Long-term increases in snow pack elevate leaf N and photosynthesis in *Salix arctica*: responses to a snow fence experiment in the High Arctic of NW Greenland

A Joshua Leffler¹ and Jeffery M Welker

Department of Biological Sciences, University of Alaska–Anchorage, Anchorage, AK 99508, USA

E-mail: ajleffler@uaa.alaska.edu

Received 15 January 2013
Accepted for publication 31 May 2013
Published 27 June 2013
Online at stacks.iop.org/ERL/8/025023

Abstract

We examine the influence of altered winter precipitation on a High Arctic landscape with continuous permafrost. Gas exchange, leaf tissue element and isotopic composition (N, δ¹³C, δ¹⁵N), and plant water sources derived from stem and soil water δ¹⁸O were examined in *Salix arctica* (arctic willow) following a decade of snow-fence-enhanced snow pack in NW Greenland. Study plots in ambient and +snow conditions were sampled in summer 2012. Plants experiencing enhanced snow conditions for 10 years had higher leaf [N], photosynthetic rate, and more enriched leaf δ¹⁵N. Enhanced snow did not influence stomatal conductance or depth of plant water use. We attribute the higher photosynthetic rate in *S. arctica* exposed to deeper snow pack to altered biogeochemical cycles which yielded higher leaf [N], rather than to enhanced water availability. These data demonstrate the complexity of High Arctic plant responses to changes in winter conditions. Furthermore, our data depict the intricate linkages between winter and summer conditions as they regulate processes such as leaf gas exchange that may control water vapor and CO₂ feedbacks between arctic tundra and the surrounding atmosphere.

Keywords: Thule, Greenland, *Salix arctica* (arctic willow), gas exchange, carbon, nitrogen, and oxygen isotope composition, leaf nitrogen, photosynthesis, snow fence

Online supplementary data available from stacks.iop.org/ERL/8/025023/mmedia

1. Introduction

Increased precipitation in the High Arctic associated with global climate change is expected to influence plant function and ecosystem processes (Welker et al 2005, Schimel et al 2004, Buckeridge and Grogan 2008, Christiansen et al 2012). Higher snowfall has been observed in the High Arctic (Kohler et al 2006, Min et al 2008), and recent studies document increased transport of atmospheric moisture northward and greater discharge of rivers into the Arctic Ocean in Eurasia (Peterson et al 2002, Zhang et al 2013). During winter, deeper snow pack can increase soil temperature resulting in greater CO₂ flux and enhanced nutrient cycling (Brooks and Williams 1999, Schimel et al 2004, Rogers et al 2011). The effects of enhanced snow depth persist during summer, reducing...
soil temperature post-snowmelt, increasing soil moisture, and delaying leaf production (Wipf and Rixen 2010, Cooper et al 2011, Rogers et al 2011). Warmer soils during winters with enhanced snow clearly stimulate microbial activity and result in greater soil N availability (Schimel et al 2004, Buckeridge and Grogan 2008). The influence of greater soil moisture on carbon gain is less well understood and depends on the plant communities examined (Oberbauer et al 2007, Lafleur and Humphreys 2007, Nobrega and Grogan 2008).

Plant and ecosystem function were altered at the same study site following five consecutive winters of experimentally enhanced snow pack in northwest Greenland (Rogers et al 2011). Deep snow led to higher soil [N] and leaf [N] in Salix arctica (arctic willow) and higher over-winter CO₂ efflux, summer gross ecosystem productivity, and summer ecosystem respiration; leaf-level photosynthesis was not measured. Understanding the influence of enhanced snow pack on photosynthesis is important because plant productivity may have a greater influence on net ecosystem exchange than soil respiration in Arctic ecosystems (Griffis and Rouse 2001, McFadden et al 2003) although this is not universally the case (Lafleur and Humphreys 2007). Moreover, carbon gain by Salix sp. may be a key factor in the carbon balance of High Arctic ecosystems (Steltzer et al 2008) since shrubs are becoming more abundant in the region (Wahren et al 2005, Wipf and Rixen 2010, Callaghan et al 2011a). Increased shrub abundance is likely to have a complex influence on active layer depth with potential feedbacks on climate (Blok et al 2010, Bonfils et al 2012).

