

Carbon dioxide fluxes of tundra vegetation communities on an esker top in the low-Arctic

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Abstract Previous studies have shown that carbon dioxide fluxes vary considerably among Arctic environments and it is important to assess these differences in order to develop our understanding of the role of Arctic tundra in the global carbon cycle. Although many previous studies have examined tundra carbon dioxide fluxes, few have concentrated on elevated terrain (hills and ridge tops) that is exposed to harsh environmental conditions resulting in sparse vegetation cover and seemingly low productivity. In this study we measured carbon dioxide (CO₂) exchange of four common tundra communities on the crest of an esker located in the central Canadian low-Arctic. The objectives were to quantify and compare CO₂ fluxes from these communities, investigate responses to environmental variables and qualitatively compare fluxes with those from similar communities growing in less harsh lowland tundra environments. Measurements made during July and August 2010 show there was little difference in net ecosystem exchange (*NEE*) and gross ecosystem production (*GEP*) among the three deciduous shrub communities, *Arctous alpina*, *Betula glandulosa* and *Vaccinium uliginosum*, with means ranging from -4.09 to $-6.57 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and -7.92 to $-9.24 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. *Empetrum nigrum* communities had significantly smaller mean *NEE* and *GEP* (-1.74 and $-4.08 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). Ecosystem respiration (*ER*) was similar for all communities (2.56 to $3.03 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), except the *B. glandulosa* community which had a larger mean flux ($4.66 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Overall, fluxes for these esker-top communities were near the upper range of fluxes reported for other tundra communities. *ER* was related to soil temperature in all of the communities. Only *B. glandulosa* *GEP* and *ER* showed sensitivity to a persistent decline in soil moisture throughout the study. These findings may have important implications for how esker tops would be treated in construction of regional carbon budgets and for predicting the impacts of climate change on Arctic tundra future carbon budgets.

Keywords tundra carbon exchange, net ecosystem exchange, gross ecosystem productivity, ecosystem respiration, low-Arctic, esker top, xerophytes

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1 Introduction

Knowledge of carbon dioxide (CO₂) fluxes between Arctic tundra and the atmosphere is important in quantifying the global carbon cycle and is therefore critical in

understanding global climate change (McGuire et al., 2009; Euskirchen et al., 2017; Jeong et al., 2018). Flux studies also provide information for testing and validation of ecosystem models used to predict the impacts of climate change on tundra ecosystems and their potential feedbacks to the atmosphere (Lorant et al., 2012). CO₂ exchange is influenced by climate, vegetation cover and soil conditions, requiring studies in many different environments to develop

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a more complete picture for the Arctic biome. Indeed, Arctic tundra is an especially diverse and complex environment, plant properties and species composition can vary over spatial scales ranging from sub-meter to regions. At the local scale (meters to kilometers) species composition is controlled by soil physical and chemical properties, topography and moisture, all of which are interrelated to some extent (Walker 2000; Spadavecchia et al., 2008). The distribution of snow (Evans et al., 1989) and moisture (Walker et al., 1989) are particularly important in controlling local-scale vegetation distribution. Despite these generalized environmental controls, the same communities (or species) are found in a range of environments; many plants adopt different growth forms depending on the harshness of environmental conditions, with more erect and less dense structures found in favourable microclimates and more compact and low stature forms found in harsh microclimates (Bliss, 1956; Walker et al., 1994).

Much of the continental Low Arctic of Canada is non-mountainous with low relative relief, but it still possesses a variety of terrain types with presumably different CO₂ exchange characteristics. The local surface elevations are controlled by bedrock topography and surficial geology, where the highest features are remnant glacial deposits such as kames and eskers (Dredge et al., 1999). These wind-swept, sparsely vegetated landforms are characterized by coarse, well-drained, sandy soils. The unprotected condition and sparse vegetation result in low snow accumulation, which exposes vegetation to the harsh winter weather. Plant communities on these raised features are less diverse than in the surrounding landscape, yet contain similar species (Obst, 2008). Given the variation in community structure and climatic conditions, it is not clear *a priori* if and how the CO₂ exchanges of esker top communities differ among themselves or from those of the more ubiquitous lowland tundra communities.

The broad goal of this study was to characterize CO₂ exchange for the dominant plant communities occurring on the top of an esker complex in the central Canadian Low Arctic. Measurements were made during the midday period, thus represent daily maximum fluxes. The objectives were to quantify the mean fluxes and patterns of CO₂ exchange over the study period, examine CO₂ flux responses to environmental controls (light intensity, temperature and soil moisture) and finally, to qualitatively compare these results with the fluxes previously reported for similar vegetation types from surrounding lowland environments. The specific questions we address are: (1) Do CO₂ fluxes vary among esker-top communities? and (2) Are these fluxes anomalous within the range of fluxes for similar communities growing in less harsh tundra environments?

2 Study site

The research site was located near Daring Lake, NWT,

Canada: 64°52'N, 111°35'W. This low-Arctic terrain lies in the southern Arctic ecozone (Marshall et al., 1996) and is characterized by numerous lakes and bedrock controlled topography with continental bedrock outcrops, interspersed with upland and lowland tundra. The local landscape is dissected by a prominent esker, which runs west-southwest to east-northeast. Although the total length of the esker system is about 100 km measurements were focused on a small section to the northeast of Daring Lake (Figure S1, see Electronic Supplementary Material). The top of the esker at this location is ~432 m a.s.l. and is ~30 m from the lake surface. Soils in the region are primarily composed of glacial till and are sandy-stoney in nature with minor silt content. Organic layer thicknesses vary from negligible, such as on the esker top, to a few tens of centimeters, as commonly found in low-lying wet areas. Soils in and around Daring Lake, including on the top of the esker, are described in Campeau et al. (2014). Continuous permafrost underlies the region to a depth of >160 m and may reach depths of 350 m depending on regional conditions (Dredge et al., 1999). Climate data have been collected since 1996 at an automatic weather station located ~340 m SSE of the research sites (elevation 421 m). Mean annual temperature and precipitation are -9.4 °C and ~250 mm, respectively. Mean monthly temperatures are above freezing from June to September, with the warmest month being July (13.3 °C). Snow melt generally occurs in mid-late June, thus providing a short growing season from late June to late August. Average monthly precipitation for June to September was 32 mm·month⁻¹ for the years since 1996.

