

Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska

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Citation: Euskirchen, E. S., M. S. Bret-Harte, G. J. Scott, C. Edgar, and G. R. Shaver. 2012. Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska. *Ecosphere* 3(1):4. <http://dx.doi.org/10.1890/ES11-00202.1>

Abstract. Understanding the carbon dioxide and water fluxes in the Arctic is essential for accurate assessment and prediction of the responses of these ecosystems to climate change. In the Arctic, there have been relatively few studies of net CO₂, water, and energy exchange using micrometeorological methods due to the difficulty of performing these measurements in cold, remote regions. When these measurements are performed, they are usually collected only during the short summer growing season. We established eddy covariance flux towers in three representative Alaska tundra ecosystems (heath tundra, tussock tundra, and wet sedge tundra), and have collected CO₂, water, and energy flux data continuously for over three years (September 2007–May 2011). In all ecosystems, peak CO₂ uptake occurred during July, with accumulations of ~51–95 g C/m² during June–August. The timing of the switch from CO₂ source to sink in the spring appears to be regulated by the number of growing degree days early in the season, indicating that warmer springs may promote increased net CO₂ uptake. However, this increased uptake in the spring may be lost through warmer temperatures in the late growing season that promote respiration, if this respiration is not impeded by large amounts of precipitation or cooler temperatures. Net CO₂ accumulation during the growing season was generally lost through respiration during the snow covered months of September–May, turning the ecosystems into net sources of CO₂ over measurement period. The water balance from June to August at the three ecosystems was variable, with the most variability observed in the heath tundra, and the least in the tussock tundra. These findings underline the importance of collecting data over the full annual cycle and across multiple types of tundra ecosystems in order to come to a more complete understanding of CO₂ and water fluxes in the Arctic.

Key words: Arctic tundra; ecosystem respiration; eddy covariance; evapotranspiration; gross primary production; net ecosystem exchange; water balance; water use efficiency.

Received 13 July 2011; revised 15 November 2011; accepted 21 November 2011; final version received 19 December 2011; **published** 19 January 2012. Corresponding Editor: Y. Pan.

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INTRODUCTION

In northern Alaska, warmer air temperatures across all seasons (ACIA 2005, Chapin et al. 2005) have altered a number of ecological and physical systems in northern Alaska. In particular, the carbon balance of the arctic tundra may be

shifting under a warming climate (McGuire et al. 2009). Historically, Arctic tundra has acted as a strong carbon sink because low temperatures and poor soil drainage limit decomposition more than primary production. However, some studies indicate that the Alaskan tundra is becoming a net source of CO₂ during the growing season,

with larger positive values of net ecosystem exchange (NEE, where a positive value of NEE denotes a source of CO₂, and a negative value denotes a sink; Oechel et al. 1995, Kwon et al. 2006). This switch is generally thought to be due to drying and warming of the tundra, and consequently higher rates of soil decomposition (Kwon et al. 2006, Oberbauer et al. 2007). It is also possible that earlier snowmelt and a longer growing season will increase the sink strength of the tundra, with warming in both the spring and autumn that may enhance plant production (e.g., Aurela et al. 2004). Alternatively, the tundra may have acclimated to temperature changes, and has once again turned back to a sink after acting as a source in the 1980s (Oechel et al. 2000). Since climatic factors may vary widely from year to year, there is also a large degree of interannual variability in tundra NEE, gross primary productivity (GPP), and ecosystem respiration (ER) (Kwon et al. 2006, Lafleur and Humphreys 2008, Lund et al. 2010).

Water vapor fluxes may be particularly important in determining NEE since increasing water stress has long been tied to a depression in photosynthesis for a wide range of plant species, including tundra plants (Johnson and Caldwell 1975). Much of Alaska is predicted to become warmer and drier during the growing season when the biological demand for water is greatest, with more water leaving the region through greater evapotranspiration (ET) than is provided by incoming precipitation (Hinzman et al. 2005). Such changes in water availability will likely have impacts on ecosystem productivity in tundra systems (Nobrega and Grogan 2008).

Numerous studies in the arctic tundra have shown that the metabolic activity of soil microbes continues under snow-covered, cold conditions. These studies suggest that wintertime respiratory losses of CO₂ can be significant and can determine whether an ecosystem is an annual CO₂ source or sink (Nobrega and Grogan 2007, Schimel et al. 2006). Some research suggests that deeper snow enhances respiration since the snowpack insulates the ground, creating warmer temperatures with more responsive microorganisms (Schimel et al. 2004). Other studies suggest that a deep snowpack may cause an apparent decrease in CO₂ flux to the atmosphere during winter due to the temporary formation of pockets

of high CO₂ concentration in snow above the soil surface (Gilmanov et al. 2004). This period of buildup of CO₂ within the snowpack can then result in higher rates of CO₂ efflux once the CO₂ is ultimately released.

Despite convincing evidence that the arctic environment of northern Alaska is changing, continuous observations of year-round fluxes of ecosystem CO₂, water, and energy in the various tundra ecosystems that comprise the region are relatively scarce. This is due to the logistical difficulties of collecting micrometeorological data without line power, the long snow season, long periods of extreme cold, and remote locations. Because heterogeneity of vegetation at fine spatial scales (e.g., meters) is one of the defining characteristics of the ecosystems in arctic tundra landscapes, spatial heterogeneity in the vegetation may ultimately result in large variations in the CO₂, water, and energy fluxes across a landscape.

To better understand these fluxes across the landscape and through all seasons, we chose three representative types of tundra ecosystems located within 1 km² of one another in which to make our continuous measurements of CO₂, water, and energy fluxes, including the winter season. Here, we report data for over nearly four years (September 2007–May 2011) of CO₂ and water eddy covariance measurements and associated meteorological variables. The specific objectives of this research were to (1) document the seasonal and interannual patterns in CO₂ fluxes (NEE, GPP, and ER) within and across these three ecosystems, (2) examine how surface weather (in particular, air temperature and precipitation) influences these fluxes, and (3) document growing season and interannual patterns in water use efficiency (WUE), evapotranspiration (ET), and water balance (WB) within and across these three ecosystems. We expected that the NEE, GPP, ER, WUE, ET, and WB would show interannual variations due to climatic influences, and that the interannual variation in these fluxes would be similar across the three ecosystems. We also expected that the wet sedge tundra would have lower rates of respiration than either the tussock or heath tundra due to the wetter soils. Furthermore, we anticipated that the heath tundra, with sparser vegetation, would be the least productive ecosystem, with less GPP

and NEE than the tussock or wet sedge tundra.

METHODS

Study site

The study site is in the Imnavait Creek watershed (2.2 km²), in the northern foothills of the Brooks Range, Alaska (68°37' N, 149°18' W). The watershed is located in rolling hills, lying within the headwaters of the Kuparuk River Basin (8,140 km²), and is underlain with continuous permafrost, with a maximum thickness of 250–300 m near the site (Osterkamp 2005). The predominant soils are 15–20 cm of porous organic peat underlain by silt and glacial till (Hinzman et al. 1991). The surface organic layer is porous and drains when saturated, but often both the organic layer and the underlying mineral soil are saturated with water, depleting the soil of oxygen during thaw (Hinzman et al. 1991). The mean annual temperature is -7.4°C and the mean annual precipitation is 318 mm, with about 40% occurring as rain and 60% as snow. The landscape is treeless, located ~ 100 km north from latitudinal treeline. Walker et al. (1989) provide a detailed analysis of the vegetation and geology of the Imnavait Creek watershed, and Kane et al. (1989) describe the hydrology.

While the northern foothills of the Brooks Range are largely dominated by moist acidic tussock tundra vegetation, there are also areas of heath tundra on the hilltops and wet sedge tundra in the riparian areas near Imnavait Creek. We examined three different tundra types within the Imnavait watershed, including heath, moist acidic tussock, and wet sedge tundra. The moist acidic tussock tundra ecosystem is dominated by the tussock-forming sedge *Eriophorum vaginatum*, *Sphagnum* spp., and dwarf shrubs such as *Betula nana* and *Salix* spp. The dry heath tundra ecosystem, located on a ridge top, is dominated by *Dryas* spp, lichen, and dwarf shrubs. The wet sedge ecosystem, located in the valley bottom, includes the sedge *Eriophorum angustifolium* and dwarf shrubs such as *Betula nana* and *Salix* spp. In fact, our sites contained a mixture of these vegetation types. Within the 200 m footprint of our eddy flux towers, our heath site was classified as 20% heath, but also included 72% tussock tundra, with the balance made of up of

sedge meadow and bare soil. The moist acidic tussock tundra site was classified as 95% tussock tundra, with the balance being overgrown frost boils (e.g., upwellings of mud that occur through frost heave and cryoturbation in permafrost areas). The wet sedge site was classified as 52% wet sedge, and 47% tussock tundra, with the balance being made up of open water and bare soil (A. Kade, unpublished data). The soil organic layer is thickest in the wet sedge tundra (34.0 ± 2.4 cm), less thick in the tussock tundra (15.0 ± 1.4 cm), and thin at the heath tundra (2.3 ± 0.3 cm; A. Kade, unpublished data). The maximum depth of thaw is ~ 40 cm at the heath site, ~ 60 cm at the wet sedge site, and ~ 70 cm at the tussock site (A. Kade, unpublished data).