If greater snow pack is having an influence on photosynthesis, it could be through the alleviation of drought stress, an enhancement of nitrogen availability, or a combination of both (Osmond 1987, Evans 1989). Drought stress may be mitigated by the additional water increasing soil moisture content or by delayed melt preventing water stress from developing because leaf expansion and water use are delayed (Cooper et al 2011, Wipf and Rixen 2010). If the primary mechanism is alleviation of water stress, we should observe higher photosynthesis (A), stomatal conductance (g) and transpiration (E) under enhanced snow pack. Additionally, we may observe that plants are using water from more shallow soils in areas of deeper snow; water use from various depths can be discerned using oxygen isotope composition (δ¹⁸O) of soil and stem water (Dawson et al 2002). Alternatively, if deep snow pack is increasing the availability of mobile forms of N (Schimel et al 2004) we should observe higher A, lower sub-stomatal [CO₂] (ci) and greater leaf [N], but no significant difference in g. Additionally, if high leaf [N] is the result of enhanced microbial activity, we would observe significant differences in leaf nitrogen isotope composition (δ¹⁵N) between plants experiencing ambient and deep snow conditions (Craine et al 2009).

In this study, we examined photosynthetic gas exchange, leaf tissue [N] and δ¹⁵N, and stem and soil δ¹⁸O in S. arctica following ten years of experimentally enhanced snow pack in northwest Greenland. We ask if (1) gas exchange differs in this species between ambient and enhanced snow plots, and

if (2) any differences in gas exchange can be attributed to a response to water availability, or a through a relationship with leaf [N].

2. Materials and methods

An increased snow depth experiment was established near Thule Air Base in northwest Greenland (76°32′N, 68°42′W, 170 m elevation) in 2002; this study was conducted in 2012. Vegetation is a dwarf-shrub/herb tundra dominated by Salix arctica and Dryas integrifolia similar to a local long-term climate change experiment (Sullivan et al 2008). Mean annual precipitation and temperature (1951–2006) is about 120 mm and −11 °C, respectively. June, July and August 2012 (figure 1) were warmer (5.3 versus 4 °C) and wetter (127 versus 40 mm) than average.

Snow depth was enhanced using a snow fence (15 m long × 1.2 m tall), consisting of vertical slats of wood approximately 5 cm wide with similar sized spaces erected in summer 2002. Snow accumulation was enhanced on the windward and leeward side of the fence and measured near the fence on 29 May 2012. We used a 2 m grid of sample points extending 10 m from the fence in each direction, running 12 m parallel to the fence, and recorded snow depth at each point (n = 70). Snow samples were collected from a single snow pit at four depths between the surface and 1 m to determine water equivalent of depth. Snow depth was also recorded at 24 additional points around the study site not influenced by the fence. Finally, distance from the fence to where snow depth was approximately equal to that at uninfluenced points was measured (about 35 m).
The locations of study plots were selected based on snow accumulation and topography. Since soils are shallow, rocky and frozen in the spring, much of the additional water accumulated near the snow fence runs off into shallow depressions on the largely flat landscape, these run-off areas were avoided when selecting deep and ambient snow accumulation zones for study. Three study plots (1.5 m × 1.5 m) were selected in deep snow areas (+snow) and three other study plots were selected in ambient snow areas. The +snow plots were between 2 and 4 m on the windward side of the fence and the ambient snow plots was about 40 m from the fence.

Beginning in late June, and continuing until early August the study plots were sampled every week (six sampling periods). Sampling began approximately four weeks following melt in the ambient plots and two weeks following melt in the +snow plots. Leaf-level gas exchange on five leaves of *S. arctica* per study plot was measured using a portable photosynthesis system (model 6400, Li-Cor Inc., Lincoln, NB). Randomly selected leaves were measured in the field using quantum flux similar to ambient conditions at solar noon (1250 μmol m−2 s−1 for wavelengths 400–700 nm, 10% blue light), and a reference [CO2] of 400 μl l−1 inside the 2 cm2 chamber. Leaves completely filled the chamber. Air temperature during days of measurement varied between 4.7 and 11.4 ◦C; soil temperature varied between 5.8 and 10.7 ◦C; and relative humidity varied between 57 and 89% (table 1). Several leaves from each plot were collected each measurement day for analysis of [%N] (‰), carbon (δ13C) and nitrogen (δ15N) isotope composition (Dawson et al. 2002). Leaf tissue was oven dried at about 70 ◦C and ground to a fine powder in a mechanical shaker (Mini-Beadbeater-16, Biospec Products Inc., Bartlesville, OK) with 3.2 mm ball bearings. Samples were combusted in an elemental analyzer (model 4010, Costech Inc., Valencia, CA) coupled to a mass spectrometer (model Delta V, Thermo Scientific, Waltham, MA) at the University of Alaska–Anchorage. Standard deviation of standards from this analysis for [%N], δ13N and δ15N was 0.02, 0.15, and 0.03, respectively.

