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Delayed responses of an Arctic ecosystem to an extremely dry summer: impacts on net ecosystem exchange and vegetation functioning

D. Zona^{1,2}, D. A. Lipson², J. H. Richards³, G. K. Phoenix¹, A. K. Liljedahl⁴,
M. Ueyama⁵, C. S. Sturtevant⁶, and W. C. Oechel²

¹Department of Animal and Plant Science, University of Sheffield, Western Bank, Sheffield, S10 2TN, UK

²Department of Biology, San Diego State University, San Diego, CA, USA

³Department of Land, Air and Water Resources, University of California, Davis, CA, 95616-8627, USA

⁴Water and Environmental Research Center, and International Arctic Research Center, University of Alaska Fairbanks, Fairbanks, AK, USA

⁵Graduate School of Life and Environmental Sciences, Osaka Prefecture University, Japan

⁶Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, CA, USA

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Correspondence to: D. Zona (d.zona@sheffield.ac.uk)

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Abstract

The importance and mode of action of extreme events on the global carbon budget are inadequately understood. This includes the differential impact of extreme events on various ecosystem components, lag effects, recovery times, and compensatory processes. Summer 2007 in Barrow, Arctic Alaska, experienced unusually high air temperatures (fifth warmest over a 65 yr period) and record low precipitation (lowest over a 65 yr period). These abnormal conditions resulted in strongly reduced net *Sphagnum* CO₂ uptake, but no effect neither on vascular plant development nor on net ecosystem exchange (NEE) from this arctic tundra ecosystem. Gross primary production (GPP) and ecosystem respiration (R_{eco}) were both generally greater during most of this extreme summer. Cumulative ecosystem C uptake in 2007 was similar to the previous summers, showing the capacity of the ecosystem to compensate in its net ecosystem exchange (NEE) despite the impact on other functions and structure such as substantial necrosis of the *Sphagnum* layer. Surprisingly, the lowest ecosystem C uptake (2005–2009) was observed during the 2008 summer, i.e. the year directly following the extremely summer. In 2008, cumulative C uptake was ~ 70 % lower than prior years. This reduction cannot solely be attributed to mosses, which typically contribute with ~ 40 % – of the entire ecosystem C uptake. The minimum summer cumulative C uptake in 2008 suggests that the entire ecosystem experienced difficulty readjusting to more typical weather after experiencing exceptionally warm and dry conditions. Importantly, the return to a substantial cumulative C uptake occurred two summers after the extreme event, which suggest a high resilience of this tundra ecosystem. Overall, these results show a highly complex response of the C uptake and its sub-components to atypically dry conditions. The impact of multiple extreme events still awaits further investigation.

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1 Introduction

Global increase in mean temperature (Vavrus et al., 2012) and increases evapotranspiration are expected to lead to drier conditions in many regions of the world (IPCC, 2007). Heatwaves and warm spells are also showing increasing frequency and duration in most of the world (Perkins et al., 2012), including at high latitudes (Tingley and Huybers, 2013). Alaska and Canada have been subjected to a substantial drying in the last 50 yr (as shown by the increase in the Palmer Drought Severity Index using the Penman–Monteith equation, PDSI-PM, Sheffield et al., 2012). Drought and extreme temperatures are the most important extreme events to understand, as they may have a disproportionate impact on ecosystem structure and function compared to climate change trends, overtaking more rapidly the lethal thresholds for organisms (Marchand et al., 2006; Jentsch et al., 2007). Generally, arctic ecosystems are among those experiencing the fastest relative and absolute changes in climatic conditions (IPCC, 2007). It is therefore critical to understand the effect of increased climate variability on arctic tundra ecosystem functioning.

Often, temperature increase has been connected to increased productivity in northern ecosystems (Zhou et al., 2001; Chen et al., 2006; Zhao and Running, 2010; Wookey et al., 2009; Epstein et al., 2012). This occurs, at least in part, because optimum temperatures for photosynthesis in arctic vegetation are usually higher than the observed mean temperatures (Wilson, 1957; Oechel, 1976; Tieszen, 1981). On the other hand, the impact of temperature increase on ecosystem respiration (R_{eco}) can result in a net C release from northern ecosystems (Billings, 1982; Peterson et al., 1984; Piao et al., 2008). The occurrence of extreme summer temperatures might negatively affect the photosynthetic capacity of arctic plants, and increase leaf mortality due to both direct temperature stress or drying (Marchand et al., 2005, 2006) as peatlands have been shown to be sensible to drought (Lafleur et al., 2003; Riutta et al., 2007; Lund et al., 2013). Temperature increase may also decrease species richness and change the composition of Arctic plant communities' (Walker et al., 2006; Elmendorf

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et al., 2012). It is still largely unknown how the combined changes in temperature and soil moisture (i.e. drought and heat waves) will ultimately affect ecosystems (Wu et al., 2011). This is particularly true for arctic tundra, which present an extremely complex response to temperature and hydrological change due to the presence of permafrost.