Eddy covariance and microclimatic measurements

Due to the remote location of the site and the absence of line power, electrical power for the equipment at the site was provided by solar panels, wind turbines, and batteries. For the wet sedge and heath tundra sites, the power supply at each site consisted of 32 12-V deep cycle marine batteries connected to six 100-W solar panels and a wind turbine. The solar panels were the predominant source of power from April to October, while the wind turbine was the main source from November–March. The power supply at the tussock tundra site consisted of three 12-V deep cycle marine batteries connected six solar panels totaling ~ 300 W and consequently operated from approximately May to early November.

The eddy covariance system for measuring the fluxes of CO₂, water, and energy was placed on a 3 m high tripod in the center of each site. The instrumentation consisted of a 3-D sonic anemometer (CSAT-3; Campbell Scientific Instruments, Logan, Utah, USA) and an open-path infrared gas analyzer (LI-7500 IRGA; LI-COR, Lincoln, Nebraska, USA) mounted at a height of ~ 2.5 m. The main axis of the LI-7500 IRGA was tilted by 30° with respect to the horizontal to aid in draining condensation and precipitation from the optical windows. The LI-7500 IRGA and the CSAT-3 were both mounted on a shared horizontal bar and were laterally separated by 20 cm to reduce flux loss and flow distortion. The differing time delays in signals were taken into account by shifting the CSAT-3 data by one scan

(at 10 Hz) to match the fixed 302.369 ms delay (or 3 scans at 10 Hz) that is programmed into the LI-7500. This instrumentation was connected to a digital datalogging system (either a CR3000 or CR5000; Campbell Scientific Instruments) to log data at 10 Hz intervals. Raw data were collected once a month from a CompactFlash card located in the datalogger. The LI-COR 7500 was calibrated following the instructions in the manual (LI-COR 2004). Calibration was checked during each site visit. Gas analyzers were calibrated monthly at first, although this frequency was reduced to every several (3–4 months) since inspections indicated that the instruments remained stable over a several month period.

Basic microclimatic data were also collected, including photosynthetically active radiation (PAR; 2 m above the ground; LI190SB, LI-COR), air temperature (T_a) and relative humidity (Rh; 2 m above the ground; HMP45C, Vaisala, Helsinki, Finland), soil water content (SWC; water content reflectometer, CS616, Campbell Scientific Instruments), soil heat flux (G , three replicates at 5 cm below the surface, HFP01-SC, Hukseflux, Delft, Netherlands), precipitation (P ; near the ground surface; TE525MM, Texas Electronics, Dallas, Texas, USA), net radiation (R_n ; at 2 m above the ground; NR-LITE; Kipp and Zonen, Delft, Netherlands), albedo (albedometer CMA6, Kipp and Zonen), soil temperature (T_s at the surface and at 2.5 cm depth; TCAV; averaging soil TC probe; Campbell Scientific Instruments) and barometric pressure (P_a ; PB105, Vaisala). These variables were measured at 15-second intervals and stored on the datalogging systems (either a CR3000 or CR5000; Campbell Scientific Instruments). Both the processed eddy covariance and microclimatic data were averaged for 30 minute periods. Based on T_a at 2 m, the sum of growing degree days (GDD) was calculated as $GDD = \sum \max(5, T_i - 5)$, where T_i is the mean daily T_a and the base is 5°C (Molau and Molgaard 1996).

At the heath and wet sedge tundra sites, all measurements began in mid-September of 2007 for both the eddy covariance and microclimatic data. Measurements from the tussock tundra site had been ongoing since the summer of 2003 (Van Buuren 2007), although for the study presented here we only used the data from September 2007 onward to maintain congruency across the three sites for the period of analysis.

Data processing and post-processing

The automatic gain control (AGC) value (which represents optical impedance by precipitation) was computed for the IRGA and used as a QA/QC variable for both flux and radiation data, with 60 as the maximum threshold value (LI-COR 2004). The ‘WPL’ terms were applied during post-processing to the CO_2 and latent heat fluxes to account for changes in mass flow caused by changes in air density (Webb et al. 1980). In addition, corrections were applied to account for frequency attenuation of the eddy covariance fluxes (Massman, 2000, Massman 2001). To account for nocturnal CO_2 advection, we calculated a storage term and then performed a u^* correction. We calculated storage using the discrete method of estimation (e.g., Papale et al. 2006), and that this had a minimal, 2% effect, on the fluxes. Following the storage correction, we applied a u^* correction for calm periods, when friction velocity (u^*) was less than 0.1 m s^{-1} (Fig. 1). This u^* value of 0.1 was the same as that used in another eddy covariance study located near our sites, as described in Rocha and Shaver (2011). Following u^* and precipitation filtering approximately 90% of the original data remained. We applied the adjustment for instrument warming from measurements of both CO_2 and latent heat with the LI-7500 during cold periods ($T_a < 0^\circ\text{C}$), taking into account net radiation, wind speed, and temperature as suggested by Burba et al. (2008), and most recently by (Amiro 2010). This correction was generally small, $<0.025 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and resulted in no apparent uptake of CO_2 during the winter.

Data gaps occurred because of either instrument malfunction or power outages. Shorter gaps in the eddy covariance data were usually related to instrument errors during precipitation events in the summer. Longer gaps occurred due to power outages during cold temperatures or ice and snow build-up on the instruments. For data gaps in NEE of approximately 1–6 days, we gap-filled by calculating the mean diurnal variation, where a missing observation is replaced by the mean for that time period (half-hour) based on adjacent days (Falge et al. 2001). This method provided stable approximations of missing data using 7-day independent windows during the nighttime hours and 14-day windows during the

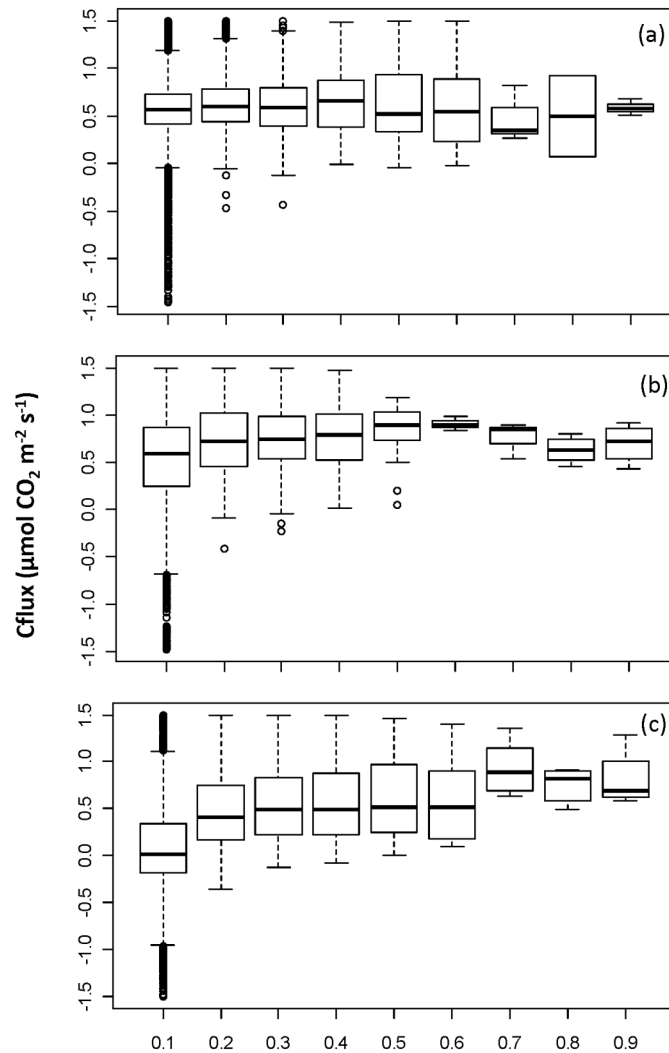


Fig. 1. Relationship between u^* and nighttime NEE (PPFD $< 50 \mu\text{mol m}^{-2} \text{s}^{-1}$) for the heath tundra (a), tussock tundra (b), and wet sedge tundra (c). The median of each u^* class is represented with a horizontal black line in the interior of the boxplot. The height of the boxes is equal to the interquartile distance with the dotted lines from the top and bottom extending to the extreme values of the data, or a distance of $1.5 \times$ interquartile distance, whichever is less. The points outside the boxes are the outliers.

daytime hours (Falge et al. 2001). Recent research comparing 15 different gap-filling techniques found that the mean diurnal variation method showed a moderate and consistent performance (Moffat et al. 2007). Consequently, we did not implement alternative gap-filling techniques. We did not gap-fill data for periods greater than six days that were due to power outages or ice on the instruments during the winter.

