



Temperature response of respiration across the heterogeneous landscape of the Alaskan Arctic tundra

Eric Wilkman^{*1}, Donatella Zona^{1,2}, Yanfei Tang¹, Beniamino Gioli³, David A. Lipson¹,
Walter Oechel^{1,4}

¹Department of Biology, San Diego State University, San Diego, California

²Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

³Istituto di Biometeorologia, Consiglio Nazionale delle Ricerche, Firenze, Italy

⁴Department of Physical Geography, University of Exeter, Exeter, UK

*corresponding author: *Eric Wilkman*

ewilkman@sdsu.edu

Phone: 619 (594) 4258

Fax: 619 (594) 7831

Key words: microtopography, ice-wedge polygons, permafrost, flux partitioning, Q_{10}

Key Points:

- Estimates of the temperature response of respiration can be simplified across heterogeneous landscapes.
- Seasonal changes in Q_{10} should be noted, with a marked decrease across the growing season.
- Ecosystem respiration estimated with eddy covariance daytime flux partitioning agrees well with chamber respiration estimates

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1029/2017JG004227

Abstract

Predictions of the response of ecosystem respiration to warming in the Arctic are not well constrained, partly due to the considerable spatial heterogeneity of these permafrost-dominated areas. Accurate calculations of *in-situ* temperature sensitivities of respiration (Q_{10}) are vital for the prediction of future Arctic emissions. To understand the impact of spatial heterogeneity on respiration rates and Q_{10} , we compared respiration measured from automated chambers across the main local polygonized landscape forms (high and low centers, polygon rims, polygon troughs) to estimates from the flux partitioned net ecosystem exchange (NEE) collected in an adjacent eddy covariance tower. Microtopographic type appears to be the most important variable explaining the variability in respiration rates, and low-center polygons and polygon troughs show the greatest cumulative respiration rates, possibly linked to their deeper thaw depth and higher plant biomass. Regardless of the differences in absolute respiration rates, Q_{10} is surprisingly similar across all microtopographic features, possibly indicating a similar temperature limitation to decomposition across the landscape. Q_{10} was higher during the colder early summer and lower during the warmer peak growing season, consistent with an elevated temperature sensitivity under colder conditions. The respiration measured by the chambers and the estimates from the daytime-flux partitioned eddy covariance data were within uncertainties during early and peak season, but overestimated respiration later in the growing season. Overall, this study suggests that it is possible to simplify estimates of the temperature sensitivity of respiration across heterogeneous landscapes, but that seasonal changes in Q_{10} should be incorporated into model simulations.

1. Introduction

Comprising an area of more than $7 \times 10^6 \text{ km}^2$ and storing over 28% ($41.0 \text{ kg} \cdot \text{SOC} \cdot \text{m}^{-2}$) of the world's soil organic matter pool, Arctic tundra ecosystems are vitally important components of the global carbon (C) cycle (Ping *et al.*, 2008). These ecosystems are sensitive to subtle changes in climate and many of these functional changes can feedback on atmospheric CO_2 and future climate regimes (Callaghan & Maxwell, 1995; Deslippe *et al.*, 2012; Pearson *et al.*, 2013). As a current estimate, the soils of the circumpolar Arctic store over $1,035 \pm 150 \text{ Pg C}$ in the near surface (0–3m), approximately twice the amount of carbon that is currently in the atmosphere and 43% of the global carbon content to this depth (Tarnocai *et al.*, 2009; Hugelius *et al.*, 2014). Historically, most of this carbon has been sequestered as the net result of photosynthetic dominance in the short summer season and low rates of decomposition as a consequence of cold, nutrient poor, and generally waterlogged conditions (Oechel *et al.*, 1993). Yet, much of this soil carbon pool is at risk of being lost to the atmosphere due to accelerated soil organic matter decomposition in warmer future climates (Grogan & Chapin, 2000; Dorrepaal *et al.*, 2009; Schuur *et al.*, 2015). Notwithstanding any acclimation and metabolic adjustments that may occur, greater soil drying, aeration, and an expansion of the seasonally thawed active layer may result in increased carbon losses to the atmosphere (Oechel *et al.*, 2000; Hinzman *et al.*, 2005; Natali *et al.*, 2012).

The sensitivity of carbon emissions from soil organic matter to current and future climate regimes is an increasingly important area of research. Despite the importance of the Arctic to the global climate system, carbon budgets are poorly constrained and models poorly capture respiration losses, particularly during the cold period (e.g., McGuire *et al.*, 2012; Fisher *et al.*, 2014; Commane *et al.*, 2017). Much of the inadequacy can be attributed to a poor understanding of the spatial patterns and controls on carbon flux in the Arctic (Hodson

et al., 2013). Summer warming, in particular, might increase both carbon loss from respiration and photosynthetic carbon uptake (Hanson *et al.*, 2000; Ueyama *et al.*, 2013). However, the complex interactions between respiration and photosynthesis, together with the complexity of their environmental controls (e.g., soil moisture, substrate quality, nutrient cycling, and vegetation categories), increase uncertainties in predictions of the carbon balance under a changing climate (Hobbie *et al.*, 2000; Trumbore, 2006; Nobrega & Grogan, 2008; Sommerkorn, 2008; Zona *et al.*, 2011).

Arctic tundra landscapes are largely characterized by patterned ground. Polygonal landscapes are generated through the formation of ice wedge polygons that underlie soils of the coastal tundra (Brown, 1967). Through the alternation of yearly freeze-thaw cycles, and the growth and subsidence of the underlying ice wedges, low-center and high-center polygons develop across the tundra (Billings & Peterson, 1980; Gamon *et al.*, 2013). Approximately 65% of the Arctic Coastal Plain in northern Alaska is underlain by polygonal landforms (Hinkel *et al.*, 2005; Liljedahl *et al.*, 2011; Liljedahl *et al.*, 2012). High-center polygonal landforms have a relatively high relief and are generally found in well-drained interstitial tundra regions, while low-center polygons are similar to high-center polygons with the exception of having an often submerged moist-aquatic center (Lara *et al.*, 2015). Adjacent to this moist-aquatic center in low-center polygons are dry-moist rims. Finally, troughs and drainage channels are found on the perimeter of the high and low center polygons. While ice wedge formation is typically limited to a few meters in depth, polygonization produces substantial biogeochemical and hydrological heterogeneity (Zona *et al.*, 2011; Davidson *et al.*, 2016).

