See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/229063267

Variation in Peak Growing Season Net Ecosystem Production Across the Canadian Arctic

ARTICLE *in* ENVIRONMENTAL SCIENCE & TECHNOLOGY · JULY 2012

Impact Factor: 5.33 · DOI: 10.1021/es300500m · Source: PubMed

CITATIONS

12

READS

57

9 AUTHORS, INCLUDING:



May Myklebust

Trent University

4 PUBLICATIONS 90 CITATIONS

SEE PROFILE



Laurier Poissant

112 PUBLICATIONS 3,280 CITATIONS

SEE PROFILE



Joel Barker

The Ohio State University

25 PUBLICATIONS 472 CITATIONS

SEE PROFILE



Martin Pilote

Environment Canada

37 PUBLICATIONS **1,196** CITATIONS

SEE PROFILE





Variation in Peak Growing Season Net Ecosystem Production Across the Canadian Arctic

Peter M. Lafleur,*,† Elyn R. Humphreys,‡ Vincent L. St. Louis,§ May C. Myklebust,† Tim Papakyriakou, $^{\parallel}$ Laurier Poissant, $^{\perp}$ Joel D. Barker, $^{\$,\#}$ Martin Pilote, $^{\perp}$ and Kyle A. Swystun $^{\parallel}$

Supporting Information

ABSTRACT: Tundra ecosystems store vast amounts of soil organic carbon, which may be sensitive to climatic change. Net ecosystem production, NEP, is the net exchange of carbon dioxide (CO₂) between landscapes and the atmosphere, and represents the balance between CO₂ uptake by photosynthesis and release by decomposition and autotrophic respiration. Here we examine CO₂ exchange across seven sites in the Canadian low and high Arctic during the peak growing season (July) in summer 2008. All sites were net sinks for atmospheric CO₂ (NEP ranged from 5 to 67 g C m⁻²), with low Arctic sites being substantially larger CO2 sinks. The spatial difference in NEP between low and high Arctic sites was determined more by CO2 uptake via gross ecosystem production than by CO₂ release via ecosystem respiration. Maximum gross ecosystem production at the low Arctic sites (average 8.6 μ mol m⁻² s⁻¹) was about 4 times larger than for high Arctic sites (average 2.4 umol m⁻² s⁻¹). NEP decreased with increasing temperature at all low Arctic



sites, driven largely by the ecosystem respiration response. No consistent temperature response was found for the high Arctic sites. The results of this study clearly indicate there are large differences in tundra CO2 exchange between high and low Arctic environments and this difference should be a central consideration in studies of Arctic carbon balance and climate change.

■ INTRODUCTION

The Arctic tundra is a vast and diverse biome covering approximately $5 \times 10^6 \text{ km}^2$ and is composed of some 15 major vegetation community classes and over 400 plant species.1 Climate in the circumpolar Arctic has changed in the latter part of the previous century driving demonstrable responses from the tundra biological and physical systems.² Such changes have potential to feedback on the Arctic climate system.³ One significant feedback could arise through the exchange of carbon (C) gases between Arctic tundra and the atmosphere, in part because of the vast store of soil organic carbon in permafrost soils⁴ and its potential vulnerability to decomposition with future climate warming.⁵ Hence, there has been recent interest in tundra-atmosphere C exchange.

Despite this awareness, the Arctic is relatively unstudied due to its remoteness and associated logistical challenges. Studies of tundra-atmosphere C exchange have been conducted at a number of disparate locations throughout the circumpolar Arctic. To date only a few regional syntheses of tundraatmosphere C exchanges have been attempted.6-8 None of these focused on the Canadian Arctic, yet the Canadian Arctic holds about one-third of the circumpolar tundra and more than half of all high Arctic tundra.9 Therefore, studies of C exchange in this region are of particular significance.

The net exchange of C between tundra and atmosphere is referred to as net ecosystem production (NEP), which is generally defined as the balance between gross ecosystem production, or photosynthesis (GEP), and ecosystem respiration (ER) with carbon dioxide (CO₂) making up the bulk of this mass exchange. When NEP is positive, the ecosystem is in a phase of net autotrophy and CO2 is being removed from the atmosphere. When negative, the ecosystem is in a phase of net heterotrophy and CO_2 is being added to the atmosphere. Warming in Arctic regions could increase soil decomposition, and hence ER, resulting in a positive feedback to the climate system, whereas enhanced productivity will result in greater removal of atmospheric CO₂ and a negative feedback. 10 Our current limited understanding of the sensitivity of C cycling to

Received: February 6, 2012 Revised: June 4, 2012 Accepted: July 10, 2012 Published: July 10, 2012

Department of Geography, Trent University, Peterborough, Ontario K9I 7B8, Canada

^{*}Department of Geography and Environmental Studies, Carleton University, Ottawa, Ontario K1S 5B6, Canada

[§]Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Department of Environment and Geography, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

¹Earth Sciences, University of Ottawa, Ottawa, Ontario K1N 6N5 & Environment Canada, Montreal, Quebec H2Y 2E7, Canada

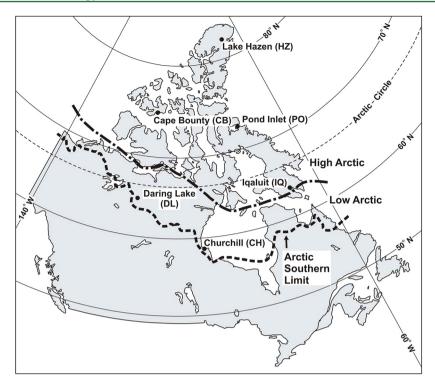


Figure 1. Location of flux tower sites in the Canadian Arctic.

climate change in the Arctic means the ultimate fate of these two processes is still not known.

