Sink or source? Responses of tundra carbon fluxes to warming in a high-Arctic polar oasis

by

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# Abstract

The Arctic is warming faster than predicted and faster than almost anywhere on the planet. Alexandra Fiord, NU is a High Arctic coastal polar oasis warming by 1ºC per decade. Snowfall, snowmelt, and precipitation patterns are changing, and the active layer is deepening. Soil moisture regimes and plant growing season length/warmth are changing, affecting the flux of CO2 into and out of the tundra (net ecosystem exchange; NEE). Tundra regions may shift from sinks to sources of CO2 emissions with the changing climate.

We examined the effects of ambient and long-term (30+ years) experimental warming on tundra net ecosystem exchange (NEE) of CO2. NEE is calculated as the sum of the rate of gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER). NEE and ER were measured in and out of passively warmed (1-3ºC) plots (n = 12) using a static chamber system connected to a portable infrared gas analyzer. Plots were divided evenly across 3 sites representing different soil moisture regimes and plant community types and measured 3 times over the growing season.

Using linear mixed models, we found that warming significantly increased the magnitudes of the GEP and ER fluxes. Plot greenness significantly explained much of the variation in GEP and NEE. There was a trend of increasing NEE with warming, as the greenness-driven increase in the GEP flux outpaced ER. This evidence suggests that longer and warmer growing seasons may increase NEE and CO2 sequestration in these plant communities. Comparison with previous results suggest that interannual variability is still greater than variation in multiyear warming trends in the High Arctic tundra.

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# List of Abbreviations

# Introduction

Arctic ecosystems are warming faster than almost anywhere on the planet (Constable et al., 2022; Rantanen et al., 2022). Terrestrial carbon cycles are beginning to change as warming differentially affects the bioclimatic and hydrological environments (Mekonnen et al., 2021). Impacts include a deepening of the active layer with permafrost degradation, longer growing seasons with decreased snow cover, changes in the surface energy balance, and physiological and phenological plant responses including ‘greening’ and increased growth (Derksen et al., 2019; Frei & Henry, 2021). Of particular concern is the potential for feedback loops in which warming encourages the transition of terrestrial carbon reservoirs from sinks to sources (McGuire et al., 2009). Tundra ecosystems contain 30-50% of the soil carbon on Earth, an estimated 500Pg C is in the top metre of permafrost soils (Hugelius et al., 2014; Tarnocai et al., 2009). Warming is accelerating microbial activity and soil organic matter decay in the active layer, generating a permafrost-carbon feedback and hastening the leak of stored greenhouse gases into the atmosphere (Antala et al., 2022; Koven et al., 2011; Schuur et al., 2015; Skeeter et al., 2022). The High Arctic does not have the same enormous wetland/delta C stocks that are found further south, but remains a significant part of the Arctic carbon budget and a potentially volatile reservoir for greenhouse gases (mostly CO2) as the region continues to warm (Schuur et al., 2015).

Plants, microbes, and animals mediate the boundary between atmospheric CO2 and terrestrial carbon sequestered into the ecosystem. Net ecosystem exchange (NEE) is the flux carbon across that boundary, into or out of the ecosystem. NEE is defined as the difference between gross ecosystem productivity (GEP), the total CO2 drawn into the ecosystem in photosynthesis, and ecosystem respiration (ER), the total respiratory losses of plants and soil to the atmosphere ( 1 ).

( 1 )

Ecosystem respiration includes growth, maintenance, and photo-respiration by autotrophs along with heterotrophic respiration from microbes and other soil dwelling detritivores.

The NEE balance determines whether Arctic ecosystems store or release carbon. A positive NEE flux indicates that the tundra is sequestering atmospheric CO2 where a negative NEE flux represents the net release; the response of this flux to warming will inform a feedback loop either accelerating or decelerating climate change (Davidson & Janssens, 2006). If the respiration response (change in ER flux) is stronger, a positive feedback loop will promote increasing CO2 release with warming as rates of decomposition and heterotrophic respiration rise (Shaver et al., 2000). Conversely, if there is an increase in photosynthesis and growth (the GEP flux increases), a negative feedback loop would slow the release of CO2 from High Arctic soils.

There is significant heterogeneity in plant community types arrayed across unevenly warming bioclimatic gradients in the High Arctic, and ecosystem carbon balance responses to climate change are equally heterogenous (Jónsdóttir et al., 2022; Street et al., 2007). Despite this, closed chamber studies consistently observe that experimental warming increases the magnitude of the photosynthetic (GEP) and respiratory (ER) fluxes (Edwards, 2012; Hobbie & Chapin, 1998; Huemmrich et al., 2010; Jónsdóttir et al., 2022; Lupascu et al., 2014; Oberbauer et al., 2007; Shaver et al., 1998; Welker et al., 2004).

GEP is most significantly driven by variables affecting plants’ photosynthetic rates: temperature of the plant canopy, leaf nitrogen content, and resource acquisition traits including plant/canopy height, leaf area, and greenness (Arndal et al., 2009; Campioli et al., 2013; Happonen et al., 2022; Jónsdóttir et al., 2022; Street et al., 2007). Field experiments have demonstrated the link between tundra nutrient availability and increases in GEP-supporting traits like growth, canopy cover, and photosynthetic rates (Betway-May et al., 2022; Mekonnen et al., 2021), and shown that nitrogen and phosphorus fertilization may increase GEP more than warming (Oberbauer et al., 2007; Shaver et al., 1998).

Over 75% of ER occurs below ground in roots, mycorrhizae, and microbial communities; ER is driven largely by plant and soil microbial activity (Segal, 2013). Canopy temperature (Jónsdóttir et al., 2022) and soil temperature (H.-J. Kwon et al., 2006) are thus key drivers of ER. Soil moisture often determines these warming affects, as soil saturation significantly soil oxygen content and thus aerobic decay belowground respiration rates (M. J. Kwon et al., 2019; Oberbauer et al., 2007). Lowering the water table can turn the tundra from a sink to a source (Huemmrich et al., 2010), despite also encouraging more vigour in plants (Hudson & Henry, 2009).

The complex of factors driving GEP and ER are complex and interactive, and as a result NEE is sensitive to short-term hydrological and climatological shifts (Grant et al., 2011), as seen in the variable responses to warming and high interannual variability observed in NEE studies, even within the same site (Table S1). Studies often find NEE to be positive (a sink) with variable warming responses between years or sites (Hobbie & Chapin, 1998; Shaver et al., 1998; Welker et al., 2004), or variable in direction and warming response (Oberbauer et al., 2007). Some studies have found a negative feedback loop (positive and increasing NEE; Boelman et al., 2003; Edwards, 2012; Huemmrich et al., 2010), more rare is NEE found to be a source with variable to decreasing warming responses (Jónsdóttir et al., 2022).

Eddy covariance studies evaluating NEE on a larger scale may corroborate that many High Arctic terrestrial ecosystems are currently net sinks for CO2 (Grant et al., 2011; McFadden et al., 2003) though CO2 sequestration can occur alongside methane release (Skeeter et al., 2022). Outside the growing season, NEE has a lower, and more negative flux (Arndal et al., 2009; Hobbie & Chapin, 1998; Welker et al., 2004). Wintertime and shoulder-season respiration often result in net CO2 and CH4 release (Pirk et al., 2016; Skeeter et al., 2022).

Spectral vegetation indices based on remote sensing techniques are used as proxies for functional traits (Agger, 2022). The greenness excess index (GEI) can be accurately measured at the plot and individual scale with digital consumer grade cameras (Nijland et al., 2014), and is able to detect differences in vegetation cover and vigour and chlorophyll content (Agger, 2022; Beamish et al., 2016). GEI is well suited to distinguishing plant tissue from soil, an advantage over the normalized difference vegetation index (NDVI), the most common spectral vegetation index in use (Nijland et al., 2014). It has been shown to be an acceptable proxy for SLA, plant cover, and chlorophyll content (Beamish et al., 2016; Edwards & Henry, 2016), and has thus been correlated with increases in GEP (Ahrends et al., 2009; Boelman et al., 2003; Street et al., 2007).

