Effects of Fine-Scale Topography on CO2 Flux Components of Alaskan Coastal Plain Tundra: Response to Contrasting Growing Seasons

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Abstract

Arctic regions hold considerable reservoirs of soil organic carbon. However, most of this carbon is in a potential labile state, and expected changes in temperature and water availability could strongly affect the carbon balance of tundra ecosystems. Plant community composition and soil carbon are closely tied to microtopography and position relative to the water table. We evaluated CO$_2$ fluxes and moss contribution to ecosystem photosynthesis in response to fine-scale topography across a drained lake bed in Barrow, Alaska, during two contrasting growing seasons. CO$_2$ exchange was assessed through static chamber measurements in three vegetation classes distinguished by plant dominance and topographic position within low-centered polygons. Gross primary production (GPP) and ecosystem respiration (ER) were the lowest under high soil moisture conditions in 2006. ER responded more strongly to wet conditions, resulting in a larger summer sink in 2006 than in 2005 (64 vs. 17g CO$_2$ m^{-2}, respectively). Microsites responded differently to contrasting weather conditions. Low elevation microsites presented a strong reduction in ER as a result of increased water availability. A maximum of 48% of daytime GPP and 33% of seasonal daytime GPP was contributed by moss on average across microtopographic positions. The interaction between fine-scale microtopography and variation in temperature and water availability can result in considerable differences in CO$_2$ sink activity of the polygonal tundra.

Introduction

As a result of their large reservoirs of soil carbon (1672 Pg; Tarnocai et al., 2009), arctic ecosystems play a crucial role in the global carbon cycle (Oechel et al., 1993; Chapin et al., 1995; Schuur et al., 2008; Tarnocai et al., 2009). A considerable part of the arctic soil carbon (191–495 Pg) is stored under labile conditions in the seasonally active layer and the upper most permafrost (0–100 cm deep; Post et al., 1982; Tarnocai et al., 2009), where an increase in temperature can thaw the upper layer of the permafrost, exposing soil carbon to microbial decomposition (Schuur et al., 2008). Recent climate models have shown that the long-term cooling trend of the Arctic has reversed and the current warming is expected to continue to increase the average temperature of the globe (Solomon et al., 2009). Additionally, a temperature increase is likely to be accompanied by a shift of the hydrological regime, potentially causing drying in some areas and thermokarst erosion and flooding in others (Schuur et al., 2008). In the Arctic, changes in hydrology and temperature regimes are likely to alter ecosystem respiration (ER) and gross primary production (GPP), resulting in major shifts in the net ecosystem CO$_2$ exchange (NEE) and soil carbon losses (Oberbauer et al., 1991; Oechel et al., 1993; Chapin et al., 1995; Shaver et al., 2006).

Considerable attention has been directed toward the direct effects of warming on the CO$_2$ balance of tundra ecosystems (Kwon et al., 2006; Shaver et al., 2006; Schuur et al., 2008; Tarnocai et al., 2009). However, in the medium-term, indirect effects of climate warming on the water table via increased evapotranspiration (Rott and Obleitner, 1992) and deeper active

layer depths have the potential to be as great or greater than direct effects on the CO$_2$ balance. Although increased evapotranspiration as a result of warming could have a slight cooling effect on the soil surface (Heijmans et al., 2004), potentially reducing ER in the short-term, in the long-term, warming could lower the water table and increase the depth to permafrost, strongly increasing oxidation of the organic matter and limiting water access (Johansson et al., 2006; Schuur et al., 2008).

In the Arctic, the depth to the permafrost, water availability, plant cover, and productivity are strongly associated with microtopography (Oberbauer et al., 1991; Engstrom et al., 2005; Schuur et al., 2007). Although climate, soil type, and topography are among the primary drivers of permafrost presence and active layer thickness (Gomersall and Hinkel, 2001; Johansson et al., 2006), plant community composition, particularly the presence of bryophytes such as mosses, also plays an important role in regulating soil temperatures and depth of thaw (Beringer et al., 2001; Heijmans et al., 2004). Mosses such as *Sphagnum* influence the energy transfer between atmosphere and soil as a result of the cooling effect on the soil produced by high evaporation rates and the insulating effect of the thick organic layers (Heijmans et al., 2004; Gornall et al., 2007). As a result, mosses can potentially reduce depth of thaw, ER, and plant productivity (Brooker and van der Wal, 2003) by reducing soil temperature.