The region contains a variety of tundra communities that generally follow moisture gradients (Obst, 2008). The lowest-lying, wet areas are characterized by sedge fen, wet sedge meadow and sedge-moss hummocks dominated by *Carex* sp. Mesic terrain is characterized by birch hummock, cotton-grass tussock, heath-mat and heath-lichen tundra. The driest areas, such as esker tops, are dominated by xerophytic herb tundra consisting of scattered patches of low shrubs and herb vegetation.

3 Measurements

Vegetation around Daring Lake region was characterized by ground surveys and remote sensing to produce a map of ecosystem units based on land cover and vegetation communities defined in Obst (2008). From this information, four commonly occurring vegetation communities on the esker ridge top were selected for carbon dioxide flux measurements. The four community types were identified by the dominant species: bearberry (*Arctous alpina* L. Nied.), bilberry (*Vaccinium uliginosum* L.), dwarf birch (*Betula glandulosa* Michx.), and crowberry (*Empetrum nigrum* L.). Flux measurements were situated in an area where all four vegetation types were in close proximity (< 100 m), enabling movement of the measuring equipment

between sampling locations. For each community, 5 sample plots (1 m × 1 m) of uniform cover were randomly selected and square aluminum collars (dimensions 40 cm l × 40 cm w × 12.5 cm d) were installed in the centre of each plot. Collars were inserted through the vegetation and into the soil down to a depth of about 5–10 cm (depending upon stoniness). Insertion of collars can cause root damage and potentially influence flux measurements. Such effects were minimized in the current study because of (1) the large size of the collar, and (2) measurements were delayed by a minimum of 2 d after collar installation to allow the environment time to adjust to collar placement.

3.1 CO₂ flux measurements

CO₂ fluxes were measured during daily campaigns when fluxes were measured on all collars for each community type and at 5 locations on bare ground between the midday hours of 10:00 and 16:00 local time to minimize the effects of low sun angles and as such represent daily maximum fluxes. During each measurement campaign (i.e., one day) the sampling order was determined by randomly selecting a vegetation community type and randomly selecting the order of collars to sample within that community. This process was repeated for the remaining community types. Ideally, measurement campaigns were to have been conducted for all sample plots every 2–3 d. However, this schedule varied due to weather and technical problems; on a few occasions flux measurements occurred on successive days and the longest gap between campaigns was 7 d. A few campaigns did not include all 25 collars because of technical problems.

Fluxes were measured with a closed-flow chamber system consisting of a non-dispersive infrared gas analyzer, IRGA (LI840, LI-COR, Lincoln, NE, USA), which measured CO₂ and H₂O concentrations, as well as a sample chamber constructed of clear acrylic sheeting (6.0 mm thickness). The chamber measured 40 cm wide, 40 cm long and 40 cm tall, with an interior volume of 64 L. Air was continuously circulated from the chamber to the IRGA via a small pump (model UN89, KNF Neuberger, Trenton, NJ) at a constant rate of 0.9 L·min⁻¹ through 1.5 m sample tubes (beva-line, 3.2 mm i.d.). The bottom of the chamber had a 27 mm wide seat, angled 90° outward from the chamber wall with a foam seal (5 mm) glued to the bottom of the seat. The chamber was placed on the aluminum sample collars and secured with clamps on each side. A small fan circulated air inside the chamber during measurement periods. Air temperature inside (T_{cham}) and outside (T_{air}) the chamber were measured with fine wire (0.35 mm) shielded thermocouples. Photosynthetic photon flux density ($PPFD$, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was measured outside the chamber with a quantum sensor (Kipp and Zonen PAR-LITE, Campbell Scientific, Logan, UT, USA). To prevent the T_{air} and $PPFD$ sensors from blocking light entering the chamber, they were mounted on a small wooden platform ~0.4 m in height

placed within 1 m of the chamber. Signals from all the instruments were recorded on a data logger (CR1000, Campbell Scientific, Logan, Utah, USA) every second during measurement periods and later transferred to a computer for processing. The logging function was turned off after each measurement to conserve memory space in the logger.

The measurement process for a given collar consisted of three steps: (1) the clear chamber was fixed on the collar and the data logger was activated for a 2 min recording period; (2) the logger was paused and the chamber was removed from the collar, then waved in the air to bring the internal environment back to ambient conditions; (3) the chamber was fixed on the collar again, covered with an opaque plastic shroud, and after a minimum of 3 min the data logger was activated for another 2 min recording period. The two measurements made on each collar represented net ecosystem exchange (NEE —without shroud) and ecosystem respiration (ER —with shroud). Gross ecosystem production (GEP) was computed as NEE minus ER . Here we adopt the sign convention where fluxes into the ecosystem are reported as negative and fluxes out of the ecosystem are reported as positive.

Fluxes were calculated according to the following equation, after Shaver et al. (2007):

$$Flux = \frac{\rho_a V \Delta C}{A \Delta t} \quad (1)$$

where ρ_a is air density ($\text{mol}\cdot\text{m}^{-3}$), calculated with the Ideal Gas Law using average H₂O vapour concentration and average T_{cham} during the sampling period; V is the effective chamber volume (m^3), calculated by summing the chamber volume and the volume contributed by the offset of the ground surface to the top of the collar, which was calculated by averaging 20 depth measurements taken from the top of the collar to the ground surface (the volume of sample tubes and the internal volume of the IRGA were considered negligible in comparison to the overall volume); A is the surface area of the collar (0.16 m^2) and $\Delta C \cdot \Delta t^{-1}$ is the change in CO₂ concentration (expressed as the mixing ratio) over time ($\mu\text{mol}\cdot\text{mol}^{-1}\cdot\text{s}^{-1}$) determined by computing the linear slope of the CO₂ concentration versus time. CO₂ and water vapour concentration were converted to mixing ratios for computing fluxes to account for water vapour dilution. During data analysis it was discovered that one of the *V. uliginosum* collars locations gave consistently erroneous readings (likely due to leaking around the collar or foam seal) and this was discarded from the measurements. Hence, $n=4$ for this community and $n=5$ for all other communities and the bare ground plots. In addition, on two occasions of hot weather abnormally high (>30 °C) temperatures were recorded in the flux chamber during measurements at all communities and anomalous flux readings were obtained. These measurements were excluded from the data analysis.

