

Title: Tundra is a consistent source of CO₂ at a site with progressive permafrost thaw during six years of chamber and eddy covariance measurements.

Authors: Gerardo Celis^{*,1,2}, Marguerite Mauritz¹, Rosvel Bracho⁴, Verity G. Salmon³, Elizabeth E. Webb², Jack Hutchings², Susan M. Natali⁵, Christina Schädel¹, Kathryn G. Crummer⁴, Edward A.G. Schuur^{1,2}

*Corresponding author; email: gerardo.celis@nau.edu

¹Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA,

²Biology Department, Bartram Hall, University of Florida, Gainesville, Florida 32611, USA

³Environmental Sciences Division, Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN, USA,

⁴School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA,

⁵Woods Hole Research Center, Falmouth, Massachusetts, USA.

Key points:

- Arctic tundra ecosystem is an annual net source of CO₂.
- Winter CO₂ release offsets growing season CO₂ gain.
- Active layer thickness is a significant driver of NEE, GPP, and R_{eco}.

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Abstract:

Current and future warming of high latitude ecosystems will play an important role in climate change through feedbacks to the global carbon cycle. This study compares six years of CO₂ flux measurements in moist acidic tundra using autochambers and eddy covariance (Tower) approaches. We found that the tundra was an annual source of CO₂ to the atmosphere as indicated by net ecosystem exchange using both methods with a combined mean of 105 ± 17 g CO₂-C m⁻² y⁻¹ across methods and years (Tower 87 ± 17 and Autochamber 123 ± 14). The difference between methods was largest early in the observation period, with Autochambers indicated a greater CO₂ source to the atmosphere. This discrepancy diminished through time and in the final year the Autochambers measured a greater sink strength than tower. Active layer thickness (ALT) was a significant driver of NEE, GPP, and R_{eco} and could account for differences between Autochamber and Tower. The stronger source initially was attributed lower summer season gross primary production (GPP) during the first three years, coupled with lower ecosystem respiration (R_{eco}) during the first year. The combined suppression of GPP and R_{eco} in the first year of Autochamber measurements could be the result of the experimental setup. Root damage associated with Autochamber soil collar installation may have lowered the plant community's capacity to fix C, but recovered within three years. While this ecosystem was a consistent CO₂ sink during the summer, CO₂ emissions during the non-summer months offset summer CO₂ uptake each year.

Index terms (Max 5): 1615, 0428, 0439, 0702, 0718

Keywords (Max 6): Carbon fluxes, Climate change, Tundra, Arctic, Permafrost,

1 Introduction

High latitude ecosystems are among the global ecosystems that will experience greatest increases in air temperature by the end of the century due to climate amplification [IPCC, 2014]. These ecosystems store large stocks of carbon (C) in soils, in particular in perennially frozen soils (permafrost), which currently contain approximately 1330-1580 PgC in the form of frozen soil organic matter [Tarnocai *et al.*, 2009; Hugelius *et al.*, 2014; Schuur *et al.*, 2015]. Current warming in high latitude regions is associated with soil warming and permafrost thaw [Romanovsky *et al.*, 2011; IPCC, 2014], which has the potential to release large amounts of stored C to the atmosphere. An estimated 130 to 160 Pg C will be released by 2100 under a high warming scenario (i.e., RCP 8.5; [Schuur *et al.*, 2015]), and these C emissions are expected to accelerate the rate of global climate change [Koven *et al.*, 2011].

The net contribution of CO₂ from high latitudes to the atmosphere will depend on the balance between two major processes: (a) decomposition and/or physical release of soil C reserves [Xue *et al.*, 2016] and (b) the capacity of vegetation to fix atmospheric CO₂ during the growing season [Schimel, 1995; Lucht *et al.*, 2002; Walker *et al.*, 2012]. The drivers that will influence CO₂ fluxes can be physical and/or biological [McGuire *et al.*, 2009]. Physical drivers that have the potential to alter CO₂ fluxes are: longer snow free periods [Groendahl *et al.*, 2007; Euskirchen *et al.*, 2009; Lund *et al.*, 2012], increased temperature [Rustad *et al.*, 2000; Davidson and Janssens, 2006] reduced soil moisture [Oberbauer *et al.*, 2007; Sharp *et al.*, 2013; Natali *et al.*, 2015], and increased nutrient availability [DeMarco *et al.*, 2014; Salmon *et al.*, 2016]. Biological drivers potentially tied to fluxes are: improved species performance [Chapin and Shaver, 1985; Oberbauer *et al.*, 2013], shift in plant communities [Walker *et al.*, 2006; Schuur *et al.*, 2007; Myers-Smith *et al.*, 2011; Hollister *et al.*, 2015] and herbivory [Welker *et al.*, 2004; Kelsey *et al.*, 2016]. The warming of soils and thawing of

permafrost stimulate soil organic matter decomposition [Mackelprang *et al.*, 2011; Schädel *et al.*, 2014; Xue *et al.*, 2016] and increase heterotrophic respiration from soils resulting in a positive feedback to the atmospheric CO₂ concentration, but will depend on snow accumulation [Nowinski *et al.*, 2010; Blanc-Betes *et al.*, 2016] and changes in soil community abundance and composition [Mohan *et al.*, 2014; Morgado *et al.*, 2015; Parker *et al.*, 2015; Semenova *et al.*, 2015; Geml *et al.*, 2016; Morgado *et al.*, 2016]. Increased CO₂ loss may however be counteracted by increases in net primary production (NPP) as plant productivity increases [Epstein *et al.*, 2012] and the plant community shifts from graminoid to shrub dominance [Sturm *et al.*, 2005; Walker *et al.*, 2006; Myers-Smith *et al.*, 2011; Pearson *et al.*, 2013; Hollister *et al.*, 2015]. There is considerable variability among observational studies and modeling approaches [Koven *et al.*, 2011], with some reviews showing annual CO₂ emissions exceed CO₂ uptake [Belshe *et al.*, 2013], while others indicate that the tundra is a net CO₂ sink [McGuire *et al.*, 2012 and references therein]. There is growing evidence that winter is an important driver of annual estimates since cold season losses which can offset summer season gains [Fahnestock *et al.*, 1999; Welker *et al.*, 2000; Euskirchen *et al.*, 2012; Grogan, 2012; Oechel *et al.*, 2014]. Yet, winter remains one of the most uncertain periods of the Arctic CO₂ balance. In the past it has been difficult to constrain Arctic CO₂ fluxes due to spatially and temporally sparse measurements, and differences in measurement techniques. Better estimates of both the magnitude and direction of CO₂ fluxes (i.e., net source or sink) is critical for understanding the strength of the Arctic carbon-climate feedback.