5 The near-desert like precipitation is able to sustain extensive arctic wetlands partly due to the high soil water storage capacity and low drainage constrained from the shallow active layer (the ground that experience seasonal freeze and thaw). However, despite these factors, there is evidence that reduced precipitation can reduce C uptake at least in more southerly of these high latitude ecosystems, due to soil drying and increase in
10 R_{eco} (Angert et al., 2005; Piao et al., 2008).

Overall, there is a need to understand how temperature and hydrological change affects high latitude ecosystems. Therefore, in this study we investigated the impact of an extremely low precipitation and very warm summer (2007) on an arctic tundra ecosystem in Barrow, Alaska. We hypothesized that (i) warm and dry conditions would
15 decrease net ecosystem C uptake due to drought stress to vegetation and the increase in R_{eco} at higher temperatures. Therefore, we also expected (ii) the overall cumulative C uptake of the ecosystem to be lower during this atypical warm and dry summer. To investigate how the entire ecosystem (larger scale) and different vegetation components (smaller scale) were affected by this extreme event, we compared net ecosystem
20 exchange (NEE), to plot scale net mosses' (*Sphagnum* ssp.) CO_2 uptake, and to a vascular plant development (leaf area index, LAI). *Sphagnum* mosses do not have roots, and rely on capillary transport of water between and within the short structure of its photosynthetic tissues (Price et al., 2009). They are therefore very sensitive to the surface moisture conditions, which lead us to hypothesize that (iii) mosses were
25 the vegetation component most affected by the extreme high temperature and drought event.

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2 Materials and methods

2.1 Study site

The study area was located in a vegetated drained lake basin at the Barrow Environmental Observatory (BEO), about 10 km east of the town of Barrow, Alaska, with basin area of about 0.3 km². The area is characterized by low elevation, moderate slopes (Brown, 1967), the presence of continuous permafrost with a seasonal thaw depth of up to ~ 40 cm (Hinkel et al., 2001), and wet sedge tundra vegetation (Brown, 1967). This tundra vegetation is composed of *Carex aquatilis*, *Eriophorum vaginatum* and *Dupontia fisheri*, and dominated by mosses (mostly *Sphagnum* ssp.) which are about 80% of the living biomass (Zona et al., 2009, 2011). Long-term average meteorological conditions of the site are reported in Table 1.

2.2 Eddy covariance measurements

CO₂ fluxes were measured with eddy covariance (EC) towers. Three EC towers were installed at the beginning of summer 2005 for a large scale manipulative experiment (Zona et al., 2009, 2012). For the present study, data from the control (South) section not subjected to manipulations were used (South tower 71°16'51.17" N, 156°35'47.28" W, ~ 4.5 m a.s.l.). As at the end of July 2009 the South section was also subjected to increase water table, therefore we only used data until end of July. In contrast to the previous published studies which mostly investigated the impact of flooding on CO₂ and CH₄ fluxes (Zona et al., 2009, 2012), this study focuses on the impact of a naturally occurring extreme event on NEE, gross primary production (GPP), R_{eco} , net *Sphagnum* CO₂ exchange (NSE), and LAI.

Flux processing of the CO₂ fluxes, gap filling, quality control, and footprint analysis followed standard procedures; details are described in Zona et al. (2009, 2012) and in Sturtevant et al. (2012). As we previously reported (Zona et al., 2012), the footprint analyses (Hsieh et al., 2000; Kljun et al., 2004) performed on the eddy co-

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variance fluxes showed that most ($\sim 90\%$) of the fluxes corresponded to a fetch 80 m upwind from the tower. The percent data coverage of the NEE data was 47 % in 2005, 43 % in 2006, 55 % in 2007, 45 % in 2008, and 46 % in 2009. The flux partitioning to estimate GPP and R_{eco} , and estimation of flux uncertainties, were performed using standard online methodologies, as used in Fluxnet (<http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/>), and in Reichstein et al., 2005, and in Lasslop et al., 2010).