The C sink/source strength of an ecosystem is evaluated on an annual basis as CO2 exchange is a year round process. In tundra, small effluxes occur through the winter and shoulder (spring and fall) seasons and can accumulate to be a significant component of the annual budget. $^{11-13}$ If net CO₂ uptake is going to occur during the year, it takes place in the snow-free growing period, which is typically less than 100 days in the Arctic. ¹⁴ Consequently, the period of net CO₂ uptake (positive NEP) generally lasts only two to three months (June–August) with maximum daily values achieved in midsummer (July). July on the tundra is the period when average air temperature is usually at its maximum, light is not yet limiting, and plants are rapidly increasing their leaf area 18 resulting in maximum GEP. 19 Despite the short duration of this uptake period, studies suggest that the NEP at this time is most influential in determining the temporal^{15,20,21} and spatial^{22,23} variability in tundra NEP. Hence, there is a need for further studies on this critical period of maximum NEP and its spatial variation.

In this study, we present observations of NEP from seven tundra sites in the Canadian Arctic obtained during the fourth International Polar Year in 2008. Our analyses focused on the midsummer (July) period, when all sites were snow-free and vegetation was actively growing. The objectives of our analyses were to characterize the magnitude and variation in peak summer tundra NEP across the Canadian Arctic, and investigate the environmental factors that explain spatial variation in CO₂ exchange across this vast region of the Arctic.

MATERIALS AND METHODS

We quantified summer NEP measurements from seven sites in Canada spanning a latitudinal range from 58° to 81° N (Figure 1). Although the sites represent a variety of ecological and physical conditions found in the Canadian Arctic, they broadly

fall into two groups: (1) high Arctic tundra which corresponds to most of the Canadian Arctic Archipelago landmass and (2) low Arctic tundra, comprising the northern portions of the North American continental surface. Three sites, Daring Lake fen (DL-f), Daring Lake mixed (DL-m), and Churchill (CH), lie in the low Arctic zone. CH and DL-f are classified as wetland (wet sedge) tundra (Table 1) and DL-m is a mixed upland tundra site with low shrubs and dwarf shrubs, tussocks, and sedges. High Arctic sites include Lake Hazen (HZ), Cape Bounty (CB), and Pond Inlet (PO) and are representative of sparsely vegetated polar semidesert tundra. Iqaluit (IQ) is mixed upland tundra composed of tussock, sedge, and dwarf shrub. Despite its relatively low latitude IQ is represented as high Arctic in some classifications and middle-low Arctic in others.²⁴ Therefore, it is a transitional site between high and low Arctic.

Climate patterns across the range of the study sites followed expected trends. Mean annual temperature (MAT) at the high Arctic sites was $7-10~^{\circ}\text{C}$ lower than at the low Arctic sites (see Supporting Information, SI, Table S1). CH was the warmest site ($-6.9~^{\circ}\text{C}$), and MAT at DL ($-8.9~^{\circ}\text{C}$), and IQ ($-9.8~^{\circ}\text{C}$) were similar. Mean annual precipitation at high Arctic sites was roughly half that at the low Arctic sites and IQ (average of 364 mm).

NEP was measured at all sites (except PO) with the eddy covariance (EC) technique, and supported by environmental measurements. The EC instruments consisted of a sonic anemometer to measure fluctuations in vertical wind speed and temperature (DL-f, DL-m, and CB: model R3-50, Gill Instruments, Lymington, UK; IQ: model Windmaster Pro, Gill Instruments; CH and HZ: model CSAT3, Campbell Scientific, Logan, UT, USA) and an open path infrared gas analyzer (IRGA) to measure fluctuations of CO₂ and water vapor concentrations (model LI-7500, LI-COR Inc., Lincoln, NE, USA) at a frequency of 10 Hz. The height of the EC

Table 1. Sites and Acronyms, Latitude and Longitude, Description of Vegetation, and Soil Characteristics within the Flux Tower Footprint^a