Studies related to CO₂ fluxes measurements are often collected at different spatial scales. Small-scale (<1 m²) measurements are used to understand the dynamics of manipulative experiments (e.g. the International Tundra Experiment, ITEX [Henry and Molau, 1997]) and local processes that affect CO₂ cycling. Small-scale measurements provide important

mechanistic insights for CO₂ fluxes, but can be difficult to scale and be biased by site selection [Fox *et al.*, 2008]. Eddy covariance towers are used at larger scales (>10,000 m²) to observe landscape dynamics and can incorporate a wide range of microsite conditions and vegetation types, which affect the CO₂ balance [Belshe *et al.*, 2012], but may not capture mechanistic processes. The process of data comparison for landscape-level analysis is further complicated by the fact that many studies only utilize one method to measure CO₂ fluxes at a given site. It is well documented that measured CO₂ flux estimates vary depending on the method employed [Björkman *et al.*, 2010; Riederer *et al.*, 2014; Webb *et al.*, 2016] and co-located measurements of CO₂ fluxes using different methods can differ due to the small scale changes in the local plant community, time of day, and time of year [Oechel *et al.*, 1998; Smith *et al.*, 2003; Myklebust *et al.*, 2008]. Accurate quantification of the arctic CO₂ balance relies on the ability to combine and compare chamber and tower based data but there is a scarcity of research on how these two methods differ from one another. The present study provides an opportunity to compare these two measurement techniques and determine both the magnitude and direction of CO₂ fluxes (i.e., net source or sink) in a rapidly thawing tundra ecosystem.

This study examined the dynamics of ecosystem CO₂ exchange using two complementary methods of measuring CO₂ fluxes: (a) plot-scale experiment (<1m² scale using autochambers) and (b) landscape observation (>10,000 m² using Eddy covariance) measurements. We addressed the following questions: (1) Is tundra a net annual CO₂ source or sink at a site with permafrost thaw? (2) What are seasonal and interannual changes in CO₂ magnitude, and what environmental variables drive these changes? (3) Do measurements at different scales (eddy covariance tower and autochambers) show the same magnitude and variability?

2 Methods

2.1 Site descriptions and setup

Carbon dioxide flux measurements were measured within a discontinuous permafrost zone at the Eight Mile Lake (EML) research site near Healy, Alaska, USA [Schuur *et al.*, 2007; 2009; Vogel *et al.*, 2009; Lee *et al.*, 2010; 2011; Natali *et al.*, 2011; Belshe *et al.*, 2012; Natali *et al.*, 2012; Trucco *et al.*, 2012; Hicks Pries *et al.*, 2013a; 2013b; Natali *et al.*, 2014; 2015; Salmon *et al.*, 2016; Webb *et al.*, 2016; Mauritz *et al.*, 2017]. The site contains a permafrost borehole which has documented rising permafrost temperatures since 1985 [Osterkamp and Romanovsky, 1999] and within the past three decades the site has experienced varying levels of disturbance associated with permafrost thaw [Schuur *et al.*, 2007]. The site vegetation community depends on permafrost degradation. Low and intermediate thaw stages are dominated by the graminoid *Eriophorum vaginatum*, a tussock-forming sedge, whereas in the transition to extensively thawed permafrost shrubs (evergreen - *Rhododendron subarcticum* and deciduous - *Vaccinium uliginosum*) become dominant [Schuur *et al.*, 2007]. Landscape-scale CO₂ fluxes have been monitored since June 2008 using the eddy covariance approach (hereafter called Tower; 63° 52' 42"N, 149° 13' 12"W). Small scale CO₂ fluxes were measured at the plot level (0.36m²) from the Carbon in Permafrost Experimental Heating Research project (hereafter called Autochamber; 63° 52' 59"N, 149° 13' 32"W), which was initiated in September 2008 and was designed to simulate anticipated increases in soil and air temperatures [Natali *et al.*, 2011]. Because the goal of this analysis was to evaluate how permafrost thaw impacts CO₂ fluxes under ambient climate forcing, only control plots, which did not receive any warming treatment, were used in this analysis. Control plots were selected from within the blocked split-plot warming experiment which used snow fences and open top chambers OTCs to simulate warming; there were two control plots (60x60cm) at each of the six snow fences so we used a total of 12 replicate plots for this study. Further description of

the field site and warming experiment can be found in [Natali *et al.*, 2011; 2012].

Autochamber plots are located just outside the tower fetch and soil classification, climatic conditions, topography and vegetation community were similar between Autochamber and Tower [Schuur *et al.*, 2007; Natali *et al.*, 2011; 2012]. A high-resolution active layer thickness (ALT) survey (n=310) in 2008 and 2009 at the Tower showed that ALT ranges at Tower and Autochamber plots encompassed similar ranges throughout the study period [Belshe *et al.*, 2012]. The Tower included few areas with more extensive permafrost thaw than was documented at Autochamber. Based on 2009 plot-level census (Tower n= 225 and Autochamber n=12) vegetation is dominated by moist acidic tussock tundra comprising an average mixture of ~11-29% sedges (*Eriophorum vaginatum*), ~23-25% deciduous and ~25-29% evergreen shrubs (*Vaccinium uliginosum*, *Rubus chamaemorus*, *Betula nana*, and *Rhododendron subarcticum*), and ~20-39% nonvascular plants (*Sphagnum* spp., *Dicranum* spp., feathermoss, and lichens) [Salmon *et al.*, 2016].

2.2 Environmental monitoring

An Onset HOBO (Bourne, MA) weather station measured environmental parameters including air temperature, rainfall, and photosynthetically active radiation (PAR) at Autochamber. The Tower data were collected at an adjacent station, which included PAR (Li-190SA, LI-COR Biosciences), incident radiation (Li-200SA, LI-COR Biosciences), net radiation (REBS Q*7.1, REBS Inc., Seattle, Washington), relative humidity and air temperature (Vaisala HMP45c, Campbell Scientific), and wind speed and direction (RM Young 3001, Campbell Scientific). Soil temperatures (10 cm depth) were measured continuously in each plot at Autochamber and in two locations at Tower using constantan-copper thermocouples. Active layer thickness (ALT; end of summer season maximum thickness of thawed ground) was measured in each plot at Autochamber and at 9 locations

within the Tower footprint using a metal depth probe. Water table depth was measured from 12 water wells at Autochamber and 9 wells at Tower. Thaw and water table depth measurements were co-located with reported observations of the plant community and so these measurements capture the range of environmental conditions experienced by the plant communities at this site, and the range of microsites integrated by the tower.

2.3 Carbon flux measurements

Net ecosystem carbon exchange (NEE) was measured using two different approaches: (1) landscape dynamics using an eddy covariance tower and (2) localized plot measurements using autochambers. During the summer season both methods were simultaneously deployed; during the non-summer season CO₂ fluxes were estimated by a combination of manual chamber flux measurement and models parameterized with Tower measurements and method-specific soil temperatures. Negative NEE indicate CO₂ uptake by the ecosystem.