The percentage of data collected from September 2007 through August 2010 was near 95%

during the months from June–August. Winter data collection was $\sim 50\%$ during the first two cold seasons, October 2007–May 2008 and October 2008–May 2009, due in large part to power loss. We were able to gap-fill approximately 20% of the missing data during these first two cold seasons, but did not gap-fill the remaining 30% of the missing data since these were periods of data loss greater than six days where we also lost meteorological data. During the third and fourth cold seasons (October 2009–

May 2010 and October 2010–May 2011) power failures were nearly non-existent. During this period, the percentage of data collected was near 85%, and all the missing data were gap-filled. Losses during this period were attributable to ice on the instrumentation and short power outages (<2 days). Data coverage during the entire period was approximately 68% after accounting for data loss from power outages, AGC, and u^* filtering.

Energy budget closure

The ability of the instrumentation to close the energy balance demonstrates the quality of the eddy covariance measurements. After u^* and precipitation filtering, the closure of the energy budget was examined by a linear regression between the sum of sensible and latent heat fluxes ($H + LE$) and available energy ($R_n - G$) for half-hourly data from each site during dry periods. If $(R_n - G)$ is close to $(H + LE)$ then we can assume that advective losses of energy or CO_2 are small and that the eddy covariance measurements are of good quality. The energy balance closure at the heath tundra showed 90% (e.g., $H + LE = 0.9 \times (R_n - G)$; $R^2 = 0.91$) agreement during the period without snow-covered ground (mid-May to late September) and, 79% agreement ($R^2 = 0.88$) during all other months. At the wet sedge tundra site, the energy balance closure was in 87% agreement ($R^2 = 0.87$) during the period without snow on the ground, and in 83% agreement ($R^2 = 0.88$) at other times. At the tussock tundra site, we looked at the energy balance closure during the entire period of operation, which was generally without snow covered ground, and the data showed 85% agreement ($R^2 = 0.92$) in the energy budget closure calculations. The energy balance closure reported here is higher or close to the closure reported in many other eddy covariance studies (Wilson et al. 2002).

Modeling growing season ER and GPP

NEE represents the balance between gross CO_2 assimilation (gross primary productivity, GPP, where $GPP \leq 0$, because CO_2 uptake is denoted as a negative value) and ecosystem respiration (ER). While we do not directly measure GPP and ER, NEE based on eddy covariance data can be partitioned into these counterparts to provide an

approximation of ER and GPP and therefore a general understanding of the photosynthetic versus respiratory controls over NEE. ER is calculated based on ‘nighttime’ measurements ($PPFD < 50 \mu mol m^{-2} s^{-1}$) fit to an equation:

$$ER = R_0 \times Q_{10}^{T_a/10} \quad (1)$$

where T_a = air temperature, R_0 is a scale parameter, and Q_{10} is the temperature sensitivity coefficient of ER. R_0 and Q_{10} were estimated each day using a 29 day moving window and least squares method (Ueyama et al. 2009). GPP is then calculated as $GPP = NEE - ER$. We calculated ER and GPP for the June–August growing season. Bootstrapping was used to estimate the error (95% confidence interval) about the total NEE, GPP, and ER values for each June–August growing season. The bootstrap calculated the confidence interval by (1) constructing 2000 bootstrapped sample series by randomly sampling with replacement the observed total daily time series, (2) calculating an average from each constructed data series, and (3) calculating the grand mean ($\pm 95\%$ CI) from the distribution of means calculated from the bootstrapped data series (Efron and Tibshirani 1993).

Modeling NEE during the period of snow-covered ground

We examined various mathematical models (e.g., linear, power, polynomial, exponential) to determine the best fit of NEE during the period of continuously snow-covered ground (late September to mid-May, when the ecosystems were taking up little or no CO_2 and PAR was low) to the environmental variables. Thus, during this period, NEE should primarily represent ER, though there may be a time lag between when CO_2 is produced in the soil and when it is released from the snowpack. These variables included half-hourly T_{sr} as well as mean daily data for: T_{sr} , surface T_s , T_s at depth, soil water content, wind speed, atmospheric pressure, and snow depth.

Water use efficiency and water balance

We defined ecosystem water use efficiency (WUE) as the molar ratio of gross CO_2 uptake (e.g., GPP, mmol CO_2) to H_2O lost (e.g., ET, mol H_2O , when evaporation and transpiration both occur) for a given time period, such as a growing

season:

$$\text{WUE} = \frac{-\text{GPP}}{\text{ET}}. \quad (2)$$

Smaller WUE values indicate low net CO₂ uptake for a given amount of water lost from the system. Note that in this equation we multiply GPP by -1 so that WUE is a positive value. We restricted this analysis to June–August when reliable CO₂ and H₂O flux data were available, computing WUE for each 30-minute period during the day when PAR > 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, excluding rainy periods. From the 30-minute WUE, we calculated mean daily WUE.

We calculated the site water balance (WB) from mid-May–August as the difference between daily precipitation (P_{daily} ; mm/day) and daily evapotranspiration (ET_{daily} ; mm/day, from eddy covariance measurements):

$$\text{WB} = P_{\text{daily}} - \text{ET}_{\text{daily}}. \quad (3)$$

ET includes both evapotranspiration from the plant canopy and evaporation from the moss and soil surface. This estimate of water balance has been used in previous studies in high-latitudes (Rouse et al. 1992, Lafleur 1994) and elsewhere (Law et al. 2002).

RESULTS

Meteorology

Precipitation and air temperature regimes varied over the three years of the study (Table 1). The total amount of precipitation falling as rain was similar in the summers (June–August) of 2008 (196 mm) and 2009 (192 mm), but was less (172 mm) in the summer of 2010. The winter snowpack formed sometime between September 16 and September 26 each year, as air temperatures fell and precipitation events turned from rain to snow. The maximum snow depth occurred between March–May, and ranged from 0.7 m in April 2009 and March 2010 to 1.0 m during April 2011. The snowpack began to melt around May 20 each year, and was gone entirely by early June, in conjunction with rain events and above freezing temperatures. Over the measurement period, the summer (June–August) T_a was coolest in 2008 (mean \pm SE, $T_a = 6.8 \pm 5.0^\circ\text{C}$) warmer in 2009 ($8.3 \pm 5.0^\circ\text{C}$), and warmest in 2010 ($9.0 \pm 5.0^\circ\text{C}$; Fig. 1c). Mean air temperatures from September to May ranged from $-12.0 \pm$

Table 1. Mean (\pm SE) summer (June–August) and winter air temperature (T_a , September–May), summer and winter soil temperature by ecosystem type (T_s , 2.5 cm depth), excluding the first two cold season due to data loss > 6 days), early growing season (June) and later growing season (July–August) growing degree days (GDD), cumulative early and late season precipitation as rain, maximum snow depth (SD) and date recorded, and dates of snowmelt and snow return.

Variable	Year	Value or Date
T_a (summer)	2008	6.8 ± 5.0
	2009	8.3 ± 5.0
	2010	9.0 ± 5.0
T_a (winter)	2007–2008	-10.6 ± 12.8
	2008–2009	-10.3 ± 17.9
	2009–2010	-12.0 ± 11.4
	2010–2011	-11.3 ± 10.3
T_s (summer) Heath	2008	4.2 ± 2.2
	2009	4.5 ± 2.2
	2010	5.6 ± 1.9
Tussock	2008	4.8 ± 1.9
	2009	5.0 ± 2.1
	2010	6.0 ± 1.6
Wet sedge	2008	2.5 ± 1.1
	2009	2.8 ± 1.3
	2010	3.3 ± 1.7
T_s (winter) Heath	2009–2010	-2.0 ± 1.7
	2010–2011	-2.6 ± 1.0
	Wet sedge	2009–2010
GDD (June)	2008	118
	2009	96
	2010	162
GDD (July–August)	2008	166
	2009	288
	2010	264
Precipitation (June)	2008	101
	2009	59
	2010	27
Precipitation (July–August)	2008	103
	2009	89
	2010	148
Maximum snow depth (m) and day recorded	2007–2008	0.81 (5/4)
	2008–2009	0.70 (4/24)
	2009–2010	0.70 (3/11)
	2010–2011	1.01 (4/8)
Date of snow return and snowmelt	2007–2008	9/22, 5/22
	2008–2009	9/22, 5/23
	2009–2010	9/16, 5/27
	2010–2011	9/25, 5/25

Note: Soil temperature data were not collected over the winter at the tussock site, and mean values of soil temperature for the heath and wet sedge sites are not calculated during the first two winters due to data losses.