In addition to the flux measurements, soil temperature (T_{soil}) and volumetric water content (VWC) were measured

at each collar during each flux measurement period. T_{soil} was measured with a single thermocouple probes inserted 5 cm into the soil near the center of each collar. Readings from the thermocouple probes were recorded manually using a thermocouple reader (model HH501, Omega Engineering, Stamford, CT, USA). All of the thermocouples were intercompared prior to the start of the measurements and no significant differences were found ($p = 0.886$). These probes were installed at the time the collars were inserted and they remained in place throughout the experiment. VWC was measured with a soil moisture probe (Hydrosense, Campbell Scientific, Logan, UT, USA). The 12 cm probe leads were inserted into the soil at an angle so that the average water content in the top 10 cm was measured. VWC measurements were made around the outside of the collar (within 30 cm) to prevent disturbance within the sample collars. Two VWC measurements were made during each flux measurement period and the values were averaged.

3.2 Vegetation analysis

Vegetation species, composition, percent cover and leaf area index for the sample plots were determined by point frame method (Jonasson, 1988). Although larger frames are typically used, we constructed a 40 cm × 40 cm frame to fit the sample collars. The frame was subdivided into a 5 × 5 grid by stringing a thin filament at right angles across the frame every 8 cm (beginning 3 cm from the edge of the frame), thus creating 25 intersections. The point frame was suspended (approximately 20 cm) over the sample collar and a fine (1.5 mm) metal rod was lowered at each intersection to record green leaf hits, species type, and presence of lichen, moss or bare ground. Leaf area index (LAI) was determined from the point count surveys according to Warren Wilson (1959), whereby LAI was calculated by dividing the total sum of hits divided by the number of crosshairs and the ground surface area, then adjusting for over-sampling as described in Dagg and Lafleur (2010). These data are summarized in Tables 1 & 2. Dominant species comprised 81%–96% of the total biomass

in sample collars, except for the *B. glandulosa* community collars, where on average only 45% of total biomass was birch leaves. All communities had some lichen cover, with lichen being most prevalent in the *B. glandulosa* communities and least prevalent in the *E. nigrum* communities. Since most of the esker top is non-vegetated (~30%, Obst, 2008) point frame measurements were also made at the five bare ground collars, which consisted of gravelly/sandy soil with minor amounts (<3% cover) of unidentified lichens/mosses.

Point frame measurements were made on all collars on two occasions: July 23 and August 21. After the August point frame measurements, all above ground vegetation in the collars was harvested. Samples were air dried for up to 48 h then bagged and returned to the laboratory. Over the following 3 weeks, these samples were then sorted to remove woody material and the leaves were divided into two groups: the dominant species and all other species. The leaf samples were then oven dried at 60 °C for 24 h and weighed to a resolution of 0.01 g. Leaf total nitrogen (N) content was determined for sub-samples taken from the biomass samples. The sub-samples were ground and 100 mg of material was separated for chemical analysis. This material was then powdered and combusted with tungsten in a Macro Elemental Analyzer (Elementar Americas, Mt Laurel, NJ, USA) to determine nitrogen content by mass [$\text{g N} \cdot \text{g}(\text{leaf})^{-1}$]. Average species-specific nitrogen content values were calculated using specific leaf area [$\text{m}(\text{leaf})^2 \cdot \text{g}(\text{leaf mass})^{-1}$] and LAI [$\text{m}(\text{leaf})^2 \cdot \text{m}(\text{ground})^{-2}$] to obtain total foliar nitrogen [TFN ; $\text{g N} \cdot \text{m}(\text{ground})^{-2}$].

3.3 Period of study and weather

Measurements took place between July 13 and August 20, 2010. The tundra was snow-free by June 3, 2010. Bud break on *B. glandulosa* was first recorded on June 10 and first flowers on *V. uliginosum* were recorded on July 9. Mean daily air temperature over the study period was 13.9 °C and total precipitation was 22.5 mm. Mean air temperature was slightly higher than the historical averages for the period (12.4 ± 1.24 st. dev. °C) and precipitation was lower than

Table 1 Community descriptions and vegetation cover data for chamber collars. Values are mean and standard errors (s.e.) from $n = 5$ for each community. Data were estimated from point frame surveys conducted on July 23, 2010. Dominant cover is expressed as a percentage of total vascular % cover

Community & dominant species (common name)	Secondary species	Total vascular vegetation cover (s.e.)/%	Dominant species cover (s.e.)/%	Lichen cover (s.e.)/%
<i>Arctous alpina</i> (bearberry)	<i>Vaccinium vitis-idaea</i> , <i>Cladina</i> sp.	69.6 ^a (5.2)	90.1 ^a (2.5)	24.0 ^a (8.5)
<i>Empetrum nigrum</i> (crowberry)	<i>V. vitis-idaea</i> , <i>Cladina</i> sp.	54.4 ^a (4.7)	93.6 ^a (4.1)	16.0 ^a (2.8)
<i>Betula glandulosa</i> (dwarf birch)	<i>A. alpina</i> , <i>V. vitis-idaea</i> , <i>V. uliginosum</i> , <i>Cladina</i> sp.	72.0 ^a (6.6)	60.9 ^b (9.0)	41.2 ^a (6.0)
<i>Vaccinium uliginosum</i> (bilberry)	<i>V. vitis-idaea</i> , <i>Cladina</i> sp.	58.4 ^a (9.3)	93.6 ^a (4.4)	30.4 ^a (8.4)

Note: ^{a, b} Within each column, superscripts with different letters indicate statistically different group means ($p \leq 0.05$).