Gas exchange and leaf tissue data collected each week were examined with mixed model analyses using the LME4 package within the statistical computing environment R (R Development Core Team 2008). For each response variable two alternative models were compared: model 1 was a random effects model with fixed day of year and random day of year conditioned on plot, model 2 added treatment (ambient or +snow) as a fixed effect; both models were run with uncorrelated random effects and day as a factor. The most appropriate model had the lower akaike information criterion (AIC) and significance was assessed at α = 0.05 using the log-likelihood ratio of the two models. Photosynthesis (A), stomatal conductance (g) and transpiration (E) were log-transformed to meet normality assumptions. The relationship between mean photosynthesis for each measurement day and leaf temperature, air temperature, relative humidity and soil moisture were examined with Pearson correlation using the STATS package in R.

To explore the source of water used by arctic willow we measured oxygen isotope composition (δ18O) of water from soil and *S. arctica* stems collected weekly. A small soil pit was dug to about 20 cm. Soil samples were collected from the wall of the pit using a 1.25 cm dia. metal tube at depths of 5, 10, 15 and 20 cm below the soil surface. A woody stem sample, lacking green tissue, was also collected. Soil and xylem water δ18O were examined using a cavity ring-down spectrometer coupled with a heat induction module (IM-CRDS, Picarro Inc., Santa Clara, CA) which simultaneously extracts and analyzes extremely small samples of water (<3 µl). Samples were loaded into metal sample holders (heavy foil clips for stem cross sections, small tubes for soil), placed into a glass vial with a septum and inserted into the IM. The IM heated the sample vaporizing the water which was passed to the CRDS for analysis. Data are expressed in the familiar δ notation for 18O using the VSMOW standard (Dawson et al. 2002). Data were processed to remove any memory effects among samples and to adjust for drift from the standard (supplement 1 available at stacks.iop.org/ERL/8/025023/mmedia). Soil samples were also weighed and dried to determine water content.

We used xylem and soil water δ18O to estimate the fraction of water in *S. arctica* taken from 5, 10, 15 or 20 cm soil depth. Data were examined with a Bayesian stable isotope mixing model (Parnell et al. 2010) implemented in the SIAR package of R using 200 000 iterations with 50 000 discarded as burn-in. Soil gravimetric water content was incorporated into the model as prior information making the assumption that plants preferentially extract water from the wettest soil layers. The SIAR package uses a Dirichlet prior distribution which requires that the proportions of all isotopic sources (i.e., soil depths) sum to unity.

The response of A to quantum flux was measured in late July and early August. Measurements were made on two leaves per plot between 29 and 30 July, and again on two leaves per plot between 4 and 5 August. Reference CO2 was

### Table 1. Environmental conditions on the six days of measurement in 2012. Air temperature and relative humidity are mean daily values recorded at Thule Air Base, soil temperature was recorded off site at several locations.

| Date       | Day of year | Air temp. (◦C) | Soil temp. (◦C) | Humidity (%) |
|------------|-------------|----------------|-----------------|--------------|
| 30 June    | 182         | 11.4           | 10.2            | 58           |
| 6 July     | 188         | 6.4            | 8.1             | 84           |
| 13 July    | 195         | 5.7            | 7.8             | 89           |
| 20 July    | 202         | 7.1            | 10.7            | 81           |
| 27 July    | 209         | 11.3           | 6.1             | 57           |
| 3 August   | 216         | 10.1           | 9.0             | 66           |
maintained in the chamber at 400 µl l⁻¹ and light was varied between values exceeding full sunlight to nearly dark (1600, 1200, 1000, 700, 500, 300, 200, 100, 50 µmol m⁻² s⁻¹). Light curve measurements took about 30 min per leaf.

Light curve data were examined by fitting a non-linear mixed model (Peek et al. 2002) to each treatment for each set of measurement days. The model fit was the Mitscherlich equation (Potvin et al. 1990):

\[ A = A_{\text{max}}[1 - e^{-A_{\text{qe}}(\text{PPF} - \text{LCP})}] \]  

where \( A_{\text{max}} \) is the maximum photosynthesis rate at high light, \( A_{\text{qe}} \) is the apparent quantum yield or the slope of the curve at low light and LCP is the light compensation point (x-intercept) or the minimum light required to achieve net positive A. Incident light during the experiment is PPF (photosynthetic photon flux), and \( A \) is measured net photosynthesis. Each parameter of the equation was modeled using the NLME (non-linear mixed effects) package in R with a random plot effect. Separate models were run for each of the two days of data collection and for each treatment. Significant treatment effects were determined by comparing the overlap of 95% confidence intervals for each parameter during each measurement date.

3. Results

Snow depth on 29 May 2012 exceeded 1 m near the fence. Two meters leeward from the fence mean snow depth was 114 ± 12 cm (mean ± SD); 10 m from the fence, snow depth was 96 ± 13 cm. On the windward side of the fence, two meters from the fence the snow depth was 81 ± 7 cm and 10 m from the fence, the snow depth was 54 ± 5 cm (see also supplement 2 available at stacks.iop.org/ERL/8/025023/mmedia). Conversely, snow depth varied between 15 and 40 cm (mean 23 ± 6.1 SD) at snow sample points not influenced by the fence. Water content of the snow pack near the snow fence was about 37%. Snow depth in the high snow accumulation plots was 74 ± 9 cm. Data collected in previous years suggest soil temperature can be up to 15 °C warmer under deep compared to ambient snow (figure 1).

