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Evidence of Nonlinearity in the Response of Net Ecosystem CO_2 Exchange to Increasing Levels of Winter Snow Depth in the High Arctic of Northwest Greenland

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Abstract

Winter snowfall is increasing in many Arctic regions and climate models predict this trend will persist in the coming century. We examined the effects of two levels of increased winter snow accumulation on soil microclimate, plant and soil nutrient status, plant phenology and ecosystem CO_2 exchange after five years of treatment in a widespread High Arctic ecosystem. Increased snow cover resulted in greater winter CO_2 efflux, altered growing season soil nutrient availability and greater leaf nitrogen concentrations during the snow-free season. Modest increases in snow cover (+0.25 m above ambient) increased gross ecosystem photosynthesis (GEP) without increasing ecosystem respiration (ER), while the deepest snow cover (+0.75 m above ambient) increased both GEP and ER. The area of intermediate snow addition was a smaller source of CO_2 to the atmosphere during the growing season when compared to the ambient and deep snow areas. The intermediate and deep snow areas apparently had similar effects on the functioning of the vegetation community (increased GEP), but divergent effects on the soil microbial respiration, as evidenced by the changes in ER. This nonlinear response to increasing snow depth demonstrates the potential for complex High Arctic ecosystem responses to changes in winter precipitation.

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Introduction

The importance of snow depth as a control on the structure and function of Arctic, alpine, and temperate ecosystems has long been recognized by ecologists (e.g. Billings and Bliss, 1959; Brooks et al., 1996; Walker et al., 1999; Groffman et al., 2001; Sturm et al., 2005; Blumenthal et al., 2008; Cooper, 2010; Nowinski et al., 2010). Approximately 55%, or 54.2×10^6 km^2, of the terrestrial northern hemisphere receives seasonal snow cover (Groisman et al., 1994). Seasonal snow cover may control the heating and cooling of terrestrial ecosystems more than any other land surface feature. The length and severity of the snow-covered season is also a major driver of biogeography (Lomolino et al., 2006). The duration and depth of snow cover affects multiple vegetation and ecosystem processes including growing season length and plant phenology which, in turn, can affect net primary production and reproductive success (e.g. Bliss, 1971; Billings, 1987; Galen and Stanton, 1995; Molau, 1996; Welker et al., 2000; Groendahl et al., 2007; Borner et al., 2008). Snow depth also impacts winter soil temperatures and nitrogen (N) mineralization (Schimel et al., 2004; Sturm et al., 2005; Borner et al., 2008) and may have cascading consequences for soil water content, plant water relations, and leaf-level photosynthesis (Dawson and Bliss, 1989; Sullivan and Welker, 2007). However, it is only recently that experimental manipulations of snow depth have been combined with plant, soil, and trace gas exchange measurements to help quantify the abiotic, biotic, and feedback consequences of snow depth changes in the Arctic (e.g., Welker et al., 2000; Schimel et al., 2004; Sturm et al., 2005; Wahren et al., 2005; Nobrega and Grogan, 2007; Morgner et al., 2010).

The majority of experimental Arctic snow depth manipulations have been conducted in the Low Arctic of Alaska and have not been as spatially extensive as summer warming experiments (e.g., Arft et al., 1999). Studies focusing on the effects of snow depth changes in the High Arctic have been lacking, with only a few findings that focused primarily on changes in plant leaf waxes (Rieley et al., 1995) and soil carbon (C) effluxes (Morgner et al., 2010). These limitations constrain our ability to fully understand how ecosystems at the very northern reach of the global terrestrial landscape will differ in the future under new climate regimes.

Shifts in winter and summer Arctic conditions are becoming increasingly apparent at multiple scales (IPCC, 2007). Winter, summer, and annual temperatures are rising in Greenland (Box and Cohen, 2006; Sullivan et al., 2008a) and annual minimum sea ice extent is in steep decline (Stroeve et al., 2008). Increased snowfall has been observed in parts of the Arctic, including Greenland (Dai et al., 1997; ACIA, 2004; Kohler et al., 2006; Min et al., 2008), and is predicted to continue (ACIA, 2004; Singarayer et al., 2006).

Understanding the effects of changing winter precipitation is especially important in the far north, since winter can last for up to 10 months. Snowfall can account for more than 50% of annual precipitation and any increases in snow may raise overwinter soil temperatures, allowing greater rates of C and N mineralization (e.g. Schimel et al., 2004), which may alleviate strong nutrient limitations seen in the High Arctic (Wookey et al., 1993; Robinson et al., 1995; Arens et al., 2008). In addition, deeper snow in the High Arctic may ease water limitations to plant growth and gas exchange (Welker et al., 1993; Wookey et al., 1993; Robinson et al., 1995, 1998).

Recently, a series of studies on Greenland, Ellesmere Island, and Svalbard have quantified the magnitudes of soil carbon pools (Horwath et al., 2008) and CO_2 exchange (Jones et al., 2000; Soegaard and Nordstroem, 1999; Lloyd, 2001; Elberling, 2003; Welker et al., 2004; Arens et al., 2008; Sullivan et al., 2008b;

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Morgner et al., 2010) in the world's northernmost landscapes. Findings from these studies emphasize the following: (1) growing season length is an important control on the magnitudes and patterns of gross ecosystem photosynthesis (GEP), summer and winter ecosystem respiration (ER), and, consequently, net ecosystem exchange (NEE); (2) CO_2 exchange in High Arctic ecosystems can be very responsive to changes in temperature and nutrient availability; (3) pools of soil carbon that may be available to microbes under warmer conditions (summer or winter) are an order of magnitude greater than previously reported, indicating the potential for a strong positive feedback to warming.

This project addressed three interrelated questions. After five years of experimental manipulation, how have two levels (2× and 4× ambient) of experimentally increased winter snow depth altered: (1) the magnitudes and patterns of soil physical and chemical traits (temperature, soil water, soil N availability); (2) winter rates of soil CO_2 efflux and growing season magnitudes and patterns of GPP, ER, and NEE; and (3) the seasonality and magnitudes of leaf nitrogen concentration and vegetation greenness?

Materials and Methods

STUDY SITE

The study site is located on the Pituffik Peninsula in Northwest Greenland, near Thule Air Base, USAF (76°32′N, 68°42′W, elevation 180 m a.s.l.). Two 1.2 m tall snow fences were constructed during the summer of 2002 in prostrate dwarf-shrub, herb tundra (Walker, 2005). The fences were aligned perpendicular to the prevailing winter wind direction. *Dryas integrifolia* (M. Vahl) is the dominant vascular plant species, while *Salix arctica* (Pall.) and *Carex rupestris* (All.) are subdominant. From records dating to 1971, the Air Base has a mean annual precipitation of 12.2 cm and a mean annual temperature of −11.6 °C. The snow fences were established downwind of the experimental site described in detail by Sullivan et al. (2008a). Abiotic conditions at the site are monitored by a weather station equipped to measure soil and air temperature, solar radiation, wind speed, and precipitation.