Autochamber NEE ($\mu\text{mol CO}_2\text{-C m}^{-2} \text{ s}^{-1}$) and ecosystem respiration ($R_{\text{eco}} \mu\text{mol CO}_2\text{-C m}^{-2} \text{ s}^{-1}$) were measured using automated CO₂ flux systems during the summer (May-September) of 2009-2014. Automated flux chamber (0.36 m² x 0.25 m) measurements were made continuously (every 1.5 hours) at 12 plot locations and averaged per fence (n = 6). Automated chamber measurements were supplemented with weekly manual chamber measurements from October to November, in order to capture fall-season dynamics and before snow-cover impeded further measurements. For both automated and manual measurements air was circulated within the chamber and CO₂ concentrations were sampled in 2 s intervals at 1 L min⁻¹, for 1.5 min, using an infrared gas analyzer (LI-820, LICOR Corp., Lincoln, Nebraska), and recorded on a data logger (Campbell Scientific CR1000 in the summer and Arduino unit in the fall). NEE flux rates were calculated using linear regression and converted from

volumetric ($\text{ppm CO}_2 \text{ m}^2 \text{ s}^{-1}$) to mass ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) using plot-specific chamber volumes and air temperatures. Flux data were quality controlled for outlying and erratic fluxes based on equipment failure and environmental conditions known to produce erratic fluxes (ie: wind speeds exceeding 7 m s^{-1}). After screening, at least 80% of total flux measurements were retained. A more detailed description of the setup and data processing can be found in [Natali *et al.*, 2011; 2014; Mauritz *et al.*, 2017].

Tower NEE was measured using eddy covariance (EC) starting May 2008 to September 2014. The system consisted of a sonic anemometer (CSAT3, Campbell Scientific, Logan, Utah) and an open path infra-red gas analyzer (Li-7500, LI-COR Biosciences, Lincoln, Nebraska) mounted on a 2 m tower from 2008 to May 2011 after which sensors were raised to 3.5 m and a Li-7500A CO₂ analyzer was installed. High frequency data for CO₂, water vapor, orthogonal wind components (*u*, *v*, and *w*), and air temperature were recorded at 10 Hz using a CR500 data logger (Campbell Scientific). Calibration was performed at least twice a year using a zero CO₂ air source, an atmospheric CO₂ standard ($\pm 1\%$), and a dew point generator (Li-610, LI-COR Biosciences) for water vapor. The internal sensor head temperature for Li-7500A was changed when mean ambient temperature reached 5°C. Fluxes were estimated from 30 minute averaged covariance of CO₂ and vertical wind speed using EdiRe software (University of Edinburgh). Fluxes were corrected for frequency loss, sensor separation, and misalignment of wind sensors with respect to the local streamline [Foken and Wichura, 1996; Aubinet *et al.*, 2000], and air density [Webb *et al.*, 1980; Burba *et al.*, 2008]. Post-processing screening eliminated data when: 1) half-hour data was incomplete, 2) frictional speed (U^*) was $< 0.12 \text{ m s}^{-1}$ [Goulden *et al.*, 1996], and 3) when variation of the half-hourly orthogonal wind components exceeded one standard deviation distance from the mean. Further detailed description (quality control and filtering) is available in [Belshe *et al.*,

2012] and percentages of measured data can be found in Table S1. The Tower footprint from the tower estimate ranged from 200 m to 350 m [Kormann and Meixner, 2001] and covered a similar vegetation and permafrost thaw gradient at both height footprints. The influence of these more extensive permafrost thaw areas on Tower CO₂ fluxes were analyzed with a spatially explicit model that accounts for microtopography caused by permafrost degradation and it was compared to a nonlinear model presented in this manuscript did not substantially differ in aggregated CO₂ predictions throughout 2008 and 2009 [Belshe *et al.*, 2012].

2.4 Gap-filling and budget calculations

Fluxes were divided into non-summer season (October 1st through April 30th the following year) and the following summer season (May 1st to September 30th) and gap-filled using season specific models.

2.4.1 Summer gap-filling

Gaps in summertime NEE due to filtering and missing values were filled using a weekly hyperbolic light-response equation during high light conditions [Thornley and Johnson, 1990] (Text S1; equation 1; PAR $\geq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ Tower and PAR $\geq 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ Autochamber). For Autochambers, hyperbolic light response curves were fit for each plot on a monthly basis and gap-filling occurred at the plot-level. Gaps in nighttime NEE (R_{eco} , PAR $< 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ Tower and PAR $< 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ Autochamber) were filled using a summer season exponential temperature response with 10 cm soil temperature at Autochamber and air temperature at Tower (Text S1; equation S2). The parameters obtained from the low PAR R_{eco} model for each summer season were used to model daytime R_{eco} . Gross ecosystem primary productivity (GPP) was estimated by subtracting R_{eco} from NEE.

2.4.2 Non-summer gap filling

Non-summer season gap-filling and cumulative CO₂ flux estimates were made separately for each shoulder season (fall, and spring) and winter in order to account for small, but detectable amounts of GPP in the autumn and spring. This method allows greater sensitivity to variation in growing season length and photosynthetic capacity (mosses and evergreens), rather than assuming the entire non-summer season only consists of R_{eco} [Webb *et al.*, 2016]. Tower measurements continued throughout the non-summer season, and manual chamber measurements extended the data at Autochamber from October-November.

In the fall shoulder season, NEE and R_{eco} at Autochamber were modeled using light and temperature response curves parameterized with weekly manual chamber measurements (equations S1 & S2). In the spring shoulder season Autochamber GPP was estimated based on measured May GPP using Tower's ratio of early spring GPP to May GPP (equation S4, text S1). R_{eco} in spring was estimated using the winter model (equation S3, text S1) for both Autochambers and Tower, because soils were typically still frozen and the area snow-covered. NEE for spring was calculated as the sum of GPP and R_{eco} (text S1) and [Webb *et al.*, 2016]). At Tower, fall and spring were estimated weekly until GPP could no longer be detected.

Winter R_{eco} fluxes were gap-filled using an exponential relationship between Tower NEE, soil temperature (10 cm depth), and day of season (starting October 1st of each year) (equation 3, text S1). Winter season R_{eco} from 2008 to 2013 was modeled with a single parameter set from Webb *et al.* [2016], due to insufficient data coverage during individual years. In 2014, data coverage was greater and new model parameters were derived using soil temperature and day of season. Winter R_{eco} for Autochamber was gap-filled using the Tower

parameters, but with plot-specific soil temperatures. Winter methods were evaluated in [Webb *et al.*, 2016].

All measured and gap-filled thirty minute CO₂ fluxes were aggregated to daily, seasonal, and yearly periods.