The polygonal tundra in the Arctic Coastal Plain has relatively small variation in elevation, but these small differences can be sufficient to create significant variation in the depth to the permafrost, water availability, and species composition. That, in turn, can affect the CO$_2$ flux components (NEE, ER, GPP;

Billings and Peterson, 1980; Oberbauer et al., 1992; Sommerkorn et al., 1999; Gomersall and Hinkel, 2001; Sjogersten et al., 2006; Sommerkorn, 2008; Sullivan et al., 2008). For instance, in the low-centered polygons, mosses commonly dominate the rims (relatively high microsites) with only slight cover of vascular plants (Webber, 1978). In these areas the GPP can be affected by low water availability as a result of the lack of a vascular system in mosses that limits their ability to uptake and conduct water (Riutta et al., 2007; Robroek et al., 2009), and low soil nutrient availability in part as a result of the slow decomposition of the moss peat (Malmer et al., 1994). Mosses also can influence the soil nutrient pool by capturing most of the atmospheric deposition and litter fall (Malmer et al., 1994; Chapin et al., 1995). Additionally, the low soil temperatures favored by the moss layer can reduce vascular stomatal conductance, further limiting growth (Brooker and van der Wal, 2003; Starr et al., 2004). Despite the expected low productivity of the moss-dominated areas, previous studies have reported the contribution of mosses to the ecosystem assimilation of CO_2 across the Arctic to range from negligible to 96% (Sommerkorn et al., 1999; Douma et al., 2007; Campioli et al., 2009). Other areas associated with wet sedge–moss cover (intermediate elevation) are very productive compared to areas dominated mostly by mosses (Nosko and Courtin, 1995). In these areas, the vascular plants offer a protective canopy that could prevent drying of the moss layer and photoinhibition (Harley et al., 1989; Murray et al., 1993). In areas dominated by wet sedge, such as the center of the low-centered polygons (low areas with frequent presence of standing water), GPP is expected to be higher than that of the moss-dominated areas because of factors such as the ability of vascular plants to control water loss, higher leaf area, and photosynthetic capacity, among others (Webber, 1978; Malmer et al., 1994; Riutta et al., 2007).

The relative differences in elevation among the microtopographic features of the polygonal tundra with respect to the water table are likely to affect the CO_2 flux components differently (Oberbauer et al., 1991; Sommerkorn, 2008; Sullivan et al., 2008; Chivers et al., 2009). In high areas (polygon rims) ER is expected to be relatively high as a result of high soil oxygen availability. Conversely, the ER of the low areas (center of low-centered polygons) is expected to be low as a result of higher water availability and anoxic soil conditions. In the case of GPP, the effect of microtopography is likely to be complex as a result of the combined effect of different vegetation covers and water availability. For instance, standing water in the center of the low-centered polygons could submerge leaf area, reducing plants' ability to exchange gas with the atmosphere, but low water availability can also decrease the GPP of the mosses in the polygon rims. The direction of NEE (sink or source) will be tightly coupled to the response of ER and GPP under each microsite. Therefore, determining the differences of the CO_2 components between the different microsites, and understanding the magnitude of these responses to the interannual variability of water and temperature, is relevant for predicting the response of polygonal tundra ecosystems to climate change.

Our goal was to determine the effect of fine-scale microtopography on the CO_2 flux components of a polygonal wet tundra ecosystem of the Alaskan Arctic Coastal Plain. Specifically, we examined the variability in CO_2 exchange across wet sedge and low-centered polygon tundra. We hypothesized that: (1) GPP of the vascular-dominated areas (low areas) should be higher than that of the moss-dominated areas (polygon rim), (2) ER of the high sites (polygon rim) should be higher than that of the low sites (vascular-dominated), and (3) NEE should be higher in the low areas than in the high areas. Because of the importance of mosses in these communities, we also examined the proportion of the total ecosystem CO_2 exchange contributed by mosses. We hypothesized that: (1) based on the high moss cover, we expect the contribution of moss to the ecosystem GPP to be high, and (2) the proportion of the moss contribution to the ecosystem GPP should change along the growing season. To test these hypotheses we used the bed of a drained thaw lake that provides an area with some of the most homogeneous conditions found in the Arctic Coastal Plain landscape.

Methods

STUDY SITE

Our study was conducted in the Barrow Environmental Observatory (BEO) in Barrow, Alaska (71.32°N, 156.62°W). The BEO is located on the Barrow Peninsula, where about 22% of the surface consists of lakes and 50% comprises drained lake basins of different ages (Hinkel et al., 2003). At Barrow, the mean annual and July temperatures are −12 °C and 3.7 °C, respectively (Oberbauer et al., 2007). Late August thaw depth is about 35 cm (Walker et al., 2003). Mean annual precipitation at the area is approximately 120 mm (Curtis et al., 1998). On average the site presented acidic soil conditions, with a pH range from 4.4 to 5.7. The study area was a 62 ha naturally drained thaw lake (Billings and Peterson, 1980). The 1.4-km-long thaw lake has a natural flow gradient (11 cm difference) oriented in a north-south direction with the lake-bed outlet on the south end. The lake bed is dominated by wet sedge tundra with low-centered polygons throughout much of the basin and few small permanent thaw ponds. The dominant species were *Carex aquatilis* Whalenb., *Eriophorum scheuchzeri* Hoppe, *Sphagnum* spp., *Dupontia fisheri* R. Br., and *Arctophylla fulva* (Trin.) Rupr. ex Andersson. The lake bed provided two scales of microtopographic variation that can potentially affect ecosystem CO_2 exchange: the north-south water flow gradient and the differences in elevation between the center (small catchments) and the edges (rims) of the low-centered polygons.