Table 2 Community biomass and total foliar nitrogen (*TFN*) characteristics. Values are mean and standard errors (s.e.) from $n = 5$ for each community. Biomass estimates included green leaves only. LAI_{PC} is leaf area index estimated from the point frame method. Data were obtained from harvests taken from all sample collars on August 21, 2010. Values for biomass and *TFN* are expressed in terms of dry weight (d. wt)

Community	Total biomass/g d. wt. (s.e.)	Biomass of dominant species/(% of total)	<i>TFN</i> of dominant species/d. wt. (s.e., %)	LAI_{PC} (s.e.)
<i>Arctous alpina</i>	21.71 ^a (2.33)	81.1	1.257 ^a (0.127)	1.4 ^a (0.20)
<i>Empetrum nigrum</i>	27.82 ^a (1.81)	95.9	0.786 ^b (0.042)	0.7 ^b (0.06)
<i>Betula glandulosa</i>	24.36 ^a (3.86)	45.2	1.527 ^a (0.087)	0.8 ^b (0.12)
<i>Vaccinium uliginosum</i>	10.43 ^b (1.07)	87.7	1.393 ^a (0.074)	0.5 ^b (0.01)

Note: ^{a,b} Within each column, superscripts with different letters indicate statistically different group means ($p \leq 0.05$).

the historical average (37.8 ± 19.8 mm). The seasonal air temperature trend was marked by three abnormally warm periods: one at the beginning of the study on Day of Year (DOY) 195–197, one on DOY 205–206 and one on DOY 218–223 (Figure 1). Precipitation was more frequent during the first half of the study (Figure 1), hence there was a distinct drying trend for all vegetation community types over the course of the study period (Figure 2a) that was most noticeable at the plots with higher moisture contents (*B. glandulosa* and *E. nigrum*). Soil temperature did not show statistically significant ($p > 0.05$) seasonal trends during the study (Figure 2b).

3.4 Statistical methods

We tested for differences in fluxes (*NEE*, *ER* and *GEP*) among the vegetation communities using a linear mixed-effects model (LME) (Laird and Ware, 1982). LME is a widely used alternative to repeated-measures analysis of variance, which requires a complete data set and equal number of observations at each time step (Breslow and Clayton, 1993). LME has no such constraints and uses all available data to test for mean differences between subjects (the fixed effect) and a random linear effect (time). LME also tests for differences in the random effect among subjects using an ANOVA procedure and Tukey's multiple means comparison test. Trends in time for fluxes and

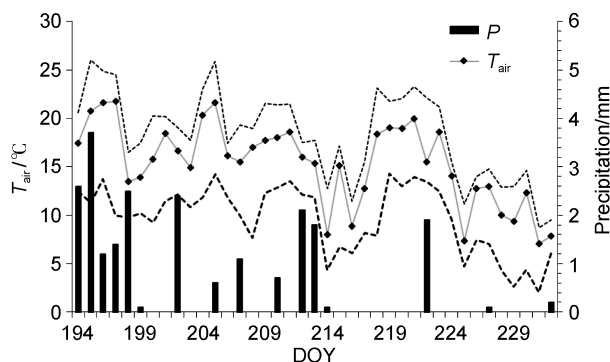


Figure 1 Seasonal trends in daily mean air temperature (T_{air}) and precipitation (P) at Daring Lake, NWT during July and August, 2010.

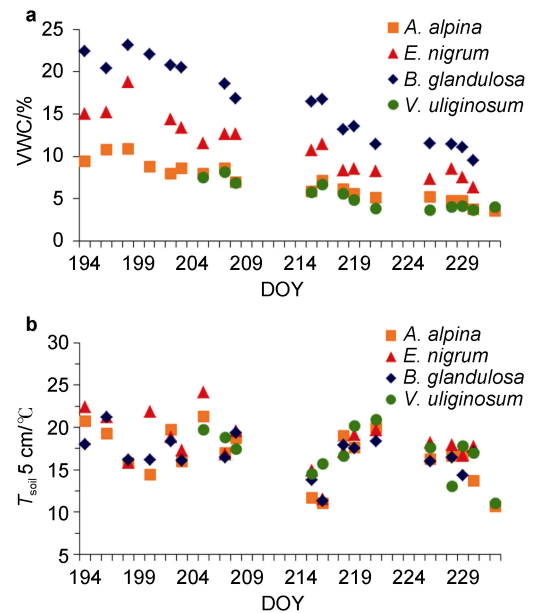


Figure 2 Seasonal trends in mean volumetric soil water content (*VWC*, **a**) and soil temperature (T_{soil} , **b**) at 5 cm depth in four vegetation communities on an esker at Daring Lake, NWT, during July–August, 2010. Points represent means for the five sample collars for each vegetation community.

independent variables were also tested with LME. All LME analyses were conducted using the R program (R Development Core Team, 2012). Specific R packages used for analysis and statistical results are given in Electronic Supplementary Material (ESM). We report differences at the significance level of $\alpha=0.05$. For other more straightforward comparisons (e.g., shaded and non-shaded bare ground fluxes, linear regressions between *GEP* and foliar *N*) standard *t*-test's with $\alpha=0.05$ were used and conducted using the software program Statistica (Statsoft Inc., Tulsa, OK, USA). Step-wise multiple regression was used to examine the response of the component CO_2 fluxes (i.e., *GEP* and *ER*) to environmental variables. The analyses were run in forward stepwise mode using the Statistica program.

