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GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Coupled long-term summer warming and deeper snow alters species composition and stimulates gross primary productivity in tussock tundra

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Abstract Climate change is expected to increase summer temperature and winter precipitation throughout the Arctic. The long-term implications of these changes for plant species composition, plant function, and ecosystem processes are difficult to predict. We report on the influence of enhanced snow depth and warmer summer temperature following 20 years of an ITEX experimental manipulation at Toolik Lake, Alaska. Winter snow depth was increased using snow fences and warming was accomplished during summer using passive open-top chambers. One of the most important consequences of these experimental treatments was an increase in active layer depth and rate of thaw, which has led to deeper drainage and lower soil moisture content. Vegetation concomitantly shifted from a relatively wet system with high cover of the sedge *Eriophorum vaginatum* to a drier system, dominated by deciduous shrubs including *Betula nana* and *Salix pulchra.* At the individual plant level, we observed higher leaf nitrogen concentration associated with warmer temperatures and increased snow in *S. pulchra* and *B. nana*, but high leaf nitrogen concentration did not lead to higher rates of net photosynthesis. At the ecosystem level, we observed higher GPP and NEE in response to summer warming. Our results suggest that deeper snow has a cascading set of biophysical consequences that include a deeper active layer that leads to altered species composition, greater leaf nitrogen concentration, and higher ecosystem-level carbon uptake.

Keywords Arctic · Climate change · Temperature · Precipitation · Carbon flux

Introduction

Arctic climate is rapidly changing (Hinzman et al. 2013). The Arctic is expected to warm by 2–9 °C by 2100 with a concomitant increase in precipitation (Held and Soden 2006; IPCC 2013). The Arctic is 1.6 °C warmer than it was during the 1960s (McBean et al. 2005; Bekryaev et al. 2010), and ground temperatures at many sites have increased 1–2 °C since the mid-1970s (Romanovsky et al. 2010). Additionally, the transport of atmospheric moisture toward the Arctic (Zhang et al. 2013), Arctic snowfall (Kohler et al. 2006; Min et al. 2008), and the discharge of fresh water into the Arctic Basin have increased (Peterson et al. 2002).

Changes in temperature and precipitation are likely to have independent and synergistic consequences for Arctic ecosystems. Arctic warming is directly causing earlier spring, later senescence, and consequently a longer growing season (Goetz et al. 2005; Euskirchen et al. 2006; Cooper 2014). Deeper snow leads to soils up to 10 °C warmer in the winter (Liston et al. 2002; Schimel et al. 2004; Leffler and Welker 2013; Pattison and Welker 2014) and increasing winter CO_2 emissions (Fahnestock et al. 1999; Sullivan et al. 2010). Warmer soils also enhance N mineralization

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(Schimel et al. 2004; Buckeridge and Grogan 2008) leading to higher leaf nitrogen concentration (Welker et al. 2005; Leffler and Welker 2013; Pattison et al. 2015). A synergistic result of greater precipitation and warmer conditions may be the transport of labile C and N deeper into the soil, altering biogeochemical processes throughout the active layer (Schaeffer et al. 2013) and promoting the establishment of deep-rooted species.

Warmer and wetter conditions are likely driving Arctic greening (Jia et al. 2003; Tape et al. 2006), increased vegetation cover (Hudson and Henry 2009), and a transition toward shrub-dominated plant communities (Sturm et al. 2001; Wipf and Rixen 2010; Elmendorf et al. 2012; Tape et al. 2012) that are functionally distinct from other tundra. Shrubs trap considerable snow (Liston et al. 2002), alter melt rate and albedo (Liston et al. 2002; Cohen et al. 2013; Loranty et al. 2014), and can influence hydrology of the system by promoting run-off or run-on of melt water depending on topography (Tape et al. 2011). Furthermore, shrubs deposit litter that decomposes more slowly than that of graminoids (Chapin et al. 1986) potentially altering soil C and N processes.

Concomitant changes in winter and summer climates are occurring and our ability to examine the independent and or synergistic consequences of them is enhanced with long-term experiments. One long-term ITEX (International Tundra Experiment) experiment (Henry and Molau 1997; Welker et al. 1997; Jones et al. 1998) has examined the independent and combined effects of deeper snow in winter and warmer summers since 1994. Researchers have measured growth and phenology; soil carbon, nitrogen, and microbial dynamics; gas fluxes; and growth and physiological responses of woody and herbaceous species in moist and dry tundra.

The influence of these climate scenarios on plant communities, plant function, and ecosystem processes has changed over time. Initially, winter soil respiration was significantly greater under deep snow in the dry tundra site, a result observed later in moist tundra (Schimel et al. 2004); plant community change was not observed despite advanced phenology (Walker et al. 1999). Three years following initiation, greater carbon loss through autotrophic and heterotrophic respiration was observed in warmed compared to ambient temperature plots in dry tundra (Welker et al. 1999). In a similar timeframe, the combined influence of enhanced snow and warming increased net annual carbon loss by nearly 50 % in the moist-tussock tundra site (Welker et al. 2000). Warming and additional snow enhanced leaf nitrogen concentration, but the effects were not uniform among species: nitrogen concentration of *Betula nana* and *Salix pulchra* responded to deep snow in combination with warming, but only deep snow increased leaf nitrogen concentration in *Ledum palustre* (Welker et al. 2005). Following 8 years of the experiment, changes in plant community composition were observed: canopy height and cover by the shrub *Betula nana* increased, and lichen cover decreased (Wahren et al. 2005). Vegetation changes were largely confined to the deeper snow areas while warmer temperatures had little effect (Wahren et al. 2005). Deep snow stimulated nitrogen mineralization during winter (Schimel et al. 2004) and net nitrogen mineralization occurred earlier in the year (Borner et al. 2008). Finally, Pattison and Welker (2014) observed net photosynthesis, transpiration, and stomatal conductance in *Eriophorum vaginatum* to be higher in ambient and deep snow compared to the reduced snow in moist tussock tundra; for *Salix pulchra*, only transpiration and stomatal conductance were influenced, while snow depth did not significantly alter gas exchange in *B. nana*.