EXPERIMENTAL DESIGN

Baseline Comparison of the Lake Sections

To assess the potential effect of the north-south flow gradient, the lake bed was divided into three sections: north, central, and south (Fig. 1). To provide access with minimum disturbance, a 200 m east-west elevated boardwalk (perpendicular to the natural flow gradient) was installed in each of the sections approximately 330 m apart. To maximize the spatial distribution of the plots along each lake section, each boardwalk was divided into blocks of 30 m and within these blocks we randomly selected the location for a plot. A total of 18 plots were selected for measurements of CO_2 exchange with six along each lake section.

Assessing the Effect of Natural Microtopographic Variation

For the microtopographic comparison, plots from all lake sections were reclassified based on plant cover, moisture condition, and position in the polygon, if present. A high-resolution digital elevation model (DEM; Tweedie et al., unpublished data) was used to determine the relative elevation of all plots. Three classes were created: (1) center of the polygon or wet sedge tundra with high vascular plant cover, (2) transition areas with no clear presence of standing water and low vascular canopy cover, and (3) drier conditions at the top of the polygon rim with predominantly non-vascular canopy cover. Here, plant canopy cover is defined based on
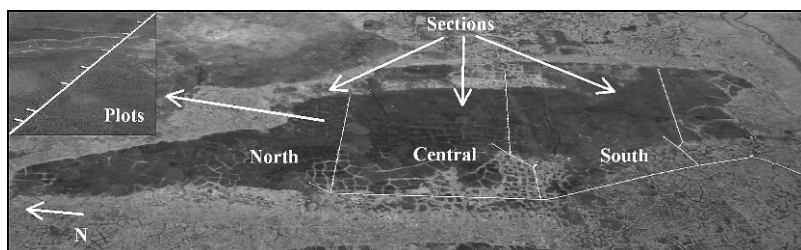
P. C. Olivas et al. / 257

the dominant growth form in the uppermost vegetation layer, which ranged from vascular-dominated canopy to only mosses. Eight of the 18 plots were categorized as vascular-dominated, six were intermediate, and four were moss-dominated polygon rims.

Microclimate and Water Level

Means of air temperature (°C) and photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) were recorded every 30 minutes and stored on a Campbell Scientific CR10X data logger at a weather station located at the center of the lake bed. Temperature was measured with a CS500 sensor (Campbell Scientific, Logan, Utah, U.S.A.) and PAR with a quantum sensor (Li-190, LI-COR Inc., Lincoln, Nebraska, U.S.A.). Thaw depth at each of the plots was measured weekly to the nearest centimeter using a metal soil probe and the top of the green moss layer as the reference. Water tables were assessed by weekly measurements of the levels of permanent ponds inside the basin using a differential global positioning system.

Ecosystem CO_2 Exchange

Carbon dioxide fluxes were measured using an infrared gas analysis system (LI-6200, LI-COR Inc., Lincoln, Nebraska) with static-chamber techniques (Oberbauer et al., 2007). The chamber was cylindrical (51 cm tall by 43 cm diameter) made of transparent acrylic (95% transmissibility and 6.35 mm wall thickness) with two internal fans to ensure air mixing. A small diameter tube was connected to the inside and outside of the chamber to minimize pressure gradients that can affect flux measurement (Daunicht and Brinkjans, 1995). The volume of the chamber was adjusted for the presence of standing water.

We used a polyethylene skirt attached to the bottom of the chamber weighted with a heavy metal chain to increase sealing and reduce CO_2 leakage during the 2005 sampling campaign (Saleska et al., 1999). Relatively smooth topography and frequent standing water facilitated this technique. At the end of the 2005 growing season, white PVC pipe bases were installed to provide a sealable base for the chamber. In 2006, fluxes were measured using these bases and by coupling the chamber to the base. The chamber plus the base volume was adjusted for each plot.

NEE was measured by placing the chamber over the base (plot) and recording the rate of change in the CO_2 concentration inside of the chamber. We measured the rate of change in concentration every second and recorded the average rate of CO_2 exchange over an integration time of 30 seconds. This was done three times over a period of one and a half minutes. We allowed CO_2 mixing between chamber and infrared gas analyzer system before initiating the measurements. We recorded only the exchange rates that did not show a strong sequential trend (upward or downward) because that would be an indication that the rates of exchange had not yet equilibrated between the ecosystem, chamber, and the analyzer, resulting in under- or overestimation of the CO_2 exchange rates. We repeated the measure-

ments until a steady rate of exchange was obtained, but avoided leaving the chamber on the plot for extended periods to prevent unrealistic CO_2 concentrations and humidity inside the head space of the chamber (Oberbauer et al., 2007). The average of the last two exchange rates was used for the flux calculations. To calculate the CO_2 exchange rates, we used the default equations provided by LI-COR (LI-COR Inc., 2001). ER was measured with the same method, but with a black cloth over the chamber to prevent photosynthesis. GPP was estimated as the difference between NEE and ER. We present NEE, ER, and GPP using an ecosystem perspective where positive numbers mean ecosystem uptake.