4 Results

4.1 Carbon dioxide fluxes

Time series of CO₂ fluxes indicated that fluxes for all communities decreased over the course of the study period (Figure 3). LME modelling analysis of time trends revealed that all four communities showed a significant (decreasing) time trend in *ER* with no interaction between time and community, suggesting that the time trend in *ER* was similar for all communities (see ESM Tables 1S–3S for full statistical results). *GEP* and *NEE* had significant decreasing (i.e., less negative values) time trends for all communities, except *E. nigrum*. Comparison of LME marginal means indicated some difference among communities (Figure 4,

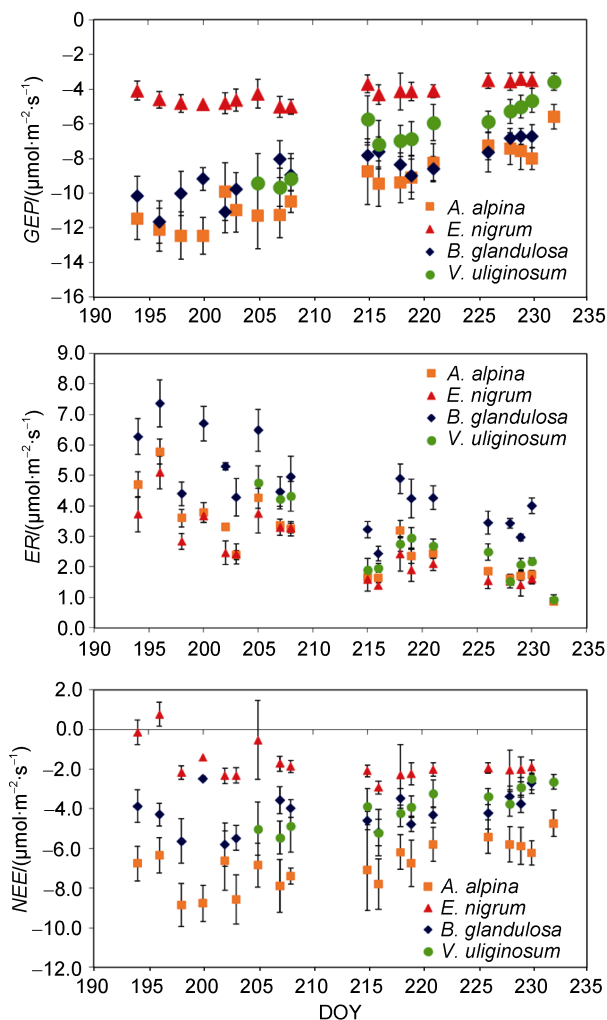


Figure 3 Seasonal trends in carbon dioxide (CO₂) fluxes for four vegetation communities on an esker near Daring Lake, NWT during July–August, 2010. *GEP* is gross ecosystem production, *ER* is ecosystem respiration and *NEE* is net ecosystem exchange. Negative values indicate CO₂ uptake by the ecosystem. Points represent daily averages from the sample collars and error bars show ± 1 standard error. $n=5$ for each community except *Vaccinium uliginosum* where $n=4$. DOY is day of year.

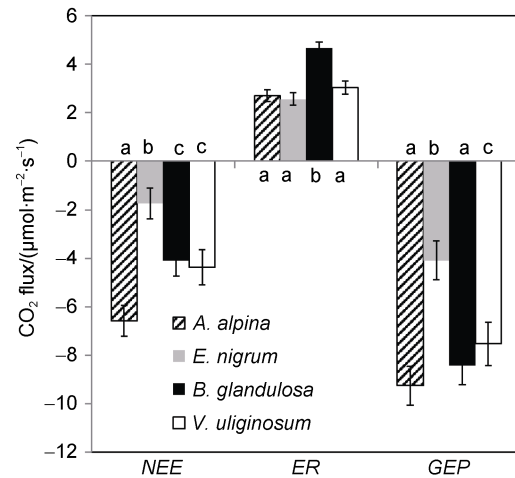


Figure 4 Comparison of LME marginal mean CO₂ fluxes from all plots for four vegetation communities on an esker at Daring Lake, NWT during July–August, 2010, acronyms as in Figure 3. Negative values indicate uptake by the ecosystem. Error bars show standard errors. Similar lower case letters indicate statistically similar means within each group at significance $p=0.05$.

Table 3). *B. glandulosa* had higher mean *ER* (4.66 ± 0.25 (s.e.) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) compared to the other communities, which had similar means ($2.56\text{--}3.03$ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Mean *GEP* for *E. nigrum* (-4.08 ± 0.80 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was significantly smaller (less negative) than for the other three communities, with no significant difference in *GEP* among *V. uliginosum* (-7.52 ± 0.89 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), *B. glandulosa* (-8.41 ± 0.80 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and *A. alpina* (-9.24 ± 0.80 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Differences in *NEE* among the communities were less clear. *E. nigrum* had the smallest mean *NEE* (-1.74 ± 0.64 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and was statistically different from the other three communities at $p=0.1$, but was different only from *A. alpina* at $p=0.05$. There was weak evidence ($p=0.1$) that *A. alpina* mean *NEE* (-6.57 ± 0.64 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was greater than for *B. glandulosa* (-4.09 ± 0.64 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), but was not different from *V. uliginosum* mean *NEE* (-4.38 ± 0.73 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Fluxes from bare ground collars were an order of magnitude smaller than those from the vegetated plots, with means <1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Figure 5). As expected, bare ground *NEE* was predominantly positive, indicating net CO₂ loss to the atmosphere. Unexpectedly, there was a small but significant difference in mean *NEE* measured for the clear (0.53 ± 0.03 s.e. $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and shrouded (0.63 ± 0.03 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) chamber measurements (paired *t*-test, $p < 0.05$). There were no trends in time for these fluxes ($p > 0.05$) and no relationships were found between fluxes and environmental variables (soil temperature and *VWC*) for the bare ground collars.