2.3 Environmental conditions

Soil moisture, soil temperature at different depths (surface, 5 cm, 10 cm, 20 cm, and 30 cm), air temperature, relative humidity, photosynthetically active radiation PAR, and net radiation were measured near the EC tower, as described in Zona et al. (2009, 2012). Surface temperature was estimated from the infrared radiation emitted from the vegetation surface and collected with a Apogee infrared sensor (Apogee Instruments, Inc.™, Logan Utah, USA) pointing towards the main footprint of the EC towers (Zona et al., 2009). Diffuse radiation was measured using a Sunshine Sensor (Delta-T Devices, Cambridge, UK). The sunshine status threshold is 120 Wm^{-2} (therefore when the diffuse radiation was below this value, the sensor reported a diffuse radiation equal to zero). These environmental conditions were assumed to be fairly representative of the general environment experience by the mosses and were used for the statistical analysis.

Potential evapotranspiration (PET) during 1999–2009 was calculated using the Penman–Monteith equation (Monteith, 1975) using field measurements from EC tower (above) and Harazono et al. (2006) assuming a ground heat flux of 10 % of net radiation. Long-term records (1949–2013) of daily precipitation and air temperature were retrieved from the National Climatic Data Center (NCDC) archive for Barrow Airport (STN 700260, WBAN 27502, <http://www.ncdc.noaa.gov/cdo-web/#t=firstTabLink>). Precipitation was adjusted for undercatch according to Yang et al. (1998). Long-term (1999–2009) incoming solar radiation (direct and diffuse) was obtained from the Atmospheric Radiation Measurement (ARM) program (<http://ncvweb.archive.arm.gov/>). The start

aquatilis, *Dupontia fisheri*, *Eriophorum* sp.) was also measured directly in the biomass samples collected in mid-August 2006. All leaves of these species were scanned next to a scale object of known area as described in Olivas et al. (2011), and the total leaf area of these three species was divided by the plot area, giving a reasonable comparison to LAI measured with the LAI-2000 (the difference in these estimates was ~ 9%; Zona et al., 2011).

2.6 Statistical analyses

T tests (SYSTAT 13, Systat Software Inc., Chicago, IL, USA) were used to test if NEE, GPP, R_{eco} , NSE, LAI were significantly different between the summers of 2006 and 2007. These tests were performed for data divided into intervals (12–30 June, 1–26 July, 27 July–16 August, 17–30 August). These intervals (with slightly different length) were selected because they correspond to the typical phases of vegetation development during the growing season in the Arctic (early season after snow melt: 12–30 June; peak season with maximum vegetation development: 1–26 July; late season after 27 July until the end of August). The late season period was divided into two sub-periods (27 July–16 August, 17–30 August) after we noticed that the environmental conditions changed substantially on 16 August 2007 when rainfall suddenly increased the water table and moisture content (see Results).

3 Results

3.1 Environmental conditions

From a visual inspection, snow melt occurred on 12–13 June in 2005, on 13 June in 2006, on 10–11 June in 2007, and on 12 June in 2008, and on 9 June in 2009. These estimates were in fairly good agreements with the end of snowmelt estimated from the degree-day method (which was calibrated with ablation measurements in 2008–2009), estimating a snow melt on 15 June (2005), 11 June (2006), 9 June (2007), 9

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June (2008), and 5 June (2009). This second method was used to estimate the long term (1999–2009) snow melt average, which was 10 June. Monthly air temperatures from NOAA’s long-term record showed that the period July-end August 2007 was the warmest over the 129yr record on the North Slope of Alaska (Jones et al., 2009).

In Barrow, June-end August 2007 represented the lowest precipitation during a 65 yr period (1949–2013, Table 1). At our site, the mean air temperature (5.4 °C) in summer 2007 was two degrees higher than the long term mean of 3.2 °C, and the total summer precipitation was 13 mm, which is less than 20 % of the long term average (72 mm) (Table 1). The atypical weather of summer 2007 was associated with much higher evaporative demand, much higher difference between precipitation and potential evapotranspiration (P-PET), higher cumulative incoming solar radiation and lower diffuse radiation than the long term average (Table 1), and higher VPD (Liljedahl et al., 2011). The summer of 2007 also had lower soil moisture (Fig. 1) and higher surface temperatures and radiation than the more typical summers (Table 1) and occasional periods of high VPD with high solar radiation and low diffuse radiation (Fig. 2).

3.2 NEE, GPP, and R_{eco} , NSE, and LAI

The higher temperatures in summer 2007 (Fig. 1) led to an early activation of the ecosystem, as shown by the rapid C uptake right after snow melt as compared to the previous summer (Fig. 3a and b). During the beginning of the summer, both GPP and R_{eco} were significantly higher in 2007 than in 2006 (Table 2). Even though the ecosystem was a net C sink in the early season, we measured C loss from the *Sphagnum* layer (i.e. positive NSE) (Fig. 3c) during this period. We therefore conclude that the substantial CO₂ uptake during the last two weeks of June (negative NEE, Fig. 3b) was due to an early activation of vascular plants in 2007, even if the LAI was still fairly low during this period (Fig. 3d).