	Churchill (CH) 58° 39.913′ N 93° 49.860′ W	Daring Lake Fen (DL-f) 64 52.111' N 111 34.488' W	Daring Lake Mixed (DL-m) 64° 52.131′ N 111° 34.498′ W	Iqaluit (IQ) 63° 47.415' N 68° 33.603' W	Pond Inlet (PO) 72° 41.565′ N 77° 57.457′ W	Cape Bounty (CB) 74° 54.885′ N 109° 34.415′ W	Lake Hazen (HZ) 81° 49.355′ N 71° 22.834′ W
${\rm Tundra\ classification}^b$	Wet sedge	Wet sedge	Low shrub/Tussock, sedge-dwarf shrub	Tussock, sedge-dwarf shrub	Semidesert	Semidesert	Semidesert
Vegetation – dominant plant functional types (and genus) and per- cent cover* or percent of total leaf area index (LAI)# (if known)	Brown moss (Scorpidium, Tomenthypnum, Dicra- num), Graminoid (Carex), Evergreen shrub (Ledum), Deciduous shrub (Betula, Salix), Li- chen	*Graminoid (Carex) (94%), Deciduous shrub (Betula) (3%), Evergreen shrub (Andromeda) (3%), *Moss (Sphagrum) (100%)	*Evergreen shrub (Ledum, Empetrum, Loiseleuria) (58%), Graminoid (Carex) (20%), Deciduous shrub (Behula, Vaccinium) (15%), Herb (Rubus) (6%)	Lichen, Moss (Aulacom- nium), Evergreen shrub (Empetrum, Ledum, Rodo- dendrum, Casiope, Dryas), Graminoid (Eriophorum), Deciduous shrub (Salix)	*Lichen (28%), Moss (7%), Evergreen shrub (<i>Dryas</i> , Cassiope) (20%), Deciduous shrub (Salix) (10%), Graminoid (Carex, Luzula) (1%), Herb (<i>Oxytropis</i>) (3%)	*Moss (58%), Green and senescent Gra- minoid (21%, 37%), Lichen (19%), De- ciduous shrub (<i>Salix</i>) (8%), Forb (4%)	*Cryptogamic crust (56%), Lichen (12%), Evergreen shrub (<i>Dryas</i>) (5%), Moss (2%), Graminoid (<i>Carex</i> , <i>Kubresia</i>) (1%), Deciduous shrub (<i>Salix</i>) (1%)
Vascular LAI ^c mean (s.d.) 0.47–0.60 ^d SOC (measured) 11.7 (20 cm 14.6 (25 cm	0.47–0.60 ^d 11.7 (20 cm) 14.6 (25 cm)	0.57 (0.12) 5.8 (20 cm) 38 (60 cm)	0.70 (0.21) 10.8 (20 cm) 22.4 (70 cm)	0.21 (0.11) n/a	0.34° n/a	0.26 (0.11) 3.5 (20 cm) n/a	0.07° 6.8 (20 cm) 22.2 (60 cm)
Mapped ^{f} SOC for top 20 cm	6.5, 10.4	9.4	3.3, 11.0	0.6, 8.8	2.2	2.0, 3.6	2.2, 4.6
ALT_{max} in m (±s.d.)	1.10 ± 0.10	0.63 ± 0.02	0.81 ± 0.13	n/a	$0.80 \pm n/a$	0.60 ± 0.07	0.88 ± 0.14

2008 before the end of August. s.d. is standard deviation. N/A indicates data were not available. Dassifications after ref 9. Includes only live green vascular structures + leaves, based on point-count sampling unless otherwise indicate. Likely range from ref 25. Derived from percent cover estimates. Value derived from the nearest one to two polygons from the Canadian Soils Data Base. 26 ^aLAI is one-sided leaf area index not including cryptograms. SOC is soil organic carbon content (kg m⁻²) measured on site for given soil depth in parentheses. ALT_{max} is maximum active layer thickness in

instrumentation varied from 2.5 m to as much as 4.5 m over the short stature Arctic surface (vegetation height between ~2 and \sim 25 cm). NEP was calculated as the sum of the flux of CO₂ and the rate of change in CO2 stored below the EC instrument height for 30 min intervals, except CH where fluxes were computed every 60 min. NEP did not account for fluxes of methane or dissolved organic carbon, which were assumed to represent only small contributions to the carbon balance of these sites. A three-axis coordinate rotation was applied to CO₂ flux measurements at all sites. Data were quality controlled by removing fluxes made when the diagnostic signal of the IRGA indicated the optical path was obstructed (typically rain periods), when average vertical wind speed or CO2 concentrations were outside the range of normal limits and during other instrument malfunction. Night-time data were also filtered for all sites using a 0.1 m s⁻¹ friction velocity threshold. This value was experimentally derived previously for the DL-m and DL-f sites, and given that all sites were similarly aerodynamically smooth, the threshold was applied uniformly to all but HZ. At HZ, dark periods did not occur and it was assumed that sufficient convection limited the occurrence of underestimates in NEP. See Supporting Information for more details on flux processing.

At PO, fluxes were measured with the Bowen ratio flux gradient technique.²⁷ The instrument package (Campbell Scientific) consisted of a closed-path IRGA (model LI-6262, LI-COR), with switched intake of air from two levels above the surface (0.5 and 2.0 m). At each level, air temperature was measured with a fine wire thermocouple, and vapor density was measured with the IRGA. These measurements were used to derive the Bowen ratio (ratio of sensible to latent heat fluxes), then based on conservation of energy, fluxes of sensible and latent heat were computed from measurements of available energy (i.e., net radiation minus soil heat flux). Assuming similarity of the eddy diffusivities for heat and CO2, the eddy diffusivity for heat was computed and applied to the CO2 concentration gradient measured with the IRGA to derive the flux of CO₂ for 60 min intervals. Fluxes were computed in a data logger using a program supplied by Campbell Scientific Inc. At PO, NEP data were quality controlled primarily by removing poorly constrained estimates of the eddy diffusivity typically occurring during stable conditions and associated with Bowen ratio values outside the expected range. In addition, fluxes beyond 3 standard deviations of the monthly mean were

Ancillary data included measurements of photosynthetically active radiation (PAR) and air temperature (*T*). PAR was measured with quantum sensors at most sites. At PO only net all-wave radiation was measured. PAR was estimated from modeled incoming global solar radiation and a relationship with measured net radiation developed for IQ where both variables were measured. Short gaps in PAR and air temperature were linearly interpolated. Longer gaps occurred at the beginning of July at HZ and end of July at PO and IQ. Air temperature records were filled using data from the nearest Environment Canada weather station (see SI Table S1), while PAR records were filled with the mean diurnal PAR values calculated from the nearest available 4–7 day period with similar precipitation regime (as recorded at the nearest Environment Canada weather station).