In 2014, we sampled species composition, leaf gas exchange, leaf nitrogen concentration of *S. pulchra* and *B. nana*, surface spectral properties (NDVI), and ecosystem carbon flux to assess the influence of enhanced snow and higher summer temperature following 20 years of experimental climate scenarios in the ITEX moist tussock tundra system. Since numerous studies have documented shrub expansion in northern Alaska (Sturm et al. 2001; Wipf and Rixen 2010; Elmendorf et al. 2012; Tape et al. 2012), we predict these treatments will (1) force plant communities toward greater shrub cover by (2) enhancing shrub leaf nitrogen concentration and net photosynthesis, which will (3) ultimately lead to greater carbon uptake at the ecosystem level due to higher biomass of shrubs. Furthermore, we predict (4) that altering winter conditions will have a greater influence on these processes because of the length of the Arctic winter and the consequences of deep snow on soil temperature and active layer depth (Liston et al. 2002; Schimel et al. 2004; Nowinski et al. 2010; Leffler and Welker 2013; Pattison and Welker 2014).

Materials and methods

Study site and experiment

We conducted this study at the Toolik Lake Field Station in northern Alaska, USA (68.6°N, 149.6°W, 760 m asl), a Low Arctic ecosystem in the northern foothills of the Brooks Range. Mean temperatures in winter are below −30 °C and mean summer temperatures are above 10 °C (Cherry et al. 2014). The growing season is typically ca. 15 May until ca. 15 September (Cherry et al. 2014). The plant community is predominately tussock tundra (Walker et al. 1994) dominated by dwarf shrubs including *Betula nana*, *Salix pulchra*, *Ledum palustre*, *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, and the sedge *Eriophorum vaginatum*.

This ITEX experiment was established in 1994 (Henry and Molau 1997; Welker et al. 1997; Jones et al. 1998) to examine the interacting effects of enhanced winter snowpack and elevated summer temperature on tundra structural and functional traits, including species composition, plant physiological traits, soil properties, and ecosystem processes. Snowpack is enhanced with a wooden snow fence 2.8 m tall and 60 m long, which produces a drift ca. 3 m deep at the fence (Walker et al. 1999; Pattison and Welker 2014). Snow accumulates earlier and melts later (ca. 2–3 weeks) in the deepest snow zone (Walker et al. 1999). The study site has a slight slope and melting snow from the snow fence does not result in additional standing water. Permanent plots for summer warming and ambient treatments were established ca. 25 m from the fence where snow depth is typically ca. 2 m deep. Warming was accomplished using hexagonal passive-solar open-top chambers (Jones et al. 1998; Walker et al. 1999) 50 cm tall × 2 m base with sides at 60°. Chambers are made of Sun-Lite HP fiberglass (Solar Components, Manchester, NH, USA) and are in place between early June and late August. Chambers warm the air 2–5 °C and warm the soil 1–2 °C (Walker et al. 1999; Welker et al. 2005). A similar arrangement of warming and ambient temperature plots were established nearby but in an area not influenced by the snow fence. Ambient snow depth is typically between 0.5 and 1.0 m deep (Walker et al. 1999). In 2014, we collected data in four experimental plot types replicated five times: typical snow/no warming (+O), enhanced snow/no warming (+S), typical snow/warming (+T), and enhanced snow/warming (+S+T).

We collected data between 20 June and 12 August 2014. Summer 2014 was cool and wet (Fig. S1; Toolik Environmental Data Center). Mean temperatures in June, July, and August were 6.7, 9.6, and 7.7 °C, respectively, compared to mean monthly temperatures (1989–2010) of 8.9, 11.4, and 9.1 °C, respectively (Cherry et al. 2014). Total precipitation for June, July, and August was 72, 106, and 53 mm, respectively, compared to mean precipitation (1989–2010) of 44, 84, and 62 mm, respectively (Cherry et al. 2014). Summer 2014 was in the 14th percentile for temperature and the 82nd percentile for precipitation; precipitation occurred nearly every day from mid-June through late July (Fig. S1).

Measurements

Air and soil temperatures in experimental plots were recorded every 2 h using microloggers (iButton model 1921; Maxim Integrated, San Jose, CA, USA). Belowground, we installed iButtons at 5 cm depth in the 20 study plots. Aboveground, we installed iButtons in all +T and +S+T plots (i.e., the plots with OTCs), and two each of the +O and +S plots (i.e., the plots without OTCs). Air temperature iButton loggers were installed at 30 cm above the soil surface and shielded from solar radiation. Active layer depth was measured weekly in each plot by twice driving a metal rod into the soil until it contacted permafrost.