During peak season (1–25 July), mosses were responsible for a substantial C uptake both in 2007 and in the previous “normal” summer 2006 (Fig. 3c and Table 2). During the abnormally warm summer 2007, surface temperatures (Fig. 1) were below or at the

optimum for photosynthesis in *Sphagnum* (between about 20°C, Harley et al., 1989, and 25°C, Gerdol and Vicentini, 2011), limiting the possibility of stress induced by temperature. Peak season NEE in the warm and dry 2007 was not significantly different than 2006 (Fig. 3b, Table 2) despite the major differences in environmental conditions.

5 However, the similar NEE was the result of very different GPP and R_{eco} , both of which were significantly more positive during peak season in 2007 compared to 2006.

In contrast, later in the season, the C uptake rate in 2007 was much lower than in 2006 (Fig. 3b). During this period GPP was similar between 2006 and 2007, but the greater R_{eco} in 2007 resulted in lower net CO₂ uptake from the entire ecosystem (Fig. 3a and b and Table 2). The observed decrease in C uptake in 2007 coincided with the water limitation of the C assimilation from *Sphagnum* (as shown by the positive NSE, Fig. 3c) with *Sphagnum* water content below 900% (Figs. 2 and 4). The water limitation of the *Sphagnum* C uptake was confirmed by the significant correlation between NSE and *Sphagnum* WC in July–August 2007 ($r^2 = 0.76$; $P < 0.05$), suggesting a water limitation that was not observed in 2006. The early-season light stress and late season water stress (Fig. 4) resulted in a seasonal NSE close to zero in summer 2007. These results suggest that a combination of unusually warm air temperatures and high radiation input (both resulting in a greater evaporative demand), negatively affect the functioning of a dominant Arctic tundra vegetation component (e.g. *Sphagnum* spp.) if precipitation is sparse. We noticed a substantial necrosis of the *Sphagnum* mat towards the end of summer 2007 (Fig. 5), which is consistent with the observed water limitation of NSE and the decrease in ecosystem net C uptake rates. The observed reduction in NEE, and GPP after the end of July may therefore be due to a decline in *Sphagnum* C uptake and *Sphagnum* being a more important late season contributor to ecosystem C gain (Zona et al., 2011).

25 During the final part of the season (17–31 August), the *Sphagnum* layer showed a partial recovery, as shown by the C assimilation of NSE from 17–30 August (Fig. 3c). This occurred after a major rainfall in mid-August (9 mm), which increased *Sphagnum* WC (Fig. 2). However, we do not think that our NSE measurements were able to ac-

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curately quantify the actual percentage of the *Sphagnum* mat that was able to recover from the water stress. Therefore, even if part of the *Sphagnum* mat was able to regain C uptake after rewetting, another substantial percentage might have been irreversibly damaged (Fig. 5).

5 The LAI of vascular plants (Fig. 3d) was not significantly different between the two summers in any of the tested periods (Table 2). Summer 2006 and 2007 also presented a similar peak NDVI (Olivas et al., 2010). As the top of the *Sphagnum* layer was mostly brown (Zona et al., 2011), NDVI mainly captured the vascular plant development. Surprisingly, total C uptake during the extreme summer 2007 (59 gCm^{-2}) was fairly similar to previous summers. A total C uptake 51 gCm^{-2} was observed in summer 2006; and in summer 2005 the ecosystem was a C sink of 64 gCm^{-2} , but the eddy covariance tower started collecting data two weeks later (1 July instead of mid-June). The first two weeks of June are usually a slight C source (2.3 gCm^{-2} in 2006), which suggest that the total summertime C uptake in 2005 was probably slightly lower than the measured value and therefore, fairly similar to both 2006 and 2007 summers. On the contrary, summer 2008, which experienced air temperature and solar radiation near the long-term average (although slightly below normal summer precipitation), experienced the lowest cumulative C gain (14 gCm^{-2}); less than 70% that of summer 2006 (51 gCm^{-2}). This reduction exceeded the typical contribution of mosses to the overall summer season C uptake (estimated to be about 40% by Zona et al., 2011). Summer 2009, on the other hand, presented a fairly substantial cumulative C uptake of 55 gCm^{-2} (until 28 July).