2.4.3 Uncertainty estimates

Uncertainties for Tower NEE were assessed using bootstrapping [Liu *et al.*, 2009]. Light response and temperature models were fit to measured data using seasonal resolution (summer and non-summer) described above and residuals were binned based on PAR (5 bins) for light response models and soil temperature (10 bins) for temperature models. In each bin category artificial data sets (1000) were created by adding predicted model values to randomly drawn and replaced residuals, and models were refit in order to gap fill data. The 95% CI were obtained from 1000 complete flux time series for seasonal cumulative fluxes (see Text S2 for more details). Autochamber uncertainties were based on standard errors of replicate plot measurements (n=12).

2.5 Data analysis

Annual (October through September of the following year) NEE, GPP and R_{eco} were compared within a given year between the Tower and Autochamber methods using 95% confidence intervals generated from uncertainties. Differences were considered significant if the 95% confidence interval of the estimated aggregate fluxes did not overlap. Interannual differences in Autochamber fluxes were compared using an analysis of variance (ANOVA) and a post hoc Tukey test. Tower interannual differences were based on 95% confidence intervals generated from uncertainty analysis. The relationship of daily growing season NEE, GPP and R_{eco} were compared between Tower and mean Autochamber estimates for each year using linear regressions.

In order to determine whether ALT and WTD, two major physical drivers for this ecosystem, could explain variation in fluxes we analyzed the relationship of summer season NEE, GPP and R_{eco} cumulative fluxes with ALT and WTD using a linear mixed effects model [Bates *et al.*, 2015]. Water table depth and ALT were fixed effects and method a random effect. We used a backward step-wise model selection to eliminate variables that resulted in less than 5 AIC change (only WTD eliminated). All data processing and analyses were performed using the *R* platform [R Development Core Team, 2015] and a significance level of $\alpha = 0.05$

3 Results

3.1 Fluxes

3.1.1 Net Ecosystem Exchange

On an annual basis, fluxes from both methods were a net CO_2 source during the six years with an average of $87 \pm 17 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ measured with Tower and $123 \pm 14 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ measured with Autochamber with a combined mean of $105 \pm 17 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$. For the first three years Autochamber released significantly more CO_2 than Tower (Figure 3a & Table S3). Annual differences were driven by both summer and non-summer season differences. During the non-summer season, fluxes differed between methods in two of the six years with Autochamber having lower fluxes in the third year and higher NEE fluxes in the sixth (Figure 1c). Over six years, the summer season sink strength increased significantly at Autochamber from almost neutral, -7 ± 7 , to a sink of $-105 \pm 11 \text{ g CO}_2\text{-C m}^{-2}$ (Figures 2, 3b & Table S3), reaching similar levels to those of the Tower. Tower NEE fluxes decreased over time, where net uptake decreased over time ranging from -134 g to $-53 \text{ CO}_2\text{-C m}^{-2}$, with lowest net uptake during years five and six (Figures 2, 3 & Table S3). Summer season NEE light response curves also indicated a progressive increase in C fixation at Autochamber,

reaching similar parameters to Tower in the later years and surpassing it in the final year (Figure 4, 2S & Table S2).

Daily NEE fluxes (measured and gap-filled data) during the summer season were significantly correlated between Tower and Autochamber in all six years (each year at least $p < 0.01$, $r^2 \geq 0.71$; Figure 1). As the years progressed, the fluxes became more similar to each other in magnitude (Figure 1a & 1f) and the slope approached 1 (2009 slope = 0.35 and 2014 slope = 0.99). Comparing methods using only measured data, when both were sampled in the same half-hourly period, found that the direction of NEE (i.e., CO₂ source or sink) was similar 79-86% of the time, and methods became more similar over time. When considering the transition point from sink to source, the date when cumulative NEE became positive was similar for Tower and Autochamber and occurred between August 25th and August 30th, only a 6 day range across five of the six years. The transition between sink and source was consistent despite interannual variation in spring snowmelt, which varied on average 12 days over the 6 years (Table 1). The first year of observation, 2009, was an exception; Autochamber NEE changed from a net CO₂ sink to a source on August 4 was 22 days earlier than the other years (Table 2). In contrast the Tower switched on August 27, 2009, consistent with all other years.

3.1.2 Gross Primary Production

Daily GPP was significantly correlated between methods during all five years (each year at least $p < 0.01$, $r^2 \geq 0.77$; Figure 1g to 1i). Annual GPP was lower during the first three years at Autochamber than at Tower, with the magnitude of the difference dropping by almost half in each subsequent year (Figure 3d Table S3). Tower GPP uptake was greatest in the first year of measurement (-471 g CO₂-C m⁻²) and then decreased to a relatively consistent level

by the third year (-396 to -423 g CO₂-C m⁻²). In contrast, Autochamber showed a progressive increase over time (Figure 3d), such that GPP was small during the first year (-205 g CO₂-C m⁻²) but increased by ~100 g CO₂-C m⁻² in the second year, held that increase in the third year, and then increased again in years four (~180 CO₂-C m⁻² more than the first year), five (~200 CO₂-C m⁻² more than the first year), and six (~250 CO₂-C m⁻² more than the first year; Figures 2 & 3d & Table S3). The Autochamber increase over time was driven by increased GPP in June, July and August of each year (Figure S2 & Table S2). Summer season GPP had similar trends to annual GPP (Figure 2 & 3e & Table S). Non-summer season contributed relatively little to annual GPP (-0.4 to -21 g CO₂-C m⁻² both methods) and showed an increase with both methods over time (Figure 3f, Table S3). Autochamber had a significantly lower uptake in four of the six years compared to Tower (Table S3) for non-summer season.

3.1.3 Ecosystem Respiration

Daily R_{eco} was significantly correlated between methods during all six years (each year at least $p < 0.01$, $r^2 \geq 0.44$; Figure 1). Annual R_{eco} was significantly lower in Autochamber during the first year (Autochamber: 387 g CO₂-C m⁻² Tower: 545 g CO₂-C m⁻²; Figure 3g Table S3). After 2009 Autochamber R_{eco} and Tower were well correlated with no observable trend over time. Summer season R_{eco} trends were similar to annual fluxes. Tower R_{eco} ranged from 302 to 355 g CO₂-C m⁻² and Autochamber R_{eco} 198 to 347g CO₂-C m⁻² (Figure 2 & 3h & Table S3). During the summer season R_{eco} and GPP were tightly coupled in both methods, with high seasonal cumulative GPP occurring during periods with high seasonal cumulative R_{eco}. The ratio of R_{eco}/GPP for the summer season was consistent between years, where Tower was on average 0.78 and Autochamber 0.85 (Table S4). Non-summer season R_{eco} with Tower was 163 to 211 g CO₂-C m⁻² and 144 to 228 g CO₂-C m⁻² with Autochamber, which

accounts for 37% and 39% of annual respiration fluxes, respectively (Figure 3g & 3i, Table S3).