Landscape heterogeneity has been shown to influence the patterns and controls of CO₂ fluxes in both Arctic and non-Arctic systems (Vourlitis & Oechel, 1997; Riveros-Iregui & McGlynn, 2009; Pacific *et al.*, 2011; Zona *et al.*, 2010; Zona *et al.*, 2011; Sturtevant *et al.*,

2013; Knowles *et al.*, 2015; Steilstra *et al.*, 2015; Davidson *et al.*, 2016). Polygonal units are characterized by heterogeneity in water table, thaw depth, and vegetation type (Zona *et al.*, 2010; Zona *et al.*, 2011; Davidson *et al.*, 2016). As a result, mean ecosystem respiration has been seen to vary substantially amongst polygonal units (Sommerkorn, 2008; Zona *et al.*, 2011). The difference in water table height across polygonized landscapes is one of the main drivers of spatial heterogeneity in vegetation and CO₂ and CH₄ fluxes (Zona *et al.*, 2011; Davidson *et al.*, 2016). Water table mediates both aerobic and anaerobic processes in wetland systems (Blodau, 2002; Lipson *et al.*, 2012). A higher water table generally limits the diffusion of oxygen, thus favoring methanogenesis and anaerobic fermentation over aerobic respiration in the soil. Conversely, greater soil oxygen availability, and therefore a lower water table, regularly stimulates aerobic respiration. In general, soil drying and increasingly aerobic conditions increase the rates of soil respiration (Billings *et al.*, 1983; Freeman *et al.*, 1993; Moore & Knowles, 1989; Oechel *et al.*, 1998). However, changes in water table and temperature may have different effects dependent on particular surface features. More mesic and waterlogged soil sites have also been shown to have increased mineralization rates and soil microbial N pools than drier hummock dominated sites across Siberian tundra zones (Biasi *et al.*, 2005). Dissimilarities in permafrost depth, pore water chemistry, nutrient availability, plant cover, and productivity have also been linked with microtopographic features in polygon-dominated tundra ecosystems (Engstrom *et al.*, 2005; Schuur *et al.*, 2007; Baumann *et al.*, 2009; Newman *et al.*, 2015; Davidson *et al.*, 2016). Nutrient availability (Damman, 1978; Chapin *et al.*, 1979) and plant species distributions (Andrus *et al.*, 1983; Ohlson & Dahlberg, 1991) have also been seen to vary with landscape heterogeneity, thus affecting the carbon dynamics in these systems (Moore & Knowles, 1989; Christensen *et al.*, 2000). As such, differences in vegetation type, and their effects on shading, soil temperature, and hydrological characteristics are tightly linked to the water level in defining the spatial

heterogeneity of these ecosystems (Billings & Peterson, 1980; Chu & Grogan, 2000; von Fischer *et al.*, 2010; Zona *et al.*, 2011; Davidson *et al.*, 2016).

Though past studies have underscored the importance of spatial heterogeneity to carbon cycling and trace gas emissions (Arbo *et al.*, 2013), there are still large uncertainties in the temperature sensitivity of respiration across these different microtopographic features in the Arctic Coastal Plain. The difficulties in collecting continuous Arctic greenhouse gas fluxes has limited our understanding of the temperature sensitivity of respiration, with only a few studies reporting continuous year-round CO₂ flux from tundra ecosystems (Sullivan *et al.*, 2008; Lüers *et al.*, 2014; Oechel *et al.*, 2014; Euskirchen *et al.*, 2017). Importantly, previous studies that measured CO₂ and CH₄ fluxes across the different microtopographic features from these tundra ecosystems were only collected within a short temporal resolution (e.g. once a day or once a week, von Fischer *et al.*, 2010; Olivas *et al.*, 2011; Zona *et al.*, 2011; McEwing *et al.*, 2015; Davidson *et al.*, 2016).

Broadly, the relative activity of biological and chemical reactions, including respiration, has been generally approximated to double for every 10°C increase in temperature, based on a theoretical Q₁₀ of 2 (Tjoelker *et al.*, 2001; Anderson, 2010; Mahecha *et al.*, 2010). These fixed Q₁₀ values are widely used in ecosystem models (Potter *et al.*, 1993; Mahecha *et al.*, 2010; Foereid *et al.*, 2014). Conversely, several studies have suggested that Q₁₀ is variable, with values ranging from 1 to more than 12 (Hamdi *et al.*, 2013; Gritsch *et al.*, 2015), and reaching 4.5 in Arctic tundra ecosystems (Ueyama *et al.*, 2013). Globally, Q₁₀ seems to be amplified in Arctic ecosystems in comparison to temperate and tropical regions, perhaps due to an inverse correlation with mean annual temperature across biomes (Bekku *et al.*, 2003; Zhou *et al.*, 2009). In Arctic soils the temperature sensitivity of CO₂ production is often larger than 2, with experiments conducted at field-relevant temperatures (Nadelhoffer *et al.*, 1991; Mikan *et al.*, 2002; Chowdhury *et al.*, 2015), or lower than 2, commonly during

the winter in Alaska (Oechel *et al.*, 2014). Several studies suggest that soil respiration and Q_{10} decline with increasing temperature (Paembonan *et al.*, 1991; Tjoelker *et al.*, 2001; Hamdi *et al.*, 2013), yet others have shown the opposite trend (Stockfors & Linder, 1998; Atkin *et al.*, 2000a; Lipson, 2006; Oechel *et al.*, 2014). The picture becomes more complicated when the effect of soil moisture is considered. Correlations between Q_{10} and soil moisture levels have been shown to be either positive (Craine & Gelderman, 2011), negative (Luan *et al.*, 2013), or non-significant (Fang & Moncrieff, 2001). Moreover, Q_{10} has been shown to vary substantially even with uniform soil moisture levels (Craine *et al.*, 2010). This variance could also be due to the quality and degradability of soil organic carbon (SOC) in Arctic soils, as recalcitrant SOC is more sensitive to warming than fresh and labile organic matter (Davidson & Janssens, 2006; Lefèvre *et al.*, 2014). The controlling factors of Q_{10} at regional scales thus remain uncertain. It is therefore important to continue to investigate the spatial patterns and controls on carbon loss and temperature sensitivities in Arctic systems.

Parameterizing ecosystem level responses to climate change in the Arctic requires a fine-scale understanding of how microtopography, soil microbial processes, and thermal regimes control biogeochemical cycling (Stoy *et al.*, 2013). Recent data syntheses and modeling studies of Arctic tundra net CO_2 flux have suggested that the tundra is either a CO_2 sink or a CO_2 source, with large uncertainties in these estimates (McGuire *et al.*, 2012; Belshe *et al.*, 2013; Fisher *et al.*, 2014). This uncertainty is related to the poor availability of continuous CO_2 data to both parameterize and validate ecosystem models in the Arctic (McGuire *et al.*, 2012). Nonetheless, several studies have shown that the spatial and temporal variation in the patterns and controls of CO_2 fluxes are large even at the meter scale (Morrissey & Livingston, 1992; Vourlitis *et al.*, 1993; Vourlitis & Oechel, 1997). Most larger scale modelling studies have used the flux partitioned net ecosystem exchange (NEE) from eddy covariance towers to estimate respiration across a variety of ecosystems (Reichstein *et*