To estimate the longer term implications of the 2007 extreme summer event, we compared the light response curve of NEE in 2007 to those observed from 2005 to 2009. The light response of NEE showed the least C uptake at saturation during the 2008 summer (which followed the warm event, Fig. 6), despite fairly similar meteorological conditions to 2005, 2006, and 2009 summers (Table 1). This minimum cumulative C uptake in summer 2008 was not the result of a higher R_{eco} as shown by the NEE intercept at zero light (Fig. 6). During summer 2009 NEE presented values similar to other

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addition, mosses affect surface albedo due to their sensitivity to moisture (Harris et al., 2005). The unique physical structure of mosses acts as a control on tundra evapotranspiration rates (Price et al., 2009; Liljedahl et al., 2011). Therefore, the thermal and hydrologic regimes can be strongly impacted by negative impacts on this vegetation component.

The similar net C uptake over the entire summer (recorded at the ecosystem scale) showed that vascular plants were able to compensate for the lack of functionality of mosses during the extreme weather event. In fact, a typical NEE at light saturation and cumulative C uptake were observed in the extreme summer 2007, which deviates from the findings presented by Lund et al. (2013) which showed a decrease in cumulative C uptake with drought. A similar compensation was also observed in grassland ecosystems subjected to extreme events (Jentsch et al., 2011). Surprisingly, the minimum ecosystem C uptake was observed the summer immediately following the extreme summer event. This is particularly surprising as Arctic plants are well adapted to grow at low temperatures (Chapin, 1983, 1987; Koroleva, 1996). The results suggest that vascular plants experienced an increased physiological activity (Lichtenthaler, 1996) in 2007 and might have undergone difficulties to readjust to the cooler, but typical, conditions after experiencing the unusually warm temperatures (Marchand et al., 2005). The observed negative lag-effect, i.e. the reduced C uptake in 2008, which was represented by fairly typical summer air temperatures and precipitation, would lead to the hypothesis that the ecosystem momentarily lost its “low-temperature acclimation”. Moreover, an important vegetation component, such as mosses, which suffered substantial stress due to dry conditions, required an entire summer to recover to their functionality, which probably only occurred in summer 2009. This interpretation was supported by the observed minimum CO₂ uptake rates for similar environmental conditions in 2008 compared to other years (Fig. 6), and by the substantial cumulative C uptake and photosynthetic capacity observed in summer 2009. The fact that the disturbance imposed on the system during the extreme year was only transitory, and that a full recovery (at least in terms of NEE) was observed in summer 2009, would imply

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a considerable resilience of the ecosystem to this extreme weather event. However, the impact of additional subsequent extreme events can have a much more damaging impact on the ecosystems (Marchand et al., 2005) and should be quantified by additional longer-term studies.

5 Conclusions

The results of NEE, GPP, and R_{eco} NSE, and related measurements of *Sphagnum* WC imply that ecosystem C uptake in arctic tundra may not be immediately affected by extreme summer weather (high air temperatures and evaporative demand and low precipitation) such as in summer 2007. Instead, some arctic ecosystems appear to exhibit year-long lag responses where the decrease in C uptake does not occur until the following summer. Longer term studies are urgently needed to refine our understanding of the ecosystem's ability to readjust (or not) to typical conditions after experiencing extreme weather events. Here, we showed that the ecosystem was able to recover substantial photosynthetic capacity just two years after the occurrence of the extreme event. However, this study represented five years and included only one extreme event. Additional longer term studies should investigate the impact of multiple subsequent extreme events and also the changes in community composition after disturbance.

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Table 1. Meteorological and hydrological conditions at the Barrow Environmental Observatory, Alaska, for the indicated periods in 2005–2009 compared to long-term means. Summer 2007 experienced the lowest precipitation over the period 1949–2009 (followed by 1991, 19 mm) and was the 5th warmest summer. Values represent end-of-snowmelt through August unless otherwise stated. Precipitation values in parentheses 2005–2009 represent the total for June through August).

Variable	2005	2006	2007	2008	2009	Long-term	Long-term period
Mean air temperature, °C ^a	3.3	2.9	5.4	3.3	3.8	3.2	1949–2013
Cumulative incoming solar radiation, MJ	1333	1311	1542	1344	1376	1327	1999–2009
Total diffuse solar radiation, MJ	733	850	774	859	917	824	1999–2009
Snow water equivalent (SWE), mm ^b	100	138	95	155	127	120	1995–2009
Summer precipitation, mm ^c	74 (86) ^a	61 (65) ^a	13 (13) ^a	56 (67) ^a	89 (91) ^a	72 ^a	1949–2013
Potential evapotranspiration (PET), mm ^d	165	134	208	147	155	157	1999–2009
Precipitation-PET, mm	–91	–72	–194	–91	–66	–86	1999–2009

^a Represents Jun through Aug.