Leaf-level instantaneous gas exchange differed between the ambient and +snow conditions. Significant differences among treatments were evident in A (figure 2, table 2). During late June and early July (DOY 182 and 187), A was nearly identical in +snow and ambient plots but differences became apparent during the height of the growing season in mid-July (DOY 195 and 202) and remained higher through early August (figure 2). For the entire growing season, mean
Figure 3. Leaf tissue N concentration (a), nitrogen isotope composition (b) and carbon isotope composition (c) throughout summer 2012. Values are the median ±95% confidence intervals.

Table 2. Mixed model analysis of gas exchange and leaf tissue response variables. Model 1 for each response variable included day as a fixed factor and day/plot as a random effect; model 2 for each response variable included treatment × day as a fixed factor and day/plot as a random effect. Response variables include net photosynthesis (A), stomatal conductance (g), sub-stomatal \([\text{CO}_2]\) (ci), transpiration (E), total leaf \([\text{N}]\) (N), nitrogen isotope composition (\(\delta^{15}\text{N}\)), and carbon isotope composition (\(\delta^{13}\text{C}\)). Subscripts indicate the models detailed above. Significant \(P\)-values (\(P < 0.05\)) indicate that model 2 is preferred over model 1, hence the treatment effect is significant.

| Model | df  | AIC   | Log likelihood | \(\chi^2\) | \(P\) |
|-------|-----|-------|----------------|-----------|-------|
| \(A_1\) | 28  | 87.61 | -15.81         |           |       |
| \(A_2\) | 34  | 85.06 | -8.532         | 14.55     | 0.024 |
| \(g_1\) | 28  | 95.55 | -19.77         |           |       |
| \(g_2\) | 34  | 98.26 | -15.13         | 9.284     | 0.158 |
| \(ci_1\) | 28  | 1648  | -79.59         |           |       |
| \(ci_2\) | 34  | 1651  | -791.6         | 8.462     | 0.059 |
| \(E_1\) | 28  | 51.05 | 2.477          |           |       |
| \(E_2\) | 34  | 38.05 | 14.97          | 25.00     | <0.001 |
| \(N_1\) | 28  | 1.705 | 27.15          |           |       |
| \(N_2\) | 34  | -58.87 | 63.43         | 72.57     | <0.001 |
| \(\delta^{15}\text{N}_1\) | 28  | 106.3 | -25.14         |           |       |
| \(\delta^{15}\text{N}_2\) | 34  | -0.14 | 34.07          | 118.4     | <0.001 |
| \(\delta^{13}\text{C}_1\) | 28  | 47.71 | 4.147          |           |       |
| \(\delta^{13}\text{C}_2\) | 34  | 50.79 | 8.603          | 8.911     | 0.179 |

A in +snow areas was 26% higher than in ambient areas. In contrast, g did not differ significantly between treatments. Curiously, a small difference in E was significant, but a similar difference in ci was only marginally significant (table 2). During the first half of the growing season gas exchange typically increased, then became more variable later in the summer (figure 2), but A was consistently higher and ci was consistently lower in +snow plots. We observed a significant correlation between A and relative humidity (\(r = 0.833, P = 0.040, n = 6\)) during summer 2012. Correlations between A and air temperature (\(r = -0.807, P = 0.052\)), or soil temperature (\(r = 0.424, P = 0.402\)), or soil moisture (\(r = 0.007, P = 0.984\)) were not significant.

Analysis of dried leaf tissue suggests increased snow depth altered leaf \([\text{N}]\) and leaf \(\delta^{15}\text{N}\) (figure 3). For the entire growing season, mean leaf \([\text{N}]\) in +snow plots was 20% greater than in the ambient areas and this difference was significant (figure 3, table 2). Differences between treatments were most pronounced during the height of the growing season in mid-July (DOY 195 and 202) when leaf \([\text{N}]\) was 27% higher. Leaf \(\delta^{15}\text{N}\) was 2.5% enriched in the +snow plots compared to ambient plots, also a significant difference (figure 3, table 2). No treatment effect was observed for leaf tissue \(\delta^{13}\text{C}\). Leaf \([\text{N}]\) declined considerably from June
Figure 4. Relationship between net photosynthesis ($A$) and incident light (PAR) during (a) 29–30 July 2012, and (b) 4–5 August 2012. Solid lines indicate the parameter estimate and 95% confidence interval about the asymptotic photosynthetic rate ($A_{\text{max}}$) for ambient conditions; dashed lines indicate the same for +snow conditions.

