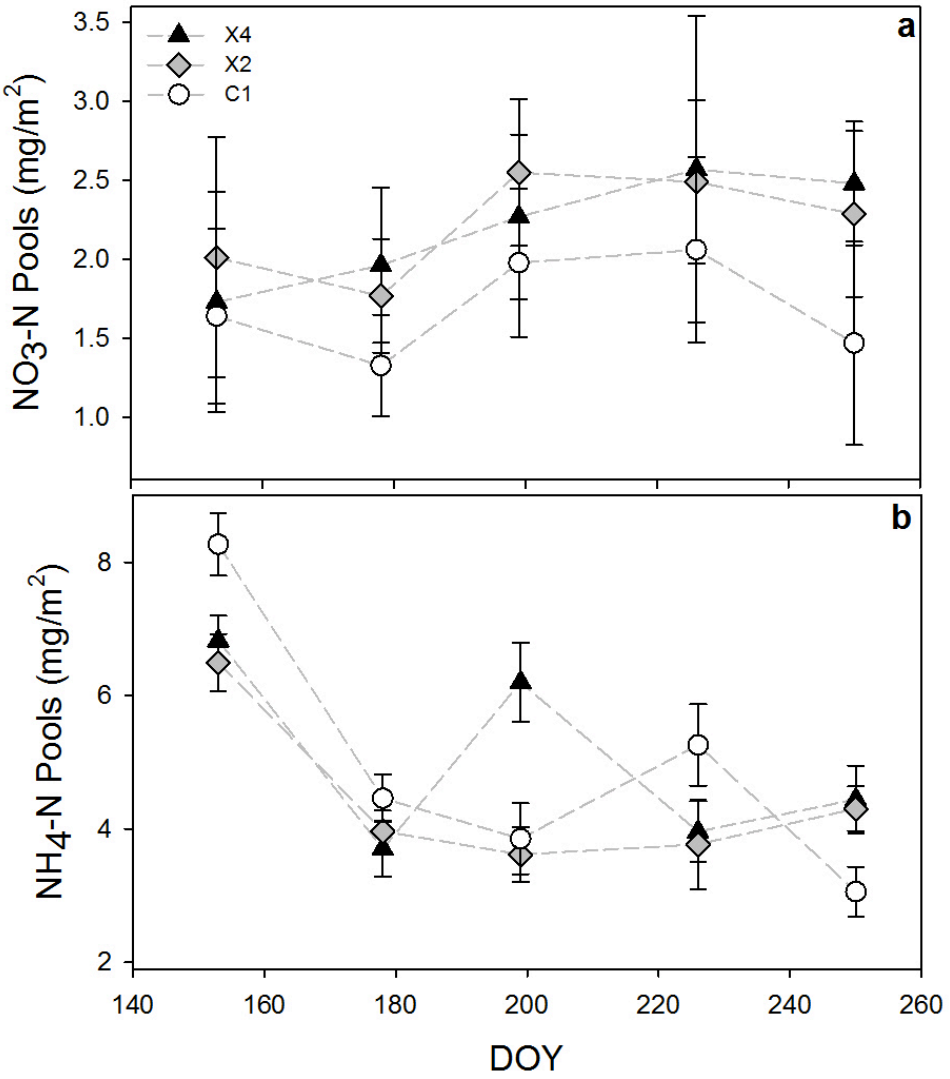

Figure A7. Pools of NO_3^- (a) and NH_4^+ (b) in surface soils (0-15 cm) for the 2012 growing season. Error bars equal ±1 standard error.

Table A1. Mean gravimetric soil moisture content by treatment for each sampling date during the growing season. Values within parenthesis equal one standard error, *p*-values from one-way ANOVA testing for any differences among treatments. Significant differences for within-row pairwise comparisons are indicated by different superscripted letters.

	Gravimentric Soil Moisture (%)			
DOY	**Control**	**X2**	**X4**	***p*-value**
153	31.1 (5.4)	26.5 (7.7)	30 (7.7)	0.82
178	12.4 (0.5)^{a}	11.3 (0.7)^{ab}	9.9 (0.7)^{b}	0.02
199	8.9 (0.2)^{a}	8.4 (0.3)^{a}	7.3 (0.3)^{b}	0.003
226	7.3 (0.3)^{a}	6.9 (0.4)^{ab}	6.0 (0.4)^{b}	0.03
250	8.1 (0.2)^{a}	7.5 (0.2)^{a}	6.5 (0.2)^{b}	0.0002

Table A2. Mean net photosynthesis by functional group for each sampling date showing Values within parenthesis equal one standard error, *p*-values from two sample t-test for differences between functional groups. Units of net photosynthesis are μmol CO_2 m^{-2} s^{-1}.

	Net Photosynthesis		
DOY	**Grass**	**Forb**	***p*-value**
172	17.2 (1.5)	18.8 (1.9)	0.40
184	18.2 (1.9)	20.1 (2.6)	0.27
198	12.1 (2.1)	17.7 (2.7)	0.004
226	-9.3 (2.1)	8.9 (2.7)	<0.001
248	-2.2 (1.9)	9.0 (2.9)	<0.001

Table A3. Average percent of total P that is an available form (PO_4^--P) with depth for each treatment. Values in parentheses equal one standard error, *p* values are from one-way ANOVAs for a difference among treatments. Significant differences for within-row pairwise comparisons are indicated by different superscripted letters.

	Percent Total P as PO_4-P			
Depth (cm)	**Control**	**X2**	**X4**	***p*-value**
0-10	2.2 (0.4)	3.4 (0.5)	3.4 (0.5)	0.09
10-20	1.5 (0.3)^{a}	2.5 (0.4)^{b}	2.5 (0.4)^{b}	0.03
20-30	1.4 (0.1)^{a}	2.0 (0.2)^{b}	2.1 (0.2)^{b}	0.01
30-40	1.7 (0.1)^{a}	2.2 (0.2)^{b}	2.1 (0.2)^{b}	0.02
40-50	1.9 (0.1)	2.2 (0.2)	2.1 (0.2)	0.26

Table A4. Mean net N mineralization by snow depth treatment for 2012 growing season. Negative values indicate microbial immobilization of NH_4^+. Values in parentheses equal one standard error, *p* values for one-way ANOVA. Significant differences ($p<0.05$) for within-row pairwise comparisons are indicated by different superscripted letters.

	Mean Net Mineralization (mg kg^{-1} day^{-1})			
Incubation	**Control**	**X2**	**X4**	***p*-value**
1	-0.08 (0.05)	-0.06 (0.06)	0.03 (0.06)	0.23
2	-0.08 (0.01)	-0.05 (0.02)	-0.03 (0.02)	0.13
3	-0.07 (0.01)[a]	-0.01 (0.01)[b]	-0.02 (0.01)[b]	0.004
4	-0.07 (0.01)[a]	0.01 (0.02)[b]	0.02 (0.02)[b]	0.006
5	0.05 (0.01)	0.00 (0.02)	0.03 (0.02)	0.09