At each fence, 20 × 40 cm CO_2 flux plots were delineated within three larger, pre-established main plots at each of three levels of winter snow accumulation: ambient (control, 0.25 m), intermediate (0.55 m), and deep (1.1 m). Ambient plots used in this study are the same control plots used in the factorial warming × irrigation experiment described by Sullivan et al. (2008a) and are within 10 m upwind of the snow fences. The ambient plots were not located downwind of the snow fences due to spatial constraints within the study site. Although the snow addition plots were distributed across two fences, we treat each plot as a replicate in our statistical analyses (i.e., $n = 6$). Snow naturally accumulates on the leeward side of the fences, creating a continuously tapering drift. Carbon dioxide flux plots were established in areas containing all three of the dominant and sub-dominant plant species. Bare soil and vegetated areas each comprise approximately 50% of the ground surface in each larger plot. Only the vegetated halves of the plots were monitored for CO_2 fluxes in the present study. Mid-summer measurements made over bare soil showed negligible rates of GEP and very low rates of ER (Czimczik and Welker, 2010; Sullivan, unpublished data). Landscape scale CO_2 fluxes can, therefore, be approximated as one-half of the rates presented in this paper.

PATTERNS OF OVERWINTER SOIL TEMPERATURES AND CO_2 EFFLUX

Soil temperature was recorded hourly at 5 cm depth during the winter of 2006–2007 using HOBO data loggers (Onset Computer Corporation, Bourne, Massachusetts) installed in each treatment. Only one probe in each treatment captured data throughout the winter due to destruction of other replicates by local animals. Mean overwinter temperatures were calculated over the period of 1 October through 1 April for all treatments.

Overwinter respiration collars were installed in vegetated areas of each snow depth ($n = 8$) on 21 August 2006. All aboveground vegetation was removed from the inside of the collar before capping for the winter. Collars were constructed of a 16 cm inner diameter, 15 cm long section of PVC pipe inserted 5 cm into the soil. The collars were fitted with a PVC cap containing a suspended packet with ~10 g of granular soda lime. The soda lime in each packet was dried to constant mass before deployment. The soda lime adsorbs CO_2 released from soil during the winter and the mass difference between the beginning and end of winter indicates the wintertime efflux of CO_2. Soda lime packets were removed from the respiration collars at snowmelt, dried to constant mass, and weighed (Edwards, 1982). Any CO_2 adsorbed during drying was accounted for by a set of blanks ($n = 8$) which were kept in a freezer during the deployment, dried with the field samples, and weighed at the same time. The change in mass observed for the blanks was then subtracted from the weight of all deployed soda lime packets. A mass correction was applied to account for H_2O formation during adsorption of CO_2 (Grogan, 1998).

GROWING SEASON PATTERNS OF SOIL AND LEAF MINERAL NITROGEN

Estimates of plant-available soil mineral nutrients were obtained using PRS Nutrient Probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada), which adsorb soil anions and cations. The probes are designed to mimic the uptake rate of *in situ* plant roots (Qian and Schoenau, 1994) and were inserted in each plot during three time periods in the growing season of 2007; early (13 June–13 July), middle (13 July–3 August), and late (3–22 August) summer. Each probe was placed in an intact *Dryas integrifolia* individual to minimize differences in microsite and species-dependent nutrient supply and uptake rates. Probes were removed at the end of each time period and a new probe was inserted into the same incision in a given plot. The probes were washed with de-ionized water and refrigerated after removal. All probes were sent to Western Ag Innovations for analysis after the field season. The units used to express nutrient availability are micrograms of nitrogen per 10 square centimeters of probe surface area per time period of burial. Total growing season mineral N supply was calculated as the sum of the three supply rates of consecutive burial periods for each treatment.

Leaf samples were collected in each main plot outside of the CO_2 flux monitoring area from *Salix arctica* and *Dryas integrifolia* individuals following each flux measurement. Approximately two to three leaves were harvested from each individual in the plot. Each leaf sample was then oven-dried at 60 °C for 24 hours and ground into a fine powder. Leaf samples were weighed out at 4.0 ± 0.3 mg into tin capsules on a Sartorius CP2P Microbalance (Sartorius Corporation, Edgewood, New York) and analyzed for % C and N using a Costech 4010 Elemental Combustion System (Costech Analytical, Valencia, California) at the University of Alaska Anchorage Environment and Natural Resources Institute

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Stable Isotope Laboratory. Each composite leaf sample for a species from a single plot was analyzed once; each plot was treated as a replicate for a given treatment.

GROWING SEASON PATTERNS OF NDVI

Measurements of the plot-level normalized difference vegetation index (NDVI) were made using a multispectral digital camera (Tetracam ADC, Chatsworth, California) mounted on a tripod 80 cm above the soil surface. Images of each CO_2 flux plot were taken and used to compute NDVI (Tucker, 1979), which is derived from the reflectance of red (R) and near-infrared light (NIR) as follows:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{R})/(\mathrm{NIR} + \mathrm{R}) \quad (1)$$

where NIR is reflectance at 835–870 nm and R is reflectance at 635–667 nm. NDVI images were captured from all of the study plots on the same dates as CO_2 flux measurements.

GROWING SEASON PATTERNS OF PHENOLOGY

Salix arctica and *Dryas integrifolia* vegetation phenology was monitored weekly during the growing season of 2007. Dates of snowmelt, first leaf bud burst, and first yellowing or browning of leaves were recorded. International Tundra Experiment (ITEX) phenological monitoring protocols were used (Molau and Edlund, 1996).

GROWING SEASON PATTERNS OF MIDDAY AND DIURNAL CO_2 FLUXES

Midday CO_2 fluxes were measured weekly in each plot ($n = 6$) using a closed system clear acrylic chamber in-line with a LI-COR 6200 (LI-COR Inc., Lincoln, Nebraska) portable photosynthesis system (Vourlitis et al., 1993). The infra-red gas analyzer was calibrated using CO_2-free air and a gas of known CO_2 concentration (500 ± 2 ppm) on a bi-weekly basis to avoid instrumental error. Instrumental drift did not exceed 2 ppm during any two weeks between calibration dates. Fluxes were calculated using CO_2 concentrations and chamber microclimate data logged every 2 seconds during the 30 second measurement period following Hooper et al. (2002). Before each NEE measurement the chamber was vented, allowing the interior to reach the ambient CO_2 concentration. The NEE measurement was then made. The chamber was then vented again, an opaque shade cloth was placed over the chamber, and the ER measurement was taken.

In this study, GEP is assigned a positive value, indicating carbon assimilation by the ecosystem, while ER is assigned a negative value, indicating carbon loss from the ecosystem. The sum of these two values yields the net ecosystem exchange (NEE) of CO_2 with the atmosphere. Positive NEE values indicate net ecosystem CO_2 gain, while negative values indicate net CO_2 loss. It is important to note that NEE (clear chamber) and ER (dark chamber) were measured directly, while GEP is a calculated value (i.e., GEP = NEE − ER).