We measured species composition in each plot by estimating cover using a point-frame. The quadrat (1 m^2) had 100 intersections in a 10 × 10 grid. We made measurements by lowering a pin at each intersection and recording the first and second species touching the pin. We calculate cover as the proportion of pin hits by each species (i.e., repeated cover; Wilson 2011). Species composition was measured mid-July.

Leaf gas exchange was quantified on two common shrub species, *B. nana* and *S. pulchra*, between 7 and 23 July. These species were present in all experimental plots. One fully expanded leaf of each species per plot was used in a 2 × 3 cm chamber of a portable photosynthesis system (model 6400XT; Licor, Lincoln, NE, USA). Gas exchange data were collected as 'light curves' where the photosynthetic response was measured as light was decreased from saturating photon flux (i.e., 1600 $\mu mol\ m^{-2}\ s^{-1}$) to darkness using an onboard light source. Here, however, we report gas exchange parameters only at saturating irradiance. During measurements, inlet [CO_2] and chamber humidity were maintained at 400 $\mu L\ L^{-1}$ and 50 %, respectively. Data were collected between 1000 and 1900 hours AKDT. Area of the measured leaf was determined using a flatbed scanner (Perfection V700; Epson America, Long Beach, CA, USA) and image analysis software (Winfolia 2011a; Reagent Instruments, Ste-Foy, Quebec, Canada).

Leaf tissue was collected from *B. nana* and *S. pulchra* species every 2 weeks. Several fully expanded, terminal leaves were collected and oven dried at 70 °C. Leaves were ground to a fine powder in a mechanical shaker (Mini-Beadbeater-16; Biospec Products, Bartlesville, OK, USA) with 3.2 mm steel ball bearings. Leaf nitrogen concentration was determined with an elemental analyzer (model 4010; Costech, Valencia, CA, USA). Standard deviation for N measurements was 0.02 $\mu g\ g^{-1}$.

We quantified net ecosystem exchange (NEE), autotrophic and heterotrophic dark ecosystem respiration (R_e), and gross primary production (GPP) in each experimental plot during July and August. We used a clear acrylic chamber, 70 × 70 cm wide × 40 cm tall with an additional 40 cm extension when necessary to accommodate larger shrubs, connected to a second photosynthesis system (model 6400; Licor). We measured NEE under six successively lower light levels (i.e., a light curve) using shade cloth of increasing opacity. Chamber PAR was typically between 0 and 1200 $\mu mol\ m^{-2}\ s^{-1}$ during measurements. The chamber was sealed to the ground using a rubber and plastic 'skirt' and heavy chain. When closed, fans inside the chamber maintained air circulation. The chamber was vented to the atmosphere between each successive measurement. Upon completion of each light curve, we fit a hyperbolic model to the data:

$$A = R_e - \frac{(A_{\max} \times \mathrm{PAR})}{k + \mathrm{PAR}} \quad (1)$$

where R_e is dark ecosystem respiration, $A_{\max}$ is maximum CO_2 uptake, PAR is incident photosynthetically active radiation, and k is PAR at 0.5 $A_{\max}$ (Williams et al. 2006). Model fitting was performed using function NLMER within package LME4 in the statistical computing environment R (R Core Development Team 2013). From the model fit for each curve, we calculated NEE standardized to PAR = 600 μmol m^{-2} s^{-1} (NEE_{600}) and determined GPP_{600} as the sum of NEE_{600} and R_e (Chapin et al. 2002); our estimate of GPP therefore includes autotrophic and heterotrophic respiration. Volumetric water content in each plot was determined with a 12-cm TDR probe (Model Hydrosense II; Campbell Scientific, Logan, UT, USA) each time measurements of carbon flux were performed (ca. every 1–2 weeks).

Multispectral reflectance above the canopy of each plot was measured to calculate the normalized difference vegetation index (NDVI) as a measurement of canopy cover. We used a spectrophotometer (Unispec-DC; PP Systems, Amesbury, MA, USA) for reflectance measures between 300 and 1100 nm (3 nm bandwidth) with an upward-facing optic covered by a diffuser and a downward-facing optic with an angle-of-view of 20°. The two optics were "cross-calibrated" each use with a reflectance standard. Weekly measurements were made within 3 h of solar noon at ca. 2 m above a plot. We calculated NDVI using 620–670 nm for the red band and 841–876 nm for the infrared band.

Data analysis

Data were analyzed in the R statistical computing environment (R Core Team 2013). All analyses except for species cover were mixed models with random time or day of year effects to account for repeated measures on the same study plots. Fixed effects included "snow", "temperature", and "snow × temperature" interaction. We examined significance of these effects for response variables by fitting full models of main effects and the interaction and reduced models with the effect of interest removed and compared full and reduced models with a likelihood ratio test (Zurr et al. 2009). All models were examined for normal distribution of residuals; tissue nitrogen concentration was log transformed to satisfy this assumption. All confidence intervals are derived from bootstrapping (1000 iterations) parameter estimates in the mixed models and computing the 2.5 and 97.5 % quantiles. All models were fit using function LMER within package LME4. Analysis of NDVI data was restricted to dates following 1 July (i.e., $NDVI_{max}$). The dependence of NEE and GPP on NDVI was estimated using ranged major axis (model II) regression (package LMODEL2). We consider $P < 0.05$ to be significant.