Table 3. Non-linear mixed model fit of the Potvin et al. (1990) equation for a photosynthetic light response curve. Confidence intervals (95%) assume a normal distribution around the parameter estimate.

| Parameter | 29–30 July Value (upper, lower CI) | 4–5 August Value (upper, lower CI) |
|-----------|-----------------------------------|-----------------------------------|
| Ambient   | $A_{\text{max}}$ 10.73 (8.00, 13.46) | 8.005 (7.04, 8.97) |
|           | $A_{\text{qe}}$ 0.0036 (0.0023, 0.0050) | 0.0037 (0.0027, 0.0046) |
|           | LCP 28.65 (−11.35, 68.65) | 31.69 (7.24, 56.15) |
| +snow     | $A_{\text{max}}$ 13.14 (9.32, 16.96) | 11.14 (9.76, 12.51) |
|           | $A_{\text{qe}}$ 0.0038 (0.0021, 0.0056) | 0.0033 (0.0021, 0.0044) |
|           | LCP 25.40 (−22.39, 73.20) | 27.73 (−3.67, 59.14) |

* Denotes parameter estimates that differ between ambient and +snow conditions based on a comparison of confidence intervals.

through August while little seasonal trend was observed in leaf $\delta^{15}$N or $\delta^{13}$C.

Light curves further suggest greater photosynthetic capacity by plants in +snow plots (figure 4). While the overall curves do not differ significantly between +snow and ambient conditions, $A_{\text{max}}$ was 22% higher in +snow plots in late July and 39% higher in early August, with the latter being significant (table 3). Light compensation point and $A_{\text{qe}}$ were similar among treatments.

We observed few clear patterns in xylem or soil $\delta^{18}$O, or soil moisture during the growing season (supplements 3 and 4 available at stacks.iop.org/ERL/8/025023/mmedia). Xylem water $\delta^{18}$O in *S. arctica* was relatively constant in +snow areas with a slight positive trend during the season; $\delta^{18}$O was more variable in the ambient snow area. Overall, $\delta^{18}$O of xylem water was $−15.9 ± 3.4 \%$ in ambient areas and $−17.2 ± 2.0 \%$ in +snow areas. Soil gravimetric moisture content, averaged across the summer, was $21 ± 13 \%$ and $16 ± 14 \%$ in the +snow and ambient plots, respectively. Water extraction by soil depth did not differ between +snow and ambient treatments and declined with depth in each (figure 5). The uppermost 5 cm of soil contributed 38% and 39% in +snow and ambient treatments, respectively. Soils at 10, 15 and 20 cm contributed 24, 20 and 18% of the stem water in the +snow plots, and 24, 21 and 16% in the ambient plots.

4. Discussion

Nearly ten years of increased snow depth has enhanced photosynthesis ($A$) in *S. arctica*, which we attribute to higher leaf $[N]$. Plants in plots with greater snow accumulation had higher $A$ and maximum photosynthesis ($A_{\text{max}}$), and marginally lower sub-stomatal $[CO_2]$ ($ci$), but did not differ from ambient plots in stomatal conductance ($g$) or depth of water extraction. Hence, we cannot conclude that additional water provided by the enhanced snow pack near the snow fence alone had a substantial influence on $A$. Rather, greater snow accumulation increased winter soil temperature and likely altered N-cycling (Schimel et al. 2004, Buckeridge and Grogan 2008) leading to greater N uptake by *S. arctica*, higher leaf $[N]$, and ultimately higher $A$.

High leaf $[N]$ is consistently linked to high $A$ because leaf $[N]$ is indicative of RUBISCO content, an N-dense
protein (Evans 1989). In the High Arctic of Svalbard, leaf [N] was closely associated with differences in $A_{\text{max}}$ between *Salix polaris*, *Dryas octopetala* and *Saxifraga oppositifolia* (Muraoka et al. 2008). Moreover, large scale arctic-wide studies indicate a tight linkage between biomass, leaf N and ecosystem photosynthetic capacity, regardless of species composition (Williams and Rastetter 1999, van Wijk et al. 2005). Leaf [N] and $A$ responded positively to experimental additions of nitrogen (Baddeley et al. 1994) as did gross ecosystem productivity in a polar semi-desert ecosystem within 10 km of our study site in NW Greenland (Arens et al. 2008). Our observation of a close linkage between photosynthetic performance and leaf [N] further emphasizes the important role N limitation plays in arctic ecosystem processes (Schimel et al. 2004).