4.2 Environmental responses

GEP is often strongly related to both *PAR* and air temperature. However, since these two environmental variables

Table 3 Tukey’s test comparisons among multiple means for differences in CO₂ fluxes among the plant communities. ns is no significant difference. ***, ** and * represent significant differences at $p < 0.001$, $p < 0.05$ and $p < 0.1$, respectively

	Species	<i>A. alpina</i>	<i>E. nigrum</i>	<i>B. glandulosa</i>
NEE	<i>A. alpina</i>			
	<i>E. nigrum</i>	***		
	<i>B. glandulosa</i>	*	*	
	<i>V. uliginosum</i>	ns	*	ns
ER	<i>A. alpina</i>			
	<i>E. nigrum</i>	ns		
	<i>B. glandulosa</i>	***	***	
	<i>V. uliginosum</i>	ns	ns	**
GEP	<i>A. alpina</i>			
	<i>E. nigrum</i>	***		
	<i>B. glandulosa</i>	ns	***	
	<i>V. uliginosum</i>	ns	**	ns

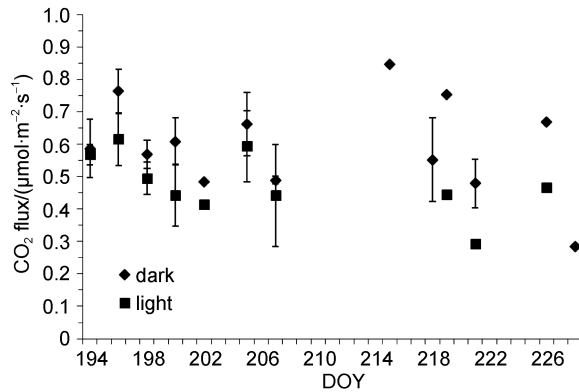


Figure 5 Comparison of CO₂ fluxes measured at bare ground collars for light (ambient) and dark (shrouded) conditions on an esker at Daring Lake, NWT during July–August, 2010. Data are means from 5 sample collars, error bars are standard errors.

trended weakly over time during the study, it was difficult to discern their influence on *GEP* and the other fluxes. In a multiple regression with time (DOY) and both *PAR* and *T_{air}* as predictor variables, DOY was shown to be the dominant variable influencing *GEP* for all species, but *PAR* was weakly significant (explaining $\leq 5\%$ of the total variation in *GEP*) for *V. uliginosum* and *A. alpina* only. This latter result was not surprising because our experiments did not include a shading effect (i.e., the use of shades with different opacities to change *PAR* in the chamber) and measurements were taken only near midday, hence variability in *PAR* was restricted. Somewhat surprisingly, *T_{air}* was not a significant variable for any community. We used the same multiple regression approach for *ER*, with time (DOY) and soil temperature (*T_{soil}*) as predictor variables (results not shown). For all communities, both variables were significant in the

regression models, with DOY being the dominant variable in all models except the *B. glandulosa* model, where *T_{soil}* contributed 42% to the total explained variance in *ER* and DOY contributed only 16%. For all other communities, *T_{soil}* contributed between 9% and 14% of the total explained variance. Since many models of *ER* use non-linear relationships with temperature, we plotted *ER* against *T_{soil}* and derived the best fit exponential relationship for each community. For individual communities the best fit model explained between 28% and 45% of the variance in *ER* (not shown). However, the models for the *E. nigrum*, *V. uliginosum* and *A. alpina* communities were not significantly different, so a best-fit model was derived for data pooled from all three of these communities; this pooled-data model explained 33% of the variation in *ER* (Figure 6). A separate model was derived for *B. glandulosa*, achieving a slightly better explained variance ($r^2=45\%$) and showing higher *ER* sensitivity to *T_{soil}* (i.e., a larger value of the model exponent) compared to the other communities.

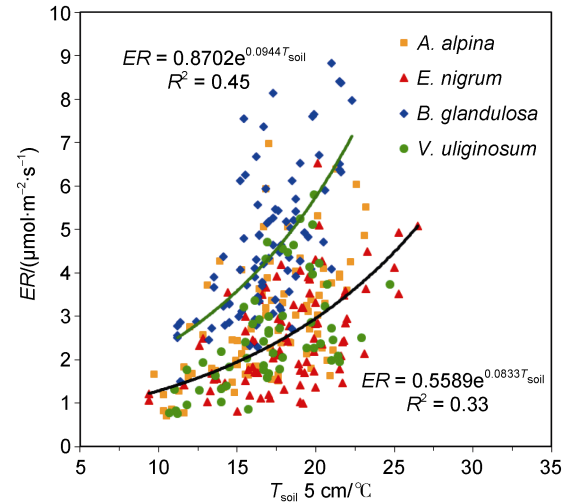


Figure 6 Relationship between ecosystem respiration (*ER*) and soil temperature (*T_{soil}*) measured at 5 cm depth in four vegetation communities on an esker at Daring Lake, NWT during July–August, 2010. Equations given are for *Betula glandulosa* collars (upper left) and all other collars (lower right).

Linear regression showed that the component fluxes *GEP* and *ER* were positively related with *VWC* (ESM-Figure S2, Table S4). However, since both *VWC* and the CO₂ fluxes trended strongly over time (Figure 2a; Table S1) these relationships were confounded. To address this issue we regressed *VWC* and each of the CO₂ fluxes (*GEP* and *ER*) against time (DOY), then regressed the residuals for *VWC*-DOY against the residuals for flux-DOY. Only the *B. glandulosa* model produced significant results (Figure 7). Both *GEP* and *ER* demonstrated a significant trend of decreasing absolute magnitude with decreasing *VWC*. The larger slope coefficient for *ER* (-0.59 , compared with -0.34 for *GEP*) suggested that *ER* was somewhat more sensitive to soil moisture changes.