al., 2005; Lasslop *et al.*, 2010). While these methodologies are well established for temperate ecosystems, where nighttime facilitates the calculation of the respiration component, there are still uncertainties with the application of these algorithms to fluxes from Arctic sites with no dark periods during the summer (Zamolodchikov *et al.*, 2003; Groendahl *et al.*, 2007; Kutzbach *et al.*, 2007; Runkle *et al.*, 2013). Several studies have found substantially different estimates between ecosystem respiration (ER) measured by soil chambers and estimations from eddy covariance fluxes (Janssens *et al.*, 2001, Fox *et al.*, 2008). Chamber estimates can be biased due to soil modifications (e.g. abscission of roots and mycorrhizae when placing chambers in the soil), the potential for anomalous chamber heating, the creation of pressure gradients, and unsatisfactory placement of sampling units within the tower footprint (Dabberdt *et al.*, 1993; Vourlitis *et al.*, 1993; Norman *et al.*, 1997; Rochette *et al.*, 1997; Subke *et al.*, 2009). Tower estimates, on the other hand, may be biased due to advection, lack of energy balance closure, or diurnal footprint variability (Wilson *et al.*, 2002; Baldocchi, 2003; Oren *et al.*, 2006). The eddy covariance technique gives a single integrated flux within the tower footprint. This can potentially bias or overestimate the emission estimates if there is variation in the land cover within the footprint. Conversely, closed chamber measurements may increase spatial representativeness of plant communities to a degree, but can have a reduced temporal coverage in comparison to tower measurements (Stoy *et al.*, 2013). It is well documented that measured CO₂ flux estimates vary depending on the method employed (Oechel *et al.*, 1998; Björkman *et al.*, 2010; Riederer *et al.*, 2014). Thus it is often important, if possible, to combine both techniques, as the information gained from each technique is complimentary and essential for understanding spatial and temporal patterns in fluxes.

To better refine our understanding of the sensitivity of spatial variability and the controls on carbon fluxes to projected near-term warming, we measured respiration rates

across different polygonal types in the coastal Arctic landscape. The goal of this study was to investigate the spatial patterns of Arctic growing season respiration, the environmental controls on respiration, the performance of currently used flux partitioning methods to estimate respiration from the NEE measured by eddy covariance flux towers in the Arctic, and to estimate the temperature response of respiration (Q_{10}) across different ecosystem types. For this study we combined data from automated soil chambers that measured continuous soil CO₂ measurements, with tower fluxes gathered in the footprint of an eddy covariance tower in the highly-polygonized tundra in northern Alaska (Utqiagvik). We hypothesize that landscape heterogeneity influences both the absolute rates and the temperature response of respiration, that temperature sensitivity will vary during the growing season, and that current flux partitioning methods do not properly capture the respiration rates from arctic tundra ecosystems.

2. Methods

2.1. Site Description

The study area is located near Utqiagvik (previously named Barrow), Alaska, at the northernmost point of the mainland United States (71.32°N, 156.62°W) (Fig. 1a). Utqiagvik is located within the Arctic Coastal Plain, where the landscape consists of thaw lake basins and areas of interstitial tundra, with approximately 65% of the ground covered by flat, high, and low center ice-wedge polygons (Brown, 1967; Billings & Peterson, 1980). The study site is a region of interstitial polygonized tundra (Fig. 1b) located in part of the Barrow Environmental Observatory (BEO), a 30.21 km² study area dedicated to terrestrial and atmospheric climate research. Vegetation in Utqiagvik is broadly dominated by mosses (*Sphagnum spp.*), sedges (*Carex aquatilis*, *Eriophorum spp.*), and grasses (*Dupontia fisheri*, *Arctophila fulva*), with mosses dominating high sites (e.g. polygon rims) and *Carex*

dominating low (e.g. polygon centers) sites (Olivas *et al.*, 2011). Previous vegetation surveys noted that high-center polygons consisted of *Polytrichum* moss and lichen-dominated communities with a highly reduced vascular plant cover (Davidson *et al.*, 2016). Polygon rims and flat centers were dominated by a mixture of graminoids, including the sedge *Eriophorum russeolum*, the grass *Poa arctica*, and the rush *Luzula arctic*, with limited smatterings of *Dicranum* mosses, liverworts, and lichens. The sedge *C. aquatilis* dominated vascular plant canopies in polygon troughs and low-center polygons.

In Utqiagvik the maximum active layer is generally ~35 cm and the organic layer, which overlies silty mineral horizons, has a general thickness of 12 to 15 cm (Walker *et al.*, 2003). Mean annual precipitation is 120 mm, while mean annual (January-December) and July temperatures are -11.3°C and 3.7°C respectively. Soil parent materials in the North Slope of Alaska are marine sediments of Pleistocene age that have been altered by thaw-lake processes (Sellmann & Brown, 1973). The organic C content in the top 100 cm of these soils ranges from 37 to 139 kg m⁻³ (Bockheim *et al.*, 2004) and soil bulk density of the organic layer in the study site is 0.06 g cm⁻³ on average (Lipson *et al.*, 2013). Soil pH values range from 5.1 at the low-center polygons to 4.5 at polygon rims (Lipson *et al.*, 2012).

2.2. Ecosystem Respiration Measurements

At the beginning of June 2007, fourteen acrylic soil collars were inserted into the surface moss layer with a serrated knife. These fourteen sampling plots were clustered together (across a 30 m diameter area in the SW portion of the footprint of the nearby Barrow-BEO eddy covariance tower). The landscape included two high-center polygons, three polygon troughs, four low-center polygons, and five polygon rims (Fig. 1b, c). All collars were inserted at least 24 hours before measurements began to reduce the impact of disturbance on respiration from collar installation. A 16-port multiplexed chamber array

system was used for measuring ecosystem respiration once every hour (LI-8100 Multiplexor, LI-COR Biosciences, Lincoln, Nebraska). These dynamic, opaque chambers are mechanically lifted from their soil collar base, thus minimizing alterations to sun exposure, wind, and precipitation in the sampling plots (Fig. 1c). Automated chamber data was collected every hour from June 18th to August 2nd, 2007 totaling 13,628 soil flux measurements during the entire sampling period.

Respiration rates were calculated from the measured increase in gas concentration within the chamber headspace, as described in McEwing *et al.* (2015). The linear increase in CO₂ concentration inside the chamber headspace was used to estimate the fluxes based on the following equation

$$F_o = S \frac{V \cdot M \cdot 273.16}{A \cdot V_m(273.16 + T)} 3600$$

F_o Flux at the time of chamber closure ($\mu\text{g C CO}_2 \text{ m}^{-2}\text{h}^{-1}$)

S Time derivative (slope) CO₂ concentration change over time (ppm s^{-1})

V Chamber volume (m^3)

A Chamber area (m^2)

M Molecular mass of CO₂ (g mol^{-1})

V_m Ideal gas mole volume ($0.224 \text{ m}^3 \text{ mol}^{-1}$)

An eddy covariance tower (Barrow-BEO, Zona *et al.*, 2016) that measured net ecosystem exchange (NEE) in proximity of the chambers was used to estimate respiration rates based on the two flux partitioning methods (Reichstein *et al.*, 2005; Lasslop *et al.*, 2010). More details on the instruments, calibrations, and data processing steps for tower derived fluxes can be found in Zona *et al.*, 2016.

2.3. Environmental Parameters

Water table and thaw depth values were recorded once a week at every chamber location. PVC pipes of 2.2 cm diameter, perforated every cm throughout their lengths, were permanently inserted into the soil and used for these water table measurements (Zona *et al.*, 2009; Olivas *et al.*, 2011). Thaw depth measurements were taken within 5 cm of the chambers using a graduated metal cylinder (Brown *et al.*, 2000; Zona *et al.*, 2009). Surface temperatures and atmospheric pressures were also measured within the chamber headspace during flux data collection. Air temperature and air pressure were collected inside each chambers with the same temporal resolution of the CO₂ measurements used to estimate the fluxes (i.e. 13,628 data points for the entire sampling period). Thaw depth was collected weekly right outside of each of the chamber collars from mid-June to the end of July. Water table measurements was only measured from the beginning to the end of July as these measurements required the installation of PVC pipes in proximity of each chamber's collar (which was completed by late June).