3.2 Fluxes and environmental factors

Summer season active layer thickness was significantly shallower with Autochamber for the first two years than with Tower ($p < 0.001$; Figure S1). There was a significant relationship ($p < 0.01$, Figure 5 Table S7) between summer season fluxes (NEE, GPP, R_{eco}) and Active layer thickness (ALT). GPP had a stronger relationship with ALT ($r^2 = 0.84$, Figure 5b; higher CO_2 uptake increased with greater ALT), than R_{eco} ($r^2 = 0.59$; Figure 5c & Table S7), followed by NEE (Figure 5a & Table S7). There was no relationship between fluxes and WTD (Table S7).

4 Discussion

Annual CO_2 fluxes were consistent in demonstrating that the tundra ecosystem was a net annual source of CO_2 to the atmosphere (mean $105 \pm 17 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ across methods and years) during our study period. Our Tower measurements ($87 \pm 17 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$) were higher than other eddy covariance studies, which have reported annual tundra CO_2 fluxes that vary from -6.4 to $68.7 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ [Euskirchen *et al.*, 2012; Belshe *et al.*, 2013; Lüers *et al.*, 2014; Oechel *et al.*, 2014; Zona *et al.*, 2014]. Autochamber measurements ($123 \pm 14 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$) were within the range of other studies, which have reported annual fluxes from the tundra between -109 to $194 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ - chamber measurements [Grogan and Iii, 1999; Trucco *et al.*, 2012; Kim *et al.*, 2016].

Active layer thickness was identified as a key driver of cumulative GPP, NEE and R_{eco} throughout the summer season and explained differences between Tower and Autochambers in the first two years. Increased GPP and R_{eco} were related to deeper thaw, which is similar to other studies at EML [Vogel *et al.*, 2009; Trucco *et al.*, 2012]. Increased plant productivity as a result of active layer deepening is associated with increased nutrient availability as permafrost thaws [Finger *et al.*, 2016; Salmon *et al.*, 2016], although autotrophic respiration also increases [Hicks Pries *et al.*, 2015]. Active layer thickness incorporates several characteristics of the soil environment including soil moisture, soil structure, and soil temperature [Trucco *et al.*, 2012]. Increased ALT was also related to increases in R_{eco} by stimulating heterotrophic respiration as a result of increased organic matter decomposition under higher temperatures and increased moisture [Hicks Pries *et al.*, 2013b], and the availability of deep soil C [Schuur *et al.*, 2009; Hicks Pries *et al.*, 2013a; Koven *et al.*, 2015].

Summer season daily fluxes of NEE, GPP, and R_{eco} were correlated between Autochamber and Tower, with R_{eco} showing less correlation and more variability between methods, consistent with other tundra sites that compared these two types of measurement methods [Zamolodchikov *et al.*, 2003; Kade *et al.*, 2012]. Even though daily GPP and NEE fluxes were highly correlated between methods, they differed in magnitude for the first three years; Autochamber measurements had lower uptake for the first three years. This is contrary to what has been observed by other studies comparing chambers and eddy covariance, which have shown higher net CO_2 uptake from chamber measurements [Fox *et al.*, 2008; Kade *et al.*, 2012]. The discrepancy between Tower and Autochamber in magnitude of NEE, GPP, and R_{eco} and light sensitivity model parameters (Table S2) in the initial years may have derived from the unintended effects of experimental setup of the Autochamber system. Chamber bases for autochamber measurements were installed to a depth of 5-8 cm, which

may have severed rooting systems and reduced fine root respiration [Wang *et al.*, 2005; Heinemeyer *et al.*, 2011]. In Arctic plant communities, belowground biomass is concentrated near the surface [Sullivan and Welker, 2005; Sullivan *et al.*, 2007; Iversen *et al.*, 2015], and stored root C and respiration can contribute substantially to C flux dynamics [Hopkins *et al.*, 2013; Cahoon *et al.*, 2016]. Fine root production also coincides with whole plant belowground allocation of C resources and reserves [Olsrud and Christensen, 2004]. Any alteration to belowground resources can therefore affect plant seasonal responses above- and belowground. Autochamber was dominated by the tussock-forming sedge *Eriophorum*, which has a quick fine root turn-over rate of ~1 year [Shaver and Billings, 1975] and has a late summer season growth pulse of fine roots [Kummerow and Russell, 1980; Shaver *et al.*, 1986; Cahoon *et al.*, 2016]. We observed a reduction in R_{eco} during the first year only at Autochamber when compared to Tower fluxes. The severing of *Eriophorum* roots and/or root disturbance during installation in the autumn prior to measurements, could have delayed production of fine roots in the following season (year one of this study), which would have altered fine root litter inputs during that year and might explain the low R_{eco} during that year. Fine root decomposition accounts for a large proportion of respiration inputs to tundra soil [Loya *et al.*, 2004]. Not only was R_{eco} lower during the first year for Autochamber, but GPP was also lower and the ecosystem became a net source of CO_2 earlier in the summer season than any other year (Table 2). The use of reserves for root growth and/or repair or access to spring nutrients could compromise summer plant performance for the first three years. Although summer season NEE was significantly different in the sixth year, GPP and R_{eco} were similar between methods.

Interannual NEE variability can be influenced by environmental factors that determine the start and end of the summer season. The timing of snow melt plays an important role for determining the annual CO₂ balance for the Arctic [Aurela *et al.*, 2004; Lund *et al.*, 2012], and late snow-melt can delay phenology [Ernakovich *et al.*, 2014] resulting in lower annual NEE, but can vary depending on vegetation type [Humphreys and Lafleur, 2011]. Mbufong *et al.* [2014] found that tundra peak productivity in July was unrelated to the start of the summer season and in fact R_{eco} was a stronger driver of interannual NEE flux variability than the timing of growing season start. In our study, snow melt in the fifth year (2013) of monitoring at Tower and Autochamber was exceptionally late in comparison with other years (Table 1), yet that year did not have the lowest summer season NEE uptake. The low GPP during the month of May in 2013 was compensated for by increased carbon fixation in the following months. This indicates that tundra plants are capable of reaching high productivity by upregulating photosynthesis [Bosiö *et al.*, 2014] in a short period of time (Table S2 & Figure 4). Other environmental drivers of respiration such as temperature and moisture play an important role in the net CO₂ balance of the season [Euskirchen *et al.*, 2012] such as increased temperatures can offset ecosystem uptake by increased respiration late in the summer season, but respiration can also be inhibited by increases in precipitation as decomposition is slowed down under wet conditions.

Autochamber and Tower methods were remarkably consistent in capturing biological down regulation of ecosystem productivity and becoming a net source of CO₂ within a small window in August, regardless of the start of the summer season. This down regulation was likely due to the onset of senescence, which is thought to be regulated mostly by photoperiod in tundra plants [Shaver and Kummerow, 1992].