Diurnal CO_2 fluxes were sampled on five dates during the growing season. Only the ambient and intermediate plots were snow-free on the first diurnal measurement date (27 June). Carbon dioxide fluxes were measured in all treatments on the subsequent four dates (4 and 18 July, 1 and 16 August). NEE was measured at 0:00, 6:00, 12:00, and 18:00 using the method described above. Plot-level daily mean NEE was regressed against midday NEE to determine if midday NEE measurements could be used to predict daily mean NEE.

Plot-level measurements of midday soil temperature (5 cm depth), photosynthetically active radiation (PAR) and volumetric soil moisture (0–12 cm depth) were taken immediately following each flux measurement with a VWR Traceable Temperature Probe (VWR Instruments, West Chester, Pennsylvania), a LI-COR 190SA Quantum Sensor (LI-COR Inc., Lincoln, Nebraska) and a Hydrosense time-domain reflectometry (TDR) probe (Campbell Scientific, Logan, Utah), respectively.

STATISTICAL ANALYSIS

Data were tested for normality and homogeneous variances using the Shapiro-Wilk test and Bartlett's test, respectively, using the Explore function in SPSS version 16.0.1 (SPSS Inc., Chicago, Illinois). Appropriate transformations were performed if necessary. The Regression function in SPSS 16.0.1 was used to determine the relationship of midday NEE and daily mean NEE. Treatment effects for overwinter CO_2 flux were tested using a one-way ANOVA in SPSS ($\alpha = 0.05$) with snow depth as the main factor.

Treatment effects for all time series data (CO_2 flux rates, leaf and soil nutrient concentrations) were tested using two-way repeated measures ANOVA ($\alpha = 0.05$) with snow depth and date as factors (Zar, 1999). Repeated measures analyses were performed using PROC MIXED in SAS version 9.1 (SAS Institute, Cary, North Carolina). Snow depth and sampling date were fixed effects and plot was the random effect. Repeated measures analyses included only those sampling dates in which data were available for all treatments. Error covariance structures were chosen by the lowest absolute value of Akaike's Information Criterion. A post-hoc Tukey's HSD test was used to identify significant differences across treatments and dates in all analyses.

Results

PATTERNS OF OVERWINTER ABIOTIC MEASUREMENTS AND CO_2 EFFLUX

Mean overwinter soil temperatures for the ambient, intermediate, and deep snow treatments were −15.0, −13.9, and −12.4 °C, respectively (Fig. 1). The maximum soil temperature difference across treatments of 7.5 °C occurred on 31 January 2007 between the ambient and deep areas. Overwinter CO_2 efflux was significantly different between the intermediate and ambient snow depth treatments ($p = 0.03$, $n = 8$; Fig. 2). Soda lime traps in the ambient snow areas adsorbed the smallest mean amount of CO_2 (33.1 ± 6.6 g CO_2 m^{-2}), while traps in the intermediate and deep snow areas adsorbed 2 to 3 times as much CO_2 (104.5 ± 15.3 g CO_2 m^{-2} and 77.7 ± 21.7 g CO_2 m^{-2}, respectively). CO_2 efflux from the deep snow treatment was not significantly different than the ambient ($p = 0.09$, $n = 8$) or intermediate treatments ($p = 0.17$, $n = 8$).

GROWING SEASON PATTERNS OF ABIOTIC MEASUREMENTS

There were no significant treatment differences in point measurements of growing season soil temperature ($p = 0.18$, $n = 6$; Fig. 5F) or PAR ($p = 0.34$, $n = 6$; Fig. 5E). Soil water content, however, was significantly affected by the increased snow treatments ($p < 0.001$, $n = 6$; Fig. 5D). The ambient and

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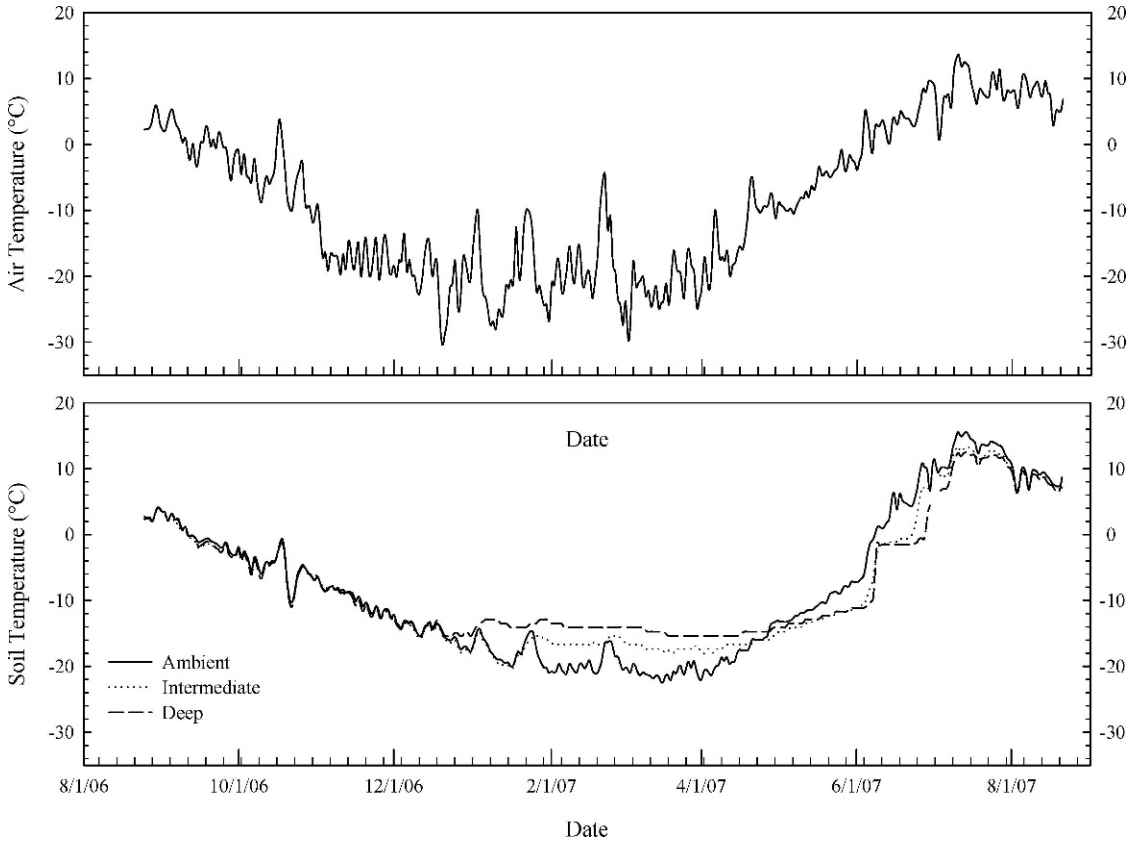


FIGURE 1. Air and soil temperatures at the study site from 24 August 2006 through 24 August 2007.

intermediate treatments were significantly different ($p = 0.023$, $n = 6$). There was no difference between the ambient and deep ($p = 0.125$, $n = 6$) or deep and intermediate ($p = 0.827$, $n = 6$) treatments. The largest difference in volumetric soil water content across two treatments (~10%; the intermediate and ambient snow depths) occurred immediately after snowmelt in the intermediate area. The ambient area had been snow-free for three weeks and soil water had decreased to 26%, while the mean soil water content in the intermediate area was at 36% after emergence from snow cover. Soil water decreased in all treatments after snowmelt until early August, when the ambient area had the lowest soil water content (9%) of any treatment during the growing season. Rain events then brought all treatments to equal levels of soil water for the remainder of the season.