There is an established body of data and literature examining the effects of long term and experimental warming on the tundra carbon balance, and illustrating its continued volatility. Climate change-magnified variations in snowmelt, hydrology, and active layer depth all bear unpredictable effects on the already significant intra- and interannual variability seen in NEE. In this thesis I investigate the current state and trend of net ecosystem exchange at Alexandra Fiord. We hypothesize that experimental warming will bring an increasing trend in NEE, and expect to see additional relationships between the ecosystem carbon fluxes–NEE, GEP, and ER–and soil moisture, GEI, air temperature, and soil temperature. I spent June through August 2022 on the beautiful coastal lowland at Alexandra Fiord, NU, measuring NEE measurements. The plots have experienced over thirty years of continuous experimental warming and my CO2 flux measurements were the first on these plots in over a decade and the fifth since 2000. This work contributes to the longest running warming experiment in the circumpolar High Arctic and, through comparison with previous results, furthers our understanding of how NEE and terrestrial ecosystem carbon balances are responding to climate change.

# Methods

## Study site

Our study was conducted across three sites at Alexandra Fiord, or Sanannguavvik, (78º53'N, 75º55'W). The sites are arranged on an 8km2 deglaciated lowland on the eastern shore of Ellesmere Island, Qikiqtaaluk Region, Nunavut, Canada. The three sites in this study sit on Crown land surrounded by Grise Fiord Inuit Owned Land under the Nunavut Land Claims Agreement. At approximately 30m elevation, the area is nearly flat, sloping northward towards the fiord waters. It is surrounded by steep scree slopes on the east and west sides and glaciers to the south. Alexandra Fiord is a relatively well-vegetated polar oasis compared to the surrounding polar semi-deserts that characterize much of the high-arctic (Svoboda, 1994).

Extreme local variation in hydrology, substrate composition, and soil moisture regime create distinct habitats and plant communities across the lowland. The wet “MEAD” site is a hydric sedge, moss, and dwarf-shrub wetland site dominated by *Eriophorum angustifolium, Carex stans,* and *Carex membranacea*, with flowing surface water throughout most of the growing season. The moist “DRYAS” site is considered a prostrate dwarf-shrub herb tundra with mesic to hydric soils and less surface water during the growing season. DRYAS is dominated by the woody dwarf shrub *Dryas integrifolia* with prevalent *Cassiope tetragona*, *Arctagrostis latifolia,* and *Carex misandra*. The relatively dry “WILL” site is also a prostrate dwarf-shrub herb tundra but has considerably snow accumulation, and melted out five days earlier than DRYAS in the 2022 season. WILL is characterized by sandy xeric to mesic soils and is dominated by the woody dwarf shrub *Salix arctica*. A large variety of other plants are also present, notably *Luzula confusa, Poa arctica,* and *Papaver radicatum.*

## Experimental design

Alexandra Fiord a founding site of the International Tundra Experiment (ITEX), and we experimentally warm our plots using open top chambers (OTCs) which heat the enclosed area by 1-3ºC relative to ambient temperature while leaving airflow, RH, and insolation relatively unchanged (Hollister et al., 2022). This warming is within the modeled predictions of Arctic warming and less than the annual temperature variability; OTCs simulate a warm year at a site (Henry et al., 2022). The CO2 plots have pentagonal OTCs of the ‘oversize’ ITEX standard measuring 0.5 m tall with 1.5 and 2.0 m between parallel sides at the top and bottom respectively (Marion et al., 1997).

Eight plots were designated at each of the three sites, with warming chambers installed on half of the plots at each site in 1992: N = 24, nsite = 4. Plots without OTCs are referred to as control or “C” plots and those with OTCs are referred to as warmed or treatment/“T” plots. Plots were haphazardly designated within each site boundary and treatments were alternately assigned along the north/south gradient of the site.

## Data Collection

### CO2 Flux measurements

In July and August 2022, we measured growing season net ecosystem CO2 exchange (NEE) and ecosystem respiration (ER) using an infrared gas analyzer (IRGA; Li-6800, LI-COR Biosciences, Lincoln, NE, USA) connected to a custom-made 75 x 75 x 30cm (168.75L) plexiglass chamber (for details see Welker et al., 2004). 75 x 75cm metal collars were permanently installed in every plot in 1999 to a depth of 15cm, forming a closed system with the chamber and IRGA when all components are attached. The IRGA measures CO2 concentration once per second in parts per million (ppm) within the chamber as two fans circulate air. Daytime fluxes were measured between 10:30 and 16:30 (at times of maximum insolation) four times throughout the season, with sites measured on adjacent days. Weather and full-spectrum insolation were comparable on adjacent measurement days (SUPP FIG 1), we assume that flux measurements were unaffected by changing insolation or relative humidity. Due to logistical complications and mechanical issues the second of four measurements were only obtained for the WILL site.

Each flux measurement lasted at least 125 seconds and we omit the first 5 seconds in which the IRGA would stabilize. NEE was measured during ambient light conditions, followed by the chamber being removed for at least 30 seconds to aerate the plot and chamber, followed by an ER measurement in which the plot was covered by an opaque polyethylene cloth fitted over the chamber. Flux measurement periods were kept short (<130s) and the chamber air continuously circulated to further reduce the effect of sudden enclosure.

We used linear regression used to calculate NEE and ER as the rate of change in CO2 concentration during the two-minute measurement period. While there is some concern about the suitability of linear regression to model this flux (Kutzbach et al., 2007), visual inspection of our results indicate that it is appropriate for our data, as R2 values were found to be up to 0.99 (Figure S1). Results are expressed in μmol CO2 m−2 s−1 from the ecosystem perspective where fluxes into the atmosphere are treated as negative and fluxes into the ecosystem as positive (as per Boelman et al., 2003; Edwards, 2012; Oberbauer et al., 2007; Shaver et al., 1998). We calculated GEP as the sum of NEE and RE at each plot (Equation 1).

### Temperature measurements

Custom made temperature probes for litter (3cm depth) and air (5cm height) temperature were fitted to the IRGA chamber. Data output from the Li-Cor 6800 and temperature probes were written to proprietary storage modules with a CR-21 datalogger (Campbell Scientific, Inc., Edmonton, AB, Canada).

We measured soil and air temperature using HOBO® Pendant 8K and 64K dataloggers (Onset Computer Corporation, Bourne, MA, USA) positioned immediately adjacent to the chamber bases within the plots for the duration of the field season. Soil pendants were inserted 5cm into the soil and air pendants were mounted 10cm above the ground under porous white plastic shields to reduce insolation effects. The pendants recorded temperature every fifteen minutes.

### Soil moisture measurements

Each day that CO2 flux measurements were recorded, we recorded soil moisture at the focal site. In addition, soil moisture was recorded at all plots/sites periodically throughout the season to enrich the moisture record. Readings were taken with a Hydrosense soil moisture probe (Campbell Scientific, Inc., Edmonton, AB, Canada) at three points along the north/south axis of each plot and averaged.

### Greenness Excess Index (GEI)

We took digital colour photographs with a Canon EOS Rebel T5 (Canon Inc., Japan), with an 18MP, 5184 x 3465 pixels (px) sensor. The camera settings were consistent throughout the study period (Canon’s “intelligent auto” mode) and we assumed that visible wavelengths (RGB) would be similarly captured. Photos were manually taken from 1.5m above the ground at nadir.

A picture containing text, window

Description automatically generatedAs per Agger (2022), I processed the images individually in Adobe Photoshop 24.3.0 (Adobe Inc., San Jose, CA, USA, 2022). Photographs for each plot were stacked as layers and each was warped with the *Perspective Warp* feature so that the CO2 chamber base was perfectly square. This warp corrects for any deviations from nadir that occurred (Figure 1A). I then used the *Auto-Align Layers* feature, which automatically aligns images based on shared content, followed by manual adjustments to visually ensure a near-perfect match of the CO2 chamber base from one layer to the next. I cropped the aligned set to a 1:1 ratio just outside the lip of the chamber base before importing it to Adobe Lightroom Classic 12.2.1 (Adobe Inc., San Jose, CA, USA, 2023). I resized all image sets to a common 2000 x 2000px resolution and applied a common 1:1 crop to remove the chamber base (Figure 1C). The final set consisted of 211 photographs, each one 1750 x 1750 pixels covering an on-the-ground area of approximately 0.5625m2.