2.4. Temperature Sensitivity

The temperature response of respiration from the chamber measurements was estimated based on a best fit exponential regression model between the hourly respiration and both air and soil temperature, with separate fits for each ecosystem type. Unfortunately, the loss of soil temperature data from individual chambers forced us to use either soil temperature data collected at the surface in proximity of the eddy covariance tower (in a high-center polygon ecosystem type), or air temperature collected from each chamber. Soil temperature data collected across the different ecosystem types used in this study showed similar values (Zona *et al.*, 2011; Davidson *et al.*, 2016), likely due to the short and sparse vegetation limiting shading effects from different ecosystem types. To address the potential

limitation of using just one soil temperature for all the Q_{10} estimates collected in proximity of the eddy covariance tower, we also calculated Q_{10} using the chamber air temperatures and the results were very similar to the Q_{10} calculation using soil temperatures. The calculation of respiration Q_{10} for the chambers was performed on weekly periods to include enough data to allow the building of reasonable temperature responses of respiration.

2.5. Statistical Analysis

To address temporal and spatial pseudoreplication, the relative importance of each environmental variable in explaining the weekly averaged ecosystem respiration was determined using linear mixed effects models (lme4 package in R, R Core Team, 2015). The mixed models included the relevant fixed effects (ecosystem type, thaw depth, water table depth, and soil temperature), the week of measurement, and the chamber number as continuous and categorical random effects. These mixed models were chosen given the violation of independence (within a repeated measures design, the same plots are measured multiple times during an experiment). Weekly averages were chosen for this analysis as the thaw depth and water table were only collected once a week. Ecosystem respiration data were log transformed to meet normality and homoscedasticity assumptions. The following variables were tested as explanatory variables (fixed effects) of the spatial variability in ecosystem respiration: ecosystem type, thaw depth, water table depth, and soil temperature. As water table values were only collected starting in July, weekly log transformed ecosystem respiration was modeled as a function of the various environmental parameters including a dataset both with water table ($n = 69$; all of July) and without data ($n = 97$; June and July). Model performance was evaluated on Akaike information criterion (AIC) values, on the significance of the partial F-test, and on the marginal coefficient of determination (similar to the explanatory power of the linear models) for generalized mixed-effects models as output

by the r^2_{GLMM} function within the MuMIn package in R (Nakagawa & Schielzeth, 2013; Johnson, 2014). This r^2_{GLMM} function (Nakagawa & Schielzeth, 2013) was used to estimate both the marginal R^2 which describes the percentage of the variance in the respiration explained by fixed effects, and conditional R^2 (i.e. percentage of the variance explained by both fixed and random effects). To assess the co-variance among the independent variables, correlation coefficients were assessed for all combinations. We also performed a partial correlation analysis to test how much the explanatory power of a variable increased, once we accounted for other variables. All statistical models were defined as significant at $p < 0.05$. As the sampling plots were stratified by microtopographical category, we also tested the difference in ecosystem respiration between these categories through a one-way ANOVA and pairwise comparisons. All statistical analyses were carried out in the statistical software R, version 3.2.3 (R Core Team, 2015).

3. Results

3.1. Environmental Parameters

Throughout the growing period high-center polygons had the shallowest thaw depths, while low-center polygons had the deepest thaw depths (Fig. 2a). For all topographic categories, averaged thaw depth increased with the progression of the growing season. Throughout the growing period high-center polygons and polygon rims had deeper water tables, while low-center polygons had shallower water tables (Fig. 2b). Air temperature, measured inside each chamber, also increased from June to July (Fig. 2c).

3.2. Ecosystem Respiration

During mid- to late June, ecosystem respiration was the highest in polygon troughs, followed by low-center polygons, polygon rims, and finally high-center polygons (Fig. 2d).

This pattern remained throughout July as well. Ecosystem type was a dominant control explaining the variability in respiration in both datasets. Thaw depth, water table, and soil temperature were also significant controls on growing season respiration (Table 2 & 3).

There was a significant amount of collinearity amongst the environmental variables (Supplementary Table 1), and the explanatory power of ecosystem type increased after controlling for the other variables (Supplementary Table 2). The exclusion or inclusion of data points without water table measurements (i.e., June 18 – July 29 vs. July 2 – July 29) led to different model results (i.e. the model applied to the entire dataset without water table $n=97$ and that with the reduced dataset that also included water table $n=69$). However, the relationship between thaw depth and ecosystem respiration was only significant in the reduced model ($n=69$).

Ecosystem respiration, measured by the chambers across all the microtopographic features, was fairly stable across the season and relatively comparable with the estimated respiration using the daytime flux partitioning by Lasslop *et al.* (2010), especially for the beginning of the season (see Fig. 3). On the other hand, the flux partitioning by Reichstein *et al.* (2005) appeared to substantially overestimate the measured respiration rates (Fig. 3).

3.3. Q_{10} Estimates

The regressions between chamber air and tower soil temperatures and ecosystem respiration generated highly significant relationships (p -values <0.001 for all the regressions) (Table 1, 2, & Supplementary Fig. 1).

In general, temperature sensitivities decreased from June to July, but they were surprisingly similar, and within each other's confidence intervals, for most of the period across all microtopographic units (Fig. 4). During the month of June average Q_{10} , estimated from the chamber data, were on average 2.45 ± 0.207 decreasing to 1.67 ± 0.119 during the

first two weeks of July, and to 1.58 ± 0.11 during the last two weeks of July. Overall Q_{10} was highest early in the summer, and lowest during the peak growing season (Fig. 4).

4. Discussion

4.1. Soil Hydrology across Microtopographic Landscape Forms

Water table depth varied across each polygonal unit and with the progression of the growing season. By August the driest microsites, the polygon rims and high-center polygons, had the deepest water tables in comparison to polygon troughs and low-center polygons. As microtopographic areas with higher elevation are further above the water table and therefore drier, their higher elevation results in significant drainage throughout the growing season and thus a lower water table (Engstrom *et al.*, 2005). The deepest thaw depths occurred in the low-center polygons during the late growing season. Thermokarst dynamics and the formation of ice-wedge polygons results in water drainage in the low-center polygons and troughs, thus leading to shallower water table levels (Hussey & Michelson, 1966; Billings & Peterson, 1980). The shallower water table in these lower elevation areas results in a higher heat conductance into the soil (Hinzman *et al.*, 1991) supporting the increase in active layer depth (Shiklomanov *et al.*, 2010; Fig. 2a, b). The increased heat conductance in wetter microtopographic areas is likely responsible for their deeper thaw depth, despite the similar soil temperature between low center, and polygon rims (Zona *et al.*, 2011). The increased ground heat fluxes, and deeper thaw depths in these polygonal units can also stimulate decomposition therefore increasing respiration rates (Minke *et al.*, 2009), as discussed in the following section.