Analysis of soil and air temperature and thaw depth required a slightly different approach. Since temperature was measured every 2 h, we used a random fractional day effect to account for repeated measures of multiple plots. For thaw depth, we used rate of thaw (i.e., depth/time) as our response. To accomplish this, we included a day × site × temperature fixed effect in the full model and deleted this term from the reduced model; a significant result in this analysis indicates the slope of the line describing thaw depth over time differed among experimental treatments.

We analyzed species cover data with non-metric multidimensional scaling (NMDS) and permutational MANOVA (perMANOVA) using functions metaMDS and ADONIS within package VEGAN and with a Poisson GLM for cover of three common species. NMDS is an unconstrained iterative community ordination technique based on relative rather than absolute differences among samples (Kruskal 1964; Fasham 1977; Clarke 1993; McCune and Grace 2002). Our NMDS used a Bray–Curtis plot × species distance matrix. We computed centroids and 2-D 95 % confidence intervals for each treatment (function ORDIELLIPSE). We used PERMANOVA to partition variation in the plot × species distance matrix among the different treatments and to test the significance of these factors (Anderson 2001). The model was iterated 1000 times. The ADONIS formulation of perMANOVA is based on sequential sums-of-squares (type I). Significance is determined with a pseudo-F ratio and partial r^2 indicates the fraction of variation in the distance matrix explained by each effect. Median cover by three common species (*Eriphorum vaginatum*, *Salix pulchra*, and *Vaccinium uliginosum*) was examined with a Poisson GLM testing a full model with snow and temperature main effects and interactions against reduced models with terms deleted. All factors in the model were treated as fixed since cover was measured only once.

Results

Treatments influenced air and soil temperature (Table 1). Although significant at $P < 0.05$, median air temperature of +O and +S plots were within 0.5 °C of each other, approximately the resolution of the iButton sensor. Conversely, the +T treatment raised the median air temperature throughout the summer by ca. 1.1 °C (Fig. 1). Soil temperature at 5 cm depth was significantly altered by deeper snow and passive warming. Soils in +T, +S, and +S+T plots were 1.0, 1.8,

Table 1 Results from likelihood ratio test of temperature, soil moisture, and rate of thaw in experimental treatments to alter summer temperature (*temp*) and winter snow depth (*snow*)

Response	Effect	*df*	χ^2	*P*
Air temperature	Temp	2	1510	<0.001*
	Snow	2	136	<0.001
	Temp × snow	1	121	<0.001
Soil temperature	Temp	2	636	<0.001*
	Snow	2	2440	<0.001*
	Temp × snow	1	17.8	<0.001*
Soil moisture	Temp	2	10.8	0.005
	Snow	2	17.6	<0.001*
	Temp × snow	1	6.04	0.014*
Thaw rate	Temp × day	4	39.0	<0.001*
	Snow × day	4	37.0	<0.001*
	Temp × snow × day	1	3.95	0.047*

Full model $df = 6$ except for thaw rate where $df = 10$; reported *df* is the difference between full and reduced models

* Significant at $P \lesssim 0.05$ for soil moisture and rate of thaw

and 2.5 °C warmer than soils in the +O plots, respectively. The warming effect on air temperature was most evident near solar noon; +T and +S+T treatments were 2–3 °C warmer than +O treatments near mid-day and differences among treatments were negligible near solar midnight (Fig. 1).

Temperature and snow depth interacted to influence rate of soil thaw and soil moisture (Table 1). Rate of thaw (Fig. 2) was lowest in +O plots (0.83 cm day^{-1}) and accordingly higher in +S, +T, and +S+T plots (1.1–1.3 cm day^{-1}). Volumetric soil moisture (Fig. 2) was ca. 64 % in the +O plots and ca. 48 % in others.

Species composition differed among treatments (Fig. 3). The perMANOVA following NMDS suggests the snow depth effect accounted for 26 % ($F = 6.45$, $P < 0.001$) of the variation in species composition while temperature accounted for <1 %. Neither warming ($F = 1.73$, $P = 0.112$) nor the interaction between snow and warming ($F = 1.08$, $P = 0.362$) significantly altered species composition. Three species were most heavily weighted on the first NMDS axis (*E. vaginatum*, *S. pulchra*, and *V. uliginosum*). On an individual species basis, in the +O and +T plots, *E. vaginatum* repeated cover averaged ca. 50 %; in the +S and +S+T plots, *E. vaginatum* repeated cover averaged only 16 %. Temperature and snow depth were both significant effects ($\chi^2 = 186$ and 22.8, $P < 0.001$, respectively). Concomitantly, in the +S and +S+T plots, *Salix pulchra* repeated cover was ca. 38 %; in the +O and +T plots, *S. pulchra* repeated cover was ca. 18 %. Temperature and snow depth were both significant effects ($\chi^2 = 76.3$ and 44.0, $P < 0.001$, respectively). Significant differences in repeated cover among treatments were also observed for the shrub *Vaccinium uliginosum* ($P < 0.001$), but high cover was not necessarily linked to either warmer or deeper snow conditions.