^b SWE is from CALM (Brown et al. (2000)) snow depth measurements with snow density set to 0.32 gcm⁻³.

^c Adjusted according to Yang et al. (1998).

^d Penman–Monteith method (Monteith (1975)) assuming a ground heat flux of 10% of the net radiation.

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Table 2. Statistical results for the significance of the difference of net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (R_{eco}), net *Sphagnum* exchange (NSE), and leaf area index (LAI), between 2006 and 2007 (t tests with Bonferoni adjustment) for the indicate periods (n.s. = not significantly different). Descriptive data on the flux C components are dysplaied in Fig. 3.

Period	NEE	GPP	R_{eco}	NSE	LAI
12–30 Jun	$P < 0.001$ $F = 40$	$P < 0.001$ $F = 51.2$	$P < 0.001$ $F = 61.6$	n.s.	–
1–26 Jul	n.s.	$P < 0.001$ $F = 24$	$P < 0.001$ $F = 142.3$	n.s.	n.s.
27 Jul–16 Aug	$P < 0.001$ $F = 25.2$	n.s.	$P < 0.001$ $F = 396$	$P = 0.059$ $F = 6.9$	n.s.
17–30 Aug	$P < 0.001$ $F = 16.5$	$P < 0.001$ $F = 19.5$	$P < 0.001$ $F = 177.3$	n.s.	n.s.

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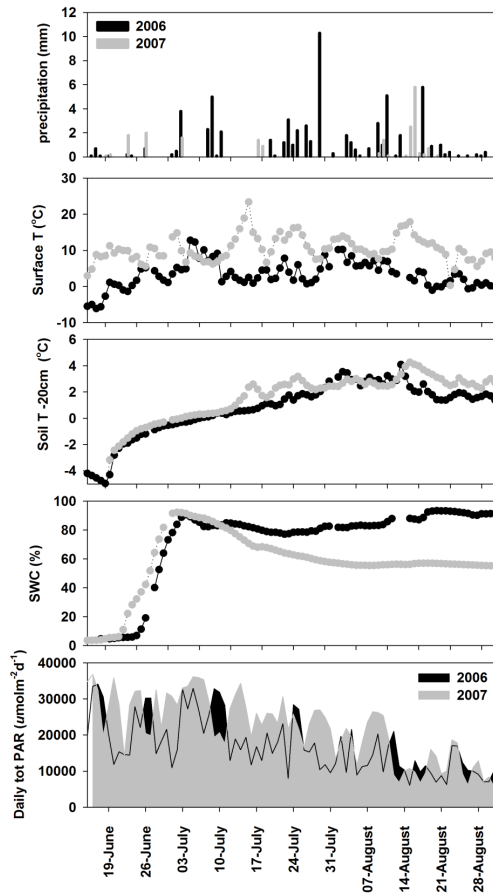


Fig. 1. Environmental conditions (daily total precipitation, surface temperature, soil temperature at –20 cm, soil water content (SWC) in the 0–10 cm layer, and photosynthetically active radiation (PAR)), at the Barrow Environmental Observatory, Alaska during summer 2006 and 2007.