11.4°C during September 2009–May 2010 to $-10.3 \pm 17.9^\circ\text{C}$ during September 2008 to May 2009 (Table 1). Soil temperatures were coldest at

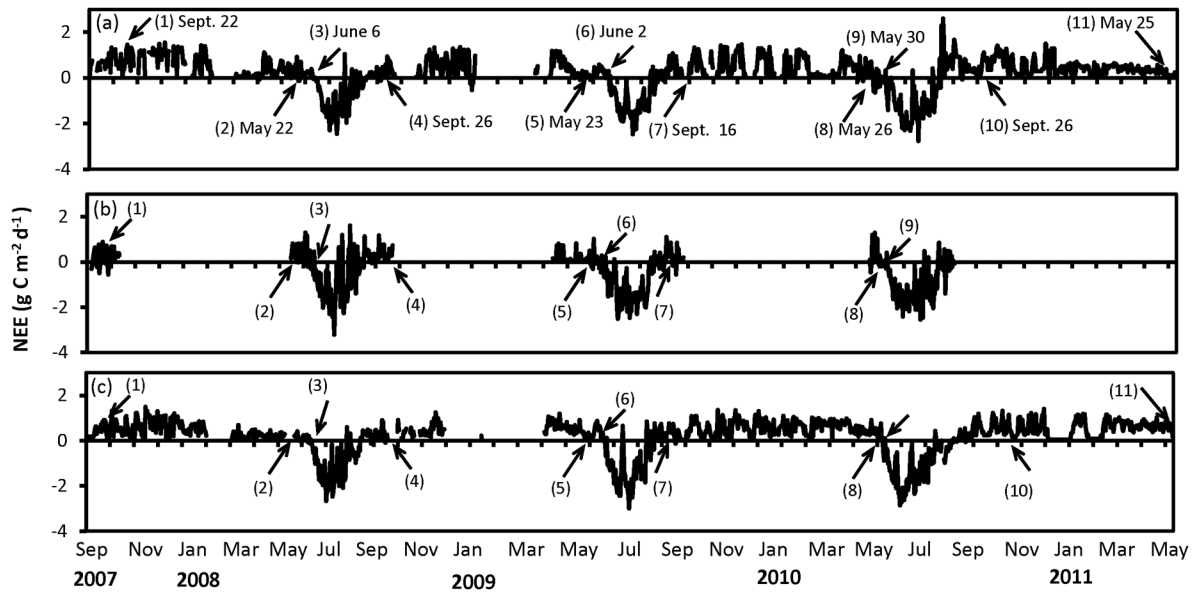


Fig. 2. Seasonal trends of NEE at the heath tundra (a), tussock tundra (b), and wet sedge tundra (c) from September 2007 to August 2010. The arrows point to approximate dates of: (1) snow return in 2007, (2) snow free ground in 2008, (3) leaf-out in 2008, (4) snow return in 2008, (5) snow free ground in 2009, (6) leaf-out in 2009 (7) snow return in 2009, (8) snow free ground in 2010, (9) leaf-out in 2010, (10) snow return in 2010, (11) snow free ground in 2011. Dates of snow return and snow free ground are determined by albedo measurements. A positive value of NEE denotes a source of C, and a negative value denotes a sink.

the wet sedge site compared to the heath and tussock sites in summer, and also when compared to the heath site in winter (Table 1). GDD in June ranged between 96 in 2008 to 162 in 2010, while GDD in August varied between 166 in 2008 to 288 in 2009 (Table 1). Notably, GDD in June 2010 (162) was nearly equal to GDD during all of July and August of 2008 (166), indicating that the early part of the growing season in 2010 was quite warm.

Seasonal patterns and interannual variation of NEE

All three ecosystems switched from source to sink (positive to negative NEE) several weeks after the snow melted, and switched from sink to source well before the snow reappeared (Fig. 2). The springtime switch from source to sink generally corresponded to the timing of leaf-out, with the first full leaves of shrubs and sedges visible in all three ecosystems by \sim June 6 in 2008, by \sim June 2 in 2009, and by \sim May 30 in 2010. In 2008 and 2009, in the heath and wet sedge tundra, the ecosystems switched from source to

sink by \sim June 18, and returned to a source of CO_2 by \sim August 7 (Fig. 2a, c; Fig. 3a, d, c, f). At the tussock tundra (Fig. 2b; Fig. 3b, e), there was a distinct difference between 2008 and 2009 in the length of time that the ecosystem accumulated CO_2 . In 2008, the ecosystem switched from a source to sink on \sim June 13, and returned to a source of CO_2 by July 28. In 2009, the period of time over which the tussock tundra acted as a sink was nearly 20 days longer, switching from source to sink at \sim June 4, and returning to a source by \sim August 7. In the warm spring of 2010, all three ecosystems behaved differently than during the springs of 2008 and 2009, switching from a source to sink approximately two weeks earlier, by \sim June 2. The heath tundra acted as a source of CO_2 through most of August 2010, while the tussock and wet sedge tundra remained a CO_2 sink until \sim August 28, 2010 (Fig. 3, g–i).

These differences in the duration of net CO_2 uptake between June–August created differences in cumulative CO_2 uptake between 2008 and 2010 (Table 2). This was most pronounced in the

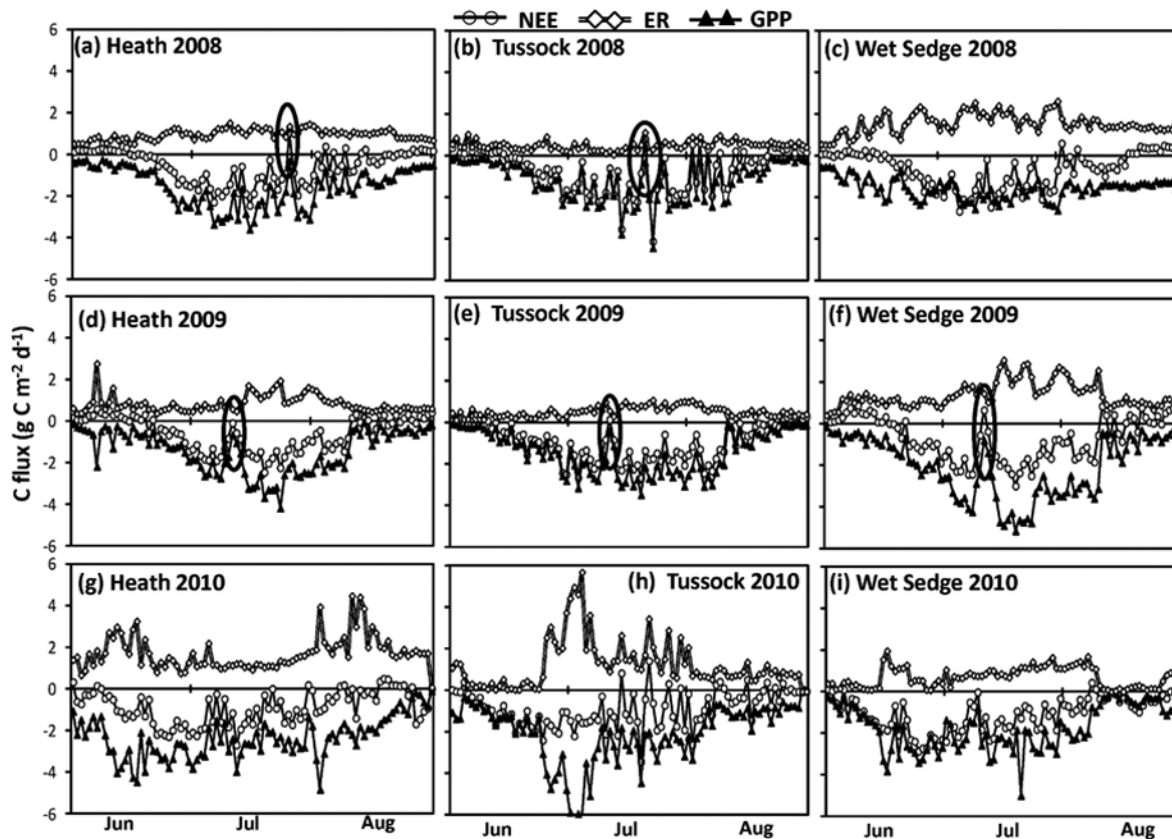


Fig. 3. Daily NEE, GPP, and ER for the heath tundra (a, d, g), tussock tundra (b, e, h), and wet sedge tundra (c, f, i) for the June–August of 2008 (a–c), 2009 (d–f), and 2010 (g–i). The ovals indicate periods where both GPP and NEE increased. Positive values of NEE and GPP denote a sink, and negative values denote a source.

wet sedge tundra, which accumulated of 59 g C/m^2 during June–August 2008 and 95 g C/m^2 during June–August 2010. The tussock tundra uptake from June–August ranged from 62 g C/m^2 in 2008 to 84 g C/m^2 in 2009. The heath tundra showed little interannual variability in cumulative CO_2 uptake between June–August of 2008 to 2010, ranging from 51 g C/m^2 in 2008 to 58 g C/m^2 in 2010 (Table 2). The bootstrapping analysis of NEE indicated an uncertainty between ± 14 to $\pm 21 \text{ g C/m}^2$ June–August, depending on the year and ecosystem (Table 2).