Leaf-level gas exchange data reveal differences in stomatal conductance by *S. pulchra* among the temperature and snow depth treatments that are borderline significant (Table 2). Stomatal conductance of *S. pulchra* was greatest in +O plots and nearly 50 % lower in the +S+T plots; other +S and +T treatments were intermediate. In contrast, stomatal conductance by *B. nana* was not affected by either

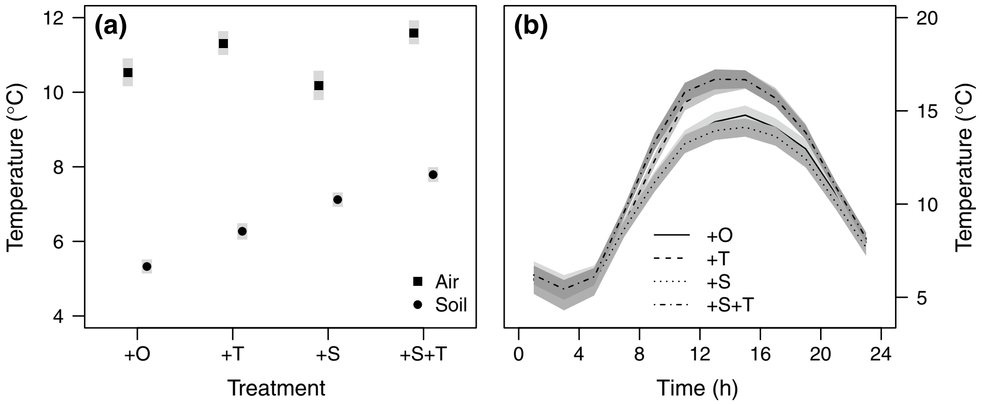

Fig. 1 The influence of summer warming and snow depth on air and soil temperature for the period 20 June–9 August 2014 (**a**), and a diurnal/nocturnal course (**b**). Values are median boot-strap parameter estimates from the mixed-model analysis with a random time-of-day effect. *Shading* indicates the 95 % confidence interval of parameter estimates. For season-long temperature, symbols are air temperature (*filled squares*) and soil temperature (*filled circles*). Treatments are: control (*+O*, *solid line*); warming (*+T*, *dashed line*); deep snow (*+S*, *dotted line*); and deep snow combined with warming (*+S+T*, *dashed-dotted line*)

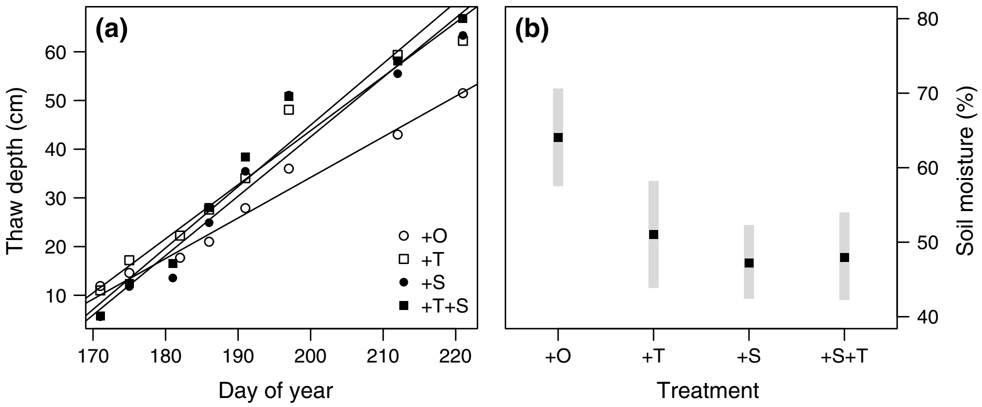

Fig. 2 Depth of thaw (**a**) and volumetric soil moisture content (**b**). Values are median boot-strap parameter estimates from the mixed-model analysis with 95 % confidence intervals. For thaw depth, values are medians for each treatment on day of measurement; best-fit lines are derived from mixed-model regression. Treatments are: control (+O, *open circles*); warming (+T, *open squares*); deep snow (+S, *filled circles*); and deep snow combined with warming (+S+T, *filled squares*). Data collected between 20 June and 9 August 2014

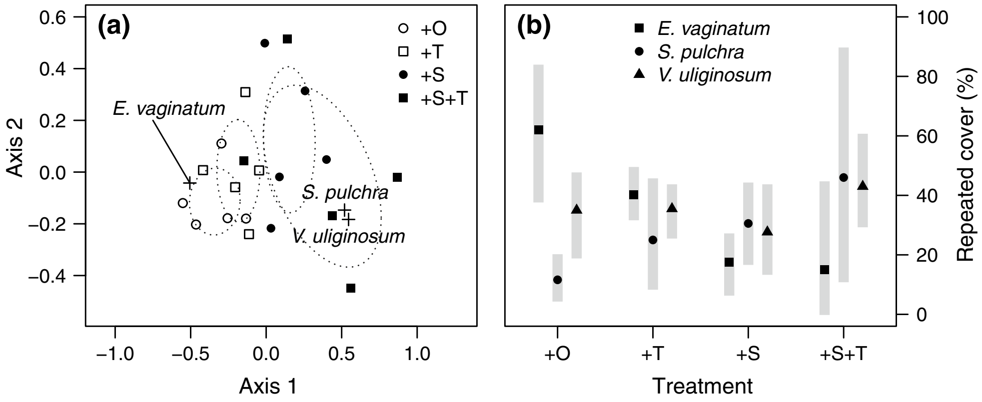

Fig. 3 Non-metric multidimensional scaling (NMDS) of plant communities (**a**), and cover of three common species in summer temperature and snow depth treatments (**b**). For the NMDS: *symbols* represent multidimensional species composition in each of the five replicate plots per treatment. *Dashed lines* represent 2-D 95 % confidence intervals of the centroid for each treatment. Noted species distinguish the +O and +T community from the +S and +S+T community. For repeated cover: values are median boot-strap parameter estimates from the Poisson GLM with 95 % confidence intervals. Species are: *Eriophorum vaginatum* (*filled squares*); *Salix pulchra* (*filled circles*); and *Vaccinium uliginosum* (*filled triangles*). Treatments are: control (*+O*, *open circles*); warming (*+T*, *open squares*); deep snow (*+S*, *filled circles*); and deep snow combined with warming (*+S+T*, *filled squares*)

treatment; the same was true for rate of net photosynthesis for both species (Fig. 4).