Non-summer season fluxes accounted for approximately 30% of the CO₂ released annually, which is within the upper range of annual budgets in other studies (10 – 30%) [Fahnestock et al., 1998; Grogan and Iii, 1999; Elberling, 2007; Kim et al., 2016]; like in other studies that estimate annual Arctic CO₂ flux, non-summer losses offset the summer season gains [Fahnestock et al., 1998; Vogel et al., 2009; Euskirchen et al., 2012; Lüers et al., 2014; Oechel et al., 2014]. Non-summer C flux estimates have many challenges and large uncertainty: direct measurements are difficult to obtain [Goodrich et al., 2016] and the differences between non-summer measurement methods can be greater than the estimates of interannual variation in CO₂ fluxes [Björkman et al., 2010; Webb et al., 2016]. In our study, non-summer season fluxes were calculated from values that were 11% measured and 89% modeled (Table S1) for the whole study period (both Tower and Autochamber used the same data set), which meant model parameterization was limited to a small quantity of data. Goodrich[2016] reported similar coverage during the winter using same type of CO₂ analyzer. Despite our small and sporadic data set, our non-summer measurements span the entire non-summer season and our model builds on extensive examination of winter fluxes done by Webb et al. [2016] . Our results represent further evidence of the influence of non-summer season CO₂ fluxes to annual C budgets from a subarctic site, which is in line with other studies throughout the Arctic [Oechel et al., 1997; Fahnestock et al., 1999; Jones et al., 1999; Welker et al., 2000; Schimel et al., 2006; Sullivan et al., 2008; Grogan, 2012; Cooper, 2014]. As we improve our data collection during winter we will be able to evaluate more precisely the mechanisms driving ecosystem CO₂ loss during this time of the year to better estimate our annual budgets of carbon.

5 Conclusion

Our CO₂ flux measurements show that during six years of measurement the tundra ecosystem was a consistent annual net source of CO₂ to the atmosphere (105 ± 17 g CO₂-C m⁻²). While this ecosystem was a CO₂ sink during the summer, CO₂ emissions during the non-summer months offset summer CO₂ uptake in every year. Active layer thickness was a significant driver of GPP, likely as a result of increased nutrient availability with deeper thaw, but also increased R_{eco} at both landscape and plot scales. Differences between fluxes at Tower and Autochamber in the first year could be related to the impact of experimental setup, and the severing of roots. This highlights the need for long-term experiments in order to make generalizations about CO₂ flux dynamics and sensitivity to environmental drivers. Further research evaluating the coupling of belowground and aboveground dynamics, and the relationship between summer and non-summer processes is needed to further our understanding of tundra C cycle dynamics and potential implications in the face of climate change.

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Table 1. Mean air temperatures, total annual precipitation (rainfall), cumulative photosynthetic active radiation (PAR), soil active layer thickness, water table depths, and snowmelt date at Eight Mile Lake, Healy Alaska, USA. Summer season data represents the period from May 1st to September 30th and non-summer season October 1st to April 30th of the following year.

Season (year of study)	Temperature (°C)			Annual rainfall (mm)	Summer Season Cumulative PAR (mole/m ²)	Active layer thickness (cm)		Water table depth (cm)		Snowmelt (date)
	Annual	Summer season	Non- summer season			Tower	Autoch.	Tower	Autoch.	
2008-2009 (1)	-3.4	9.7	-12.8	178.2	4991.7	67.6 (2.5)	55.4 (0.8)	18.5 (2.0)	27.6 (0.7)	NA
2009-2010 (2)	-1.2	9.8	-9.2	249.8	4794.9	69.9 (1.9)	58.3 (0.7)	14.8 (2.3)	20.3 (0.3)	2010-04-27
2010-2011 (3)	-3.2	8.3	-11.5	164.4	5193.2	60.0 (1.6)	56.4 (0.9)	15.1 (2.3)	23.8 (0.3)	2011-04-27
2011-2012 (4)	-3.3	9.1	-12.1	223.4	4855.3	65.3 (1.2)	60.9 (0.7)	17.3 (2.0)	22.1 (0.3)	2012-05-04
2012-2013 (5)	-4.1	9.3	-13.7	167.2	5502.3	66.3 (1.9)	62.8 (1.2)	23.6 (1.6)	23.8 (0.4)	2013-05-27
2013-2014 (6)	-0.9	9.1	-8.2	312.2	4553.4	61.1 (1.9)	65.3 (1.6)	10.4 (1.9)	14.5 (0.7)	2014-04-21
Mean (SE)	-2.7 (0.5)	9.2 (0.2)	-11.3 (0.9)	215.9 (23.8)	4981.8 (135.4)	65.0 (1.6)	59.9 (1.6)	16.6 (1.8)	22.0 (1.8)	

Table 2. The date of first change from observed summer season ecosystem CO₂ net uptake to a net source of CO₂; Date (dd-AUG-yyyy).

Tower	Autochamber
27-AUG-2009	04-AUG-2009
26-AUG-2010	26-AUG-2010
27-AUG-2011	30-AUG-2011
25-AUG-2012	29-AUG-2012
28-AUG-2013	28-AUG-2013
24-AUG-2014	31-AUG-2014

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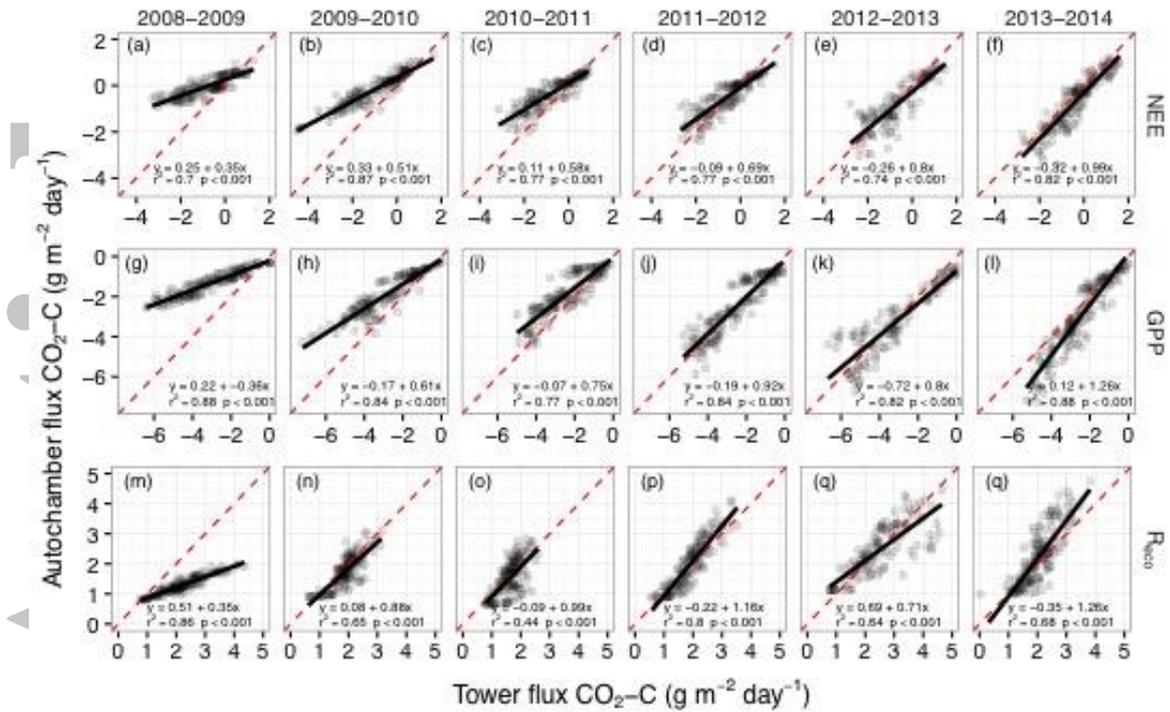