GROWING SEASON PATTERNS OF SOIL AND LEAF MINERAL NITROGEN

We found no statistically significant differences between treatments for total growing season mineral N availability ($p =$

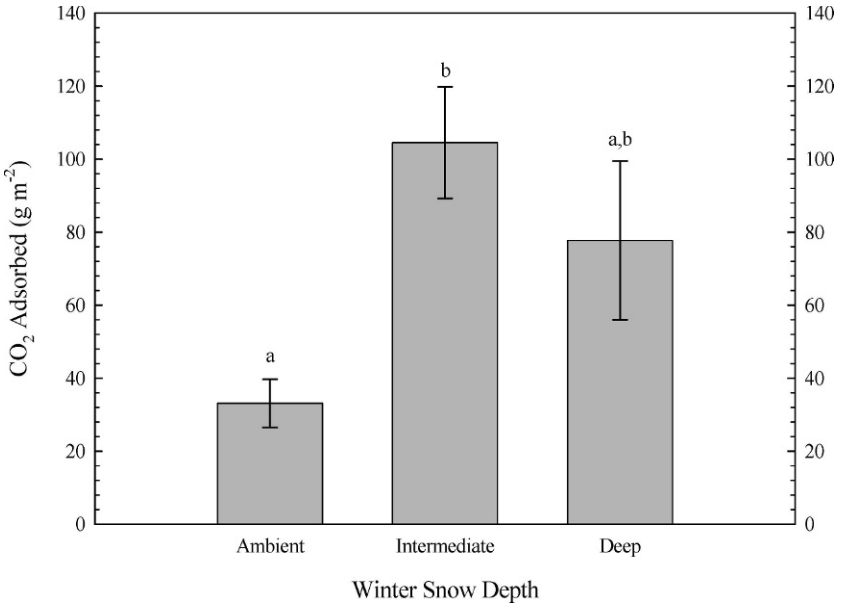


FIGURE 2. Overwinter CO_2 efflux. Values represent CO_2 adsorbed by soda lime base traps during the winter of 2007. Homogeneous subsets are significant at the $p \leq 0.05$ level. Error bars are S.E. ($n = 6$).

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TABLE 1

Growing season soil mineral N measurements. Totals are the sum of the three individual burial periods for each treatment. Superscripts denote homogeneous subsets significant at the $p \leq 0.05$ level. Homogeneous subsets apply only within a time period and not across time periods. For all S.E. terms, $n = 6$.

	Growing Season Mineral N Availability (μg N 10 cm^{-2})			
	Growing Season Period			
Snow Depth	Early (31 d)	Middle (21 d)	Late (19 d)	Total (71 d)
Ambient	14.1 ± 3.4[a]	7.6 ± 0.7[a]	2.4 ± 1.2[a]	24.1 ± 1.8[a]
Intermediate	10.6 ± 2.2[a]	6.7 ± 0.6[a]	7.9 ± 1.8[b]	25.2 ± 1.5[a]
Deep	11.4 ± 2.0[a]	6.9 ± 1.5[a]	8.8 ± 0.9[b]	27.2 ± 1.5[a]

0.741, $n = 6$; Table 1). We observed greater mean mineral N availability with increasing snow depth (ambient, 24.1 ± 1.8 μg N 10 cm^{-2} 71 d^{-1}; intermediate, 25.2 ± 1.5 μg N 10 cm^{-2} 71 d^{-1}; deep, 27.2 ± 1.5 μg N 10 cm^{-2} 71 d^{-1}), although the variability within treatments was approximately equal to the variability across treatments. Mineral N supply rates were not significantly different across treatments early in the growing season ($p = 0.201$, $n = 6$). Similarly, there were no significant differences across treatments in the middle of the growing season ($p = 0.823$, $n = 6$). Strong treatment differences then emerged late in the growing season. Areas with supplemental snow had late season mineral N availability (7.9–8.9 μg N 10 cm^{-2} 19 d^{-1}), roughly four times greater than in ambient areas (2.4 μg N 10 cm^{-2} 19 d^{-1}). The late-season difference between the ambient and intermediate snow treatments was significant ($p < 0.001$, $n = 6$), as was the difference between the ambient and deep snow treatments ($p < 0.001$, $n = 6$). There was no evidence of a significant difference between the intermediate and deep snow treatments in the late growing season ($p = 0.868$, $n = 6$).

Leaf N concentrations also varied significantly across snow depths. *Salix arctica* leaf N concentrations were significantly higher in the increased snow accumulation areas (Fig. 3). All treatments differed significantly (ambient vs. intermediate, $p < 0.001$; ambient vs. deep, $p < 0.001$; intermediate vs. deep, $p = 0.012$, $n = 6$ for all treatments). Early season *Salix arctica* leaves from deep snow area had the highest leaf % N (~4.5%), roughly 50% greater than the level found in leaves from the ambient area (~3.0%). To account for differences due to early season phenological offsets imposed by the increased snow treatments, the repeated measures analysis was also conducted using data from only the last 5 dates of leaf harvests (past the peak of the growing season; 17 July to 21 August). The leaf N concentrations in the increased snow treatments were both significantly different than in the ambient treatment over the last five harvest days (ambient vs. intermediate, $p = 0.046$; ambient vs. deep, $p = 0.001$). There was no evidence of a difference between the intermediate and deep snow treatments, however ($p = 0.141$).

Dryas integrifolia leaf N concentration was greater in the increased snow treatments, although the response was not as dramatic when compared to *S. arctica* (Fig. 3). *Dryas* plants in the deep snow area had significantly higher leaf N concentrations than plants in ambient ($p = 0.002$, $n = 6$) and intermediate areas ($p = 0.043$, $n = 6$). The maximum difference between treatments never exceeded more than 0.4% leaf N by mass. There was not a significant difference between the ambient and intermediate treatments ($p = 0.585$, $n = 6$). The leaf N concentration in the deep snow treatment was significantly different than both the ambient and intermediate treatments when repeated measure analysis was conducted using data from only the last five harvest days (ambient vs. deep, $p < 0.001$; intermediate vs. deep, $p = 0.029$). The ambient and intermediate snow treatments were not significantly different ($p = 0.267$).