To measure the carbon fluxes we divided the plots into two sets. Each set was measured once a week, and subsequently combined to determine the weekly average of the CO_2 flux components at each lake section. In each plot, the CO_2 assessments consisted of a measurement every four hours, for a total of six measurements over a period of 24 hours. Thus, at the end of the 24-hour cycle each plot had six NEE and six ER measurements. As a result of long distances between plots, the plots were sampled sequentially rather than randomly, from north-south and east-west.

Relative Contribution of Mosses to Ecosystem CO_2 Flux

For assessment of the contribution of mosses to the carbon uptake capacity of the ecosystem, three additional sites were randomly selected along each of the three lake sections in 2006. At each of the nine sites, two plots with similar vegetation cover were established, one control and one moss removal. To remove the moss GPP, we clipped only the active photosynthetic tissue of the moss layer in the manipulated plots (removed all moss green tissue). We chose moss clipping because it presented the least disruption of the baseline ecosystem respiration, and because previous studies have shown that removal of vascular canopy can cause a strong reduction of the moss photosynthetic capacity (Harley et al., 1989; Murray et al., 1993). To determine the contribution of moss to the whole ecosystem GPP, we calculated the difference in GPP between control and moss-clipped plots. We conducted four sets of flux measurements during the growing season. Each assessment included nine control and nine moss-clipped plots (replicates). The CO_2 fluxes were measured from 0800 to 1700h Alaska Daylight Time (AKDT), bracketing the time of maximum photosynthesis. For this experiment, we used a new set of plots in every sampling campaign (new plot was clipped and a new control plot was selected). Control and clipped plots were adjacent to each other and within the same microtopographic feature. This approach reduced the potential effects of spatial variation in the estimation of the moss contribution to the ecosystem GPP. The CO_2 fluxes were measured using the same technique used for the other CO_2 flux assessments; however, we used a smaller chamber equipped in the same manner as the large chamber to decrease ground disturbance in the study site as a result of the moss clipping. We standardized GPP by PAR and measured control and clipped plots the same day to reduce any temperature effect on the CO_2 fluxes.

TABLE 1

General description of the plant cover for the study site. LAI (leaf area index, $m^2\ m^{-2}$) for vascular plants, % of cover for mosses, and NDVI (normalized difference vegetation index).

		Location		
		North	Central	South
Biomass (g/m2)	Bryophytes	432 ± 29	269 ± 95†	369 ± 65
	Vascular plants	23 ± 5	48 ± 10	40 ± 14
Cover (%)	Bryophytes	0.96 ± 0.02	0.75 ± 0.23	0.82 ± 0.15
LAI (m2 m−2)	Vascular plants	0.30 ± 0.07	0.69 ± 0.19	0.57 ± 0.20
Total	LAI	1.26 ± 0.08	1.44 ± 0.42	1.38 ± 0.14
	NDVI	0.44 ± 0.03	0.37 ± 0.01	0.41 ± 0.03

† Means ± Standard Error. $N = 9$.

To estimate the seasonal GPP of moss, the average proportion of GPP contributed by moss in the nine moss experiment plots during the four flux samplings in the 2006 season was applied to the weekly flux samplings from the 18 plots. Only the measurements from 0800 to 1700h AKDT were used.

Assessing Biomass and Productivity with NDVI

Normalized difference vegetation index (NDVI) has been used as a tool to assess productivity and plant community at large scales and of remote areas because it correlates well with green biomass (Riedel et al., 2005; Steltzer and Welker, 2006). We measured NDVI at all plots through both growing seasons at each flux sampling using digital images taken with an ADC Model 4 digital camera (Dycam Inc., Woodland Hills, California, U.S.A.; La Puma et al., 2007). The pictures were taken perpendicular to the ground within one day of the flux measurements. For the determination of NDVI from the images we used Briv32 (version 1.92) with a white Teflon panel as a reflectance standard. NDVI photographs were taken near solar noon under homogeneous sky conditions.

PLANT COVER

Moss and vascular cover, biomass, and the leaf area index (LAI; m^2 of leaf area per m^2 of ground area) across the lake bed were estimated by direct harvesting near peak season (early August). Three randomly selected plots (25 × 25 cm) were established along each of the lake sections: north, central, and south. Leaf material for each vascular species was subsampled to estimate the ratio of leaf area to dry mass (specific leaf area, SLA), which was used to calculate LAI from leaf biomass. Mosses (mostly *Sphagnum*) covered more than 50% of the ground in most of the plots, whereas the LAI of vascular plants was greater than 0.5 in only 44% of the plots (Table 1). Moss cover ranged from 30 to 100% and the vascular LAI from 0.2 to 0.97.