Figure 1. Simplified Adobe Photoshop screengrabs depicting the image processing workflow for plot photos. (A) Images were individually warped to nadir, (B) resized to a common resolution, and (C) cropped to just inside the chamber base.

I calculated a greenness value from the standardized images using a function written by Alison Beamish (2011) with the rdgal package (v1.6-5, Bivand et al., 2023). Each photograph is imported as a data frame which extracts pixel values from the red (R), green (G), and blue (B) channels. To normalize irradiance variations between images, the green chromatic coordinate, or green ratio (rG) was calculated as:

( 2 )

Red (rR) and blue (rB) ratios were calculated similarly. These ratios are the camera-observed brightness in the reg, green, and blue channels, and are used to calculate the greenness excess index (GEI).

( 3 )

High GEI indicates a high proportion of green reflectance observed by the camera–which indicates a greater cover of green vegetation in the plot photo (Agger, 2022). Only GEI measurements done on the same day as flux measurements were retained for model analysis described below.

## Data loss

A corruption issue prevented data transfer between the data logger and the storage module at the start of the growing season. NEE measurements were acquired by video recording the data logger screen and manually transcribing the video. Temperature measurements were made by manually recording the readout from the chamber temperature probes at the end of the two-minute measurement period. A separate electrical fault resulted in malfunction of the chamber mounted temperature probes; in these cases, temperature data was substituted with the daytime (10:00-16:00) average from the plot’s pendant logger. In one case both the soil temperature probe and pendant logger malfunctioned, so the daytime average of all three other plots of the same (control) treatment was substituted (Table 1).

Table 1. Explanation of data collection methods by day and site. Backup methods were employed during various mechanical and electrical errors in the field.

|  |  |  |  |
| --- | --- | --- | --- |
| Site | Collection day | CO2 flux collection | Temperature collection |
| WILL | 179 | Transcribed video | Chamber probes (start and finish averaged) |
|  | 192 | Data logger | HOBO logger |
|  | 197 | Data logger | Chamber probes (continuous) |
|  | 208 | Data logger | Chamber probes (continuous) except HOBO logger for ER reading in warmed plot 12 T. |
| MEAD | 182 | Transcribed video | Chamber probes (start and finish averaged) |
|  | 195 | Data logger | HOBO logger (control 12 soil averaged from plots 11, 13, 14) |
|  | 206 | Data logger | Chamber probes (continuous) |
| DRYAS | 183 | Transcribed video | Chamber probes (start and finish averaged) |
|  | 196 | Data logger | Chamber probes (continuous) |
|  | 207 | Data logger | Chamber probes (continuous) |

## Data Analysis

Data was assembled in R using the *tidyverse* collection of packages (Wickham et al., 2019) and the *lubridate* package (Grolemund & Wickham, 2011) to create a dataframe that included all of the flux data and accompanying environmental parameters. Following the best practices for open science, I designed a coded and reproducible workflow which includes all post-collection work except image processing (Powers & Hampton, 2019; Sandve et al., 2013). A GitHub repository containing raw data; R code for manipulating my data, running analyses, and producing figures; and earlier versions of this manuscript can be found at [*https://github.com/declan-taylor/honours\_thesis*](https://github.com/declan-taylor/honours_thesis). All analyses were done in R version 4.2.2 (R Core Team, 2022).

### Carbon fluxes

Three linear mixed models were used for each NEE, ER, and GEP. Models were constructed using lme4 (Bates et al., 2015) and examined for significance using the lmerTest package and Satterthwaite's method for estimating model degrees of freedom (Kuznetsova et al., 2017). The first model included treatment as the single fixed effect and site/plot as random effects with fixed slopes.

( 4 )

To facilitate a direct comparison between sites and treatments, site was added as a fixed effect for the second iteration of my model to examine differences in plant communities not captured in other variables. Least squares means were compared for each combination of site and treatment factors.

( 5 )

Finally a full model was conducted with treatment, site, air temperature, soil temperature, soil moisture, and GEI as fixed effects, and plot as a fixed-slope random effect.

( 6 )

Air and soil were highly negatively covariate, so soil temperature was removed. Canopy temperature has been found to be a more significant predictor of carbon fluxes than soil temperature so it was prioritized (Jónsdóttir et al., 2022). Backwards model selection was done using the step() function in lmerTest which eliminates marginal fixed variables and random effect variables to reduce the model’s AIC value (Kuznetsova et al., 2017). Model fit was compared via R2 values extracted using the performance package (Lüdecke et al., 2021).

### Environmental parameters

The effect of site and treatment on each of the environmental parameters–greenness, air temperature, soil temperature, and soil moisture–was also examined. A two-way analysis of variance (ANOVA) was constructed for each of the four parameters using the stats package and significance was evaluated with a 95% confidence threshold (R Core Team, 2022).

# Results

## Carbon Fluxes

Average growing-season daytime NEE was positive at all sites in both treatments (Figure 2). GEP was always positive, and ER was always negative, but gross photosynthesis fluxes were always greater than gross respiration fluxes; the ecosystem consistently acted as a sink for CO2 (Table 2). NEE increased in response to warming and was 30.1% higher in the OTC-warmed plots (0.0195 µmol CO2 s-1 m-2) compared with the controls (0.0136 µmol CO2 s-1 m-2). A linear model with treatment as the sole fixed effect did not fit the data well (p = 0.0765, Marginal R2 = 0.03; Supplementary Table 1). Warming significantly increased the magnitude of both the GEP and ER daytime fluxes, though linear model fit remained poor. ER decreased 17.6% from -0.0135 µmol CO2 s-1 m-2 to -0.0164 µmol CO2 s-1 m-2 (p = 0.00115, Marginal R2: 0.029; Supplementary Table 2) and GEP increased 24.5% from 0.0271 µmol CO2 s-1 m-2 to 0.0358 µmol CO2 s-1 m-2 (p = 0.245, Marginal R2: 0.035; Supplementary Table 3).

Table 2. Daytime flux values averaged over the growing season. Separated by treatment and by treatment, site. Fluxes are stated in µmol CO2 s-1 m-2. Positive fluxes are those which sequester CO2 into the ecosystem, negative fluxes release CO2 to the atmosphere.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Flux | Treatment | Treatment avg flux | DRYAS avg flux | MEAD avg flux |  | WILL avg flux |
| Net ecosystem exchange (NEE) | ambient | 0.01362 | 0.0113 | 0.0074 |  | 0.0200 |
| warmed (OTC) | 0.01948 | 0.0146 | 0.0097 |  | 0.0305 |
| Gross ecosystem photosynthesis (GEP) | ambient | 0.02708 | 0.0226 | 0.0126 |  | 0.0410 |
| warmed (OTC) | 0.03586 | 0.0294 | 0.0185 |  | 0.0537 |
| Ecosystem respiration (ER) | ambient | -0.01350 | -0.0117 | -0.0052 |  | -0.0210 |
| warmed (OTC) | -0.01639 | -0.0148 | -0.0088 |  | -0.0233 |

All three fluxes varied significantly between sites, with much larger fluxes at WILL compared with DRYAS and MEAD (Figure 2). In the second model iteration, which included site and treatment as fixed effects, NEE varied significantly between DRYAS/WILL (p = 0.0122) and MEAD/WILL (p = 0.0019, Conditional R2: 0.237, Marginal R2: 0.226; Supplementary Table 4). GEP varied significantly between control and warmed (OTC) treatments (p = 0.0244), between DRYAS/WILL (p < 0.001), and MEAD/WILL sites (p < 0.001, Conditional R2: 0.417, Marginal R2: 0.414, Supplementary Table 5). ER had the best fit of any of any flux with this model iteration, with means varying significantly between warming and control plots (p = 0.0012) and all site combinations (Conditional R2: 0.758, Marginal R2: 0.721; Supplementary Table 6).

There was no perceivable trend in warming response (relative difference between ambient and OTC-warmed average daytime flux values) across sites and attempts to fit site as a random effect with random slopes and intercepts failed (the model fit was singular). Manual examination of the flux differences between treatment and control plots revealed that that the largest response in NEE to warming occurred at WILL (33.4%), while the largest GEP (32.0%) and ER (41.0%) responses occurred at MEAD (Table 3).