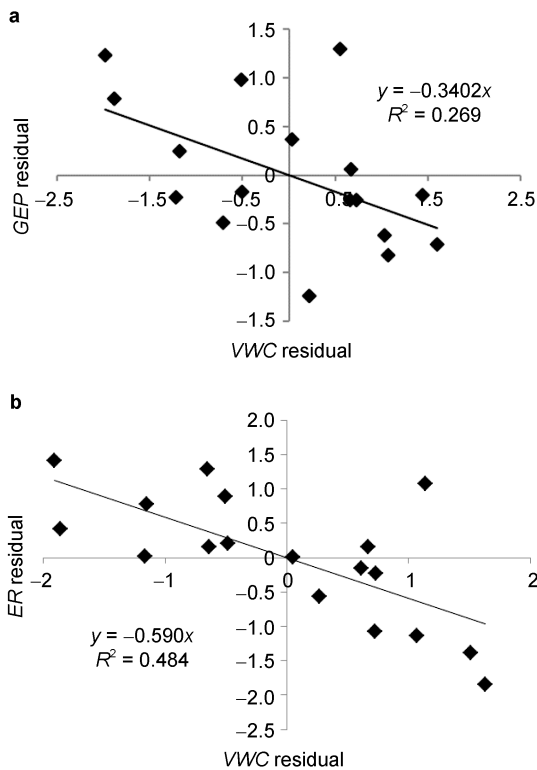


Figure 7 Relationship between (a) gross ecosystem production (*GEP*) as well as (b) ecosystem respiration (*ER*) and soil volumetric water content (*VWC*) for *Betula glandulosa* community on an esker top at Daring Lake, NWT during July–August, 2010. Data represent residuals after time trends were removed for each variable. Linear regression models shown were significant at $p=0.05$.

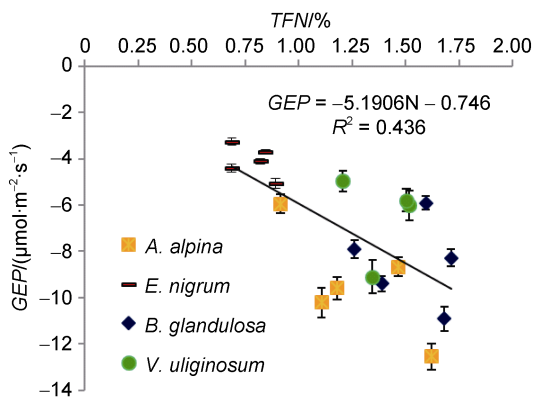


Figure 8 Relationship between gross ecosystem production (*GEP*) and total foliar nitrogen (*TFN*) for four vegetation communities on an esker at Daring Lake, NWT. Data are mean *GEP* values (error bars show ± 1 standard error) for each sample collar during July–August, 2010 and leaf *N* measured from foliage harvests taken on 23 August, 2010.

Finally, when combining data for all communities, *GEP* was linearly related to foliar *N* (Figure 8). Greater foliar *N* was associated with larger average *GEP* fluxes. In part due to the small sample sizes, no significant relationships were

found between *GEP* and foliar *N* for individual communities.

5 Discussion

This study investigated only midday CO_2 fluxes and did not include the early part of the growing period and, thus we were not able to construct complete daily or seasonal carbon balances for these communities. Although this limits our interpretations, these midday measurements form a strong basis for comparing relative maximum daily carbon sink strength and ecosystem respiration among esker top communities and their short-term response to changing environmental variables (e.g., Arndal et al., 2009; Chasmer et al., 2012).

Given the harsh environmental conditions on the esker top, we expected that the communities here would exhibit somewhat smaller CO_2 fluxes than those reported from less harsh environments. Although comparisons with other studies are fraught with difficulty because of differences in study period timing, community composition, reported units and methods of data summarization qualitative assessment is possible. Our data fall within the range of reported summer fluxes (measured with chambers) at other low- and high-Arctic sites (Christensen et al., 2000; Heikkinen et al., 2004; Welker et al., 2004; Oberbauer et al., 2007; Arndal et al., 2009; Vogel et al., 2009; Celis et al., 2017; Li et al., 2017; Wagner et al., 2019) and trend toward the upper end of this range, possibly because they are from the mid-day period only. Direct comparisons with previous flux measurements made at Daring Lake support this assessment. Both Nobrega and Grogan (2008) and Dagg and Lafleur (2011) reported mean flux measurements for birch and heath communities at lowland tundra sites near Daring Lake, with reported maximum daily values for *GEP* and *ER* being about two-thirds of those from the present study. The *LAI* values of the sample plots in these previous studies were similar or slightly smaller than those observed in our study. On the other hand, maximum instantaneous measurements from our study were similar in magnitude to those reported in Dagg and Lafleur (2010), with *GEP* values of $-3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for dry heath to $-10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for mesic birch and *ER* of $1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to $4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively.

Given the relatively high *GEP* and *NEE* fluxes observed in our study, one might have expected significant soil carbon accumulation at these sites. However, this was not the case. Soil organic layer at our measurement plots was negligible (0 to 0.3 cm) and soil carbon contents on the esker top ($6.8 \text{ kg}\cdot\text{m}^{-2}$) are twice to four times smaller than in other tundra landscapes in the Daring Lake basin (Campeau et al., 2014). The likely explanation for this divergence may relate to the harsh winter environment on the esker top. Very little snow collects on the esker tops in winter and many areas are snow free (Rees et al., 2014).

Thus, the vegetation and soil is almost completely exposed to cold and high winds. Our hypothesis is that new litter deposited by esker-top communities, which would typically make up a considerable amount of the annual soil carbon input, is carried away by aeolian forces primarily in winter and deposited on the esker slopes or valley bottoms. The hypothesis is supported by previous research on litter re-distribution in the Arctic (Fahnestock et al., 2000) and our own field observations of noticeable sediment and litter deposition on the esker slope snowpack.