Data Analysis

We first evaluated the north-south gradient, and subsequently the effect of microtopography on the seasonal means of the CO_2 flux components and NDVI. The north-south gradient effects were tested using a two-way analysis of variance (two-way ANOVA) with two fixed factors: year (two levels), and lake section (three levels). Similarly, the effects of microtopography were tested also with a two-way analysis of variance (two-way ANOVA) with two fixed factors: year (two levels), and microsite class (three levels). Thaw and NDVI were also tested using the

same technique. Here we report the actual means accompanied by the p-value calculated with the models, rather than the estimated marginal means. All means are accompanied by standard error. The analysis was done using SPSS 11.5.0 (SPSS Inc., Chicago, Illinois, U.S.A.).

To estimate whether the study site or microtopography category was a source or sink for CO_2, the area under the curve (AUC) for the seasonal NEE or GPP was calculated. The AUC was estimated using the trapezoid method, where two continuous points in the X (days) axes are subtracted (a and b) and then multiplied by the half of the addition of the two Y axes values (c and d) (units are µmol of $CO_2\ m^{-2}\ s^{-1}$). The resulting AUC was transformed to grams of CO_2 per square meter over the season (g $CO_2\ m^{-2}\ season^{-1}$).

Results

INTERANNUAL DIFFERENCES: MICROCLIMATE AND ECOSYSTEM CO₂ FLUX

Study seasons presented contrasting weather conditions that resulted in considerable differences in microclimate and ecosystem carbon flux components. The average air temperature recorded during the growing season (26 June–24 August) was considerably warmer for 2005 than for 2006 (4.6 and 3.3 °C, respectively). The seasonal PAR was very similar between years (Fig. 2). Mean growing-season thaw depth differed between years, with mean depth in 2006 (17.3 ± 0.7 cm) greater than that in 2005 (10.9 ± 0.7 cm, $F = 65.29$, $p < 0.0001$). The maximum thaw depths were 22 cm and 35 cm for 2005 and 2006, respectively. Lake sections and interaction year*lake sections effects were not significant ($F = 0.243$, $p = 0.786$; and $F = 1.212$, $p = 0.312$, respectively). However, during both years the south presented slightly deeper thaw than the north and central lake sections. The comparison across years and microtopography categories revealed that year and microtopography effects were significant ($F = 76.85$, $p < 0.0001$; and $F = 6.18$, $p = 0.006$, respectively). Deeper thaws in 2006 than in 2005 did not result in a significant interaction between year and microtopography ($F = 0.03$, $p = 0.97$). During both years, vascular-dominated plots presented deeper thaw than the polygon rim plots ($p = 0.002$), with intermediate plots not different from either. Pond levels, a measure of the lake-bed water table depth, were higher at the beginning of the season in 2005 than in 2006 (Fig. 2). However, we observed greater thaw depths and much higher mid-season water levels in 2006 than in 2005 (Fig. 2).

The estimates of seasonal NEE suggest a significantly higher carbon uptake in 2006 than in 2005 despite lower GPP (Table 2). The study area in 2005 had a seasonal uptake of 17 ± 7 g $CO_2\ m^{-2}\ season^{-1}$. For approximately the same period (21 June–22 August)
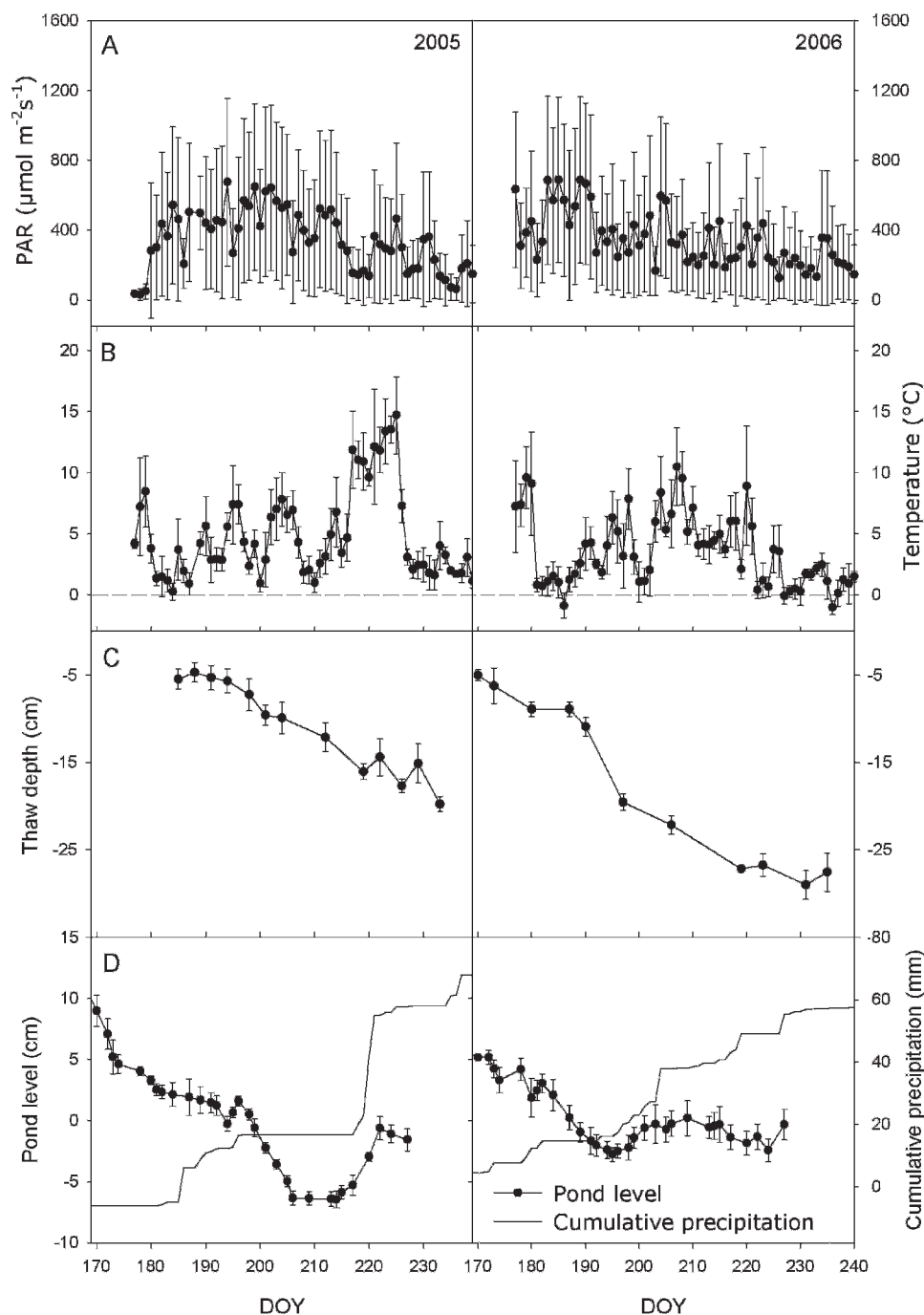
FIGURE 2. (A) Photosynthetically active radiation (PAR). Day of year (DOY). (B) Air temperature. (C) Thaw depth. (D) Seasonal water level of ponds inside the lake bed and cumulative rainfall. The values of the pond levels represent the deviation from the seasonal mean. Error bars represent ± one standard deviation for PAR and temperature, and ± one standard error of the mean for thaw and pond level for the growing seasons of 2005 and 2006.