The final models for NEE, ER, and GEP ended up being different since AIC-based backward selection retained different variables from the full models in Equation 6. NEE was significantly driven by greenness which had a strong positive influence (0.672) on net CO2 exchange (p < 0.0001; Conditional R2: 0.863, Marginal R2: 0.822; Supplementary Table 7). Plot ID was retained as a significant random effect in the final model (p = 0.0119). ER, by contrast, was affected by a wider suite of parameters. Warming (p = 0.0348) and GEI (p < 0.0001) both resulted in significantly more respiration (decreased ER), though the GEI effect was far stronger with a parameter estimate that was two orders of magnitude smaller (Conditional R2: 0.846, Marginal R2: 0.797; Supplementary Table 8). ER also varied slightly but significantly between site (p < 0.0001) and plot (p = 0.0181). GEP was driven mostly by GEI (p < 0.0001), and to a lesser extent by site (p = 0.0017; Conditional R2: 0.848, Marginal R2: 0.799; Supplementary Table 9).

All three fluxes increased in magnitude over the length of the growing season, with the WILL site displaying the largest increases in flux magnitude (Figure S2).

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Figure 2. Boxplots illustrating the effects of experimental warming by OTC (red) against control (blue) temperature regimes on gross ecosystem photosynthesis (GEP), ecosystem respiration (ER), and net ecosystem exchange (NEE). Fluxes responses are significantly different between the mesic DRYAS, hydric MEAD, and xeric WILL sites.

Table 3. Warming response, or the difference between ambient and OTC-warmed plot fluxes, for the seasonal daytime average of each flux. Fluxes reported in µmol CO2 s-1 m-2 for both the whole lowland (overall) and by site.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Flux | Overall flux difference | DRYAS flux difference | MEAD flux difference | WILL flux difference |
| Net ecosystem exchange (NEE) | 0.00586 (30.1%) | 0.00324 (22.2%) | 0.00232 (23.8%) | 0.01048 (33.4%) |
| Gross ecosystem photosynthesis (GEP) | 0.00878 (24.5%) | 0.00676 (23.7%) | 0.00592 (32.0%) | 0.01273 (23.7%) |
| Ecosystem respiration (ER) | -0.00288 (17.6%) | 0.00316 (21.3%) | 0.00225 (41.0%) | 0.00360 (9.67%) |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Variable | ANOVA terms | df | Sum of Squares | Mean Squares | F-value | P-value | Significance |
| Soil Moisture | site  treatment  site\*treatment | 2  1  2 | 6.046  0.128  0.218 | 3.023  0.128  0.109 | 65.655  2.790  2.372 | < 2E-16  0.0991  0.1003 | \*\*\*  . |
| IRGA Air Temperature | site  treatment  site\*treatment | 2  1  2 | 166.2  6.9  3.5 | 83.09  6.88  1.77 | 7.848  0.650  0.168 | 0.00081  0.42287  0.84598 | \*\*\* |
| HOBO Air Temperature | site  treatment  site\*treatment | 2  1  2 | 564  733  142 | 282.2  733.8  71.2 | 21.689  56.403  5.474 | 6.18E-10  1.37E-13  0.00433 | \*\*\*  \*\*\*  \*\* |
| IRGA Soil Temperature | site  treatment  site\*treatment | 2  1  2 | 166.6  11.3  11.1 | 83.29  11.29  5.57 | 9.770  1.324  0.653 | 0.00017  0.25355  0.52337 | \*\*\* |
| HOBO Air Temperature | site  treatment  site\*treatment | 2  1  2 | 1511  17  144 | 755.7  17.3  71.8 | 189.76  4.338  18.019 | < 2E-16  0.0376  2.12E-08 | \*\*\*  \*  \*\*\* |
| GEI | site  treatment  site\*treatment | 2  1  2 | 0.005719  0.002719  0.001429 | 0.002859  0.002719  0.000714 | 7.948  7.558  1.986 | 0.00075  0.00750  0.14448 | \*\*\*  \*\* |

Table 4. Summary of two-way ANOVAs performed for each of the four environmental parameters: soil moisture, air temperature, soil temperature, and greenness excess index (GEI). Temperature data from the IRGA temperature probe and the HOBO pendant loggers were examined.

## Greenness

A two-way ANOVA showed significant variation in GEI across sites (p < 0.001) and treatments (p = 0.0075; Table 4). Mean GEI increased the most at WILL, slightly at DRYAS, and showed almost no change at MEAD; interaction between plot and site was not significant (p = 0.144).

GEI drove a significant amount of variation in all three fluxes, and regressions between GEI and NEE/GEP/ER corroborated the findings of my final linear mixed models (Figure 3). The overall flux-regression slopes did not meaningfully change between warmed and control plots (Figure 3, top row), though there was some variation when data was separated by site. WILL has higher flux-GEI correlations than MEAD or DRYAS, which parallel the larger warming effect seen in GEI magnitude at that site (Figure 3, bottom row). The overall GEP-GEI slopes were steep and positive (0.95, R2control = 0.751; 0.92, R2warmed = 0.814; Figure 3). ER had weaker correlation with GEI (R2control = 0.269, R2warmed = 0.463), with a negative and less steep slope (control = -0.23, warmed = -0.21). NEE and GEI were very strongly correlated, with tight regression (R2control = 0.859, R2ambient = 0.824) and a steep, positive slope (control = 0.72, warmed = 0.71; the difference between the GEP and ER regression slopes). The GEI parameter estimates were similarly positive in the final NEE (0.672) and GEP models (0.788), and negative in the final ER model (-0.116).

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Figure 3. Regressions between GEP and the various ecosystem fluxes. Shown overall (top row) and by site (bottom row), for both treatment and control. Equations and R2 values are given for regression lines not separated by treatment.

## Air Temperature

The 10cm average air temperature measured by the HOBO pendants, reading every fifteen minutes, twenty-four hours per day, was 13.5% higher in the OTC plots (11.14ºC) than the controls (9.638ºC; Figure 4a). Daytime air temperatures, or the subset of HOBO readings taken between 1000h and 1600h when insolation was highest and CO2 flux measurements were performed, were considerably higher: 14.50ºC in OTC plots and 12.75ºC in controls. The daytime warming response was smaller than the 24h difference, 12.1%, but still significant (p = 0.0376). The greatest differences were at MEAD (the overall warmest site) and WILL (Figure 4b). Temperature also varied between sites (p < 2E-16), and the treatment effect was strongly affected by site (psite\*treatment = 2.12E-08; Table 4). The 5cm air temperature measurements obtained from the IRGA temperature probes during CO2 flux measurements varied significantly with site (p < 0.001), but not with treatment (p = 0.423). MEAD was the coldest and least treatment-responsive site measured by the IRGA probes, opposite to the trend observed by the HOBOs (Figure 5b). DRYAS and WILL were found to be warmer and more responsive.

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Figure 4. Mean daily air temperature across sites and treatments (**A**). The interaction between site and treatment is illustrated in an ANOVA interaction plot (**B**) for both daytime (1000h-1600h) average 10cm air temperature, measured every 15 minutes through the growing season by HOBO pendants (orange), and sporadic 20cm IRGA measurements taken during CO2 flux readings (purple).

## Soil Temperature

Soil temperature was lower than air temperature throughout the season. Control plots averaged 8.30ºC in the daytime (1000h to 1600h) and 7.25ºC over 24h. Treatments (7.85ºC) were 5.67% colder than ambient plots in the daytime (p = 0.038) and 2.68% colder over the 24h period (7.06ºC). Figure 5a shows that the OTC-response was variable between sites; DRYAS decreased, MEAD increased, and WILL showed little response. Daytime mean HOBO soil temperature varied significantly between sites (p < 0.001), and mean treatment differences are thus significantly affected by interaction between site and treatment (p < 0.001). Figure 5b illustrates that IRGA measurements captured different site-treatment interactions than the HOBOs. Soil temperatures at DRYAS and MEAD had opposite responses to OTC presence between measurement tools. Only the effect of site was significant in the IRGA soil temperature measurements (p < 0.001; Table 4). Despite the variable OTC response, soil temperatures were much warmer during the day, daytime averages were 12.6% warmer in control plots and 10.0% warmer in OTC plots compared with their 24h equivalents.