Processes behind NEE: GPP and ER

The pattern of GPP showed seasonality similar to NEE, while ER showed less seasonality than either NEE or GPP (Fig. 3), indicating that, based on our calculations of ER and GPP, the seasonality in NEE was generally determined by GPP

rather than ER. We did see seasonality in ER in the tussock tundra in 2010 (Fig. 3h) and in the wet sedge tundra in 2008 and 2009 (Fig. 3c, f), when both GPP and ER showed similar increases in mid-July. While the ecosystems generally showed net CO_2 uptake between about mid-June and August, there were days when the ecosystems were net sources of CO_2 . These days coincided with abrupt decreases in T_{av} and also increases in GPP (see the circled data points in Fig. 3). For example, on July 23, 2008, T_a dropped to a daily mean of -1°C from a daily mean of 10°C on July 22nd, with a corresponding increase in GPP and increase in NEE, but little effect on ER. Similarly, on July 9, 2009, T_a dropped to 6°C from a mean of 13°C on July 8th, again coinciding with sharp increases in NEE and GPP, and little effect on ER, illustrating the effect of a more thermally buffered soil environment than the

Table 2. Total net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (ER) for the summer (June–August), autumn, winter, and spring (September–May; labeled ‘Winter’).

Flux (g C/m ²)	Year/Data/Season									
	2007–2008	2008–2009			2009–2010			2010–2011		
	(9/15–5/31) Winter	(6/1–5/31)			(6/1–5/31)			(6/1–5/31)		
	Summer	Winter	Annual	Summer	Winter	Annual	Summer	Winter	Annual	
Heath										
NEE	121 (22)	–51 (16)	72 (13)	21 (29)	–54 (14)	105 (17)	51 (22)	–58 (19)	119 (21)	61 (30)
GPP	–3 (0.03)	–201 (23)	–5 (0.04)	–206 (23)	–131 (18)	–7 (0.06)	–138 (18)	–214 (25)	–6 (0.05)	–220 (26)
ER	118 (22)	150 (5)	67 (13)	217 (18)	77 (7)	98 (16)	173 (23)	156 (7)	113 (21)	269 (28)
Tussock										
NEE	N/A	–62 (21)	N/A	N/A	–84 (17)	N/A	N/A	–79 (16)	N/A	N/A
GPP	N/A	–108 (20)	N/A	N/A	–131 (19)	N/A	N/A	–191 (25)	N/A	N/A
ER	N/A	46 (5)	N/A	N/A	47 (5)	N/A	N/A	112 (20)	N/A	N/A
Wet sedge										
NEE	105 (17)	–59 (17)	61 (14)	2 (31)	–63 (10)	145 (19)	82 (29)	–95 (15)	139 (15)	44 (30)
GPP	–4 (0.03)	–202 (23)	–4 (0.02)	–206 (23)	–190 (25)	–8 (1)	–198 (26)	–157 (20)	–7 (1)	–164 (21)
ER	101 (17)	143 (10)	57 (5)	200 (15)	127 (11)	137 (10)	264 (21)	62 (10)	132 (15)	194 (25)

Notes: Uncertainties, given in parentheses, are based on bootstrapping. A negative value of NEE or GPP denotes a sink of C, and a positive value denotes a source.

environment of the plant leaves.

While 2008 and 2009 showed little interannual variability in terms of growing season (June–August) GPP and ER across all three ecosystems, these fluxes were quite different during June–August 2010 (Fig. 3g–i). During the warm growing season of 2010, GPP was smaller and ER was larger in the heath and tussock tundra compared to the summers of 2008–2009. The wet sedge tundra showed a different response in 2010, with GPP and ER values through mid-June–July 2010 similar to those of 2008 and 2009, but with increases of GPP and decreases in ER in late July and August of 2010. While this resulted in larger values of GPP and smaller values of ER compared to those recorded from June–August in 2008 and 2009, ER was reduced so much that the wet sedge tundra showed the greatest net CO₂ uptake in 2010 compared to 2008 and 2009 (Table 2). Cumulative growing season GPP ranged from a minimum of –214 g C/m² in the heath tundra in 2010 to a maximum of –108 g C m^{–2} in the tussock tundra in 2008, with bootstrapped errors estimated between ±18 to ±25 g C/m², depending on the year and ecosystem

(Table 2). In terms of cumulative growing season ER, the maximum was also in the heath tundra in 2010 (156 g C/m²), and the minimum was in the tussock tundra in 2008 (46 g C/m²), with bootstrapped errors between ±5 to ±20 g C/m², depending on the year and ecosystem.

Temperature and precipitation controls over cumulative NEE, GPP, and ER

Although sharp fluctuations in T_a coincided with increases in GPP and net CO₂ loss on a day to day basis (e.g., the circled areas in Fig. 3), GDDs were a good predictor of cumulative NEE and GPP across all three ecosystems. GDDs were also a good predictor of cumulative ER in the heath and tussock tundra. In the wet sedge tundra, cumulative precipitation was a better predictor of ER than GDD (Fig. 4). NEE decreased by 0.18–0.28 g C/m² per unit increase in GDD (Fig. 4a–c). As noted above, in 2010 the GDD during the early growing season (166 in June) was approximately the same as that later in the growing season in July–August in 2008 (162). Consequently, the heath and wet sedge tundra ecosystems had similar C uptake during these

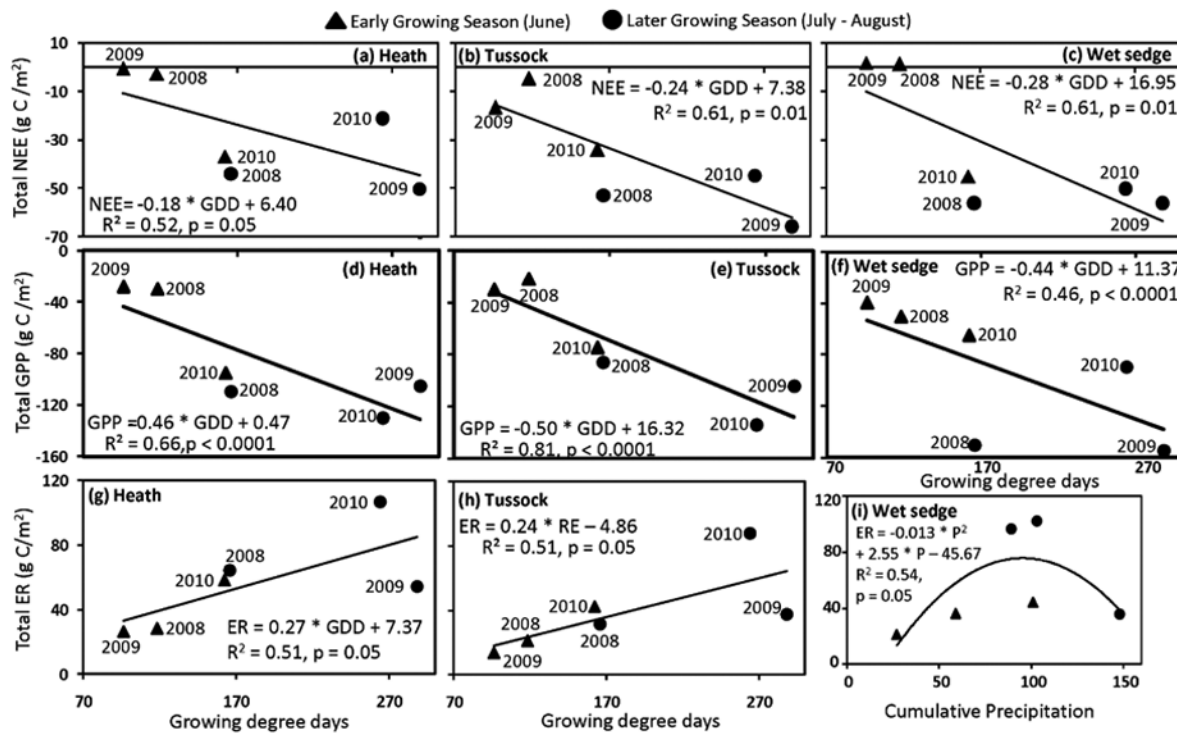


Fig. 4. Relation between NEE (a–c), GPP (d–f), ER (g–h) and growing degree days in the early growing season (30 days; June 2008–2010) and later growing season (62 days; July–August 2008–2010) for the heath tundra (a, d, g), tussock tundra (b, e, h), and wet sedge tundra (c, f). Also shown is the relation between early and late season cumulative precipitation and ER for the wet sedge tundra (i). Positive values of NEE and GPP denote a sink, and negative values denote a source.

two time periods (in the heath, -37 g C/m^2 in June 2010 and -44 g C/m^2 July–August 2008, and in the wet sedge, -46 g C/m^2 in June 2010 and -54 g C/m^2 July–August 2008). In fact, this early season heath tundra uptake in 2010 accounted for over 60% of the entire growing season net uptake in 2010 (Fig. 5a), while in 2008 and 2009, early growing season net CO_2 uptake accounted for only 3–8% of the entire growing season net CO_2 uptake. A similar pattern was seen in the tussock and wet sedge tundra (Fig. 5b, c).