4.2. Growing Season Ecosystem Respiration

Respiration increased across every polygonal type during the growing season with deeper water table and thaw depth (Fig. 2c). This decrease in water table undoubtedly increased aeration of the soil (Fig. 2a, d). The higher soil aeration, together with the increase of both active layer depth and temperature with the progression of the summer likely increased microbial activity, increasing respiration rates (Freeman *et al.*, 1993; Moore & Knowles, 1989). However, respiration rates were highest in low-centers and in troughs (Fig. 1d), despite their shallower water levels (and therefore more anoxic conditions of their soils) presumably because of the predisposition of the microbial communities in these low regions to anaerobic respiration (Lipson *et al.*, 2012). Moreover, the deeper depth of thaw in these lower elevation areas also results in a higher nutrient concentration (Lipson *et al.*, 2011), and more productive vegetation (Zona *et al.*, 2010), possibly contributing to the higher respiration rates observed (Fig. 1d). However, the collinearity of all these environmental variables (water table, thaw depth, air and soil temperature), co-varying with vegetation phenological change, makes it extremely challenging to separate each of their roles in controlling the respiratory fluxes (Supplementary Table 1, 2; Zona *et al.*, 2009). Generally, if independent variables are highly correlated, any regressive statistics will tend to assign all the predictive capacity to one regressor only, likely not representing the full complexity of the ecological processes controlling respiration.

The poor performance of the nighttime based flux partitioning by Reichstein *et al.* (2005) is consistent with the near-absence of dark conditions across the Arctic in the summer. A more reasonable comparison was found between the ecosystem scale respiration rates measured by the chambers and the ones estimated following Lasslop *et al.* (2010), given that the daytime fluxes are used in the Lasslop method. However, even if closer to the chamber respiration estimates, the respiration estimated using Lasslop *et al.* (2010) showed higher values, particularly later in the season (Fig. 3). This result could be explained by a higher air

temperature effect on the respiration portion of NEE (Runkle *et al.*, 2013), linked to the lack of inclusion in the Lasslop parameterization of the changes in soil moisture, water table, or air humidity (Runkle *et al.*, 2013).

4.3. Influence of Temperature on Respiration

While respiration rates were found to differ across the microtopographic features investigated here, the temperature response was very similar (Fig. 4). This dissimilarity in rates of respiration with the same temperature response was quite unexpected, but it may suggest stability in the thermal controls of carbon loss. Temperature was positively correlated with ecosystem respiration throughout the early and peak growing season for all polygonal features considered in this analysis (Table 1), yet R^2 values were greatest during the beginning of the growing season. During this period soils had just begun to thaw and water table depths were closest to the soil surface. Early in the growing season, before vegetation becomes active and starts absorbing carbon, soil respiration is the main process taking place in these ecosystems, thus simplifying modeling of the temperature response of ecosystem respiration (Dorrepaal *et al.*, 2009; Hicks Pries *et al.*, 2013). Later in the season, plant and soil respiration can have different temperature sensitivities, increasing the noise of the temperature-respiration regressions (Janssens *et al.*, 2004; Davidson *et al.*, 2006; Karhu *et al.*, 2014).

The temperature sensitivity of respiration can vary considerably depending on factors such as vegetation composition, water table and seasonality (Hobbie *et al.*, 2000). A similar Q_{10} across microtopographic features, even under very different water table and thaw depth levels (Fig. 4) is nonetheless surprising, as different vegetation types, with varying leaf litter qualities (Aerts & Chapin, 2000; Dorrepaal *et al.*, 2005), different rates of organic matter decomposition (Wardle, 2002), and different substrate qualities should have different

temperature sensitivities of decomposition (Fierer *et al.*, 2005). The observed similar temperature sensitivities across these very different landscapes could be attributed to a general temperature limitation to decomposition, independent from the litter and soil carbon qualities in these very cold ecosystems. Strong physicochemical protection methods could also shield organic matter from decomposition, and the perennially low Arctic soil growing season temperatures may effectively constrain any temperature sensitivities of carbon decomposition (Aerts, 2006; Conant *et al.*, 2011).

Overall, our results suggest the presence of seasonal patterns in temperature sensitivity that should be carefully considered and modeled. The seasonal decrease in Q_{10} was very similar among all these microtopographic features, with the progression of the summer (Fig. 4). This decrease is likely due to an increase in temperature (Anderson, 2010), in agreement with Tjoelker *et al.* (2001) and Carey *et al.* (2016). A decrease in water table levels (tightly related to soil moisture) at high temperatures can also explain the decreased sensitivity at elevated temperatures (Carey *et al.*, 2016). Low soil water content could affect the diffusion of soluble substrates, which can limit soil microbial respiration (Linn & Doran, 1984; Grant & Rochette, 1994). Additionally, warmer conditions could decrease autotrophic demand for ATP and enzyme capacity, ultimately reducing temperature sensitivity (Atkin *et al.*, 2000b). Finally, an increase in plant productivity with warmer temperatures during peak season could increase the soil carbon quality, decreasing the temperature sensitivity of respiration (Fierer *et al.*, 2005; Knorr *et al.*, 2005). Given the differential temperature sensitivity of respiration, accounting for these seasonal changes is critical to prevent overestimation of the predicted response of carbon loss to warming. Including this seasonality into model estimates is particularly important, given that most models use a fixed Q_{10} of 2 to simulate regional and global carbon dynamics (Lariguaderie & Körner, 1995; Xu *et al.*, 2017).

In conclusion, a similar temperature sensitivity of respiration across very different microtopographic features supports simplification of the modeling of the response of respiration to warming from these highly heterogeneous landscapes. However, the seasonal decrease in Q_{10} should be taken into consideration, as it could lead to overestimation of the response of respiration to warming in the Arctic if not included in model estimates.

Acknowledgements

This work was funded by the Office of Polar Programs of the National Science Foundation (NSF) awarded to DZ, WCO, and DAL (award number 1204263) with additional logistical support funded by the NSF Office of Polar Programs, and by the Carbon in Arctic Reservoirs Vulnerability Experiment (CARVE), an Earth Ventures (EV-1) investigation, under contract with the National Aeronautics and Space Administration, and by the ABoVE (NNX15AT74A; NNX16AF94A) Program. We would like to thank the Global Change Research Group at San Diego State University, in particular, Patrick Murphy and UMIAQ and Ukpeagvik Inupiat Corporation (UIC) for logistical support. This research was conducted on land owned by the UIC. This project has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement No. 727890, and by the Natural Environment Research Council (NERC) UAMS Grant (NE/P002552/1). We would like to thank Cole Kelleher and the team at the Polar Geospatial Center at the University of Minnesota for their help with the satellite imagery. Tower flux data has been submitted to Ameriflux and chamber data are accessible on the Pangaea repository at the following url: <https://doi.pangaea.de/10.1594/PANGAEA.890144>.

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Table 1 - Weekly soil chamber respiration ($\text{gC-CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) vs. soil temperature ($^{\circ}\text{C}$) by ecosystem type with mean least squares exponential regression fit and modeled Q_{10} . Data are shown ecosystem type and include r^2 , p values, and standard error for each Q_{10} estimate.