Soil temperature also increased throughout the growing season (Figure S3). At the start of the growing season when we deployed the HOBO pendant loggers, DRYAS and MEAD were quite cold relative to their peak-season temperatures and an increasing trend is visible. The active layer at WILL was at its seasonal average at the start of measurements as there is no increasing trend over time (Figure S3).

Chart

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Figure 5. Mean daily soil temperature across sites and treatments (**A**). The interaction between site and treatment is illustrated in an ANOVA interaction plot (**B**) for both daytime (1000h-1600h) average soil temperature, measured every 15 minutes through the growing season by HOBO pendants (orange) embedded 5cm in the soil, and sporadic IRGA measurements taken during CO2 flux readings (purple), embedded 3cm into the litter.

## Soil Moisture

Soil moisture was 63% at MEAD, the highest of any site, 33% at DRYAS, and 36% at WILL. The variance between sites was significant (p < 2E-16), and the variance between treatments was nearly significant (p = 0.099; Table 4). Control plots in MEAD were much wetter than OTC plots, where in WILL and DRYAS they were dryer, though interaction between site and treatment was not significant (p = 0.100).

# Discussion

We examined the net ecosystem exchange of CO2 (NEE) and its component carbon fluxes across temporal and environmental gradients to capture change in carbon fluxes throughout the growing season, across soil moisture gradients, and between plant communities. NEE is the balance of GEP and ER, two climactically controlled processes that vary with plant traits, ecosystem drivers, and scale. Across the Arctic, the heterogeneous magnitude and direction of GEP and ER warming responses are creating positive and negative feedback loops with global warming at different sites (Virkkala et al., 2018). There is a dearth of long-term data and measurements from more extreme High Arctic environments, especially in the Canadian archipelago, making our repeat high-Arctic experiment of particular value (Virkkala et al., 2018).

## Fluxes, greenness, and carbon sequestration

Net ecosystem exchange was positive across all treatments and sites. The average carbon balance at Alexandra Fiord (during the day in the growing season) was positive, and thus the ecosystem was acting as a sink. Experimental warming, manipulated through OTC presence increased NEE by 30% and the magnitudes of both the GEP and ER component fluxes, though the increase in GEP was larger. These results indicate that warming promotes further carbon sequestration, which can be interpreted as a negative feedback loop between climate change and atmospheric CO2 concentrations. As NEE is not itself a process but the balance between two processes–photosynthesis (GEP) and respiration (ER)–the often-overlapping drivers of these two fluxes and the interactions between them collectively determine the magnitude and direction of the ecosystem carbon balance.

### Gross ecosystem productivity

Marchand et al. (2004) outline that GEP in warmed plots may be elevated due to the acceleration of the temperature-linked biochemical processes (enzyme kinetics) in photosynthesis, or indirect effects, such as warming-driven changes in nutrient uptake, leaf area, or species composition. Tundra plants generally utilize C3 photosynthesis pathways with low temperature optima (Tieszen, 1973) and acclimatize to new temperature regimes (Billings et al., 1971; Marchand et al., 2004). Some recent closed chamber studies have found that canopy temperature, measured as a microclimatic (plot level) parameter, played a dominant role in driving variation in GEP fluxes after long-term warming (Jónsdóttir et al., 2022), but our models did not retain these parameters or observe significant differences in them between plots of different treatment manipulations. Given that our OTCs have been warming the treatment plots for over three decades, it is unlikely that direct effects are the dominant reason for this increase.

There is a well-documented link between warming and the acceleration of plant growth (Bjorkman, Myers-Smith, Elmendorf, Normand, Rüger, et al., 2018; Campioli et al., 2013; Frei & Henry, 2021; Hudson et al., 2011). Greenness, or GEI, captures the amount of active plant body in a plot by proxying plant size, leaf area, and photosynthetic capacity (Beamish et al., 2016; Boelman et al., 2003; Nijland et al., 2014). We observed our warmed plots to be greener, GEI explained the most variation in GEP of any variable, and the regression between GEP and GEI was steeply positive and very well fit. These results indicate that increased indirect effects measured from greenness are the likely drivers of increased GEP, and higher net carbon sequestration.

GEP varied significantly between sites, and site was retained as the only other significant fixed effect in our final GEP model. MEAD is dominated by graminoids and, due to the absence of large grazers on the landscape at Alexandra Fiord, is often choked with litter. DRYAS is somewhat of an intermediate site in terms of species composition, soil moisture, and litter volumes. WILL is dominated by *Salix arctica* and is relatively free of litter. GEI, GEP, and the GEI-GEP regression slope, were all highest at WILL.

In addition to questions of litter and greenness, site also captures variation in plant community. While environmental drivers of per-unit area photosynthesis rates are likely insignificant, interspecific variation in these traits and plant phenology do explain variation in GEP. WILL is a warmer site with less snowfall, earlier snowmelt, and dryer soils. In addition, woody prostrate dwarf shrubs tend to exhibit earlier bud break and faster green up than their graminoid counterparts [CITATION?]. For both of these reasons the deciduous plants at WILL were likely ahead of their counterparts at DRYAS and MEAD. Coupled with their high photosynthetic capacity (Oberbauer et al., 2007), this temporal and compositional difference likely drove much larger photosynthesis fluxes. High GEP fluxes have been associated with woody shrub presence elsewhere (Cahoon et al., 2012), though a recent review paper suggests that graminoid sites have the highest peak season GEP (Virkkala et al., 2018). However, the authors largely attribute this to leaf area and metabolic speed and leaf area is severely limited at our graminoid sites as senesced leaves make up far more of the canopy coverage than active live leaves. Inter site differences at Alexandra Fiord also may have been magnified by low soil moisture at WILL; *S. arctica* is more vigorous at dry/drained sites than elsewhere on the lowland (Beamish et al., 2016). DRYAS, also rich in prostrate dwarf shrubs, melts out later and is victim to annual seasonal flooding which has raised the water table and promoted a shift towards graminoids over the last decade.

Light intensity and incident photosynthetically active radiation (PAR) play a dominant role in photosynthesis rates (Tieszen, 1973) and have been strongly linked to NEE rates in the field (Skeeter et al., 2020). Arctic plants often photosynthesize below their saturation light levels except on the clearest midsummer days, including at our field site, meaning that GEP is highly sensitive to PAR (Edwards, 2012; Tieszen, 1973). Nitrogen commonly also limits or drives photosynthesis rates (Arndal et al., 2009; Evans, 1989). This has been corroborated by field (Betway-May et al., 2022; Jónsdóttir et al., 2022) and fertilization experiments (Boelman et al., 2003; Shaver et al., 1998). We did not measure incident PAR or the size of the nitrogen pool, but some of the unexplained variation in our models is likely due to these two parameters. Overall we can conclude that while we have not captured the full diversity of factors affecting GEP, plant community, canopy cover, leaf area, and photosynthetic capacity play significant roles in determining this flux and the overall carbon balance.

### Ecosystem respiration

Ecosystem respiration is the cumulative respiratory efflux of carbon dioxide from plants (photorespiration, growth and metabolic processes), mycorrhizal networks, soil microbes, and other detritivores. The belowground component of ER makes up approximately 75% of the ecosystem’s total CO2 release [cite]. Variation in our ER measurements was explained by site, treatment, and GEI. GEI was the largest and most significant influence, likely because of the biomass and plant/canopy size differences captured. More above-ground plant tissue is associated with higher ER fluxes because larger plants have larger root and mycorrhizal networks and higher litter production. These traits are associated with higher soil microbial activity and soil organic matter decomposition [cite; potentially Bjorkman et al 2020]. GEI fluxes were largest at WILL which has large carbon stocks and steady litter production from deciduous woody shrubs. Unlike MEAD however, high litter production at WILL does not choke the plants. Compared with GEP and NEE, the GEI-ER regression trendline was relatively shallow and poorly fit both overall and at each site, suggesting that this flux is significantly driven by other factors.