GPP decreased by $0.44\text{--}0.50 \text{ g C/m}^2$ per unit increase in GDD (Fig. 4d–f). Again, warm temperatures in early 2010 promoted reduced GPP during the early growing season compared with years 2008 and 2009 (Fig. 5b). In the heath and tussock tundra, ER increased by $0.24\text{--}0.27 \text{ g C/m}^2$ per increase in GDD (Fig. 4g, h), but there was not a significant relation between ER and GDD in the wet sedge tundra. There was a strong parabolic relation between ER and cumulative

precipitation in the wet sedge tundra, with greater cumulative precipitation inhibiting ER (Fig. 4i). The relation between ER and precipitation was not significant for the heath or tussock tundra. Early season ER as a percentage of the ER for the entire season (Fig. 5c) was more similar from 2008–2010 than early season NEE or GPP as a percentage of the total NEE or GPP (Fig. 5a, b).

Winter NEE

All of the ecosystems acted as a net sink of CO_2 during the months of June–August. However, even without accounting for data that was lost during periods >6 days of power outages or iced equipment in the snow season, both the heath and wet sedge tundra ecosystems released CO_2 during the fall, winter and spring (‘cold season’) months, from September–May (Table 2). Given that the estimated release during the first two cold seasons of measurement (September 2008–May 2008 and September 2008–May 2009) does

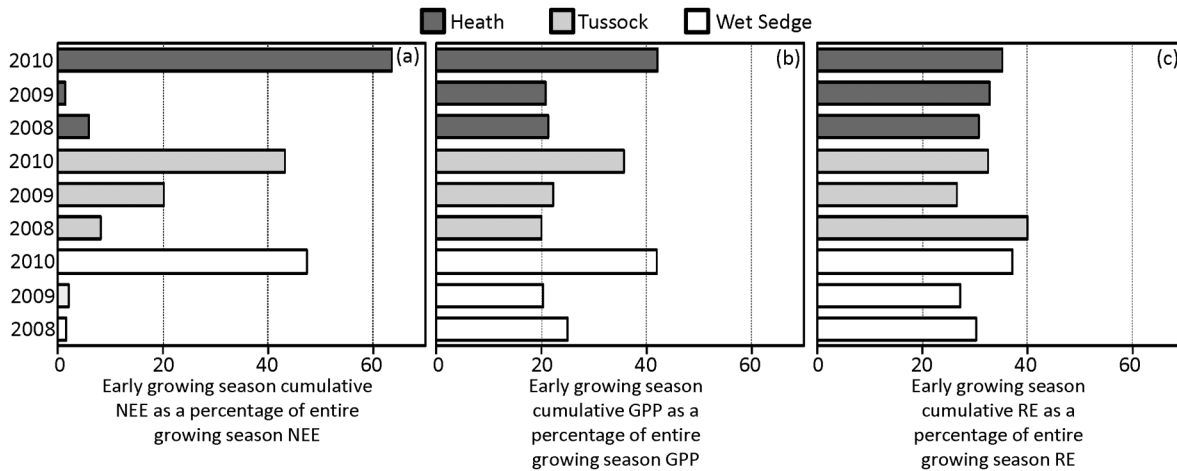


Fig. 5. Early growing season (June) cumulative NEE (a), GPP (b), and ER (c) as a percentage of entire growing season (June–August) for the heath tundra, tussock tundra, and wet sedge tundra.

not include data from 30% of the periods where we were unable to gap-fill the data (see *Methods: Data processing and post-processing*), the estimated CO₂ release is considered a ‘lower bound’ on the total amount of CO₂ released during these first two cold seasons of measurements. However, even without accounting for data loss, both the heath tundra and wet sedge tundra released slightly more CO₂ during the cold season of September 2008–May 2009 ($\sim 72 \pm 13$ g C/m² in the heath tundra and $\sim 61 \pm 14$ g C/m² in the wet sedge tundra) than what was taken up during the summer (-51 ± 16 g C/m² in the heath tundra and -59 ± 17 g C/m² in the wet sedge tundra), indicating that both ecosystems were slight sources of CO₂ during this period. During the third and fourth cold seasons, where data loss was only 15% and all of this was gap-filled, estimated losses of CO₂ were slightly larger in the wet sedge tundra (139–145 g C/m²) compared to the heath tundra (105–119 g C/m²), and both ecosystems were estimated to have acted as CO₂ sources during from June 2009–May 2011 (Table 2). Therefore, over the entire measurement period, from September 2007–May 2011, the heath tundra is estimated to have released 254 g C/m² and the wet sedge tundra released 233 g C/m², noting that these estimates of release would be slightly larger if we had not experienced power outages during the first two cold seasons that led to gaps >6 days in our day (Table 2).

Empirical modeling of NEE during the period of snow-covered ground

During the period of snow covered ground and negligible CO₂ uptake (e.g., September–May), NEE represented primarily ER (e.g., CO₂ released to the atmosphere). NEE from the heath and wet sedge tundra ecosystems were modeled with variables pertaining to daily snow depth, mean daily air temperature, mean daily atmospheric pressure, and mean daily wind speed (Table 3). At the heath tundra, there was a negative relation between snowpack depth and CO₂ release, indicating that, in deeper snow, CO₂ flux to the atmosphere decreases as it may remain within the porous spaces of the snowpack. At the wet sedge tundra, winter NEE was positively correlated with wind speed and drops in atmospheric pressure, indicating, that under high wind speeds, accumulated CO₂ within the snowpack is more rapidly released (Table 3). While half-hourly soil temperature data provided a good fit to half-hourly nighttime NEE (e.g., ecosystem respiration) during the summer at all three sites, there was not a significant relation between half-hourly winter soil temperature data and winter NEE (Table 3).

Water balance

The WB over the three June–August growing seasons of 2008–2010 differed across ecosystems (Fig. 6; Table 4). Based on the total WB by the end of the summer, there was a large amount of

Table 3. Regression analysis of summer nighttime NEE (June–August, where PPFD < 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and winter NEE (September–May) versus soil temperature (e.g., ecosystem respiration; $\text{g C m}^{-2} \text{30 min}^{-1}$), and regression analysis between daily NEE ($\text{g C m}^{-2} \text{d}^{-1}$) and other best-fit environmental variables for the heath tundra and wet sedge tundra ecosystems for the months September through May (winter).

Season	Model	R^2	N
Tussock Summer	$0.0367 \times e^x$ where $x = 0.0249 \times T_s$	0.58	1483
Heath Summer	$0.0172 \times e^x$ where $x = 0.0368 \times T_s$	0.56	1748
Winter	$0.0160 \times e^x$ where $x = 0.00802 \times T_s$	0.19 (ns)	17,695
Winter	$1.0445 \times e^x$ where $x = 0.2997 \times T_s - 0.7447 \times \text{Snow}$	0.32	974
Wet sedge Summer	$0.0367 \times e^x$ where $x = 0.0249 \times T_s$	0.66	1520
Winter	$0.0154 \times e^x$ where $x = 0.00691 \times T_s$	0.05 (ns)	17,082
Winter	$5.0390 \times e^x$ where $x = 0.0264 \times \text{Wind} - P_a \times 0.0212 + 0.00915 \times T_a$	0.52	983

Notes: Data is pooled across all study years combined. Unless noted as 'ns', models were significant at $P < 0.0001$. 'N' in the final column refers to the number of half hourly periods or days the equations are calculated from. Wind = mean daily windspeed (m s^{-1}), T_a = mean daily air temperature ($^{\circ}\text{C}$), T_s = half-hourly (for the equations incorporating only T_s) or mean daily (for the equations with other variable as well) temperature at soil surface ($^{\circ}\text{C}$), Snow = daily maximum snowpack (m); P_a = mean daily atmospheric pressure (kPa).

interannual variability in the WB of the heath (ranging from -14 mm in 2010 to 52 mm in 2008), less variability in the wet sedge (ranging from 4 mm in 2010 to 26 mm in 2008 and 2009), and almost no interannual variability in the tussock tundra (ranging from 21 mm in 2009 to 32 mm in 2008). The pattern of accumulated water differed between the years, with June of 2008 showing a negative WB that turned positive later in the summer (Fig. 6a–c). The WB was essentially positive for all of 2009 in all three ecosystems (Fig. 6d–f). In 2010, there was a long period of negative WB in all three ecosystems due to ET that was greater than precipitation (Fig. 6g–i).