Temperature and snow depth interacted to influence leaf nitrogen concentration in *B. nana* and *S. pulchra* (Table 2). Plots receiving +S and +S+T treatments had the highest leaf nitrogen concentration for both species, but the lowest leaf nitrogen concentration for both species was observed in the +T plots (Fig. 4).

Treatment temperatures significantly influenced GPP and NEE, and the temperature × snow interaction was significant for R_e (Table 3; Fig. 5). GPP was 23 % greater in the +T and +S+T compared to the +O and +S plots. NEE was 69 % greater in the +T and +S+T plots compared to the +O and +S plots. R_e was greatest in the +O and +S+T plots, and lower by 15 % in the +S and +T plots.

NDVI differed among temperature and snow depth treatments (Table 3), but there was no clear pattern in treatment influence on NDVI (Fig. S2). We observed high NDVI (ca. 0.73) in the +O plots, and lower NDVI (0.68) in the +S plots. NDVI in the +T and +S+T plots were similar (ca. 0.70). NDVI was not a significant predictor of GPP ($P = 0.296$, Fig. S2) or NEE ($P = 0.494$, Fig. S3).

Table 2 Results from likelihood ratio test of plant-level variables for birch (*B. nana*) and willow (*S. pulchra*) in experimental treatments to alter summer temperature (*temp*) and winter snow depth (*snow*)

Response	Species	Effect	*df*	χ^2	*P*
A	*B. nana*	Temp	2	0.697	0.706
		Snow	2	2.34	0.311
		Temp × snow	1	0.648	0.421
	S. pulchra	Temp	2	2.76	0.251
		Snow	2	1.30	0.522
		Temp × snow	1	1.26	0.261
g	*B. nana*	Temp	2	3.70	0.157
		Snow	2	0.044	0.978
		Temp × snow	1	0.044	0.835
	S. pulchra	Temp	2	5.96	0.051*
		Snow	2	3.26	0.196
		Temp × snow	1	0.782	0.377
Leaf nitrogen concentration	*B. nana*	Temp	2	4.86	0.088
		Snow	2	6.40	0.041*
		Temp × snow	1	3.76	0.052*
	S. pulchra	Temp	2	5.19	0.075
		Snow	2	7.31	0.026*
		Temp × snow	1	5.07	0.024*

Responses are: net photosynthesis (*A*), stomatal conductance (*g*), and leaf nitrogen concentration (leaf nitrogen concentration). Full model *df* = 6; reported *df* is the difference between full and reduced models

* Significant at $P \lesssim 0.05$

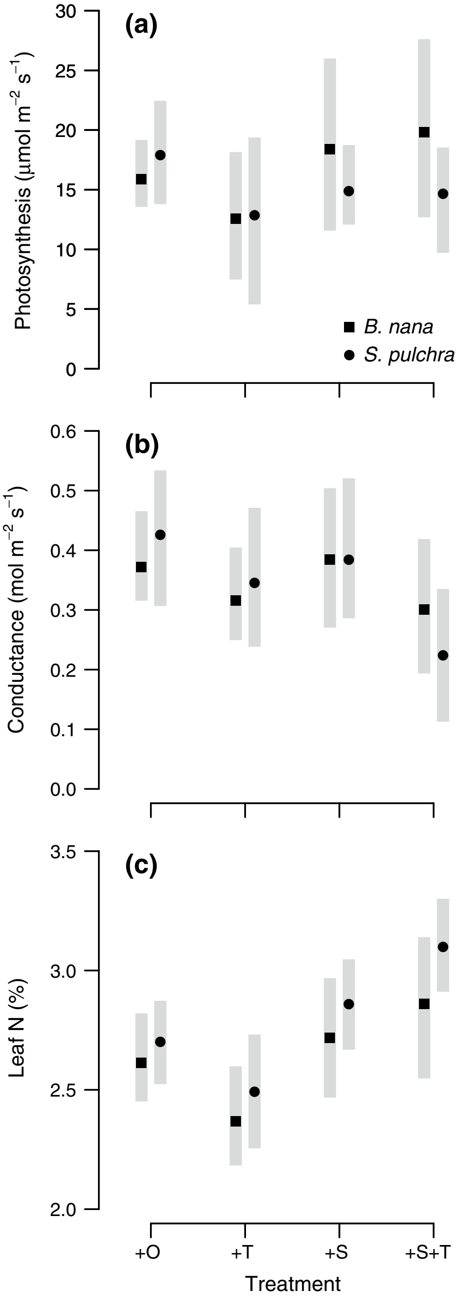

Fig. 4 Net photosynthesis (**a**), stomatal conductance (**b**), and leaf nitrogen concentration (**c**) in summer temperature and snow depth treatments. Values are the median and 95 % confidence intervals of boot-strapped mixed-model parameter estimates. Treatments are: control (*+O*); warming (*+T*); deep snow (*+S*); and deep snow combined with warming (*+S+T*). *Symbols* are *Betula nana* (*filled squares*) and *Salix pulchra* (*filled circles*). Data collected between 7 and 23 July 2014