Site and treatment variation may support an ER-climate change positive feedback loop mechanism descried by Grant et al. (2011). They suggest that warming promotes permafrost melt, which generates a deeper, warmer active layer for longer in the summer, which all enable increased decomposer activity, carbon remineralization, and CO2 efflux. ER fluxes are higher at the OTC-warmed sites, aligned with strong experimental evidence supporting the strong dependency of ER on temperature (Cahoon et al., 2012; Jónsdóttir et al., 2022), as temperature limitations on enzyme kinetics, as well as active layer freezing, can dramatically slow carbon mineralization.

It was unexpected that our data did not present a relationship between soil moisture and ER, especially given the huge variation between the hydric and often saturated soil conditions at MEAD and the rocky xeric conditions at WILL site. Huemmrich et al. (2010) and Oberbauer et al. (2007) both provided strong evidence for temperature-soil water content interactions, experimental manipulations of temperature and soil moisture found positive correlations between each of these and NEE, with synergistic effects between the factors. This anoxia-ER relationship is also well documented in low-arctic studies examining permafrost-carbon feedbacks (Knoblauch et al., 2013; H.-J. Kwon et al., 2006; M. J. Kwon et al., 2019). Limitations on our soil moisture methodology (discussed below) may be responsible for this and thus we are cautious to lend support to arguments rejecting the importance of this factor.

## Model results and excluded parameters.

NEE was 30% higher in warmed plots and GEP, ER varied significantly between sites; treatment was a small but significant predictor of variation in the ER final model. Backwards selection removed air temperature, soil temperature, and soil moisture from our GEP, ER, and NEE full models. This status, and the associated small parameter estimates of these environmental parameters, suggests that they do not explain a significant amount of variation in any of our observed fluxes. This is in contrast to much of the literature on ecosystem carbon balances, which often find trends between each flux and in situ air/soil temperature and soil moisture.

### Temperature and OTC-warming responses

Air and soil temperature were removed from the final flux models, though Figures 4b and 5b demonstrate that the temperature measurements captured by the IRGA probes during CO2 flux measurements are likely a poor and sporadic approximation of the seasonal temperature record at each site. This is the most likely explanation for the different and sometimes opposite site-treatment interactions seen in the IRGA and HOBO temperature records. Further, given that CO2 fluxes are dependent on a variety of plant traits and ecosystem drivers that are themselves dependent on long-term climatological conditions, plot treatment is likely a better candidate for warming observations than in-situ temperature.

Soil temperature responded unevenly to OTC presence but air temperature was consistently warmer. This is in line with recent ITEX-wide findings which suggest a decoupled air/soil temperature OTC response (Hollister et al., 2022). Recent ITEX analyses also suggest that there is little species composition change in and out of the OTCs (Henry et al., 2022), affirming the robustness of OTCs as a method of experimental manipulation that can guide our understanding of vegetative climate-warming responses (Hollister et al., 2022).

### Soil moisture

Soil moisture varied significantly between sites and had opposite warming responses in different sites. Water content was lower in warmed plots at DRYAS and WILL but higher at MEAD, and didn’t follow a clear seasonal trend at any of the sites. Rather than indicating a strong treatment-site interaction, these results are likely due to soil moisture varying based on local hydrological conditions unique to each site.

It is common to see interactions where soil moisture affects the warming response of plant traits (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018) and the magnitude and direction of ecosystem carbon fluxes (Oberbauer et al., 2007; Shaver et al., 1998). Especially in hydric ecosystems, soil water content can be high enough that anoxic conditions in soils limit belowground respiration (Oberbauer et al., 2007), and on an ecosystem scale a high water table can reduce the mineralization and efflux of CO2 (Knoblauch et al., 2013; M. J. Kwon et al., 2019). MEAD had the highest soil moisture the lowest ER. Huemmrich et al. (2010) suggest that the corollary to anoxic flux limitations is that soil saturation should also limit ER responses to temperature. Our data is opposite to this–at MEAD, ER has the strongest increase in magnitude with warming.

## Long term trends

Our 2022 measurements at Alexandra Fiord were the fifth since 2000, contributing another landscape-level observation to our long-term warming experiment. I examined nine other similar chamber-based studies, which represent ongoing work at Alexandra Fiord (Nunavut), Toolik Lake (Alaska), and Utqiagvik (Alaska), along with more intermittent work at other sites across the circumpolar High Arctic (Supplementary Table 10). Our results are similar to other warming manipulations on High Arctic carbon balance: GEP and ER nearly always increase in magnitude in response to warming, with variable responses in NEE. Mean daytime growing season NEE increased more often than it decreased, which is supported by landscape-scale eddy covariance work in the low arctic (Grant et al., 2011; McFadden et al., 2003; Skeeter et al., 2022). A review study of global arctic and subarctic chamber studies also found that NEE had variable warming responses (Virkkala et al., 2018). The complex of interacting environmental variables which determines fluxes and carbon balance are sensitive enough that intraanual and inter-site variability appear to be larger than long term warming responses, making it difficult to draw conclusions about climate-NEE feedback loops.

Comparing our results with previous results from our sites specifically, we can see that the negative NEE values seen in 2000 and 2001 at DRYAS have become more positive and were negligible in 2011 and now in 2022. The variable waring responses of fluxes have also become more positive. While we could speculatively associate the trend of increasingly positive NEE and warming responses with long term warming from climate change and 30+ years of OTC presence, it is also certainly driven in part by hydrological changes on the landscape. DRYAS in particular has had significant enough changes in moisture regime that it would be impossible to isolate a single driver of long term change.

Of particular interest in the long term may be the impacts of shrubification, the process by which deciduous shrubs with taller maximum canopy heights advance. As patches are infilled and prostrate shrubs increase growth and height, these plants may come to dominate tundra ecosystems as they warm (Mekonnen et al., 2018, 2021). Shrubification can affect flux rates by favouring larger plants and species with higher photosynthesis rates and increasing litter production and thus respiration (Finderup Nielsen et al., 2019; Virkkala et al., 2018). Our woody shrub-dominated site had the largest carbon fluxes, and compositional shifts towards woody shrubs have been noticed at the MEAD and DRYAS sites (i.e. those not already dominated by *S. arctica*; Edwards & Henry, 2016). Changing species composition and hydrological conditions will certainly continue to affect NEE into the future.

## Year-round fluxes

While we have seen increases in GEP, ER, and NEE during the summer, we did not measure shoulder season fluxes at Alexandra Fiord. Across the arctic, photon flux density has been shown to play a significant role in photosynthesis rates and carbon flux magnitudes, and drives diurnal and seasonal patterns in GEP and NEE (Skeeter et al., 2020). GEP ramps up through the spring with leaf bud expansion, and declines throughout the fall with decreasing daylight hours and photon flux density (Uchida et al., 2016); carbon assimilation stops completely while the active layer is completely frozen and plants are covered with snow (Pirk et al., 2016). When incident light is low but shoulder season temperatures are mild (especially typical of the early to mid-autumn), respiration does not decline with photosynthesis and instead drives a negative NEE flux (Christiansen et al., 2012), also experimentally observed at Alexandra Fiord (Welker et al., 2004). Flux magnitudes are much smaller in the winter, respiration and decomposition do continue throughout the year, with observable effluxes of both CO2 and methane (Christiansen et al., 2012; Pirk et al., 2016).

This trend prevents us from extrapolating conclusions about whether our site is a net source of carbon sequestration beyond daytime hours in the growing season. To understand the complete impact of the tundra on atmospheric CO2 concentrations, one would need to do 24-h/day measurements throughout all seasons; a logistical impossibility for researchers who do not live at their field site and are constrained to diurnal field practices. While winter and nighttime GEP fluxes are lower than the growing season daytime, Welker et al. (2004) found that the flux magnitudes at those times were small enough that they did not dominate the carbon balance and did not change NEE from a sink to a source. Growing season daytime fluxes are the largest of any time of day or year, and so remain the most important drivers of net year-round ecosystem carbon balance.

# Conclusion

Unsure how to write this.

While we were faced with challenges in when we could measure and what data was retained, our results conclusively showed Alexandra Fiord is acting as a net sink of carbon throughout the day during the growing season. Further, warming manipulations demonstrated that experimental warming, a simulation for climate change, drives larger fluxes. Greenness excess index, a proxy for biomass, leaf canopy, and photosynthetic capacity, was by far the most important driver of NEE and its component fluxes, ER and GEP. The stronger correlations between GEI and GEP/NEE compared with ER show us that plant size as measured by greenness has more balance on carbon assimilation, and efflux is likely determined by other factors including more direct links with temperature and soil moisture.