		Regression Equation	R ²	p-value	Q ₁₀	SE
16-Jun	High-center	$y = 0.0153e^{0.0736x}$	0.5451	>0.001	2.087566	0.155107
	Low-center	$y = 0.0223e^{0.0723x}$	0.677	>0.001	2.008725	0.176484
24-Jun	Rim	$y = 0.0178e^{0.0767x}$	0.3961	>0.001	2.153294	0.176042
	Trough	$y = 0.0335e^{0.0627x}$	0.5227	>0.001	1.871988	0.189103
25-Jun	High-center	$y = 0.0106e^{0.087x}$	0.3139	>0.001	2.38691	0.159215
	Low-center	$y = 0.0175e^{0.0986x}$	0.3914	>0.001	2.680487	0.240792
1-Jul	Rim	$y = 0.0125e^{0.0815x}$	0.1455	>0.001	2.259173	0.159146
	Trough	$y = 0.0198e^{0.1023x}$	0.2115	>0.001	2.781532	0.269027
2-Jul	High-center	$y = 0.0156e^{0.0726x}$	0.6712	>0.001	2.066797	0.154014
	Low-center	$y = 0.0249e^{0.0604x}$	0.7434	>0.001	1.829422	0.155969
8-Jul	Rim	$y = 0.0178e^{0.0691x}$	0.5975	>0.001	1.995869	0.154915
	Trough	$y = 0.0348e^{0.0511x}$	0.4477	>0.001	1.666958	0.151757
9-Jul	High-center	$y = 0.0222e^{0.0171x}$	0.0705	>0.001	1.819384	0.142607
	Low-center	$y = 0.0228e^{0.049x}$	0.4232	>0.001	1.632313	0.117068
15-Jul	Rim	$y = 0.0196e^{0.0346x}$	0.1608	>0.001	1.413403	0.073566
	Trough	$y = 0.0316e^{0.0322x}$	0.1435	>0.001	1.379885	0.086353
16-Jul	High-center	$y = 0.0164e^{0.0594x}$	0.3191	>0.001	1.811217	0.12411
	Low-center	$y = 0.0251e^{0.0472x}$	0.3216	>0.001	1.603198	0.117704
22-Jul	Rim	$y = 0.0209e^{0.0472x}$	0.2169	>0.001	1.603198	0.107406
	Trough	$y = 0.0296e^{0.0462x}$	0.2448	>0.001	1.587247	0.124752
23-Jul	High-center	$y = 0.0188e^{0.0x}$	0.2526	>0.001	1.818477	0.133937
	Low-center	$y = 0.027e^{0.0402x}$	0.1759	>0.001	1.494811	0.10191
29-Jul	Rim	$y = 0.0279e^{0.0218x}$	0.0545	>0.001	1.241016	0.052889
	Trough	$y = 0.0343e^{0.0376x}$	0.1368	>0.001	1.456405	0.10664

Table 2 - Weekly soil chamber respiration ($\text{gC}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) vs. chamber air temperature ($^{\circ}\text{C}$) by ecosystem type with mean least squares exponential regression fit and modeled Q_{10} . Data are shown ecosystem type and include r^2 , p values, and standard error for each Q_{10} estimate.

		Regression Equation	R2	p-value	Q ₁₀	SE
16-Jun	High	$y = 0.015e^{0.0758x}$	0.539	<0.001	2.134007	0.159259
-	Low	$y = 0.0216e^{0.074x}$	0.6813	<0.001	2.095936	0.185527
24-Jun	Rim	$y = 0.017e^{0.0815x}$	0.4005	<0.001	2.259158	0.185592
	Trough	$y = 0.0326e^{0.0655x}$	0.5283	<0.001	1.925164	0.196539
25-Jun	High	$y = 0.0101e^{0.0958x}$	0.367	<0.001	2.606484	0.176102
-	Low	$y = 0.0169e^{0.1055x}$	0.4221	<0.001	2.871967	0.259083
1-Jul	Rim	$y = 0.0123e^{0.0936x}$	0.3286	<0.001	2.549768	0.188512
	Trough	$y = 0.0184e^{0.1156x}$	0.2581	<0.001	3.159708	0.305796
2-Jul	High	$y = 0.0151e^{0.00773x}$	0.6216	<0.001	2.166307	0.163721
-	Low	$y = 0.0249e^{0.0604x}$	0.7434	<0.001	1.832684	0.156304
8-Jul	Rim	$y = 0.0178e^{0.0691x}$	0.5975	<0.001	1.995705	0.154902
	Trough	$y = 0.0346e^{0.0516x}$	0.4529	<0.001	1.675308	0.153023
9-Jul	High	$y = 0.0213e^{0.0239x}$	0.1115	<0.001	1.266841	0.050969
-	Low	$y = 0.0228e^{0.049x}$	0.4232	<0.001	1.63236	0.117074
15-Jul	Rim	$y = 0.0196e^{0.0346x}$	0.1608	<0.001	1.391941	0.070283
	Trough	$y = 0.0316e^{0.0322x}$	0.1435	<0.001	1.379876	0.086351
16-Jul	High	$y = 0.0164e^{0.0594x}$	0.3191	<0.001	1.811246	0.124113
-	Low	$y = 0.0251e^{0.0472x}$	0.3216	<0.001	1.603197	0.117704
22-Jul	Rim	$y = 0.0209e^{0.0472x}$	0.2169	<0.001	1.603182	0.107403
	Trough	$y = 0.0296e^{0.0462x}$	0.2448	<0.001	1.587231	0.124749
23-Jul	High	$y = 0.0175e^{0.062x}$	0.2505	<0.001	1.859005	0.134872
-	Low	$y = 0.0259e^{0.0429x}$	0.1706	<0.001	1.535737	0.107339
29-Jul	Rim	$y = 0.0258e^{0.0261x}$	0.0746	<0.001	1.298238	0.062197
	Trough	$y = 0.0331e^{0.0389x}$	0.1334	<0.001	1.351133	0.083949

Table 3 - Full model (n=97) linear mixed effects models of respiration on environmental parameters (significant with $p < 0.05$).

Dependent Variable	Independent Variable	R ²	n	p-value
<i>logExp_Flux</i>	<i>Ecosystem_Type</i>	0.327	69	
	- (Intercept)			<0.0001
	- <i>Ecosystem_Type</i> LOW			0.1881
	- <i>Ecosystem_Type</i> RIM			0.3031
<i>logExp_Flux</i>	<i>Ecosystem_Type + Thaw_Depth</i>	0.453	69	
	- (Intercept)			<0.0001
	- <i>Ecosystem_Type</i> LOW			0.7246
	- <i>Ecosystem_Type</i> RIM			0.5492
	- <i>Ecosystem_Type</i> TROUGH			0.0031
<i>logExp_Flux</i>	<i>Ecosystem_Type + Thaw_Depth + Water_Table</i>	0.520	69	
	- (Intercept)			<0.0001
	- <i>Ecosystem_Type</i> LOW			0.4278
	- <i>Ecosystem_Type</i> RIM			0.9527
	- <i>Ecosystem_Type</i> TROUGH			0.0005
	- <i>Thaw_Depth</i>			<0.0001
<i>logExp_Flux</i>	<i>Ecosystem_Type + Thaw_Depth + Water_Table + Tchamber</i>	0.538	69	
	- (Intercept)			0.0006
	- <i>Ecosystem_Type</i> LOW			0.5427
	- <i>Ecosystem_Type</i> RIM			0.7074
	- <i>Ecosystem_Type</i> TROUGH			0.0009
	- <i>Thaw_Depth</i>			0.0077
	- <i>Water_Depth</i>			0.0002
- <i>Tchamber</i>	0.0014			

Table 4 - Reduced model (n=69) linear mixed effects models of respiration on environmental parameters (significant with $p < 0.05$).