Water use efficiency

The seasonal pattern of WUE in all three ecosystems followed that of NEE and GPP, reaching a peak in July, with lower values recorded during June and August (Fig. 7). WUE differed across sites, with the highest daily mean WUE from June–August for all years and sites occurring in the tussock tundra in 2010 ($1.7 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$), which also corresponded to the greatest cumulative GPP estimated for this ecosystem (-191 g C/m^2 ; Table 4). In the wet sedge tundra, daily mean WUE was greatest in

2008 ($1.5 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$), again corresponding with the greatest cumulative GPP estimated for this ecosystem (-202 g C/m^2). Daily mean values of WUE in the heath tundra were similar in 2008 and 2010 ($1.2 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$), and greater than in 2009 ($0.7 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$). Values of cumulative GPP in the heath tundra were also greater in 2008 (-201 g C/m^2) and 2010 (-214 g C/m^2) compared to 2009 (-131 g C/m^2). Across all years, there was a significant relation between total monthly GPP and total monthly ET in the heath tundra, but not in the tussock or wet sedge tundra (Table 5). Taking the vapor pressure deficit (VPD) into account provided a slightly stronger relation than that between simply total monthly GPP and total monthly ET, suggesting a link between CO_2 and water fluxes through stomatal conductance (Table 5). This link seemed strongest in the tussock tundra, where R^2 increased from 0.21 in the model without VPD to 0.36 in the model with VPD (Table 5).

DISCUSSION

The impact of earlier and later growing seasons on CO_2 fluxes

Climate change in the Arctic is expected to

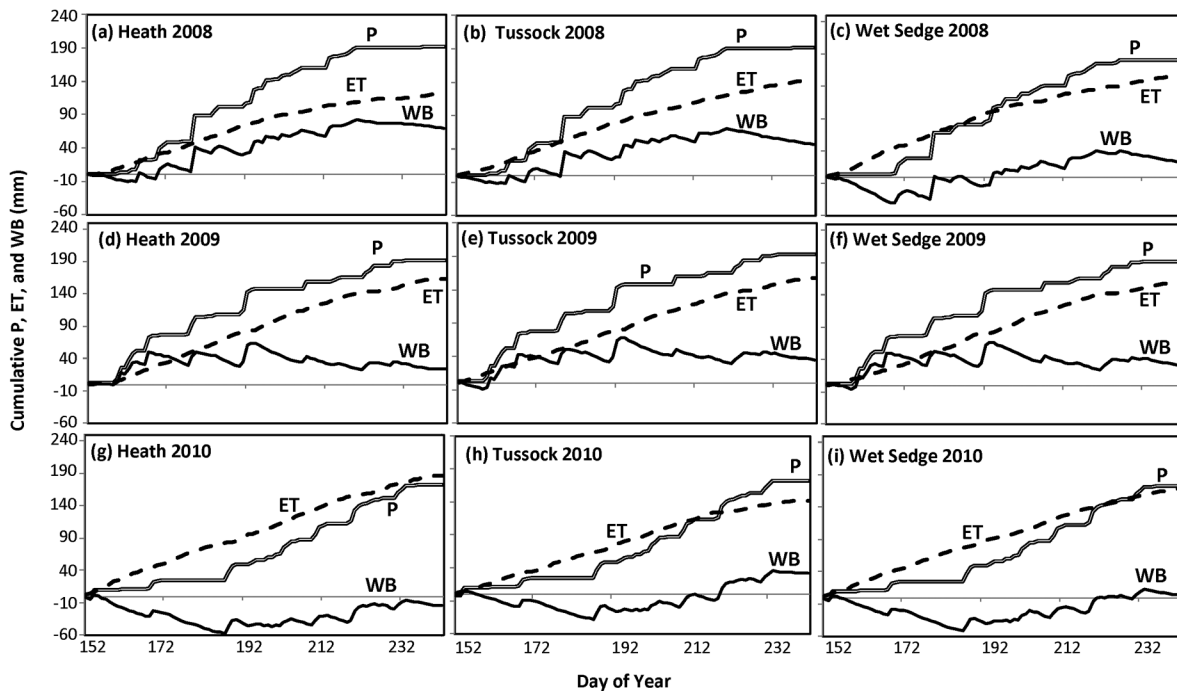


Fig. 6. Cumulative precipitation (P , mm/d), evapotranspiration (ET , mm/d), and water balance (WB , mm/d) from June–August for 2008–2010 at the heath tundra (a, d, g), tussock tundra (b, e, h), and wet sedge tundra (c, f, i).

Table 4. Summer (June–August) cumulative values of evapotranspiration (ET , mm), precipitation (P , mm), and water balance (WB , mm).

Parameter	2008	2009	2010
Heath			
ET	144 ± 5	177 ± 7	186 ± 8
P	196	192	172
WB	52 ± 5	15 ± 7	-14 ± 8
Tussock			
ET	164 ± 6	171 ± 5	142 ± 3
P	196	192	172
WB	37 ± 6	34 ± 5	30 ± 3
Wet sedge			
ET	170 ± 7	166 ± 4	168 ± 6
P	196	192	172
WB	26 ± 7	26 ± 4	4 ± 6

Note: Uncertainties for ET (\pm) are based on bootstrapping.

result in earlier springs and longer autumns. For most arctic vascular plants, dormancy is broken by the prolonged cold of winter, and they are able to become photosynthetically active and grow as soon as temperatures permit in the spring. We thus anticipate that earlier springs should result in earlier CO_2 uptake, because plant activity will closely track the warming

climate (Aurela et al. 2004). We did indeed measure greater negative cumulative GPP and NEE during the warm early growing season during June 2010 (Figs. 4, 5). The autumn is a different situation, however. The onset of dormancy in fall is photoperiodically controlled, though it can be hastened by early cold. Thus, a warmer, longer autumn will probably not result in prolonged photosynthetic uptake by arctic vascular plants. In contrast, respiration by soil microbes is mainly controlled by temperature and moisture. Unless photosynthetic C uptake by mosses and lichens is great even under the low light intensities of the arctic autumn, we would expect longer, warmer autumns to result in a greater loss of CO_2 during the autumn than currently occurs, at least under the present vegetation composition. Here, we found that during all years the ecosystems showed increases in NEE, indicating reduced photosynthesis, by the beginning of August, at the latest (Fig. 3d–f), despite differences in T_a during this month. The mean T_a was 3.4°C in August 2008, 4.8°C in August 2009, and 8.4°C in August 2010. The

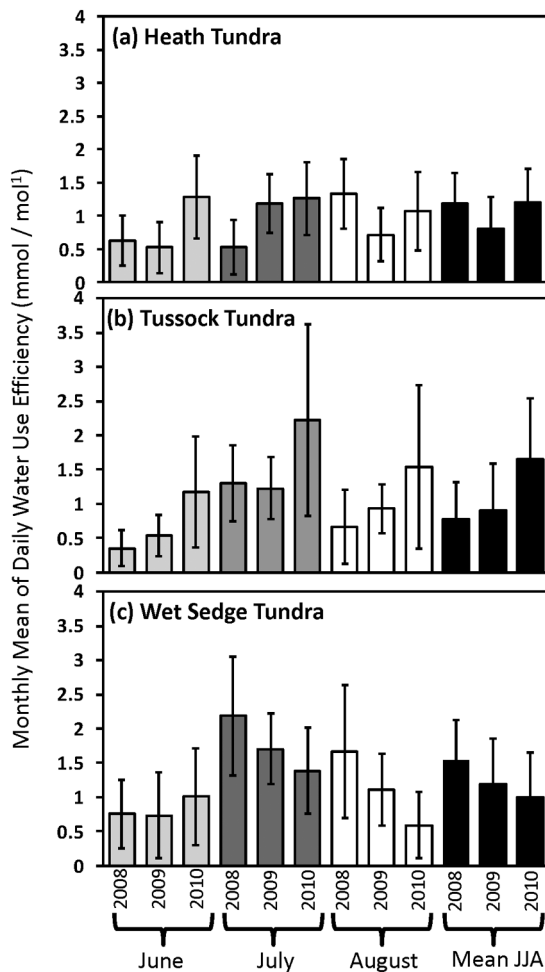


Fig. 7. Daily mean ecosystem water use efficiency (WUE_{eco} , $mmol/mol$) by month for June–August of 2008–2010 for the heath tundra (a), tussock tundra (b), and wet sedge tundra (c). The daily mean values are calculated based on 30-minute measurements. Also shown are the daily means across all three months, June–August, of each year.

heath tundra showed the greatest response to the warm August of 2010 in terms of increased respiration, which nearly offset early season CO_2 gains that occurred during the warm spring of 2010 (Fig. 3a, d, g). Interestingly, a different dynamic was found in the wet sedge tundra, where in 2010 ER was inhibited, perhaps due to more precipitation later in the growing season along with the warmer temperatures (Fig. 4i). This resulted in the greatest net CO_2 uptake in the wet sedge tundra during this period out of

any of the three growing seasons. Consequently, while warm air temperatures could have a significant influence on net CO_2 uptake during the early growing season, much of this could be offset if temperatures remain warm later in the growing season, thereby promoting respiration. Alternatively, if the ecosystem ER is inhibited by too much precipitation, then it is also possible that warmer temperatures later in the growing season will not promote greater ER. Recent work by Humphreys and Lafleur (2011) similarly found that an early snowmelt and greater spring warmth does not necessarily correspond to increased growing season CO_2 uptake.