Few studies have examined the influence of altered snow conditions on leaf-level $A$ in the Arctic. At Toolik Lake, Alaska, reduced snow pack had little influence on $A$ of several
species including *Salix pulchra* (Starr et al. 2008). However, $A_{\text{max}}$ was lower following five years compared to three years of snow removal. More recently, long-term snow reduction (about 14 years) led to lower rates of $A_{\text{max}}$, but added snow did not significantly increase $A_{\text{max}}$ in *Betula nana* or *S. pulchra* (Pattison and Welker, unpublished). Differences between our findings and these may arise from differences in growing season length or temperature between the High Arctic of Greenland and the Low Arctic of Alaska (Billings 1973).

We have experimental evidence that enhanced snow accumulation influences leaf [N]. Leaf [N] in *S. arctica* individuals from deep snow areas compared to ambient snow zones was 50% greater in early July 2007 at the same study site in Greenland (Rogers et al. 2011). Here, following several more years of enhanced snow accumulation, we observed higher leaf [N] throughout the growing season. In a separate study in NW Greenland, *S. arctica* in areas of naturally deep snow pack had high leaf [N], but not necessarily higher A (Sullivan and Welker 2007). Near Toolik Lake, Alaska, higher leaf [N] was observed in several species including woody plants such as *Betula nana* and *Dryas octopetala* following up to six years of enhanced snow (Welker et al. 2005) indicating similar processes operate at both study sites.

Enriched leaf nitrogen isotope composition ($\delta^{15}N$) in +snow compared to ambient plots is consistent with soil moisture. Nitrogen fixation with deeper snow pack (Craine et al. 2009). Nitrification results in $15^{-}\text{N}$-depleted NO$_3^-$ and $15^{\text{N}}$-enriched NH$_4^+$ (Korontzi et al. 2000, Pörtl et al. 2007). If *S. arctica* is using primarily NH$_4^+$, or if NO$_3^-$ is rapidly leached, leaf tissue in +snow plots should be enriched in $15^{\text{N}}$ as observed here. In another study, warmer soils associated with greater insolation during winter increased microbial biomass and activity (Schimel et al. 2004, Buckeridge and Grogan 2008). This higher activity appears to have slightly increased available NO$_3^-$ at Toolik Lake, Alaska (Schimel et al. 2004). A pulse of NH$_4^+$ and NO$_3^-$ was observed during melt in high snow plots at Daring Lake, Canada (Buckeridge and Grogan 2010); this pulse, however, was largely removed from the system prior to leaf out.

Despite the enhanced snow areas yielding about double the melt water as ambient areas, water alone had little influence on differences in gas exchange physiology or depth of water extraction between treatments. Other studies report minor influence of enhanced snow on subsequent soil moisture (Buckeridge and Grogan 2008, Rogers et al. 2011), while larger differences have been observed elsewhere (Cooper et al. 2011). The direct role of water in this study may have been limited for several reasons including: much of the excess water in the enhanced snow plots simply running-off during snow-melt (Dunne and Black 1971) since soils are frozen; summer 2012 was characterized by repeated rains which kept soil moisture high, preventing a strong contrast between gas exchange physiology under wet and dry soil conditions; and we have only measured leaf-level $g$ and not accounted for differences in leaf area index (Steltzer and Welker 2006) between treatments which may indicate an influence of water availability at the ecosystem scale.

We observed limited influence of atmospheric moisture deficit on the seasonal pattern of $A$ in summer 2012. Since relative humidity and $A$ were positively correlated among measurement days we conclude that atmospheric water deficit was having a minor influence on carbon gain. High vapor pressure deficit can reduce $A$ in arctic and alpine plants, even without inducing stomatal closure (Johnson and Caldwell 1975); similar to our observation that $g$ changed little throughout the summer. Although leaf [N] differs between +snow and ambient plots, it appears to have little influence on the seasonal course of photosynthesis which is likely controlled by phenology.

Our data support the contention that a changing Arctic climate is having widespread influence on ecosystem and plant processes (Post et al. 2009, Callaghan et al. 2011b). Enhanced $A$ in *S. arctica* following a decade of increased snow accumulation likely resulted from increased microbial activity when snow was present, promoted by warmer soil temperatures from insulation (Schimel et al. 2004, Buckeridge and Grogan 2008, Christiansen et al. 2012). Consequently, winter conditions influence summer plant processes and carbon gain may be enhanced by additional snow in the Arctic. Conversely, delayed melt may shorten the time available for carbon acquisition and cooler soils in the early summer can reduce growth and N-uptake potentially offsetting higher $A$ (Wipf 2010, Leffler et al. 2011).

Acknowledgments

We thank L Merrill for excellent assistance in the field and laboratory and J Hurley, CH2M Hill Polar Field Services and Greenland Contractors for coordinating logistics for working in Thule, Greenland. We thank the US Air Force and governments of Greenland and Denmark for allowing this research to take place on Thule Air Base. We appreciate R Sletten (University of Washington) providing soil temperature data. Funding was provided by grants from the National Science Foundation awarded to JMW (0631234 and 0856728).