To derive daily totals, NEP were computed for the month of July only and all sites were gap-filled in the same way. Gaps of 1 h or less were linearly interpolated. Larger gaps were filled by

modeling NEP with environmental variables as follows. Using all available measurements of NEP, PAR, and T for July, a light and temperature response curve (eq 1) was developed (also see SI, S3):

$$NEP = \frac{GEP_{\text{max}}\alpha PAR}{\alpha PAR + GEP_{\text{max}}} - R_{10}Q_{10}^{T-10/10}$$
(1)

where GEP_{max} is the maximum gross photosynthesis achieved at unlimited PAR, α is the slope of the initial NEP–PAR curve, R_{10} is the respiration at 10 °C, and Q_{10} is the rate at which ecosystem respiration changes with a 10 degree change in T. The quantity of missing 30-min data requiring gap-filling in July was as follows: 15% for DL-f, 18% for DL-m and CB, 26% for CH, 31% for IQ, 44% for HZ, and 63% for PO.

Gap-filled NEP was decomposed into component fluxes of GEP and ER. Values of ER were obtained from eq 1 (site parameters given in SI,Table S2) or when available, from nighttime measurements of NEP. Following previous works, ²⁸ nighttime was defined when PAR was less than 60 μ mol m⁻² s⁻¹. GEP was then computed as the sum of these ER values and gap-filled NEP. In this study, positive NEP and GEP indicate a net uptake of CO₂ by the ecosystem, while negative NEP and positive ER indicate a net release of CO₂ to the atmosphere. Random uncertainty estimates for July fluxes were estimated by statistical procedures (see SI, S4).

■ RESULTS AND DISCUSSION

Summer (June-August) temperature in 2008 varied by 8.2 °C among sites (see Table S1), following a latitudinal gradient of colder in the north trending to warmer in the south. Average 2008 summer (June-August) temperatures in the high Arctic were generally warmer than the long-term average, while low Arctic sites experienced near average temperatures. July 2008 temperatures followed the same patterns ranging from 4.6 °C at HZ to over 13 °C at CH and DL sites. Summer precipitation was highly variable ranging from 45 mm at HZ to about 165 mm at CH, IQ, and PO, and did not display the same latitudinal trend as temperature. Some sites were near the longterm average summer precipitation (CH and IQ), while others received lower than average totals (DL, CB, HZ), and only PO had higher than average summer precipitation. During July CH, DL, and HZ received below average precipitation, IQ was near average, and PO received more than twice average precip-

Seasonal trends in weekly mean diurnal NEP across the seven sites (Figure 2) show the evolution of CO₂ uptake across the Arctic tundra as it transitions from late winter into the growing season. Positive NEP (i.e., CO2 uptake) was initiated only after the tundra became snow free. In 2008 earlier than normal snowmelt occurred at most of the sites, varying from May 15 (IQ) to June 1 (CH), while melt at the high Arctic sites occurred near mid-June. This difference in timing is reflected in NEP trends, which showed positive NEP in early June at DL-f, DL-m, and CH, but not at CB until early July. Date of snowmelt is an important factor in tundra CO2 exchange. Although some plants can begin to photosynthesize below thin snow covers where light is sufficient and leaf temperatures can exceed the freezing point,²⁹ EC studies consistently indicate that net ecosystem scale CO₂ uptake is achieved only after snowmelt, with the period between melt and net daily uptake varying from a few days to weeks depending upon ecosystem type and weather. ^{15,16,22} Immediately following snowmelt, NEP

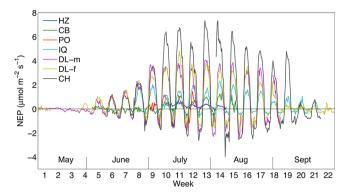


Figure 2. Seasonal trend in diurnal NEP averaged for each week from May 1 to Sept 30, 2008. Data are shown during periods when flux measurements were made at each site.

is limited by small leaf area even though PAR is near its seasonal maximum. Although we do not have seasonal measurements of LAI, previous studies indicate that tundra peak LAI is typically reached by mid- to late-July. 18,30,31 This is the period when air temperature across the Arctic is at its maximum and PAR remains sufficiently high, resulting in a broad peak of maximum NEP for much of July and into early August at all our sites (Figure 2). The remainder of our analysis focuses on this critical period when coincident data at all sites were available.

NEP and air temperature display a strong similarity in July average diurnal trends of decreasing amplitude with increasing latitude, suggesting a broad temperature control on NEP (Figure 3). PAR levels were more homogeneous among the sites. However, the importance of PAR is reflected at CH, the most southerly site, which had the greatest daytime PAR and NEP. PAR was also important at HZ, where NEP remained positive throughout the day as average PAR remained above

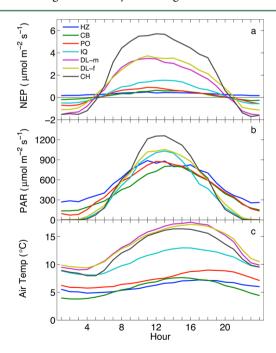


Figure 3. July 2008 daily ensemble average trends in gap-filled (a) net ecosystem production (NEP), (b) photosynthetically active radiation (PAR), and (c) air temperature. Hour 12 refers to solar noon at each site

 $250~\mu \text{mol m}^{-2}~\text{s}^{-1}$ for all hours of the day. NEP at the two DL sites displayed similar trends and magnitudes. Both of these sites had considerably greater daytime maxima NEP compared to IQ despite the similar latitude and PAR levels. This comparison reflects in part the warmer July temperature at DL (see Table S1) and the importance of biomass and productivity; DL sites had 2–3 times the LAI as IQ (Table 1).