Discussion

Twenty years of increased snow depth and warmer summer temperatures have altered the moist tussock tundra ecosystem at Toolik Lake, AK. We predicted greater shrub cover, higher leaf nitrogen concentration, higher leaf net photosynthesis, and greater ecosystem-level carbon uptake. We observed plots with additional snow accumulation to have greater cover by shrubs, specifically *S. pulchra* (Fig. 3); greater leaf nitrogen concentration in *S. pulchra* and *B. nana* in response to enhanced snow depth (Fig. 4); but no significant differences in leaf net photosynthesis by either shrub species in response to snow depth or temperature manipulation. Conversely, NEE and GPP were greater, but in response to summer warming rather than deeper snow (Fig. 5). Furthermore, we observed an increase in the depth of the active layer by ca. 15 cm, more rapid thaw, and lower near-surface soil moisture following either enhanced snow or higher summer temperature (Fig. 2). Our results suggest that increased snow accumulation and warmer conditions interact to alter ecosystem processes in Arctic tundra.

Plots associated with greater snow accumulation were more heavily dominated by shrubs; specifically, cover of *S. pulchra* increased as cover of *E. vaginatum* declined (Fig. 3). The sedge *E. vaginatum* is a wetland/bog plant replaced by shrubs in other warming experiments in the Toolik Lake region (Chapin et al. 1995). Previous examination of these plots demonstrated increased cover by *E.*

Table 3 Results from likelihood ratio test of ecosystem-level variables in experimental treatments to alter summer temperature (*temp*) and winter snow depth (*snow*)

Response	Effect	*df*	χ^2	*P*
R_e	Temp	2	9.58	0.008*
	Snow	2	8.47	0.014*
	Temp × snow	1	8.45	0.004*
GPP	Temp	2	6.14	0.046*
	Snow	2	1.02	0.600
	Temp × snow	1	0.894	0.344
NEE	Temp	2	9.08	0.011*
	Snow	2	0.273	0.873
	Temp × snow	1	0.052	0.820
NDVI	Temp	2	7.23	0.027*
	Snow	2	10.1	0.006*
	Temp × snow	1	7.22	0.007*

Responses are: ecosystem respiration (R_e), gross primary productivity (GPP), and net ecosystem exchange (NEE). Full model $df = 6$; reported *df* is the difference between full and reduced models

* Significant at $P \leq 0.05$

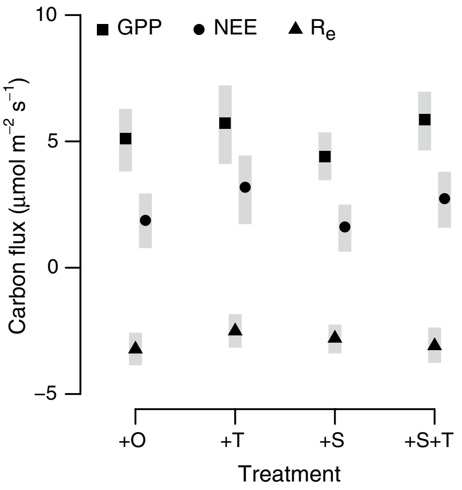

Fig. 5 Plot-level carbon flux in summer temperature and snow depth treatments. Values are the median and 95 % confidence intervals of boot-strapped mixed-model parameter estimates. Treatments are: control (+O); warming (+T); deep snow (+S); and deep snow combined with warming (+S+T). Responses are: gross primary productivity (GPP, *filled squares*); net ecosystem exchange (NEE, *filled circles*); and ecosystem respiration (R_e, *filled triangles*). Data collected between 23 June and 11 August 2014

vaginatum between 1994 and 2002; a change attributed to exceedingly wet summers (Cherry et al. 2014) rather than experimental manipulation (Wahren et al. 2005). The size, abundance, and extent of shrubs including *Alnus* (alder), *Betula*, and *Salix* have increased in Arctic systems in recent decades (Sturm et al. 2001; Tape et al. 2006) and *B. nana* and *S. pulchra* have previously increased in these enhanced snow plots (Wahren et al. 2005). There is little reason to expect uniform growth response to changing conditions among shrub species. The growth response to fertilization by *B. nana* was greater than *S. pulchra* or *Ledum palustrae*, an evergreen shrub (Bret-Harte et al. 2002) and differences in growth and reproduction among *Salix* species in response to warming were observed across Alaskan, Canadian, and European Arctic sites (Jones et al. 1997). It is possible that the response by *B. nana* to additional snow was initially rapid and has since slowed, but *S. pulchra* continues to expand in deeper snow areas.