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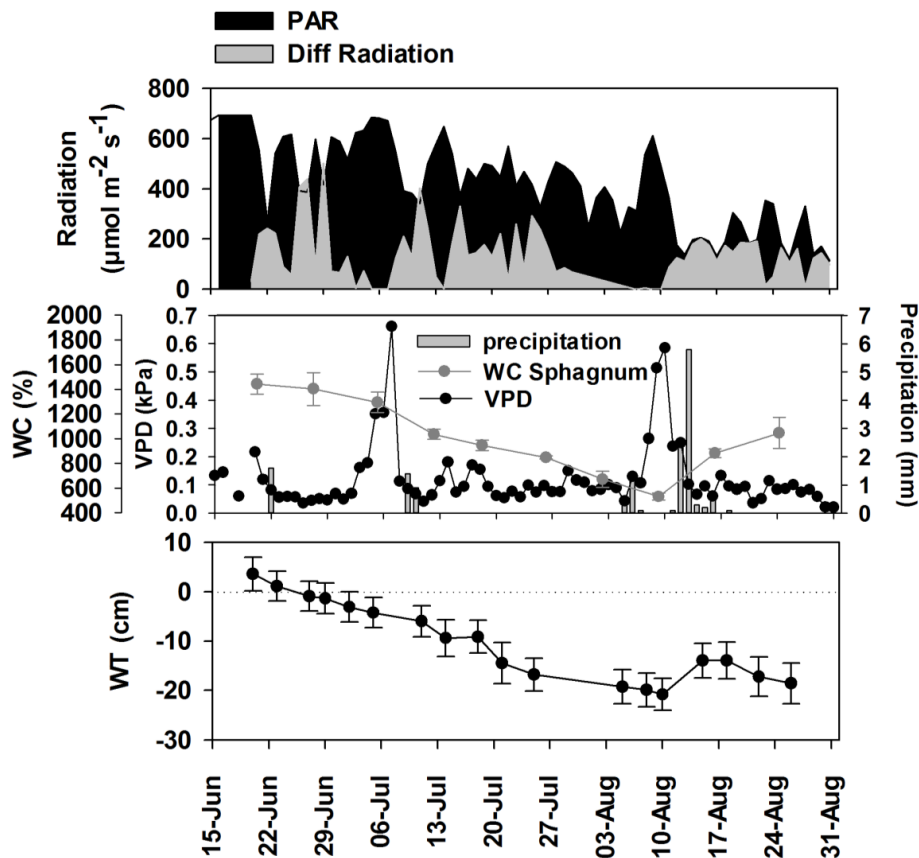


Fig. 2. Daily average weather conditions (photosynthetically active radiation (PAR), and diffuse radiation, and *Sphagnum* water content (WC), vapor pressure deficit (VPD), total daily precipitation, water table (WT)), during summer 2007 conditions at the Barrow Environmental Observatory, Alaska. Error bars are standard error of the mean.

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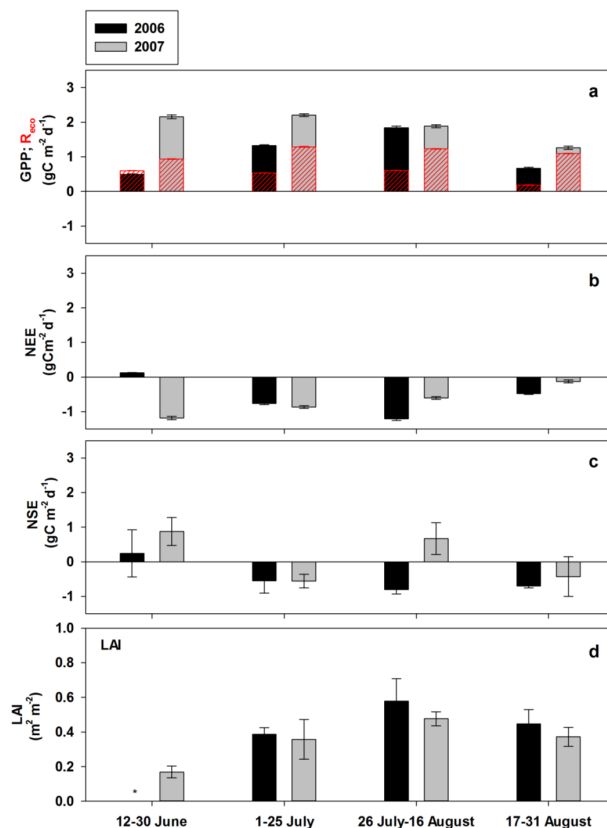


Fig. 3. Ecosystem functioning during summer in 2006 and 2007 at the Barrow Environmental Observatory, Alaska; **(a)** Gross primary production (GPP) and ecosystem respiration (R_{eco}), **(b)** net ecosystem exchange (NEE), **(c)** net *Sphagnum* exchange (NSE), and **(d)** leaf area index (LAI), averaged for each of the indicated periods. Error bars are standard errors of the mean. Negative NEE and NSE represent C uptake, while positive values represent C loss. The significance of differences between 2006 and 2007 values are reported in Table 2.