GROWING SEASON PATTERNS OF NDVI

We found no significant treatment differences in growing season NDVI ($p = 0.734$, $n = 6$; Fig. 4). The ambient snow area began the season at a mean NDVI value of 0.34 and increased

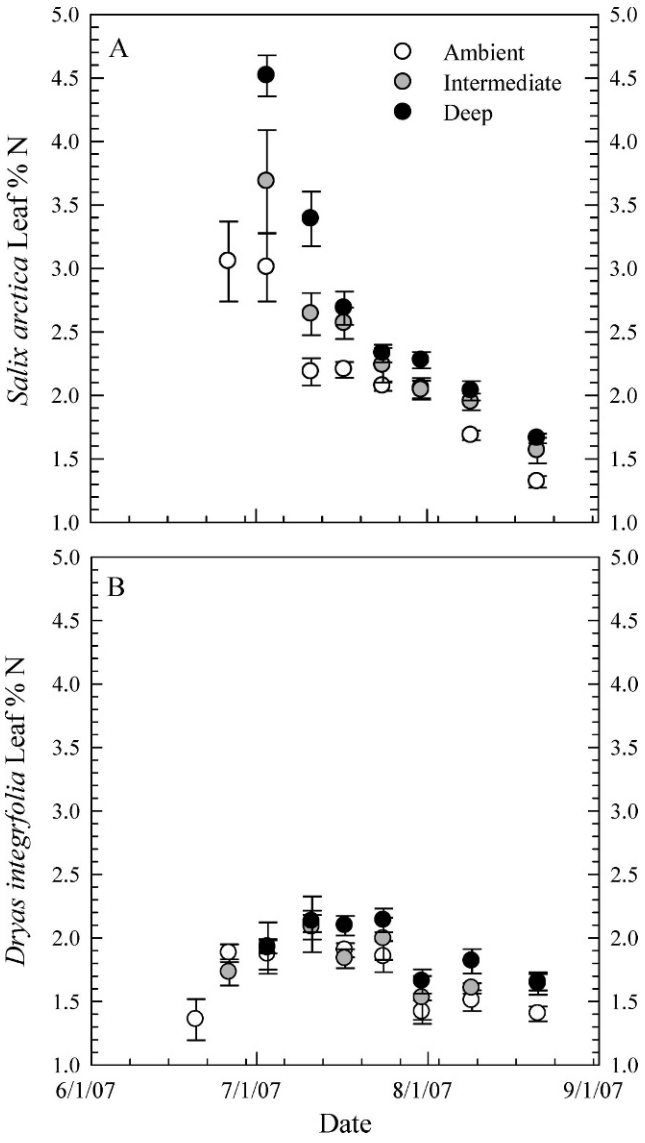


FIGURE 3. ***Salix arctica*** **(panel A) and** ***Dryas integrifolia*** **(panel B) leaf % N. Error bars are S.E. ($n = 6$).**

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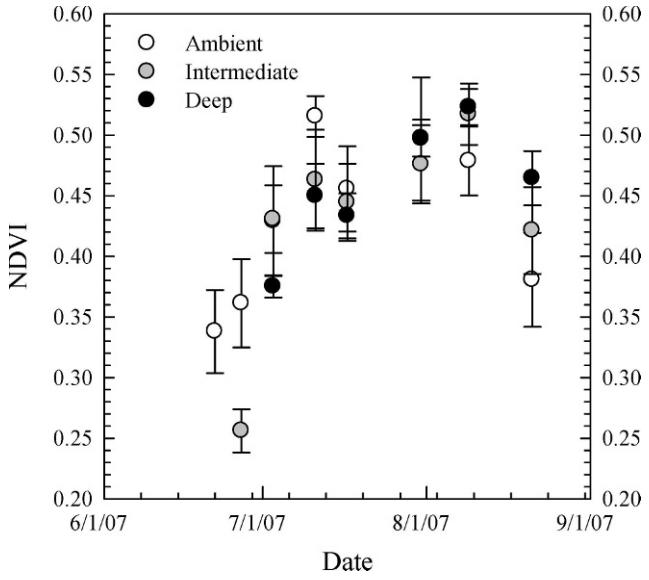


FIGURE 4. Growing season plot-level normalized difference vegetation index (NDVI) values. Error bars are S.E. ($n = 6$).

steadily until peaking at 0.52 on 11 July 2007. The intermediate and deep snow accumulation areas followed a similar pattern as the ambient, but did not reach peak NDVI values (both at 0.52) until one month later (9 August 2007).

PHENOLOGY MONITORING

Experimental snow additions altered *S. arctica* and *D. integrifolia* phenology (Table 2). Increased winter snow cover delayed the onset of leaf bud burst and leaf senescence in both species. However, plants from the increased snow areas reached phenological stages in fewer days after snowmelt than plants from ambient snow areas. For example, *S. arctica* leaves in the ambient snow area began to senesce after 61.8 ± 0.6 days, whereas *S. arctica* leaves in the intermediate and deep snow areas began to senesce after 51.8 ± 1.1 days and 48.8 ± 1.2 days, respectively.

GROWING SEASON PATTERNS OF MIDDAY CO_2 FLUXES

The NEE values measured during the first month of monitoring (11 June through 11 July) were the most negative of the growing season (Fig. 5A). Net ecosystem exchange increased across treatments from this point until 1 August, when NEE for all treatments reached positive values, indicating net ecosystem CO_2 uptake, near the peak of aboveground plant biomass as estimated by NDVI. NEE then became more negative across treatments and returned to near zero at the end of the field season. The intermediate snow depth treatment had significantly less negative rates of NEE compared to the ambient ($p = 0.036$, $n = 6$) and deep snow treatments ($p = 0.030$, $n = 6$). The ambient and deep treatments were not significantly different ($p = 0.962$).

The first GEP measurement was taken in the ambient snow area on 14 June 2007 (Fig. 5B). The intermediate and deep snow areas emerged two and three weeks later, respectively. GEP increased quickly in 2007 with warm temperatures and clear skies. The ambient snow area reached peak rates of GEP on 11 July 2007, and the intermediate and deep snow areas reached peak rates the following week. The maximum GEP rate (4.06 μmol CO_2 m^{-2} s^{-1}) in the deep snow area was the highest observed during the growing season. All treatments had declining rates of GEP after this date (18 July 2007). The ambient treatment had consistently and significantly lower rates of GEP compared to the intermediate ($p = 0.006$, $n = 6$) and deep snow treatments ($p = 0.001$, $n = 6$). There was no significant difference in GEP between the intermediate and deep snow treatments ($p = 0.728$, $n = 6$).

Ecosystem respiration rates were low (0.98 μmol CO_2 m^{-2} s^{-1}) when the control treatment became snow free in early June of 2007, but increased rapidly in the following weeks (Fig. 5C). Intermediate and deep snow treatments quickly matched the rates of the ambient treatment after emergence from the snow. All treatments reached peak ER levels on 11 July 2007, when the deep area had the highest observed mean midday respiration rate (−4.31 μmol CO_2 m^{-2} s^{-1}) of the season. ER rates within treatments fluctuated across subsequent measurement dates, generally decreasing until the end of the monitoring campaign. The deep snow treatment had significantly higher ER rates than the ambient ($p = 0.005$, $n = 6$) and intermediate ($p = 0.016$, $n = 6$) snow depth treatments during the 2007 growing season. There was no evidence of a difference between the ambient and intermediate treatments ($p = 0.962$, $n = 6$).