Although all sites had net CO_2 uptake in July, ranging from 5 to 67 g C m⁻², there was an order of magnitude difference between high Arctic (HZ, CB, PO, and IQ) and low Arctic sites (DL-m, DL-f, and CH) (Figure 4). These variations in total

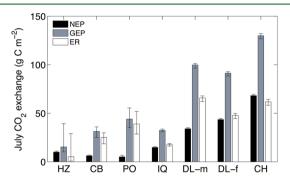


Figure 4. July 2008 monthly total fluxes for net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production (GEP). NEP is based on gap-filled measured data and ER and GEP are derived from NEP using a model. See Methods and Materials and SI for full details.

July NEP corresponded closely with variations in maximum daytime NEP (Figure 3). On a daily basis, mean NEP ranged from 0.2 to 2.2 g C m⁻² d⁻¹, which is within the range measured at peak growing season at other Arctic sites.^{20,22,30,32} We observed consistently low NEP at the high Arctic sites, but this is not characteristic of all high Arctic tundra. For example, a midsummer average NEP of ~3 g C m⁻² d⁻¹ was recorded at Zackenberg, Greenland (74.5° N),²⁸ while only ~0.4 g C m⁻² d⁻¹ was measured at Ny-Ålesund in Svalbard, Norway (79.5° N).³³ The difference between these studies can be attributed to their contrasting tundra types. Ny-Ålesund is an upland semidesert site much like our four high Arctic sites where mean daily NEP was quite similar $(0.2-0.5 \text{ g C m}^{-2} \text{ d}^{-1})$. The Zackenberg site is a fen typical of a polar oasis with an NEP similar to our three low Arctic sites (1.1-2.2 g C m⁻² d⁻¹). The occurrence of these high Arctic polar oases is rare, though, covering only about 6% of the ice-free land area in the Canadian Arctic.³⁴ The component fluxes, GEP and ER, also showed large differences in magnitude between high and low Arctic sites (Figure 4). Within high and low Arctic groups, there were subtle differences between the sites. For example, the highest latitude site (HZ) had the least amount of vegetation cover and smallest fluxes. PO and IQ had similar vegetation cover, but fluxes were smaller at IQ, especially ER, which may have been due to thinner soil and lower soil organic C at that site. In the low Arctic group, the ratio of ER/GEP was lower at the wet sites (CH and DL-f; 0.48 and 0.52, respectively) than at the upland site (DL-m; 0.65).

Overall, the trend in July C fluxes across all sites did not follow a strong latitudinal gradient. Rather, we found a step change in flux magnitudes between high and low Arctic locations, with variations within each group. This pattern is confirmed by examining the model parameters from eq 1 (see

Table S2), which unlike the flux data are relatively independent of meteorological conditions. Maximum gross ecosystem production, GEP_{max}, indicated substantially lower photosynthetic uptake of CO₂ at high Arctic (average GEP_{max} 2.4 μ mol m⁻² s⁻¹) compared with low Arctic (average GEP_{max} 8.6 μ mol m⁻² s⁻¹) sites (Figures 5a). Differences in R_{10} and night-

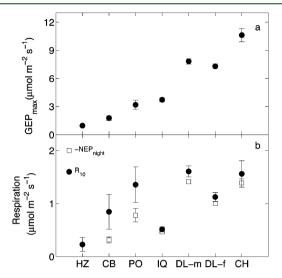


Figure 5. Mean monthly model parameters for July 2008: (a) maximum gross ecosystem production, GEP_{max} and (b) modeled base respiration (R_{10}) and ecosystem respiration (ER) derived from mean measured nighttime (PAR < 60 μ mol m⁻² s⁻¹) NEP on available data. Sample sizes for ER as follows: CB-23, PO-9, IQ-249, DL-m-287, DL-f-285, CH-166. ER for HZ not computed as it is subject to 24 h daylight in July. Error bars for GEP_{max} and R_{10} are 95% confidence intervals and for ER \pm 1 standard error.

time NEP (hence ER) were less pronounced, but tended toward smaller values at high Arctic (average $R_{10}=0.7~\mu {\rm mol}~{\rm m}^{-2}~{\rm s}^{-1})$ compared to low Arctic (average $R_{10}=1.4~\mu {\rm mol}~{\rm m}^{-2}~{\rm s}^{-1})$ sites (Figure 5b). Lower respiration rates at high Arctic sites might be expected because of minimal plant biomass resulting in less autotrophic respiration and fresh litter input to soils, which has been shown to be important for heterotrophic respiration in Arctic ecosystems. The week and R_{10} were much smaller than differences in total ER and R_{10} were much smaller than differences in total GEP and GEP_{max}, we conclude that the main factor driving differences in summer NEP between these two groups is photosynthesis rather than respiration. This is consistent with observations suggesting that assimilation drives temporal variations in NEP at a given tundra site 20,37,38 and spatial variation in NEP among tundra types. 32,39