Summer warming and additional winter snow enhanced leaf nitrogen concentration in *B. nana* and *S. pulchra* (Fig. 3). Previously in this experiment, *B. nana* and *S. pulchra*, under the combined climate scenario of deeper winter snow followed by summer warming, had the highest leaf nitrogen concentration (Welker et al. 2005), but snow depth effects in 2009 were not significantly detectable (Pattison and Welker 2014). Since additional snow and summer warming treatments raise soil temperature, warming likely accelerated nitrogen cycling and increased nitrogen available to plants (Brooks and Williams 1999; Schimel et al. 2004; Welker et al. 2005; Buckeridge and Grogan 2008; Rogers et al. 2011; Leffler and Welker 2013). Inorganic soil nitrogen measured with ion exchange resins was 65–75 % greater in the deep snow treatment in these plots (Pattison and Welker 2014). Other experiments demonstrate high leaf nitrogen concentration or enriched leaf $\delta^{15}N$ in shrubs consistent with more rapid nitrogen cycling (Craine et al. 2009) in deep snow and/or warming conditions (Rogers et al. 2011; Natali et al. 2012; Leffler and Welker 2013). Leaf nitrogen concentration of *Salix arctica* in northwest Greenland, and several shrub species in northern Sweden, was higher in naturally occurring, non-manipulated deep snow zones (Kudo et al. 1999; Sullivan et al. 2007). Leaf nitrogen concentration was also greater in *Vaccinium myrtillus* at sites under snow into mid-June compared to sites snow-free by late May (Mårell et al. 2006).

Despite higher leaf nitrogen concentration associated with warming and additional snow, leaf-level net photosynthesis was not affected in either species (Fig. 4). In general, deeper snow, warmer summer temperatures, growing season length, and fertilization have limited influence on leaf-level physiology in Low Arctic plants (Bret-Harte et al. 2001; Starr et al. 2008; Pattison and Welker 2014), although there are exceptions where increased availability of nitrogen and phosphorus did stimulate photosynthesis in *B. nana* (Chapin and Shaver 1996). In several High Arctic studies, high leaf nitrogen concentration was linked to high photosynthesis (Williams and Rastetter 1999; van Wijk et al. 2005; Muraoka et al. 2008; Leffler and Welker 2013), perhaps suggesting greater nitrogen limitation in High Arctic systems.

While net photosynthesis was not affected, warmer summer temperatures reduced stomatal conductance in *S. pulchra* (Fig. 4). We cannot link lower stomatal conductance to reduced soil moisture in this case because all manipulations were drier than the control and only warming reduced stomatal conductance. Moreover, rain was frequent in summer 2014 (Fig. S1), maintaining soil moisture content near 50 % for all treatments (Fig. 2). Phenologically advanced leaves (Woolhouse 1967) in the warmed plots might account for lower stomatal conductance.

Experimental summer warming, either independently or coupled with more snow, enhanced NEE and GPP (Fig. 5). Despite not observing greater leaf-level net photosynthesis, we observed higher carbon uptake at the ecosystem scale, similar to other tundra ecosystem carbon fixation studies in the Low and High Arctic (Welker et al. 2004; Cahoon et al. 2012; Sharp et al. 2013). In fact, other studies suggest that Arctic plants respond to warmed conditions primarily by producing more leaves (i.e., higher leaf area index) rather than through higher rates of net photosynthesis at the leaf level (Bowman et al. 1995; Sharp et al. 2013). While we did observe differences among treatments in NDVI, the treatments with the highest NEE/GPP had intermediate rather than high NDVI (Fig. S3) and NDVI is not an accurate predictor of GPP once seasonal trends are accounted for in models (La Puma et al. 2007). Differences in species composition may contribute to differences in GPP (Welker et al. 2004; Sharp et al. 2013) if species differ in photosynthetic capacity, such as that between evergreen and deciduous dwarf shrubs (Karlsson 1985). Overall, our findings are consistent with other experiments where warming enhanced GPP and NEE ca. 1 μmol m^{-2} s^{-1} in wet-sedge tundra (Boelman et al. 2003) and moist tussock (La Puma et al. 2007) tundra at Toolik Lake. Warming caused a reduction in GPP at Toolik Lake in moist tussock tundra, but an increase in GPP in dry heath in 1997 and 1998 (Oberbauer et al. 2007).

The most substantial change observed in this 20-year experiment is a shift in species composition towards dominance by shrubs, which is driven largely by increased winter precipitation. The mechanism of change appears to be increased thaw depth leading to deeper drainage and greater run-off in this system. Other tundra systems would respond differently, especially where topography promoted expansions of wetlands rather than run-off. Deeper thaw, however, was not sufficient to explain our species composition change because summer warming also increased thaw depth, but did not substantially enhance shrub abundance. Consequently, warmer soil associated with greater winter insulation is critical.

Active layer depth plays an important role in Arctic ecosystems beyond influencing species composition. Deeper thaw exposes more soil C to decomposition and subsequent release as CO_2 or CH_4 (Nowinski et al. 2010; Hicks Pries et al. 2013). Additionally, permafrost thaw allows N to leach deeper into the soil profile (Schaeffer et al. 2013), which in turn may lead to increased productivity if plants can access deeper profile N sources (Natali et al. 2012). While carbon flux differences among treatments here were modest, the plant community changes will eventually feedback to soil process, greenhouse gas fluxes, and herbivore use, resulting in different Arctic ecosystem function in the future (Hinzman et al. 2013).

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Author contribution statement JMW and SFO established the experiment, AJL and ESK designed the data collection, and AJL analyzed the data and wrote the manuscript. All authors reviewed and provided comments on the manuscript.

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