GROWING SEASON PATTERNS OF DIURNAL FLUXES

Mean diurnal NEE values were negative and significantly different for each measurement date across all treatments ($p = 0.001$, $n = 6$) for the entirety of the growing season (Fig. 6). Mean diurnal NEE of all dates (Fig. 6) in the intermediate snow area was significantly different from both the ambient ($p = 0.026$, $n = 6$) and the deep ($p = 0.001$, $n = 6$) snow areas. The ambient and deep snow areas were not significantly different, however ($p = 0.480$, $n = 6$).

Midnight NEE values were generally constant throughout the growing season in both intermediate (−1.11 to −1.54 μmol CO_2 m^{-2} s^{-1}) and deep (−1.75 to −2.01 μmol CO_2 m^{-2} s^{-1}) snow areas. Early morning (06:00), midday (12:00) and early evening (18:00) NEE values ranged between −2 and +1 μmol CO_2 m^{-2} s^{-1} and were most negative during the earliest measurement dates.

TABLE 2

Growing season phenology monitoring results. Data in the "Melt to p(n)" column represent the average amount of time elapsed (days) after snowmelt for a given phenological event to occur within a treatment. For all S.E. terms, $n = 6$.

Salix arctica Phenology	Ambient	Melt to p(n)	Intermediate	Melt to p(n)	Deep	Melt to p(n)
Snow-free date	162.0 ± 0.0	0.0	174.0 ± 0.0	0.0	180.0 ± 0.0	0.0
First leaf bud burst	168.2 ± 0.5	6.3	178.1 ± 0.5	4.2	184 ± 0.0	4.0
First yellowing of leaves	223.7 ± 0.6	61.8	225.7 ± 1.1	51.8	228.7 ± 1.2	48.8
Dryas integrifolia Phenology	Ambient	Melt to p(n)	Intermediate	Melt to p(n)	Deep	Melt to p(n)
Snow-free date	162.0 ± 0.0	0.0	174.0 ± 0.0	0.0	180.0 ± 0.0	0.0
First leaf erected	167.9 ± 0.7	6.0	178.7 ± 0.6	4.8	185.4 ± 0.7	5.5
First yellowing or browning of leaves	220.7 ± 0.9	58.8	226 ± 1.1	52.0	228.2 ± 1.0	48.3

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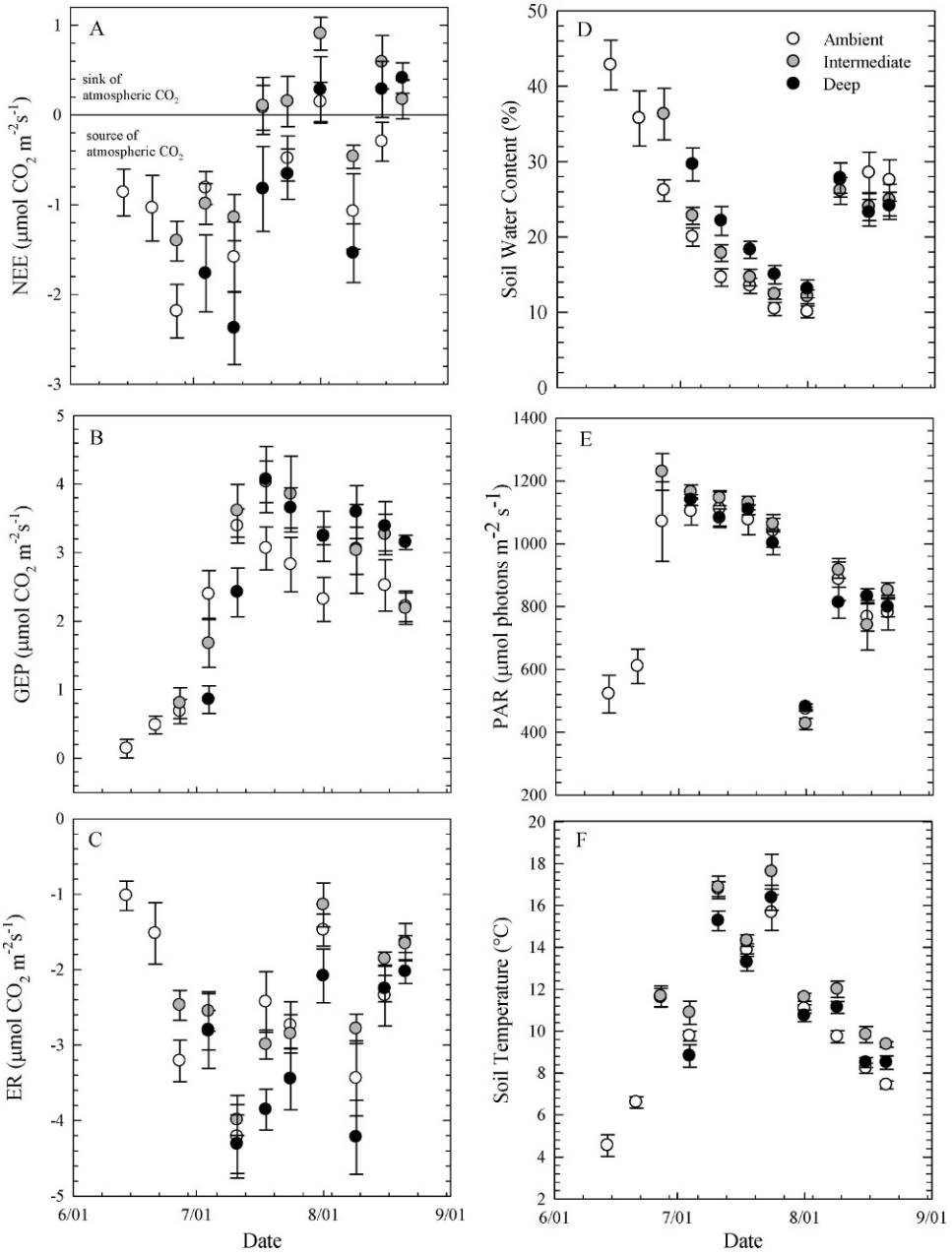


FIGURE 5. Midday net ecosystem exchange (NEE; panel A), gross ecosystem photosynthesis (GEP; panel B), ecosystem respiration (ER; panel C), soil water content (panel D), photosynthetically active radiation (PAR; panel E), and soil temperature (panel F) measurements for the growing season of 2007. Error bars are S.E. ($n = 6$).

Diurnal mean NEE increased across all treatments until 1 August 2007 when midday NEE was positive (CO_2 uptake) for all treatments. Midday NEE fluxes were a strong predictor of daily mean NEE ($r^2 = 0.80$, $p < 0.001$; Y = 0.558*X − 0.622).