Water use efficiency and water balance

Law et al. (2002) indicate that WUE for tundra ecosystems is lower than for other ecosystems, potentially due to low leaf area index (LAI), and a larger percentage of soil and bryophyte evaporation compared to transpiration in the tundra. Some studies indicate an increasing abundance of shrubs in the tundra and/or an increase in total vegetation greenness, with an increase in LAI, and a decrease in lichens and bryophytes due to decreases in light availability underneath the taller shrubs and larger plants (e.g., Cornelissen et al. 2001). Consequently, in the future it is possible that an increase in the abundance of tundra shrubs and leaf area may lead to greater WUE in these shrubbier and greener tundra sites. However, in sites that are drying, with decreases in ET, WUE may also decrease.

The relation between the WB, precipitation, WUE, and CO_2 fluxes in tundra ecosystems sites is complex. In a regional study of the CO_2 and water fluxes in Alaskan Arctic tundra, McFadden et al. (2003) found that water vapor and CO_2 fluxes were poorly coupled since water vapor exchange was largely determined by evaporation from mosses, while CO_2 exchange was controlled by the activity of vascular plants. Lafleur and Humphreys (2008) found NEE was sensitive to moisture, with lower values of net CO_2 uptake and WUE recorded during a dry year. Other studies have also found that NEE in the tundra is sensitive to dry conditions (Vourlitis and Oechel 1999, Kwon et al. 2006). Nobrega and Grogan (2008) found that peak rates of tundra net CO_2 gain occurred following a particularly large rain

Table 5. Relation between total monthly June–August GPP ($\text{g C m}^{-2} \text{ mo}^{-1}$) and ET (mm/mo) for 2008–2010 for the heath tundra, tussock tundra, and wet sedge tundra. Also given is the relation between $\text{GPP} \times \text{VPD}$ ($\text{g C m}^{-2} \text{ mo}^{-1} \text{ kPa}$) and evapotranspiration (mm/mo) for the three ecosystems.

Ecosystem type	Equation	R^2	P
Heath	$\text{GPP} = -1.01 \times \text{ET} + 0.46$	0.46	<0.001
	$\text{GPP} \times \text{VPD} = -1.14 \times \text{ET} + 17.86$	0.49	<0.001
Tussock	$\text{GPP} = -1.07 \times \text{ET} + 4.91$	0.21	>0.05
	$\text{GPP} \times \text{VPD} = -1.47 \times \text{ET} + 30.35$	0.34	<0.001
Wet sedge	$\text{GPP} = -0.87 \times \text{ET} - 13.02$	0.17	>0.05
	$\text{GPP} \times \text{VPD} = -1.47 \times \text{ET} + 29.22$	0.23	>0.05

Note: The slope of the relationship indicates the amount of carbon taken up in photosynthesis relative to the amount of water lost through evaporation and transpiration.

event, which decreased respiration and stimulated gross rates of photosynthesis, across three types of tundra in the Canadian low Arctic, including heath, dwarf birch and wet sedge tundra. This differed from the results in our study where we found that ER was depressed only in the wet sedge tundra following large amounts of precipitation, notably in July–August 2010 (e.g., Fig. 4i). Interestingly, the WB in the wet sedge tundra was slightly negative to near zero during this time, although water may flow into this system laterally (Fig. 6i).

Studies of WB in terrestrial ecosystems in the Arctic have found a drying of the ecosystem over the growing season that may lead to a negative WB by the end of summer. In a study performed in coastal arctic Alaska, Mendez et al. (1998) found that ET exceeds precipitation during the thaw period, resulting in a gradual drying of the watershed over the growing season. For a subarctic forest in northern Canada, Lafleur (1994) determined that during a five-year study period, four of the years resulted in a negative WB, with summer ET exceeding precipitation. In the Lena River Delta in Siberia, during years of extreme dryness, when summer ET exceeds precipitation, pond levels fall below the ground surface (Boike et al. 2008). Other research suggests that summer precipitation plays a minor role in the WB of the tundra ecosystems since during the summer, heavy rain events are not absorbed by mineral soils that are already near saturation (Kane et al. 1989). The results from our study show that the summer hydrology can be variable from year to year, with a negative WB possible in the early spring that can later shift to a positive WB by mid-summer or remain negative throughout the entire growing season (Fig. 6).

However, based on our studies and others discussed above, the WB dynamic is also highly dependent on the type of tundra ecosystem.

Snow season CO_2 fluxes

This study supports the conclusion that the CO_2 emission to the atmosphere during the period of snow covered ground is a large contribution to the total annual carbon budgets of arctic ecosystems (Zimov et al. 1996, Oechel et al. 1997, Nobrega and Grogan 2007). Some research has found that that nearly all of the “winter” respiration occurs in October–December, before the soils freeze, with very low rates in mid-winter when soil temperatures were very low, and a brief spike of respiration in April–May as temperatures warm (Schimel et al. 2006). There is some evidence of a similar pattern in our data (e.g., Fig. 2a, c), although this was somewhat difficult to discern due to missing data and to the timing of the CO_2 degassing, or release of CO_2 from the snowpack, as discussed below. Winter chamber measurements conducted within the footprint of the flux towers in this study detected moderate amounts of ER that were similar to those detected with the tower measurements (Kade et al., *unpublished manuscript*).

CO_2 flux from the ecosystem to the atmosphere during the winter is the result of a complex set of interactions of processes of production and storage of CO_2 in the soil and its transport to the atmosphere through the snow layer. Snow cover affects ecosystem CO_2 exchange through at least two opposite effects. First depending on thickness, porosity, and the properties of the snow surface (e.g., the snow crust), snow cover may significantly decrease CO_2 flux to the atmosphere, leading to the temporary

formation of pockets of high CO₂ concentration in the snow above the soil surface. Conversely, the main effect of snow is to increase soil temperatures by reducing heat loss from the soil to the atmosphere during winter. As a result, soil beneath snow freezes more slowly, and does not reach the very low minimum temperatures that occur in snow-free areas. In some cases, it may not freeze at all, thereby increasing CO₂ emission (Nobrega and Grogan 2007). In our study, we found that the snow cover and depth were negatively correlated with snow season CO₂ flux to the atmosphere from November to April, indicating that CO₂ is trapped in the snowpack and is not released until the wind speed increases or the atmospheric pressure drops, forcing the CO₂ from the snowpack.

Additional field studies that combine different methods to investigate driving factors causing pulses of winter fluxes are necessary. While wind velocity and the associated turbulent changes of atmospheric pressure have been documented as probable variables in determining CO₂ emissions during the Arctic winter (Coyne and Kelley 1971, Oechel et al. 1997), few long-term quantitative data are available. Time lags in soil response to environmental forcing, or other ecosystem-specific variables such as variable organic layer depth, soil carbon, mineralization, or litter quality may also be important (see also Larsen et al. 2007, Nobrega and Grogan 2008). Snow surveys in the tower footprints would be helpful to quantify the snow patchiness, and how this may then related to the winter carbon fluxes, particularly with respect to understanding the differences in the winter fluxes between the heath and wet sedge ecosystems (e.g., Table 2).

CONCLUSION

We found that the heath, tussock, and wet sedge tundra ecosystems were each a sink of CO₂, ranging from ~51 to 95 g C/m² during the June–August growing season. Our study supports the conclusion that summer uptake is generally lost through ER during the period of snow covered ground, with both the heath and wet sedge tundra acting as CO₂ sources from September 2007–May 2011. The timing of the switch from source to sink of CO₂ in the spring appears to be strongly regulated by the number

of GDD early in the season. Winter NEE was negatively correlated with snow depth and positively correlated with wind speed and drops in atmospheric pressure. Measurements at these sites are ongoing, and there is a critical need to continue to develop longer time series to address how these ecosystems may respond to changes in climate, and to understand the differences in the carbon and water fluxes across the different types of tundra in order to make regional predictions of carbon and water budgets.

ACKNOWLEDGMENTS

This research was funded by the National Science Foundation Office of Polar Programs (OPP 0632264), with a grant during the International Polar Year, ‘Collaborative Research on Carbon, Water, and Energy Balance of the Arctic Landscape at Flagship Observatories and in a PanArctic Network’. Tracy Dahl, Roy Stehle, and Martin Grill of CH₂M Hill provided expertise in building and maintaining the power systems and remote communications at the sites. Anja Kade provided information on the vegetation composition surrounding the flux towers. Masa Ueyama provided the flux partitioning tool used in this manuscript. Adrian Rocha downloaded data during the summer months of 2008 and 2009 and provided comments on an earlier draft of this manuscript. Terry Chapin and Steve Oberbauer provided valuable feedback on an earlier draft of this manuscript. We also thank two anonymous reviewers for helpful comments.

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