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As scientists we had the privilege of living and working out of six buildings on the lowland constructed by the RCMP in the early 1950s as part of a forced relocation of Inuit from Nunavik and Baffin by the Canadian government to assert their colonial sovereignty over the High Arctic archipelago. Our research site sites on Crown land, and land owned by the Grise Fiord (Aujuittuq/ ᐊᐅᔪᐃᑦᑐᖅ) Inuit under the Nunavut Land Claims agreement. I am grateful for the opportunity to have been able to visit and work at Alexandra Fiord and learn about the North.

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# Supplementary Materials

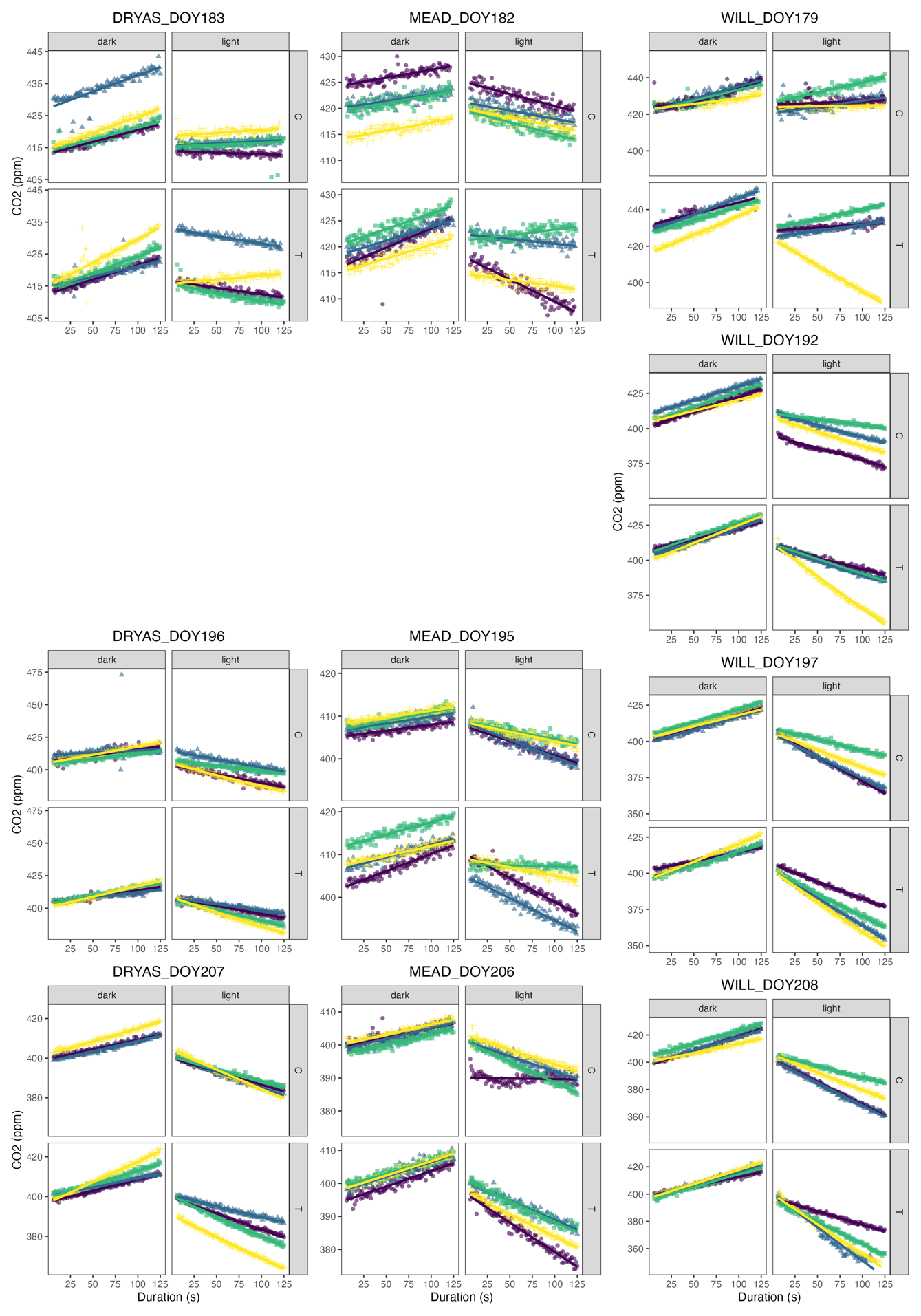


Figure S1. Raw flux data from the infrared gas analyzer separated by site, collection day (DOY), treatment (C/T), and flux, where dark is the ER measurement and light is the NEE measurement. Trendlines are basic linear models fit to each flux by plot.

Graphical user interface, chart, line chart

Description automatically generated

Figure S2. Carbon fluxes in µmol CO2 m-2 s-1 over time. Each point represents a linear model fit to CO2 concentration measurements over a two-minute interval.

Graphical user interface

Description automatically generated with medium confidence

Figure S3. Mean daily air and soil temperature, soil moisture, and greenness excess index (GEI) over the growing season. Trendlines represent smoothed conditional means to help illustrate temporal trends in the data.

Supplementary Table 1. Linear mixed effects model output from lmerTest with NEE as the response variable, treatment as a fixed effect and site, plot as random effects.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| NEE ~ treatment + (1|site/plot) | Conditional R2 = 0.272, Marginal R2 = 0.030 | | | | | | |
|  | Estimate | Std. Error | df | t value | Pr(>|t|) |  |
| (Intercept) | 0.012746 | 0.005297 | 2.478039 | 2.406 | 0.1134 |  |
| treatmentT | 0.005857 | 0.003257 | 69.194974 | 1.798 | 0.0765 | . |

Supplementary Table 2. Linear mixed effects model output from lmerTest with ER as the response variable, treatment as a fixed effect and site, plot as random effects.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ER ~ treatment + (1|site/plot) | Conditional R2: 0.807, Marginal R2: 0.029 | | | | | | |
|  | Estimate | Std. Error | df | t value | Pr(>|t|) |  |
| (Intercept) | -0.0126643 | 0.0044194 | 2.0427501 | -2.866 | 0.10079 |  |
| treatmentT | -0.0029292 | 0.0008615 | 65.6603791 | -3.4 | 0.00115 | \*\* |

Supplementary Table 3. Linear mixed effects model output from lmerTest with ER as the response variable, treatment as a fixed effect and site, plot as random effects.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| GEP ~ treatment + (1|site/plot) | Conditional R2: 0.482, Marginal R2: 0.035 | | | | | |  |
|  | Estimate | Std. Error | df | t value | Pr(>|t|) |  |
| (Intercept) | 0.02524 | 0.009612 | 2.194073 | 2.626 | 0.1087 |  |
| treatmentT | 0.008918 | 0.003875 | 68.067573 | 2.301 | 0.0245 | \* |

Supplementary Table 4. Least squares means table with NEE as the response variable, treatment and site as fixed effects, and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| NEE ~ treatment + site + (1|site:plot) | Conditional R2: 0.237, Marginal R2: 0.226 | | | | | | | | |
|  | Estimate | Std. Error | df | t value | lower | upper | Pr(>|t|) |  |
| treatmentC - treatmentT | -0.00586 | 0.00326 | 69.2 | -1.7979 | -0.01236 | 0.00064 | 0.07655 | . |
| siteDRYAS - siteMEAD | 0.00439 | 0.00438 | 14.0 | 1.0019 | -0.00501 | 0.01379 | 0.33336 |  |
| siteDRYAS - siteWILL | -0.01231 | 0.00412 | 11.1 | -2.9855 | -0.02137 | -0.00325 | 0.01225 | \* |
| siteMEAD - siteWILL | -0.01670 | 0.00412 | 11.1 | -4.0506 | -0.02576 | -0.00764 | 0.00187 | \*\* |