in 2006 the site uptake was 64 ± 5 g CO_2 m^{-2} season^{-1} (one-way ANOVA; $F = 28.31$, $p < 0.0001$). Interestingly, differences in GPP did not correspond to significant differences in NDVI between 2005 and 2006 (Table 2).

The assessment of the north-south gradient effect on the CO_2 flux components and NDVI revealed significant differences between years, only for the CO_2 fluxes; no difference between lake sections within years was observed for either. The interaction between lake section and year was not significant for any of the CO_2 flux components or NDVI (Table 2).

MICROTOPOGRAPHY AND PLANT COVER

We found that for NEE, the effect of microtopography was not significant within years; however, for ER, GPP, and NDVI the

microtopography main effect was significant (Tables 3 and 4). The interaction between microtopography and year was not significant for any of the dependent variables (Table 3).

Between years NEE was higher in each microtopographic category in 2006 than in 2005, with no difference within years (Table 4). ER rates were higher in 2005 than in 2006. Within years, ER compared across microtopographic categories showed similar patterns in both 2005 and 2006 (Table 4 and Figure 3); polygon rim plots had the highest respiration rates in both years (-0.946 ± 0.090 and -0.635 ± 0.059 SE μmol m^{-2} s^{-1} for 2005 and 2006, respectively). Vascular-dominated and intermediate plots did not differ significantly for ER rates for any of the years (Table 4 and Figure 3). The GPP rates were similar between vascular-dominated and intermediate plots in 2005 and 2006 (Table 4 and Fig. 3), but polygon rim plots had the highest mean

TABLE 2

Two-way ANOVA main effects and seasonal mean net ecosystem exchange (NEE), ecosystem respiration (ER), gross primary production (GPP), and normalized difference vegetation index (NDVI) for the study site. Bold represents significant difference at α = 0.05.

	Effect	Df	F	P-value	2005 Means	2006 Means
GPP	Year	1	**19.67**	**<0.0001**	0.848 ± 0.027[†]	0.633 ± 0.039
	Lake section	2	0.99	0.38		
	Lake section*year	2	0.13	0.88		
	Error	30				
NEE	Year	1	**14.47**	**0.001**	0.052 ± 0.032	0.211 ± 0.025
	Lake section	2	0.96	0.91		
	Lake section*year	2	0.45	0.64		
	Error	30				
ER	Year	1	**49.98**	**<0.0001**	-0.792 ± 0.034	-0.419 ± 0.037
	Lake section	2	0.70	0.51		
	Lake section*year	2	0.04	0.96		
	Error	30				
NDVI	Year	1	0.96	0.34	0.417 ± 0.006	0.424 ± 0.004
	Lake section	2	1.68	0.20		
	Lake section*year	2	0.08	0.92		
	Error	30				

[†] Seasonal means for CO_2 flux components were calculated from diurnal measurements done weekly. CO_2 flux components are in μmol m^{-2} s^{-1} using the ecosystem notation where positive rates represent uptake and negative rates losses. Means ± Standard Error.