Mean *GEP* was similar for *B. glandulosa*, *V. uliginosum* and *A. alpina*, with *E. nigrum* exhibiting smaller *GEP*. *E. nigrum* with its ‘needle-like’ leaves is the only true evergreen species observed in this study, which may help explain its low *GEP*, since evergreens are typically slow growing in Arctic environments and maximum *GEP* has been shown to be smaller in evergreen dominated communities than in deciduous communities (Street et al., 2007; Starr et al., 2008). Mean *GEP* was similar among the other vegetation types despite variations in community composition and *LAI*. *B. glandulosa* collars had the highest *LAI* and the largest percent cover of vascular plants, which also included a high coverage of *E. nigrum*. On the other hand, *A. alpina* formed dense mats within the sample collars with few other vascular species present (Table 2). The high *GEP* for *V. uliginosum* was somewhat surprising as these collars had low *LAI* with few other species present. However, *TFN* for these deciduous communities was considerably higher than for *E. nigrum*, which likely supported the high *GEP*. Despite this difference in *TFN* the positive relationship between *GEP* and *TFN* (Figure 8) is indicative of N limitation in this environment (Arndal et al., 2009). Indeed, current understanding of topographical controls on N and C cycling in Arctic tundra suggests that elevated landscapes, such as the esker top, represent extreme environments characterized by low soil organic matter, available N and N mineralization (Stewart et al., 2014). It follows that once plant communities establish themselves (likely due to niche conditions in favorable microhabitats) their presence enhances the environment to promote further growth and community sustainability.

Only *B. glandulosa* had a significantly different (higher) mean *ER* among the four communities. Many previous studies report significant differences in *ER* among different Arctic vegetation types (Welker et al., 2004; Dagg and Lafleur, 2011; Bradley-Cook and Virginia, 2018; Wagner et al., 2019), some reporting higher *ER* at shrub communities (Heikkinen et al., 2004; Nobrega and Grogan, 2008). Although *ER* measurements in this study represent both heterotrophic (soil) and autotrophic (plant) respiration processes, we hypothesize that the difference is most likely due to the autotrophic component for two reasons. Firstly, the soils at all plots were relatively dry and had low soil carbon content, which likely limits heterotrophic respiration (Bradley-Cook and Virginia, 2018). Secondly, the birch shrubs had higher *LAI* and total biomass (including stems)

than the other communities, which would support greater autotrophic respiration. However, we accept that this link is not strongly established in the literature (Virkkala et al., 2018).

The low respiration rates on bare soil we observed are consistent with other studies showing an order of magnitude lower *ER* on eroded tundra soils compared to vegetated tundra (Bradley-Cook and Virginia, 2018). Our bare soil measurements suggest that there is a small release of CO₂ occurring on the mainly un-vegetated areas of the esker top. The source of this respired carbon is not known, but it is likely from the lichens present in these plots, dead lichen organic matter and other detritus that has been deposited by wind transport and soil microbial activity.

5.1 Environmental controls on C fluxes

As demonstrated in past studies (Elberling et al., 2004; Welker et al., 2004; Grogan and Jonasson, 2005; Williams et al., 2006; Li et al., 2017; Bradley-Cook and Virginia, 2018), we found that *ER* was related to soil temperature in these communities. The model fit was not high ($r^2 = 0.33\text{--}0.45$), but it was comparable with many previous studies. *B. glandulosa* had greater base respiration and higher *ER* sensitivity to temperature than the other esker communities. If, as we hypothesize and as suggested by others (Grogan and Chapin, 2000; Grogan and Jonasson, 2005), *ER* is dominated by above-ground autotrophic respiration, the difference in *ER* response to temperature between birch and the other communities may be attributed to the larger *LAI* and biomass in the birch plots. Despite a significant decline in soil moisture for all plots over the study period (Figure 2), only *B. glandulosa* CO₂ fluxes showed sensitivity to the changes in *VWC* once time trends were removed. Both *ER* and *GEP* were negatively impacted by decreasing soil moisture. Cahoon et al. (2016) suggested that reduced mid-summer *GEP* in another Arctic shrub (*Betula nana*) was a result of drought sensitivity and laboratory and field manipulation experiments also support the idea that Arctic shrubs are drought sensitive (Illeris et al., 2004; Sharp et al., 2013). We expected that *V. uliginosum*, which is functionally similar to *B. glandulosa*, would have responded to changes in *VWC* in a similar fashion. However, since measurements at the *V. uliginosum* plot measurements did not start until 2 weeks later than at the others, the range in *VWC* was reduced and likely was not large enough to produce a statistically significant result. Fluxes for *A. alpina* showed no response to *VWC* in our study. *E. nigrum* had the smallest and least variable fluxes, probably as a result of its slow growth rate. This species is known to be somewhat drought sensitive, but inhabits a broad range of moisture conditions (Tybirk et al., 2000). Its presence on the esker top represents an extreme environment to which it has adapted.

Our findings are important because future climate warming and potential precipitation changes will impact the distribution of Arctic vegetation (Peason et al., 2013). *B.*

glandulosa is the dominant shrub in the Daring Lake region and it has been increasing in abundance across the Canadian Arctic (Myers-Smith et al., 2011). Undoubtedly, changes in moisture conditions will have a profound effect on the expansion of this species and its influence on future carbon budgets.

6 Conclusions

Our study suggests that the midday CO₂ fluxes of esker top vegetation communities in the low-Arctic are similar in magnitude and in their responses to environmental controls to those observed in lowland dry and mesic heath communities. As such, although they constitute a minor component of the landscape, construction of regional carbon budgets should pay close attention to how esker tops are included in these budgets. The high productivity of the esker top communities is not realized in high soil carbon contents and aeolian transport of mineral and organic materials to the surrounding slopes might be an important ecological process in this environment. Finally, the esker tops represent one landscape where climate change could have significant impact on the carbon budget. If warming results in less harsh winters and increased precipitation, with subsequent increases in soil moisture, this coupled with the potential for a positive feedback between shrub expansion and snow accumulation (Sturm et al., 2001; Wipf and Rixen, 2010), esker existing top communities could expand onto the un-vegetated areas and contribute to an increase in the carbon sequestration capacity of the region, albeit by a small amount because of their small proportion of the total land surface.

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