Dependent Variable	Independent Variable	R ²	n	p-value
<i>logExp_Flux</i>	<i>Ecosystem_Type</i>	0.278	97	
	- (Intercept)			<0.0001
	- Ecosystem_TypeLOW			0.1563
	- Ecosystem_TypeRIM			0.1968
	- Ecosystem_TypeTROUGH			0.0190
<i>logExp_Flux</i>	<i>Ecosystem_Type + Tchamber</i>	0.578	97	
	- (Intercept)			<0.0001
	- Ecosystem_TypeLOW			0.1235
	- Ecosystem_TypeRIM			0.3375
	- Ecosystem_TypeTROUGH			0.0522
	- Tchamber			<0.0001

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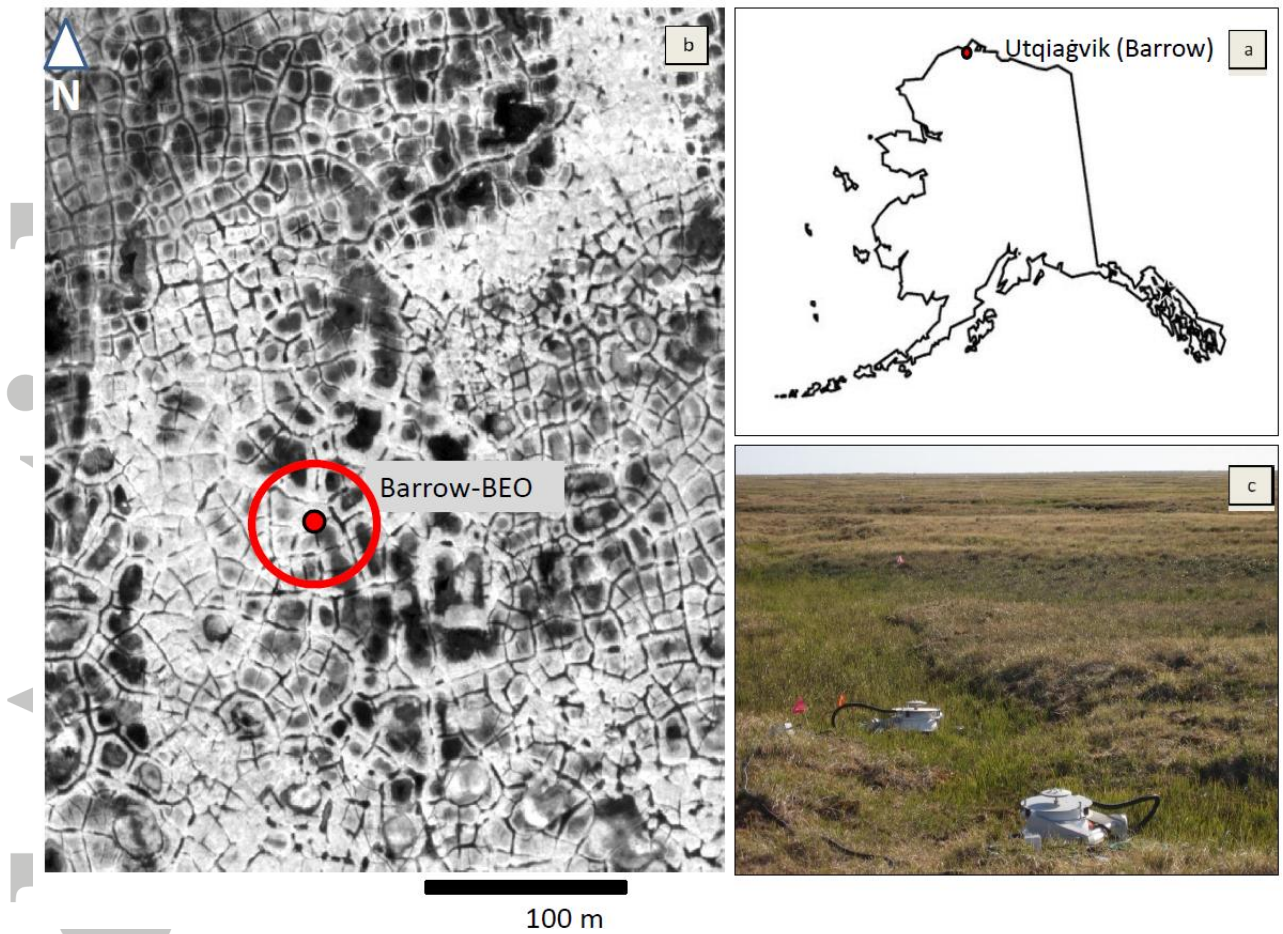


Figure 1 - (a) Utqiagvik, Alaska. (b) Study site within the Barrow Environmental Observatory. (c) A LI-COR 8100 chamber assembly within polygon troughs.

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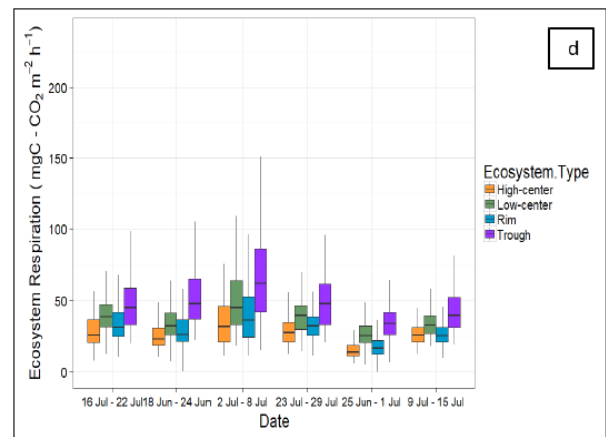
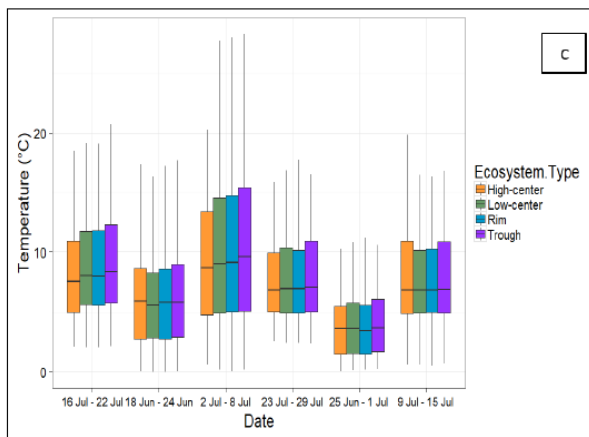
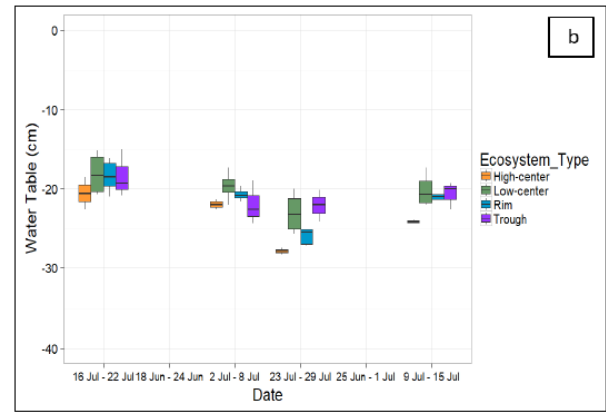
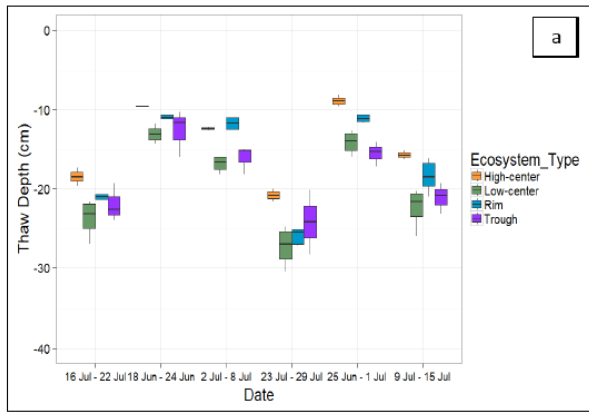