Figure 1. Daily fluxes of net Ecosystem Exchange (NEE; panels a-e), gross primary production (GPP, panels f-j), and ecosystem respiration (Reco, panels l-o) for each summer season (May 1st to September 30th, except 2013 started June 1st) for the two methods (Tower and Autochamber). Autochamber means and standard errors are based on fence replicates (n=6). The black line represents linear regression and the red dashed-line the one-to-one line. Negative fluxes indicate C uptake.

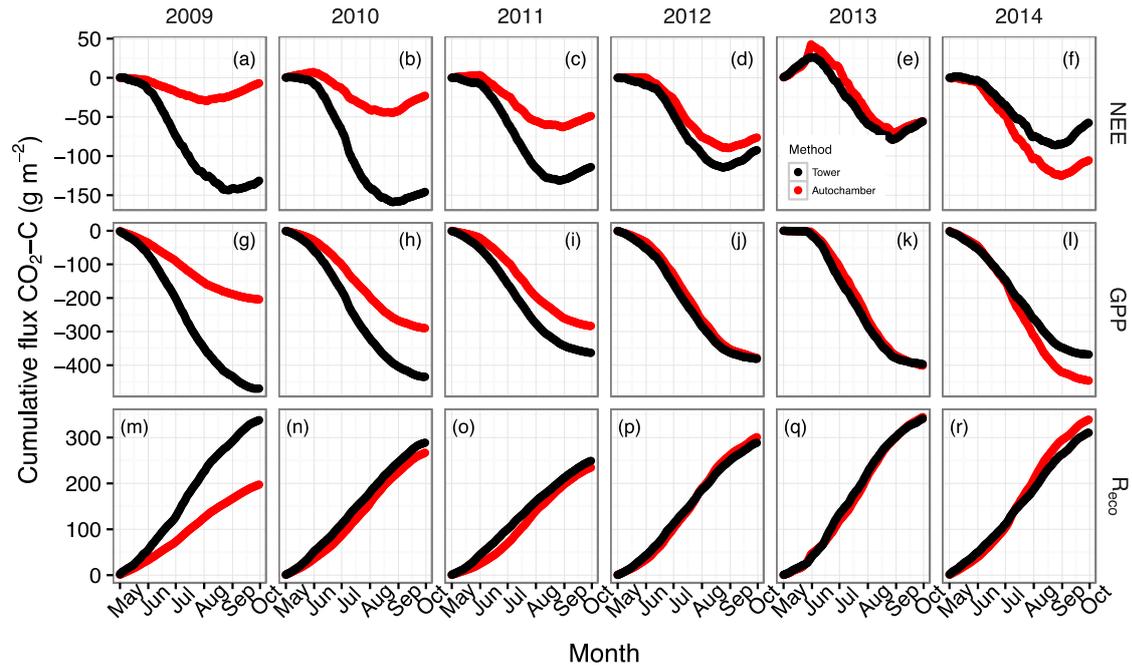


Figure 2. Summer season (May 1st to September 30th, except 2013 started June 1st) mean daily cumulative fluxes for the two methods (Tower black symbols and Autochamber red symbols). Net Ecosystem Exchange (NEE; panels a-e), gross primary production (GPP, panels f-j), and ecosystem respiration (R_{eco} , panels l-o). Note the difference in y-axis scales for each flux; negative fluxes indicate C uptake.