References

Arens S J T, Sullivan P F and Welker J M 2008 Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a High Arctic ecosystem *J. Geophys. Res.—Biogeosci.* 113 G03S10

Baddeley J A, Woodin S J and Alexander I J 1994 Effects of increased nitrogen and phosphorus availability on the photosynthesis and nutrient relations of three arctic dwarf shrubs from Svalbard *Funct. Ecol.* 8 676–85

Billings W D 1973 Arctic and alpine vegetation: similarities, differences, and susceptibility to disturbance *Bioscience* 23 697–704

Blok D, Heijmans M M P D, Schaepehn-Strub G, Kononov A V, Maximov T C and Berendse F 2010 Shrub expansion may reduce summer permafrost thaw in Siberian tundra *Glob. Change Biol.* 16 1296–305

Bonfils C J W, Phillips T J, Lawrence D M, Cameron-Smith P, Riley W J and Subin Z M 2012 On the influence of shrub...
height and expansion on northern high latitude climate
Environ. Res. Lett. 7 015503
Brooks P D and Williams M W 1999 Snowpack controls on
nitrogen cycling and export in seasonally snow-covered
catchments Hydrology. Process. 13 2177–90
Buckeridge K M and Grogan P 2008 Deepened snow alters soil
microbial nutrient limitations in arctic birch hummock tundra
Appl. Soil Ecol. 39 210–22
Buckeridge K M and Grogan P 2010 Deepened snow increases late
thaw biogeochemical pulses in mesic Low Arctic tundra
Biogeochemistry 101 105–21
Callaghan T V et al 2011a Multi-decadal changes in tundra
environments and ecosystems: synthesis of the international
polar year–back to the future project (IPY–BTF) Ambio
40 705–16
Callaghan T V, Christensen T R and Jantze E J 2011b Plant and
vegetation dynamics on Disko Island, West Greenland:
snapshots separated by over 40 years Ambio 40 624–37
Christiansen C T, Svendsen S H, Schmidt N M and Michelsen A
2012 High Arctic heath soil respiration and biogeochemical
dynamics during summer and autumn freeze–in–effects of
long-term enhanced water and nutrient supply Glob. Change
Biol. 18 3224–36
Cooper E J, Dullinger S and Semenchuk P 2011 Late snowmelt
delays plant development and results in lower reproductive
success in the High Arctic Plant Sci. 180 157–67
Craine J M et al 2009 Global patterns of foliar nitrogen isotopes and
their relationships with climate, mycorrhizal fungi, foliar
nutrient concentrations, and nitrogen availability New Phytol.
183 980–92
Dawson T E, Mambelli S, Plamboeck A H, Templer P H and
Tu K P 2002 Stable isotopes in plant ecology Annu. Rev. Ecol.
Syst. 33 507–59
Dunne T and Black R D 1971 Runoff processes during snowmelt
Water Resources Res. 7 1160–72
Evans J R 1989 Photosynthesis and nitrogen relationships in leaves of
C3 plants Oecologia 78 9–19
Griffis T J and Rouse W R 2001 Modelling the interannual
variability of net ecosystem CO2 exchange at a subarctic sedge
fen Glob. Change Biol. 7 511–30
Johnson D A and Caldwell M M 1975 Gas exchange of four arctic
and alpine tundra plant species in relation to atmospheric and
soil moisture stress Oecologia 21 93–108
Kohler J, Brandt O, Johansson M and Callaghan T 2006 A
long-term arctic snow depth record from Abisko, northern
Sweden, 1913–2004 Polar Res. 25 91–113
Korontzi K, Macko S A, Anderson I C and Poth M A 2000 A stable
isotopic study to determine carbon and nitrogen cycling in a
disturbed southern California forest ecosystem Glob.
Biogeochem. Cycles 14 177–88
Lafleur P M and Humphreys E R 2007 Spring warming and carbon
dioxide exchange over Low Arctic tundra in central Canada
Glob. Change Biol. 14 740–56
Leffler A J, Monaco T A and James J J 2011 Nitrogen acquisition
by annual and perennial grass seedlings: testing the role of
performance and plasticity to explain plant invasion Plant
Ecol. 212 1601–11
McFadden J P, Eugster W and Chapin F S III 2003 A regional study of
the controls on water vapor and CO2 exchange in arctic
tundra Ecology 84 2762–76
Min S-K, Zhang X and Zwiers F 2008 Human-induced arctic
moistening Science 320 518–20
Muraoka H, Noda H, Uchida M, Ohtsuka T, Koizumi H and
Nakatsubo T 2008 Photosynthetic characteristics and biomass
distribution of the dominant vascular plant species in a High
Arctic tundra ecosystem, Ny–Ålesund, Svalbard: implications