We used regression tree analysis (RTA) to further explore the factors contributing to spatial variation of July daily NEP across the Canadian Arctic (see SI, S5). Although several model variants were investigated, RTA showed that primary division in the tree is always between high and low Arctic sites. This division could be achieved with a number of site (e.g., LAI or mapped soil C) or climate variables. In the best fit model LAI was selected to divide high and low Arctic sites, thereafter PAR and mapped C were used to subdivide the sites, with daily average PAR and air temperature typically acting as the explanatory variables for daily NEP models at each terminal node. While some sites had unique models, the DL sites shared a common model that also included LAI as an explanatory variable. This was also the case for PO, CB, and HZ on days

with sunny conditions, but on days with low PAR, air temperature did not explain variations in daily NEP. In all cases where air temperature was present in the model, it was negatively related to daily NEP, although to varying degrees.

We further examined these relationships between daily NEP and air temperature in Figure 6a. NEP was negatively related to

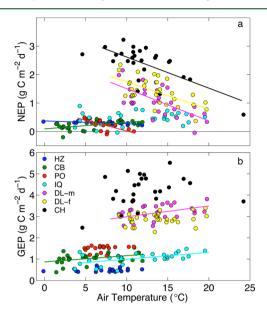


Figure 6. Response of daily (a) NEP and (b) GEP to daily average air temperature during July 2008. NEP data are 24 h totals for days with more than 24 half hours of measured data and GEP is gap-filled NEP plus measured/modeled ER for these same days. Lines are shown for significant linear relationships (p < 0.05) with coefficient of determination, linear slope value, and number of observations for each site as follows (n/s indicates not significant at p = 0.05): (a) NEP: HZ 0.27, -0.0098, 19; CB 0.27, 0.023, 29; PO 0.49, -0.076, 17; IQ n/s; DL-m 0.42, -0.113, 29; DL-f 0.39, -0.096, 31; CH 0.47, -0.109, 26; (b) GEP: HZ n/s; CB 0.18, 0.029, 29; n/s; IQ 0.32, 0.032, 27; DL-m 0.20, 0.051, 29; DL-f n/s; CH n/s.

temperature for the three low Arctic sites, where slopes of these relationships were similar (-0.9 to -0.16 g C m^{-2 o}C¹⁻, 0.39 < r^2 < 0.47). In contrast, the high Arctic sites had mostly poorer $(0.03 < r^2 < 0.49)$ and inconsistent relationships (slopes varied from -0.0098 to 0.023 g C m⁻² d⁻¹/°C). The underlying causes of these trends are driven by ER and GEP responses to temperature. As predicted by the exponential relationship (eq 1, Table S2), ER increases with air temperature at all sites. However, GEP was either unrelated or only weakly positively related to temperature at all sites in July (Figure 6b). We hypothesize that the difference in NEP response to temperature between low and high Arctic sites arises because high Arctic ecosystems rarely experience warm enough conditions whereby the exponential increase in respiration substantially offsets any possible increases in photosynthesis. Such conditions frequently prevail in peak growing season at the low Arctic sites. Although more investigation is required to confirm this hypothesis, our analyses overwhelmingly suggest that there is a distinct difference between carbon fluxes of high and low Arctic tundra and this difference is important for pan-Arctic carbon balance and climate change studies.

ASSOCIATED CONTENT

S Supporting Information

Summary of climate data for the study period, details of flux processing and uncertainty estimates, parameter estimates for the NEP light response models, and regression model results. This information is available free of charge via the Internet at http://pubs.acs.org/.

AUTHOR INFORMATION

Corresponding Author

*Phone:705-748-1011 x7487; e-mail: plafleur@trentu.ca.

Present Address

*School of Earth Sciences, The Ohio State University, 125 South Oval Mall, Columbus, Ohio 43210 USA.

Notes

The authors declare no competing financial interest.

ACKNOWLEDGMENTS

This research is part of CiCAT, an International Polar Year (IPY) project funded under the Canadian IPY Program (G.H.R. Henry, PI). Additional funding was received from the Natural Science and Research Engineering Council of Canada (NSERC) to P.M.L., E.R.H., and V.L.St.L. We acknowledge support from Polar Continental Shelf Project for logistical research at the HZ and CB sites. We also thank the following organizations and individuals for their field support: Churchill Northern Studies Centre, Steve Matthews at the Daring Lake Terrestrial Research Station, Parks Canada at HZ, the Nunavut Research Institute, Dr. Scott Lamoureux at Cape Bounty, Mike Treberg for technical support at Daring Lake and Cape Bounty, and our many field assistants. We thank two anonymous reviewers for their constructive comments.