Supplementary Table 5. Least squares means table with GEP as the response variable, treatment and site as fixed effects, and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| GEP ~ treatment + site + (1|site:plot) | Conditional R2: 0.417, Marginal R2: 0.414 | | | | | | | |  |
|  | Estimate | Std. Error | df | t value | lower | upper | Pr(>|t|) |  |
| treatmentC - treatmentT | -0.00892 | 0.00388 | 68.1 | -2.3022 | -0.01666 | -0.00119 | 0.02439 | \* |
| siteDRYAS - siteMEAD | 0.01044 | 0.00511 | 13.8 | 2.0424 | -0.00053 | 0.02142 | 0.06063 | . |
| siteDRYAS - siteWILL | -0.02141 | 0.00480 | 10.9 | -4.4585 | -0.03199 | -0.01083 | 0.00099 | \*\*\* |
| siteMEAD - siteWILL | -0.03185 | 0.00474 | 10.4 | -6.7135 | -0.04236 | -0.02134 | 0.00004 | \*\*\* |

Supplementary Table 6. Least squares means table with ER as the response variable, treatment and site as fixed effects, and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| ER ~ treatment + site + (1|site:plot), Conditional R2: 0.758, Marginal R2: 0.721 | | | | | | | | |
|  | Estimate | Std. Error | df | t value | lower | upper | Pr(>|t|) |  |
| treatmentC - treatmentT | 0.00293 | 0.00086 | 65.7 | 3.40060 | 0.00121 | 0.00465 | 0.00115 | \*\* |
| siteDRYAS - siteMEAD | -0.00628 | 0.00154 | 9.5 | -4.07750 | -0.00973 | -0.00282 | 0.00248 | \*\* |
| siteDRYAS - siteWILL | 0.00887 | 0.00149 | 8.3 | 5.95800 | 0.00546 | 0.01228 | 0.00029 | \*\*\* |
| siteMEAD - siteWILL | 0.01515 | 0.00148 | 8.1 | 10.23980 | 0.01174 | 0.01855 | 0.00001 | \*\*\* |

Supplementary Table 7. Backwards selected NEE model output from lmerTest with treatment, site, GEI, soil moisture, and air temperature as fixed effects and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Backward reduced fixed-effect table:  NEE ~ GEI + (1 | site:plot), Conditional R2: 0.863, Marginal R2: 0.822 | | | | | | | |  |
| Degrees of freedom method: Satterthwaite | | | |  |  |  |  |  |
|  | Eliminated | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |  |
| T\_air | 1 | 0.0000019 | 0.0000019 | 1 | 68.885 | 0.0548 | 0.8155 |  |
| soil\_moisture | 2 | 0.0000067 | 0.0000067 | 1 | 71.458 | 0.1946 | 0.6605 |  |
| site | 3 | 0.0000816 | 0.0000408 | 2 | 10.201 | 1.1979 | 0.341 |  |
| treatment | 4 | 0.0000855 | 0.0000855 | 1 | 67.171 | 2.504 | 0.1183 |  |
| GEI | 0 | 0.0143724 | 0.0143724 | 1 | 74.95 | 414.2193 | <2e-16 | \*\*\* |
| Backward reduced random-effect table: | | |  |  |  |  |  |  |
|  | Eliminated | npar | logLik | AIC | LRT | Df | Pr(>Chisq) |  |
| <none> |  | 9 | 254.08 | -490.17 |  |  |  |  |
| (1 | site:plot) | 0 | 8 | 250.93 | -485.85 | 6.3187 | 1 | 0.01195 | \* |
| Final model parameters | | | | | | | |  |
|  | Estimate | Std. Error | df | t value | Pr (>|t|) |  |  |  |
| (Intercept) | -0.011531 | 0.001767 | 43.988409 | -6.525 | 5.71E-08 | | \*\*\* |  |
| GEI | 0.67168 | 0.033003 | 74.949675 | 20.352 | < 2.00E-16 | | \*\*\* |  |

Supplementary Table 8. Backwards selected ER model output from lmerTest with treatment, site, GEI, soil moisture, and air temperature as fixed effects and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Backward reduced fixed-effect table:  ER ~ treatment + site + GEI + (1 | site:plot), Conditional R2: 0.846, Marginal R2: 0.797 | | | | | | | |  |
| Degrees of freedom method: Satterthwaite | | | |  |  |  |  |  |
|  | Eliminated | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |  |
| soil\_moisture | 1 | 0.00000126 | 0.00000126 | 1 | 68.5 | 0.1335 | 0.716 |  |
| T\_air | 2 | 0.00000603 | 0.00000603 | 1 | 66.643 | 0.6519 | 0.4223 |  |
| treatment | 0 | 0.00004284 | 0.00004284 | 1 | 64.997 | 4.6477 | 0.0348 | \* |
| site | 0 | 0.00068155 | 0.00034077 | 2 | 9.329 | 36.9684 | 3.68E-05 | \*\*\* |
| GEI | 0 | 0.00036758 | 0.00036758 | 1 | 66.289 | 39.8763 | 2.59E-08 | \*\*\* |
| Backward reduced random-effect table: | | |  |  |  |  |  |  |
|  | Eliminated | npar | logLik | AIC | LRT | Df | Pr(>Chisq) |  |
| <none> |  | 9 | 297.4 | -576.79 |  |  |  |  |
| (1 | site:plot) | 0 | 8 | 294.6 | -573.2 | 5.5891 | 1 | 0.01807 | \* |
| Final model parameters | | | | | | | | |
|  | Estimate | Std. Error | df | t value | Pr (>|t|) |  |  |  |
| (Intercept) | -0.008343 | 0.001258 | 17.276325 | -6.633 | 3.90E-06 | \*\*\* |  |  |
| treatmentT | -0.001548 | 0.000718 | 64.997247 | -2.156 | 0.0348 | \* |  |  |
| siteMEAD | 0.006026 | 0.001515 | 9.358372 | 3.978 | 0.00298 | \*\* |  |  |
| siteWILL | -0.006983 | 0.001512 | 9.286156 | -4.618 | 0.00116 | \*\* |  |  |

Supplementary Table 9. Backwards selected GEP model output from lmerTest with treatment, site, GEI, soil moisture, and air temperature as fixed effects and plot as a random effect.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Backward reduced fixed-effect table:  GEP ~ treatment + site + GEI + (1 | site:plot), Conditional R2: 0.848, Marginal R2: 0.799 | | | | | | | |  |
| Degrees of freedom method: Satterthwaite | | | |  |  |  |  |  |
|  | Eliminated | Sum Sq | Mean Sq | NumDF | DenDF | F value | Pr(>F) |  |
| T\_air | 1 | 0.0000010 | 0.0000010 | 1 | 67.497 | 0.0208 | 0.885821 |  |
| treatment | 2 | 0.0000028 | 0.0000028 | 1 | 64.523 | 0.0589 | 0.809033 |  |
| soil\_moisture | 3 | 0.0000184 | 0.0000184 | 1 | 71.054 | 0.3874 | 0.535642 |  |
| site | 0 | 0.0012292 | 0.0006146 | 2 | 9.725 | 13.1029 | 1.74E-03 | \*\* |
| GEI | 0 | 0.0186637 | 0.0186637 | 1 | 67.566 | 397.9046 | < 2.2e-16 | \*\*\* |
| Backward reduced random-effect table: | | |  |  |  |  |  |  |
|  | Eliminated | npar | logLik | AIC | LRT | Df | Pr(>Chisq) |  |
| <none> |  | 9 | 238.18 | -458.36 |  |  |  |  |
| (1 | site:plot) | 0 | 8 | 235.02 | -454.04 | 6.3214 | 1 | 0.01193 | \* |
| Final model parameters | | | | | | | |  |
|  | Estimate | Std. Error | df | t value | Pr (>|t|) |  |  |  |
| (Intercept) | -0.002151 | 0.002796 | 17.484044 | -0.769 | 0.452 |  |  |  |
| siteMEAD | -0.008711 | 0.003395 | 9.81802 | -2.566 | 0.0285 | \* |  |  |
| siteWILL | 0.008623 | 0.003381 | 9.647215 | 2.551 | 0.0296 | \* |  |  |
| GEI | 0.788429 | 0.039525 | 67.565897 | 19.948 | <2e-16 | \*\*\* |  |  |