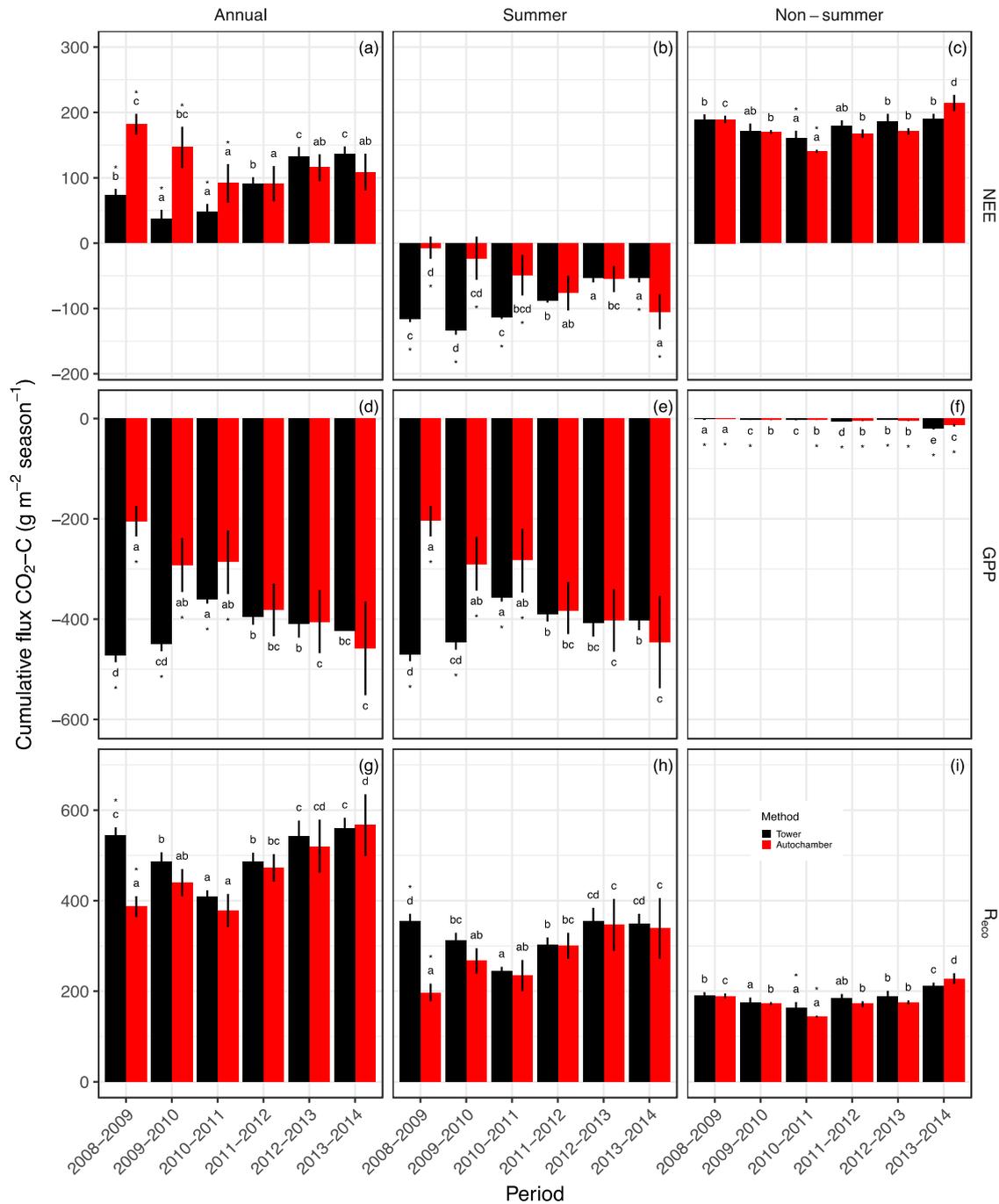


Figure 3. Annual, seasonal cumulative fluxes for the two methods (Tower black and Autochamber red) for each sampling period. Net Ecosystem Exchange (NEE; panels a-c), gross primary production (GPP, panels d-f), and ecosystem respiration (R_{eco} , panels g-i). Note the difference in y-axis scales for each flux and negative fluxes indicate carbon uptake. Means and 95% confidence intervals (Autochamber $n=6$ and Tower $n=1000$). Star (*) indicate significant differences within a period between methods. Different superscript letters

indicate significant differences between periods ($p < 0.05$) within a method; Tower black bar and Autochamber red bars for each sampling period.

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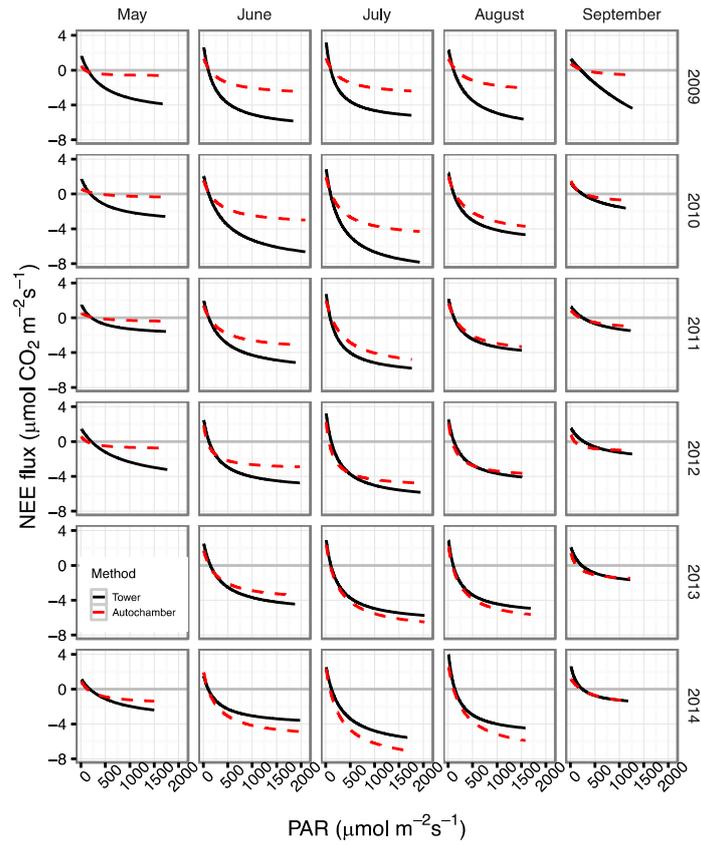


Figure 4. Summer season monthly modeled light response curves for Tower (black solid lines) and Autochamber methods (red dashed lines). May 2013 contains no data for Autochamber and Tower was excluded. For more model information see equation 1 in supplemental Text S1 and model parameters estimates Table S3.

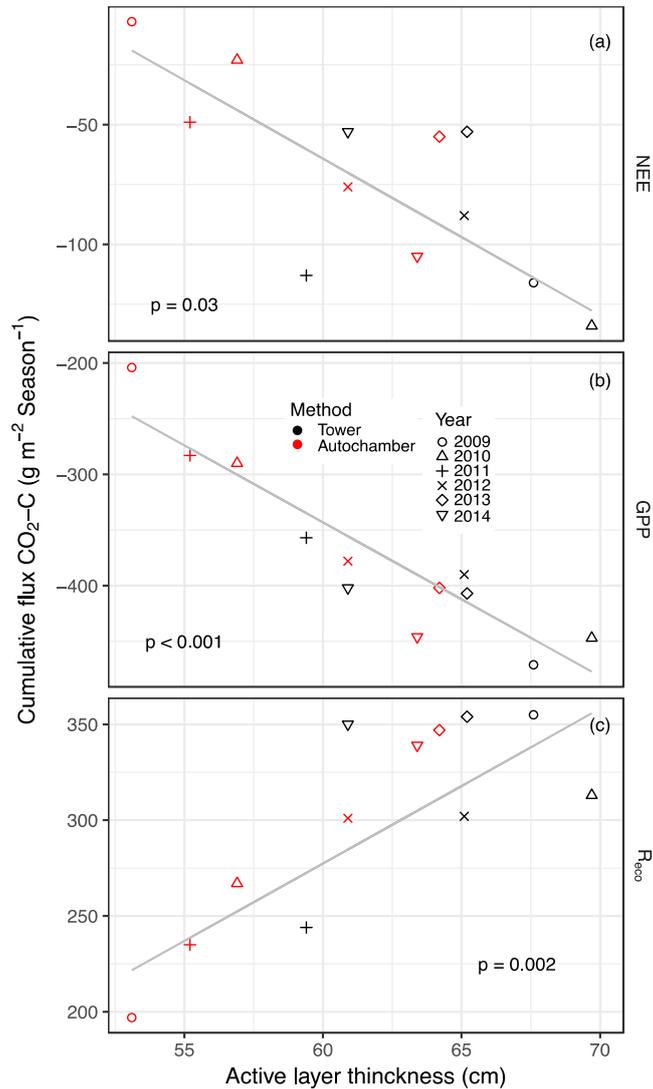


Figure 5. The relationship of summer season (May 1st to September 30th) cumulative fluxes with Active layer thickness (ALT) for the two methods (Tower black symbols and Autochamber red symbols). P-values denote significant slope parameters (Tables S7). NEE is Net Ecosystem Exchange, GPP is Gross Primary Production, and R_{eco} is Ecosystem respiration. Negative fluxes indicate CO₂ uptake. Note the difference in y-axis scales for each flux.