REFERENCES

- (1) Walker, D. A.; Raynolds, M. K.; Daniëls, F. J. A.; Einarsson, E.; Elvebakk, A.; Gould, W. A.; Katenin, A. E.; Kholod, S. S.; Markon, C. J.; Melnikov, E. S.; N.G., M.; Talbot, S. S.; Yurtsev, B. A.; CAVM Team. The Circumpolar Arctic Vegetation Map. *J. Veg. Sci.* 2005, 16, 267–282.
- (2) Hinzman, L. D.; Bettez, N. D.; Bolton, W. R.; Chapin, F. S.; Dyurgerov, M. B.; Fastie, C. L.; Griffith, B.; Hollister, R. D.; Hope, A.; Huntington, H. P.; Jensen, A. M.; Jai, G. J.; Jorgenson, T.; Kane, D. L.; Klein, D. R.; Kofinas, G.; Lynch, A. H.; Lloyd, A. H.; McGuire, D. A.; Nelson, F. E.; Oechel, W. C.; Osterkamp, T. E.; Racine, C. H.; Romanovsky, V. E.; Stone, R. S.; Stow, D. A.; Sturm, M.; Tweedie, C. E.; Vourlitis, G. L.; Walker, M/ D.; Walker, D. A.; Webber, P. J.; Welker, J. M.; Winker, K. S.; Yoshikawa, K. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Climatic Change 2005, 72, 251–298.
- (3) Chapin, F. S., III; Sturm, M.; Serreze, M. C.; McFadden, J. P.; Key, J. R.; Lloyd, A. H.; McGuire, A. D.; Rupp, T. S.; Lynch, A. H.; Schimel, J. P.; Beringer, J.; Chapman, W. L.; Epstein, E. H.; Euskirchen, E. S.; Hinzman, L. D.; Jia, G.; Ping, C. –L.; Tape, K. D.; Thompson, C. D. C.; Walker, D. A.; Welker, J. M. Role of land-surface changes in Arctic summer warming. *Science* 2005, 310, 657–660
- (4) Tarnocai, C.; Canadell, J. G.; Schuur, E. A. G.; Kuhry, P.; Mazhitova, G.; Zimov, S. A. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles* **2009**, 23, doi:10.1029/2008GB003327.
- (5) Grosse, G.; Harden, J.; Turetsky, M.; McGuire, D. A.; Camill, P.; Tarnocai, C.; Frolking, F.; Schuur, E. A. G.; Jorgenson, T.; Marchenko, S.; Romanovsky, V.; Wickland, K. P.; French, N.; Waldrop, M.; Bourgeau-Chavez, L.; Striegl, R. G. Vulnerability of high-latitude soil

- organic carbon in North America to disturbance. J. Geophys. Res. 2011, 116, G00K06 DOI: 10.1029/2010JG001507.
- (6) Weller, G.; Chapin, F. S.; Everett, K. R.; Hobbie, J. E.; Kane, D.; Oechel, W. C.; Ping, C. L.; Reeburgh, W. S.; Walker, D.; Walsh, J. The Arctic flux study: a regional view of trace gas release. *J. Biogeog.* **1995**, 22. 365–374.
- (7) Heikkinen, J. E. P.; Virtanen, T.; Huttunen, J. T.; Elsakov, V.; Martikainen, P. J. Carbon balance of eastern European tundra. *Global Biogeochem. Cycles* **2004**, *18*, GB1023 DOI: 10.1029/2003GB002054.
- (8) Laurila, T.; Soegaard, H.; Lloyd, C. R.; Aurela, M.; Tuovinen, J. P.; Nordstroem, C. Seasonal variations of net CO₂ exchange in European Arctic ecosystems. *Theor. Appl. Climatol.* **2001**, *70*, 183–201.
- (9) Bliss, L. C.; Matveyeva, N. V. Circumpolar Arctic vegetation. In *Arctic Ecosystems in a Changing Climate, An Ecological Perspective*; Chapin, F. S., III; Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J., Eds.; Academic Press: New York, 1992; pp 58–89.
- (10) Shaver, G. R.; Billings, W. D.; Chapin, F. S., III; Giblin, A. E.; Nadelhoffer, K. J.; Oechel, W. C.; Rastetter, E. B. Global change and the carbon balance of arctic ecosystems. *BioScience* **1992**, *42*, 433–441.
- (11) Euskirchen, E. S.; Bret-Harte, S.; Scott, G. T.; Edgar, C.; Shaver, G. R. Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska. *Ecosphere* **2012**, 3 (1), 4 DOI: http://dx.doi:org/10.1890/ES11-00202.1.
- (12) Fahnestock, J. T.; Jones, M. H.; Welker, J. M. Wintertime CO₂ efflux from Arctic soils: Implications for annual carbon budgets. *Global Biogeochem. Cycles* **1999**, *13*, 775–779.
- (13) Aurela, M.; Laurila, T.; Tuovinen, J.-P. Annual CO_2 balance of a subarctic fen in northern Europe: Importance of the wintertime efflux. *J. Geophys. Res.* **2002**, 107 DOI: 10.1029/2002JD002055.
- (14) Shaver, G. R.; Kummerow, J. Phenology, resource allocation, and growth of arctic vascular plants. In *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*; Chapin, F. S., III; Jefferies, R., Reynolds, J., Shaver, G., Svoboda, J., Eds.; Academic Press: New York, 1992; pp 193–212.
- (15) Groendahl, L.; Friborg, T.; Soegaard, H. Temperature and snow-melt controls on interannual variability in carbon dioxide exchange in the high Arctic. *Thoer. Appl. Climatol.* **2007**, *88*, 111–125.
- (16) Lafleur, P. M.; Humphreys, E. R. Spring warming and carbon dioxide exchange over low Arctic tundra. *Global Change Biol.* **2008**, *14*, 740–756.
- (17) Lund, M.; Falk, J. M.; Friborg, T.; Mbufong, H. N.; Sigsgaard, C.; Soegaard, H.; Tamstorf, M. P. Trends in CO₂ exchange in a high Arctic tundra heath, 2000–2010. *J. Geophys. Res.* **2012**, *117*, G02001 DOI: 10.1029/2011JG001901.
- (18) Oberbauer, S.; Starr, G.; Pop, E. Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska. *J. Geophys. Res.* **1998**, 103 DOI: 10.1029/98JD00522.
- (19) Arndal, M. F.; Illeris, L.; Michelsen, A.; Albert, K.; Tamstorf, M.; Hansen, B. U. Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high Arctic vegetation types. *Arct., Antarct., Alp. Res.* **2009**, *41*, 164–173.
- (20) Griffis, T. J.; Rouse, W. R.; Waddington, J. M. Interannual variability in net ecosystem CO₂ exchange at a subarctic fen. *Global Biogeochem. Cycles* **2000**, *14*, 1109–1121.
- (21) Nobrega, S.; Grogan, P. Landscape and ecosystem-level controls on net carbon dioxide exchange along a natural moisture gradient in Canadian low Arctic tundra. *Ecosystems* **2008**, *11*, 377–396.
- (22) Kwon, H.-J.; Oechel, W. C.; Zulueta, R. C.; Hastings, S. J. Effects of climate variability on carbon sequestration among adjacent wet sedge tundra and moist tussock tundra ecosystems. *J. Geophys. Res.* **2006**, *111*, G03014 DOI: 10.1029/2005JG00036.
- (23) Aurela, M.; Laurila, T.; Tuovinen, J. P. The timing of snowmelt controls annual CO₂ balance in a subarctic fen. *Geophys. Res. Lett.* **2004**, *31*, L16119 DOI: 10.1029/2004GL020315.
- (24) Gould, W. A.; Raynolds, M. K.; Walker, D. A. Vegetation, plant biomass and patterns of net primary productivity in the Canadian Arctic. *J. Geophys. Res.* **2003**, 108 DOI: 10.1029/2001JD000948.