Discussion

Experimental snow depth manipulations in Low Arctic, alpine, and grassland ecosystems have provided evidence that changing a landscape's snow depth regime directly influences physical, chemical, and biological processes (Brooks et al., 1996; McGuire et al., 2000; Aerts et al., 2004; Schimel et al., 2004; Chimner and Welker, 2005; Welker et al., 2005, Rixen et al., 2008). The results presented in this study are the first to show the sensitivity of a High Arctic ecosystem to multiple levels of increased winter snow depth. Our results indicate that both overwinter and growing season physical parameters are affected by increased winter snow accumulation, which in turn have significant effects on ecosystem function. The growing season of 2007 was the 6th warmest out of 30 years of local temperature records, and as of the summer of 2009, five of the ten warmest years on record in the Thule area had occurred in the past decade. If this trend persists, then the results presented in this study may be representative of the future state of this landscape.

PATTERNS OF OVERWINTER SOIL TEMPERATURE AND CO_2 EFFLUX

The mean overwinter (1 October 2006–1 April 2007) soil temperature under deep snow was approximately 2.5 °C warmer than the mean temperature under ambient snow, consistent with previous snow addition experiments (Welker et al., 2000; Brooks et al., 2004; Schimel et al., 2004). Overwinter CO_2 efflux was responsive to snow depth, being approximately four times greater under increased (~80–100 g CO_2 m^{-2}) versus ambient snow cover (~25 g CO_2 m^{-2}). Estimates from wintertime CO_2 flux experiments have shown that up to 60% of growing season carbon uptake can be respired during the snow-covered season

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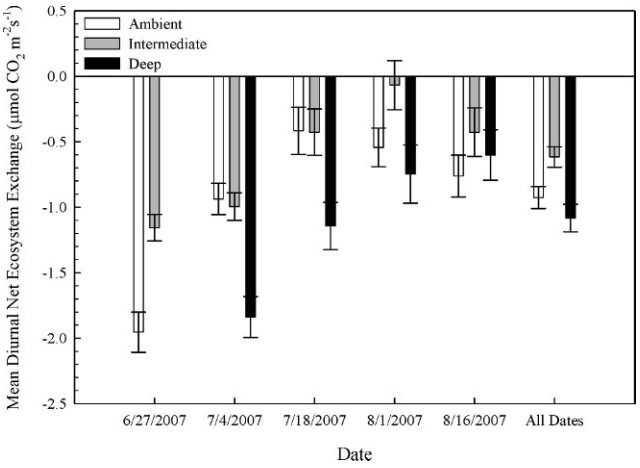


FIGURE 6. Growing season mean daily diurnal NEE measurements. Measurements were made on only four dates for the deep snow treatment due to persistent snow cover. Error bars are S.E. ($n = 6$).

(Sommerfeld et al., 1993; Winston et al., 1997; Oechel et al., 2000; Monson et al., 2002, Morgner et al., 2010).

Soil temperature diverged from air temperature first under deep snow, then under intermediate snow, but never under ambient snow cover, which closely tracked air temperature throughout the winter. It is likely that greater microbial activity during the winter in the increased snow areas contributed to the higher observed rates of CO_2 efflux in those treatments. Soil heterotrophic respiration occurs underneath the snowpack at temperatures below 0 °C and is highly sensitive to small changes in temperature, particularly when soils are near the freezing point (Mikan et al., 2002; Sullivan et al., 2008c).

The measured overwinter CO_2 efflux (25–100 g CO_2 m^{-2}) is comparable to rates observed elsewhere in cold and dry ecosystems (Fahnestock et al., 1998; Welker et al., 2004; Elberling, 2007), although the range of reported values varies widely. The soda lime base trap technique used in this study may cause an artificially large release of CO_2 from the soil due to its effect on the CO_2 concentration gradient from the soil to the chamber headspace, as described by Nay et al. (1994). Although the magnitudes of the wintertime fluxes may not be representative of natural fluxes, the results are nonetheless useful for comparison across snow depths. Additional overwinter monitoring will be extremely valuable to determine if the patterns observed in this study are indicative of long-term responses.

GROWING SEASON PATTERNS OF SOIL AND LEAF NUTRIENTS

We observed a shift in the seasonal pattern of N availability, with increased late season N availability in the increased snow accumulation treatments. Changes in soil nutrient availability are thought to be one of the most significant effects of increased winter snow accumulation on ecosystem function because tundra landscapes are generally strongly nutrient limited (Schimel et al., 2004; Sturm et al., 2001, 2005; Welker et al., 2005; Borner et al., 2008). Borner et al. (2008) also observed significantly higher rates of late growing season N availability following increased snow depth.

Total growing season N availability was not significantly different across treatments. The late season response was significantly different and nonlinear with increasing snow depth. After a jump in N availability from ambient to intermediate snow depth, there was no increase observed between the intermediate and deep snow depths in the late growing season. The nonlinear response may be due to differences in microbial community activity, composition, or biomass in the increased snow treatments. Litter deposition in the winter snowpack may have also caused or added to the observed increase in late growing season nutrient availability. Fahnestock et al. (2000) found that snow areas of high snow deposition had 10 times the amount of litter in the snowpack than in ambient areas, which amounted to an additional 14 g N m^{-2} in the deep snow areas. At our site, litter from the snowpack may be decomposing in the early and middle growing season as soil and air temperatures increase, which may then become available as mineral N in the late growing season. Soil microclimate conditions during the late growing season and early fall may be key determinants of the rate of decomposition in these systems.

The pattern of seasonal acquisition and allocation of the soil N pool among the plant and microbial community remains incompletely studied, although it appears both *Salix arctica* and *Dryas integrifolia* individuals in the increased snow treatments may have incorporated additional N resources into leaf tissue, similar to what has been observed in Low Arctic Alaska (Welker et al., 2005). *Salix arctica* leaves harvested from the deep snow areas immediately after snow melt had N contents approximately 50% greater than those of the ambient snow areas harvested immediately after snowmelt. The phenological shift caused by the delayed growing season start may account, in part, for the greater leaf N concentration in the increased snow zones. However, the difference in leaf N concentrations persisted late into the growing season as evidenced by the results of the repeated measures ANOVA of the last five leaf harvest days. Regardless of the mechanism responsible for the greater leaf N concentrations, the presence of leaves with higher N concentrations during the entire growing season likely led to greater rates of leaf-level photosynthesis in *S. arctica* within the intermediate and deep snow zones.

The leaves of *D. integrifolia*, a wintergreen shrub, had a much smaller increase in leaf N concentration in response to increased winter snow accumulation, supporting the postulate that relatively fast-growing deciduous shrubs such as *S. arctica* are the plant functional type most responsive to deep snow (Sturm et al., 2005). In one of the few long-term snow fence experiments in the Arctic, shrubs were the plant functional group most responsive to increased snow cover after eight years of snow addition at Toolik Lake, Alaska (Wahren et al., 2005). Shrub cover increased in both moist and dry tundra, and the change was most pronounced in the intermediate (0.5–2 m) and deep (2–3 m) snow areas.