GPP during both years (0.969 ± 0.040 and 0.825 ± 0.071 SE μmol m^{-2} s^{-1}, 2005 and 2006, respectively). The NDVI showed a slight increase from 2005 to 2006 (Table 2 and 4). Within years the cover types did not differ in 2005; however, in 2006 vascular-dominated plots presented lower values than those of the intermediate plots (Table 4).

The carbon uptake determined as the AUC of the seasonal NEE presented significant differences between years; 2006 presented lower respiratory losses than 2005, which translated into higher carbon accumulation per unit area despite the decrease in GPP in 2006 (two-way ANOVA, F = 25.07, p < 0.0001).

TABLE 3

Main effects of the two-way ANOVA for the seasonal means of the CO_2 flux components and normalized difference vegetation index (NDVI) across microtopographic features for 2005 and 2006.

Production	Df	F	P-value
Gross Primary Productivity			
Year	1	26.0	**<0.0001**[†]
Microtopography	2	9.46	**0.001**
Microtopography * Year	2	0.56	0.58
Error	30		
Net Ecosystem Exchange			
Year	1	13.2	**0.001**
Microtopography	2	0.34	0.72
Microtopography * Year	2	0.01	0.99
Error	30		
Ecosystem Respiration			
Year	1	82.01	**<0.0001**
Microtopography	2	13.76	**<0.0001**
Microtopography * Year	2	0.40	0.68
Error	30		
NDVI			
Year	1	0.71	0.41
Microtopography	2	4.40	**0.02**
Microtopography * Year	2	0.20	0.82
Error	30		

[†] Bold-face font represents significant difference at α = 0.05.

Within years the differences between microtopographic categories were not significant. However, in the 2005 growing season determinations of AUC for the NEE seasonal uptake for each microtopographic category revealed that all categories were net carbon sinks (Fig. 3). The intermediate microtopographic category was the strongest sink followed by the vascular and polygon rim microsites (22 ± 11, 19 ± 10, and 5 ± 14 g CO_2 m^{-2} season^{-1}, respectively). In 2006, the intermediate microtopographic category again was the strongest CO_2 sink (71 ± 6 g CO_2 m^{-2} season^{-1}) followed by the vascular (63 ± 9 g CO_2 m^{-2} season^{-1}) and polygon rim plots (53 ± 10 g CO_2 m^{-2} season^{-1}).

MOSS CONTRIBUTION TO THE ECOSYSTEM CO_2 FLUX

The proportion of ecosystem GPP contributed by moss between 0800 and 1700h AKDT, ranged from 31 to 48% with the highest values associated with vascular plant leaf area development and senescence (early and late in the growing season; Fig. 4). A second-order polynomial was the best fit for the proportion of moss contribution and day of the year; however, the relationship was not significant (R^2 = 0.69, p = 0.55). As a result, to estimate the seasonal contribution of mosses to the daytime ecosystem GPP, we used the average proportion of the moss contribution found with the moss clipping. We estimated that, on average, ~33% of the seasonal ecosystem GPP (289 g CO_2 m^{-2} season^{-1}) was contributed by mosses during the 2006 growing season (~95 g CO_2 m^{-2} season^{-1}).

Discussion

CONTRASTING GROWING SEASONS

We observed strong differences in the 2005 and 2006 growing season CO_2 flux components for the lake bed, likely in response to differences in thaw depth, standing water level, and temperature (Tables 2 and 3 and Fig. 2; Oberbauer et al., 1992; Oechel et al., 1993; Hobbie and Chapin, 1998; Shaver et al., 2006). Although soil temperature is an important regulator of ER, especially in Arctic and peatland ecosystems (Oberbauer et al., 1992, 2007; Ostendorf, 1996; Oechel et al., 1998), under conditions of high soil moisture content ER is likely to be low, reducing CO_2 losses,

TABLE 4

Seasonal mean CO_2 flux components and normalized difference vegetation index (NDVI) ± SE for 2005 and 2006 separated by microtopography category. See Table 2 for explanation of variable abbreviations.