- (25) Griffis, T. J.; Rouse, W. R. Modelling the interannual variability of net ecosystem CO_2 exchange at a subarctic fen. *Global Change Biol.* **2001**, 7, 511–530.
- (26) Tarnocai, C.; Lacelle, B. Soil Organic Carbon of Canada Database; Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Research Branch: Ottawa, Ontario, Canada, 1996; digital database.
- (27) Angell, R. S.; Svejcar, T.; Bates, J.; Nicanor, Z. S.; Johnson, D. A. Bowen ratio and closed chamber carbon dioxide flux measurements over sagebrush steppe vegetation. *Agric. For. Meteor.* **2001**, *108*, 153–161.
- (28) Nordstrom, C.; Soegaard, H.; Christensen, T. R.; Friborg, T.; Hansen, B. U. Seasonal carbon dioxide balance and respiration of a high arctic fen ecosystem in NE-Greenland. *Theor. Appl. Climatol.* **2001**, *70*, 149–166.
- (29) Starr, G.; Oberbauer, S. F. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* **2003**, *84*, 1415–1420.
- (30) Soegaard, H.; Nordstrom, C. Carbon dioxide exchange in a high-Arctic fen estimated by eddy covariance measurements and modeling. *Global Change Biol.* **1999**, *5*, 547–562.
- (31) van Wijk, M. T.; Williams, M.; Laundre, J. A.; Shaver, G. R. Interannual variability in plant phenology of tussock tundra: modelling interactions of plant productivity, plant phenology, snowmelt and soil temperature. *Global Change Biol.* **2003**, *9*, 743–758.
- (32) McFadden, J. P.; Eugster, W.; Chapin, F. S., III. A regional study of the controls on water vapour and CO_2 exchange in Arctic tundra. *Ecology* **2003**, *84*, 2762–2776.
- (33) Lloyd., C. R. On the physical controls of the carbon dioxide balance at a high Arctic site in Svalbard. *Theor. Appl. Climatol.* **2001**, 70, 167–182.
- (34) Freeman, B.; Svoboda, J.; Henry, G. H. R. Alexandra Fiord -- An Ecological Oasis in the Polar Desert. In *Ecology of a Polar Oasis*; Svoboda, J., Freeman, B., Eds.; Captus University Publication: Toronto, 1994; pp 286.
- (35) Elberling, B.; Jakobsen, B. H.; Berg, P.; Sondergaard, J.; Sigsgaard, C. Influence of vegetation, temperature and water content on soil carbon distribution and mineralization in four high Arctic soils. *Arct., Antarct., Alp. Res.* **2004**, *36*, 528–538.
- (36) Grogan, P.; Jonasson, S. Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biol.* **2005**, *11*, 1–11.
- (37) Rennermalm, A. K.; Soegaard, H.; Nordstroem, C. Interannual variability in carbon dioxide exchange from a high Arctic fen estimated by measurement and modeling. *Arct., Antarct., Alp. Res.* **2005**, *37*, 545–556.
- (38) Johnson, L. C.; Shaver, G. R.; Cades, D. H.; Rastetter, E.; Nadelhoffer, K.; Giblin, A.; Laundre, J.; Stanley, A. Plant carbon-nutrient interactions control CO₂ exchange in Alaskan wet sedge tundra ecosystems. *Ecology* **2000**, *81*, 453–469.
- (39) Street, L. E.; Shaver, G. R.; Williams, M.; van Wijk, M. T. What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in Arctic ecosystems? *J. Ecol.* **2007**, *95*, 139–150