for their role in ecosystem carbon gain J. Plant Res. 121 137–45
Nobrega S and Grogan P 2008 Landscape and ecosystem-level
controls on the net carbon dioxide exchange along a natural
moisture gradient in Canadian Low Arctic tundra Ecosystems
11 377–96
Oberbauer S F et al 2007 Tundra CO2 fluxes in response to
experimental warming across latitudinal and moisture
gradients Ecol. Monogr. 77 221–38
Osmond C B 1987 Photosynthesis and carbon economy of plants
New Phytol. 106 (Suppl.) 161–75
Parnell A C, Inger R, Bearhop S and Jackson A L 2010 Source
partitioning using stable isotopes: coping with too much
variation PLoS One 5 9 e9672
Peek M S, Russe-Cohen E, Wait D A and Forseth J N 2002
Physiological response curve analysis using nonlinear mixed
models Oecologia 132 175–80
Peterson B J, Holmes R M, McClelland J W, Vörösmarty C J, Lammers R B, Shiklomanov A I, Shiklomanov I A and
Rahmstorf S 2002 Increasing river discharge to the Arctic
Ocean Science 298 2171–3
Pörlt K, Zecheimacher-Boltenstern S, Wanek W, Ambus P and
Berger T W 2007 Natural 15N abundance of soil N pools and
N2O reflect the nitrogen dynamics of forest soils Plant Soil
295 79–94
Post E et al 2009 Ecological dynamics across the Arctic associated
with recent climate change Science 325 1355–8
Potvin C, Lechowicz M J and Tardif S 1990 The statistical analysis
of ecophysiological response curves obtained from
experiments involving repeated measures Ecology
71 1389–400
R Development Core Team 2008 R: A Language and Environment
for Statistical Computing, Reference Index Version 2.15.1
(Vienna: R Foundation for Statistical Computing)
Rogers M C, Sullivan P F and Welker J M 2011 Evidence of
nonlinearity in the response of net ecosystem CO2 exchange to
increasing levels of winter snow depth in the High Arctic of
northwest Greenland Arct. Antarct. Alp. Res. 43 95–106
Schimel J P, Bilbrough C and Welker J M 2004 Increased snow
depth affects microbial activity and nitrogen mineralization in
two Arctic tundra communities Soil Biol. Biochem. 36 217–27
Stagg G, Oberbauer S F and Alhquist L E 2008 The photosynthetic
response of Alaskan tundra plants to increased season length
and soil warming Arct. Antarct. Alp. Res. 40 181–91
Steltzer H, Hufbauer R A, Welker J M, Casalis M, Sullivan P F and
Chimner R 2008 Frequent sexual reproduction and high
intraspecific variation in Salix arctica: implications for a
terrestrial feedback to climate change in the High Arctic
J. Geophys. Res.—Biogeosci. 113 G03S10
Steltzer H and Welker J M 2006 Modeling the effect of
photosynthetic vegetation properties on the NDVI–LAI
relationship Ecology 87 2765–72
Sullivan P F and Welker J M 2007 Variation in leaf physiology of
Salix arctica within and across ecosystems in the High Arctic:
test of a dual isotope (Δ13C and Δ18O) conceptual model
Oecologia 151 372–86
Sullivan P F, Welker J M, Steltzer H, Sletten R S, Hagedorn B,
Arens S J T and Horwath J L 2008 Energy and water additions
give rise to simple responses in plant canopy and soil
microclimates of a High Arctic ecosystem J. Geophys.
Res.—Biogeosci. 113 G03S08
van Wijk M T, Williams M and Shaver G R 2005 Tight coupling
between leaf area index and foliage N content in arctic plant
communities Oecologia 142 421–7
Wahren C-H A, Walker M D and Bret-Harte M S 2005 Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment *Glob. Change Biol.* **11** 537–52
Welker J M, Fahnestock J T, Sullivan P F and Chimner R A 2005 Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska *Oikos* **109** 167–77
Williams M and Rastetter E B 1999 Vegetation characteristics and primary productivity along an arctic transect: implications for scaling-up *J. Ecol.* **87** 885–98
Wipf S 2010 Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations *Plant Ecol.* **207** 53–66
Wipf S and Rixen C 2010 A review of snow manipulation experiments in Arctic and alpine tundra ecosystems *Polar Res.* **29** 95–109
Zhang X, He J, Zhang J, Polyakov I, Gerdes R, Inoue J and Wu P 2013 Enhanced poleward moisture transport and amplified northern high-latitude wetting trend *Nature Clim. Change* **3** 47–51