Increased leaf N concentration in areas of increased snow cover could have multiple implications for ecosystem function. In addition to increasing rates of leaf-level photosynthesis (Field and Mooney, 1986; Evans, 1989), increased leaf N concentrations and decreased leaf C:N ratios lead to higher quality forage for herbivores (Klein and Bay, 1991). Decreased leaf C:N ratios also lead to increased litter quality, which can bring about more rapid leaf litter decomposition and turnover by soil invertebrates, fungi, and bacteria (Enriquez et al., 1993; Hobbie et al., 2000). Increasing decomposition and more rapid litter turnover times may then accelerate a biophysical feedback cycle of snow-shrub-microbial interactions (Schimel et al., 2004; Sturm et al., 2001, 2005.)

GROWING SEASON PATTERNS OF PHENOLOGY

The phenology monitoring results show that increased winter snow accumulation has significant impacts on the timing of vital

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events in plant development. Increased winter snow accumulation delayed the onset of plant development by two to four weeks due to extended snow cover. *Salix arctica* and *Dryas integrifolia* in the increased snow depth areas then developed more rapidly compared to ambient snow area plants and delayed senescence by 5–8 days, compared with plants in ambient areas (Table 2). The delayed senescence contrasts with results in Low Arctic Alaska and partially explains the greater growing season averaged GEP under both levels of increased snow. Borner et al. (2008) found that, despite different times of emergence from the snow, senescence began in all treatments at approximately the same time for *Betula nana* and *Salix pulchra*, both deciduous shrubs.

GROWING SEASON PATTERNS OF NDVI AND CO_2 FLUXES

The rates of NEE, GEP, and ER observed in this study (Figs. 5A–5C) are similar to those seen in other studies of High Arctic prostrate dwarf-shrub, herb tundra ecosystems (Jones et al., 2000; Lloyd, 2001; Welker et al., 2004). The maximum rates of CO_2 exchange are only one-half those observed in a nearby fen at Thule, where aboveground biomass and NDVI are much greater (Sullivan et al., 2008b). During most of our midday measurements, the ecosystem was a net source of CO_2 to the atmosphere (Fig. 5A). The mean rate of NEE in the intermediate snow area was, however, 75% higher than mean NEE rates in the ambient or deep snow area (i.e. the intermediate area lost significantly less CO_2 to the atmosphere at midday). The ambient snow area was a net source of CO_2 to the atmosphere on 8 out of 11 sampling days and the deep area was a net source on 5 out of 8 sampling days. In contrast, the intermediate snow area was a net atmospheric CO_2 source on only 4 out of 9 sampling days.

These results as a whole suggest a balance between parameters controlling carbon exchange that are significantly affected by increased snow depth. The first parameter, soil nutrient supply, was greater in the late growing season in plots where snow was deeper during the previous winter (Table 1). Even relatively small nitrogen additions in High Arctic prostrate dwarf-shrub, herb tundra near our study site dramatically stimulated both GEP and ER (Arens et al., 2008) and in similar vegetation types on Svalbard (Robinson et al., 1995). More plant available N in the late growing season appears to have resulted in higher leaf N and greater photosynthetic rates throughout the growing season in the increased snow plots.

The second parameter, soil water availability, is also greater with increased snow (Fig. 5D). Greater soil water availability may reduce the potential for midday and/or midsummer water stress allowing for higher rates of leaf gas exchange (e.g., Welker et al., 1993).

The third parameter, growing season length, is shorter with increased snow and is one of the primary controls over net ecosystem exchange (Churkina et al., 2005; Groendahl et al., 2007). Thus, areas with intermediate snow depth in winter may be in an optimal snow depth condition for midday carbon uptake due to a balance of these three parameters. The intermediate snow depth area has increased nutrient and water availability, as does the deep snow area. Yet the area of intermediate snow depth has a slightly longer growing season (~10 days) than the deep snow area which allows plants to capitalize on additional soil water and nutrient resources without the constraint of a more severely shortened growing season.

Our results showed that GEP increased in both the intermediate and deep snow areas, yet ER increased only in the deep snow treatment area (Figs. 5A–5C). We hypothesize that plants in the intermediate area were able to compete more effectively with soil microbes for the greater nutrient and water resources than plants in the deep area where the length of the growing season was more severely constrained. Additionally, the deep snow areas may have a deeper active layer which could expose buried organic matter to decomposition. Horwath et al. (2008) found pockets of very old soil C buried deep in the soil profile of a similar ecosystem near Thule. Meanwhile, Nowinski et al. (2010) found that long-term snow additions have nearly doubled the active layer depth in moist acidic tundra near Toolik Lake, Alaska, and that CO_2 is being released from the deepest part of the active layer in that treatment. This effect may be contributing to the high observed ER rates in this study, although very rocky soils have prevented our research team from taking spatially and temporally extensive active layer measurements.

Deeper snow conditions had no significant effect on growing season NDVI (Fig. 4), which is closely correlated with the leaf area index in this ecosystem (Steltzer and Welker, 2006). Increased photosynthetic rates are therefore likely due to increased leaf-level photosynthesis associated with higher leaf nitrogen concentration and improved plant-water relations (e.g., Sullivan and Welker, 2007).

Our diurnal NEE measurements expanded upon the patterns observed in the midday measurements. The intermediate snow treatment had consistently higher rates of NEE than the other treatments, as demonstrated by the mean diurnal NEE values across all sampling dates (Fig. 6). We observed six measurements of positive mean NEE across all sampling times in the intermediate snow treatment during our diurnal campaign, twice the number in the ambient and three times the number in the deep treatments. On 1 August 2007, NEE was positive at three of the four sampling times in the intermediate snow treatment; only at midnight was NEE negative. These results reinforce our postulate that a combination of factors result from the intermediate snow depth which create an optimal scenario for growing season net CO_2 uptake. Daily mean rates were more negative than midday rates at all snow depths, lending more evidence that on a seasonal and yearly basis, this ecosystem is currently a source of CO_2 to the atmosphere. A combination of factors is likely causing this site to be a source of atmospheric CO_2. However, a site cannot be a perennial source of CO_2 without a large supply of labile carbon for respiration, otherwise the soil and plant communities could quickly exhaust the supply of available carbon. Soil studies at this site have shown the presence of old (thousands to tens of thousands of years old) carbon stores. In addition, the soils of this area are highly cryoturbated (Horwath et al., 2008). The dynamic nature of the soil may expose older carbon stocks to the active layer of the soil, which provides a large supply of carbon to the heterotrophic soil community. Recent work at our study site has shown that the older carbon is being mineralized during the time of maximum thaw depth (Czimczik and Welker, 2010).

The ecological research community is beginning to fully appreciate the complexities of Arctic ecosystem responses to changes in climate (e.g., Post et al., 2009). The nonlinear responses of NEE to multiple levels of increased winter snow depth demonstrate that the response to a small perturbation may not be indicative of the response as the magnitude of the perturbation grows. Our results show that even the direction of the ecosystem response may change (e.g., NEE) as the driver increases in magnitude. Moreover, results of our study show that changes in winter can have cascading consequences for ecosystem function that persist throughout the subsequent growing season. The potential for complex ecosystem responses to climate change

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reinforces the need for long-term studies that employ multiple levels of experimental manipulation (e.g., Sullivan et al., 2008a).

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