Figure 2 - (a) Weekly thaw depth (cm) by ecosystem type. (b) Weekly water table (cm) by ecosystem type. (c) Weekly chamber air temperature derived respiration ($\text{mgC-CO}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) across ecosystem type. (d) Weekly soil surface air temperatures ($^{\circ}\text{C}$) measured with the soil chamber headspace. Displayed are median, interquartile range, and standard deviations.

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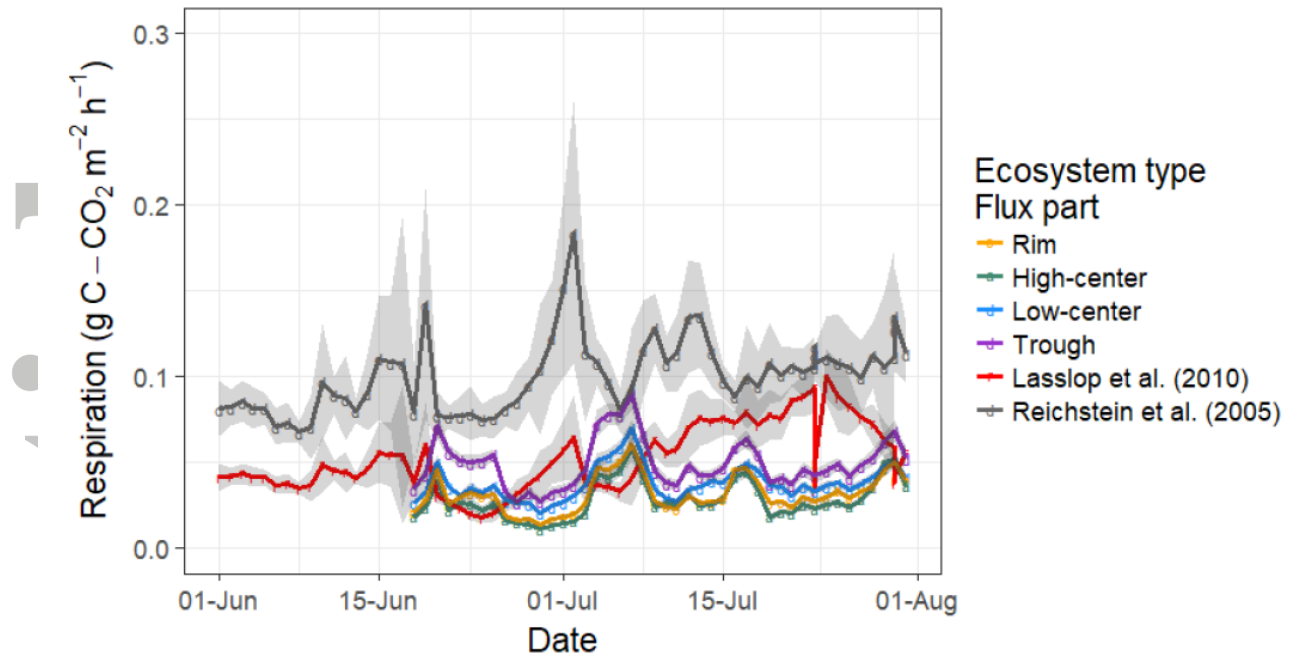


Figure 3 - Daily chamber respiration (gC-CO₂·m⁻²·h⁻¹) across ecosystem type compared to estimated tower respiration.

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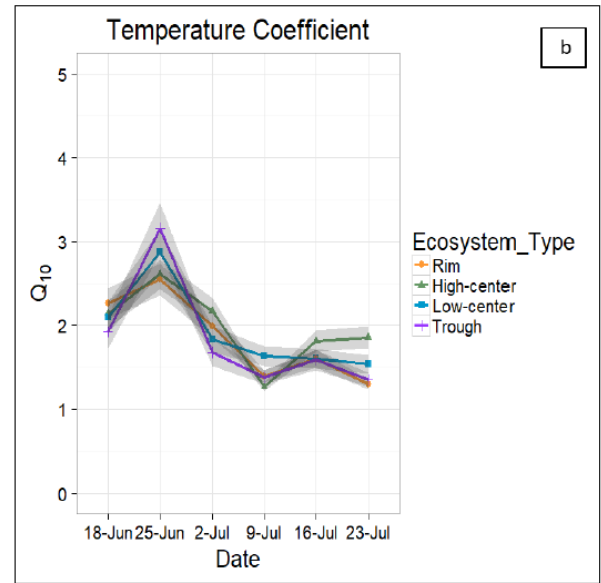
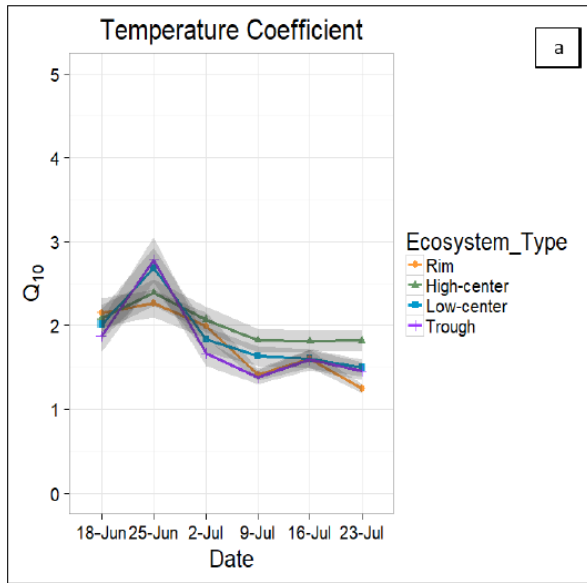


Figure 4 - (a) Chamber air derived growing season Q_{10} . (b) Soil tower derived growing season Q_{10} . Shaded areas represent 95% confidence intervals.

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