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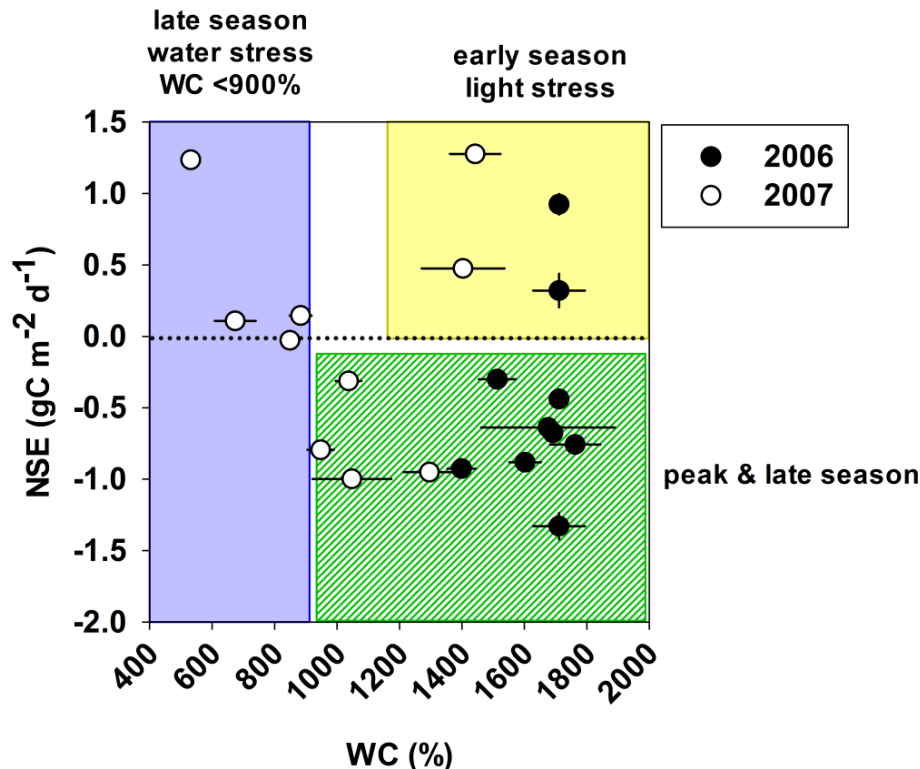


Fig. 4. Daytime (08:00–18:00LT) net *Sphagnum* exchange (NSE) vs water content in the *Sphagnum* layer (WC) during the 2006 and 2007 growing seasons. Negative NSE values represent C uptake, while positive values represent C loss. Note photoinhibition early in the season in both years, and the water limitation (increase in NSE with decrease in WC below 900%) in summer 2007. Mosses were water saturated on 13 and 25 June 2006 (WC was not measured as water table was above or at the *Sphagnum* surface, and it was assumed to be equal to the maximum observed WC in summer 2006 for graphing purposes).



Fig. 5. Close-up photograph of the *Sphagnum* layer during mid-August 2006 and 2007. Notice necrosis of the *Sphagnum* layer in August 2007.

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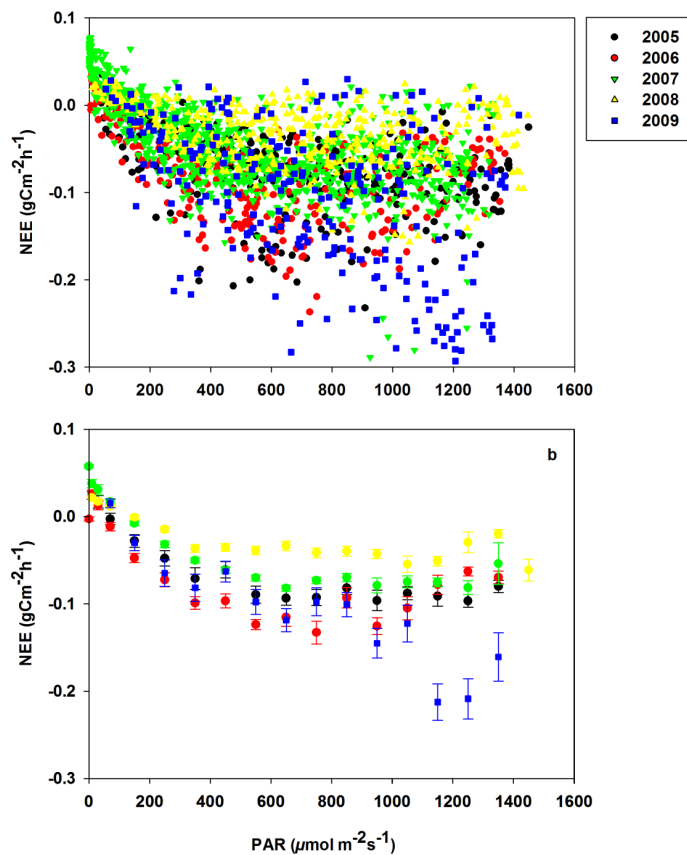


Fig. 6. Light response curves of net ecosystem exchange (NEE) during the 2005–2009 growing seasons. Displayed are data filtered for a similar temperature range and to remove water stress ($VPD < 0.3$ kPa).

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