Variable	Category	2005 Means[+]	2006 Means
GPP	Vascular-dominated	0.821 ± 0.034 [a]	0.600 ± 0.057 [a]*
	Intermediate	0.805 ± 0.047 [a]	0.548 ± 0.024 [a]*
	Polygon rim	0.969 ± 0.040 [b]	0.825 ± 0.071 [b]*
NEE	Vascular-dominated	0.048 ± 0.044 [a]	0.212 ± 0.049 [a]*
	Intermediate	0.076 ± 0.022 [a]	0.227 ± 0.024 [a]*
	Polygon rim	0.021 ± 0.123 [a]	0.187 ± 0.050 [a]*
ER	Vascular-dominated	−0.764 ± 0.029 [a]	−0.384 ± 0.046 [a]*
	Intermediate	−0.726 ± 0.054 [a]	−0.321 ± 0.020 [a]*
	Polygon rim	−0.946 ± 0.090 [b]	−0.635 ± 0.059 [b]*
NDVI	Vascular-dominated	0.403 ± 0.010 [a]	0.414 ± 0.005 [a]
	Intermediate	0.427 ± 0.008 [a]	0.435 ± 0.008 [b]
	Polygon rim	0.428 ± 0.014 [a]	0.427 ± 0.006 [ab]

[+] Means were evaluated using a two-way ANOVA. Means of the CO_2 flux components are in $\mu mol\ m^{-2}\ s^{-1}$. Means with different letters differ significantly within years and * means significant difference between years at $\alpha = 0.05$. Sample size 8, 6, and 4 plots for vascular-dominated, intermediate, and polygon rim plots, respectively, for each year.

regardless of soil temperature (Oberbauer et al., 1992; Oechel et al., 1998). The observed increase in NEE in 2006 might suggest that greater thaw depth and soil moisture favored above-ground productivity; however, our results suggest that the observed increase in NEE in 2006 occurred more as a result of a greater reduction in ER than an increase in GPP.

While it seems reasonable to attribute differences in CO_2 flux components to soil temperature or soil water level, predicting the direction and magnitude of differences poses a serious challenge as a result of indirect linkages among the soil environmental factors, particularly those driven by water table. High soil moisture, by increasing soil thermal conductivity, can increase thaw depths that in turn can lower the water table relative to the surface. Furthermore, standing water reduces the surface albedo, increasing water and soil surface temperature and potentially thaw depth. Conversely, low soil moisture reduces soil temperatures and thaw because of the low thermal conductivity of dry organic soils, particularly beneath *Sphagnum* moss (Brooker and van der Wal, 2003; Heijmans et al., 2004). In a warm, dry year such as 2005, active layer thickness and subsurface soil temperatures can be lower than those during a cool, wet year such as 2006.

MICROTOPOGRAPHY

We found no evidence of a north-south flow gradient effect; however, the microsite comparison indicates that significant effects of microtopographic position occurred (Tables 2 and 3). Such differences in CO_2 flux components in response to microtopography can arise from differences in vegetation or soil factors in response to vegetation properties and/or level of the water table, including soil water availability, aeration, temperature, thaw depth, and nutrient availability.

Our results complement the results of previous research about the importance of microtopography and hydrological gradients in controlling ecosystem structure (Webber, 1978) and function by determining the response of the carbon flux components to changes in microtopography (Sommerkorn, 2008; Sullivan et al., 2008). Previous studies of CO_2 fluxes in the Arctic have mostly focused on understanding the responses and differences of the carbon flux components along large moisture gradients, especially dry and wet conditions (Moosavi and Crill, 1997; Oberbauer et al., 2007) rather than on differences in microtopography.

Despite very small differences in the topography across the low-centered polygons in the basin (generally around ~10 cm), plant communities differ strongly with microtopographic position. Polygon rims presented high bryophyte cover with low vascular plant presence; as a result, the moss layer had little or no canopy protection against high irradiances. The few individuals of vascular species present in the polygon rims have shallow roots usually confined to the moss layer, shorter and fewer leaves, and low leaf angles. Conversely, in the intermediate and vascular-dominated plots (polygon basins), vascular plants were abundant with large leaves, steep leaf angles, and a dense root system beneath a moss layer (if present).

We expected the polygon rim plots to have lower GPP rates than the other two plot types because of the low photosynthetic capacity of the mosses; our results suggest, however, that weather conditions, such as light and temperature, were such that they favored productivity of polygon rim plots. The differences in GPP were not significant between vascular-dominated and intermediate microsites during the dry and wet condition (2005 and 2006), but significant differences were seen in the polygon rim plots having the highest GPP in both years (Table 4). Additionally, the higher elevation of the polygon rims relative to the surrounding areas allows moisture to run off to lower areas creating dry conditions that can prevent submersion of the leaf area, benefiting GPP, but that also increases soil oxygen availability, enhancing ER (Oechel et al., 1998). Furthermore, high ER rates are generally associated with high GPP (Bubier et al., 2003; La Puma et al., 2007), but whether that is true for mosses is uncertain. The decrease in ER rates of polygon rims between years suggests that the increase in water availability increased soil anoxia (Oberbauer et al., 1992); however, other factors such as temperature could have also affected the ER rates. Similarly, as a result of the combined effect of the higher water availability in 2006 and relative low elevations of vascular-dominated and intermediate plots, the soil oxygen availability likely decreased, significantly reducing the ER rates even more than those of the polygon rims (Table 4). Higher ER of polygon rims compared to those of the other microsite resulted in the lowest average NEE, though overall NEE did not differ significantly (Table 4).

The sensitivity of CO_2 fluxes of the three microtopographic categories to interannual variation, and the difference of the magnitude of the responses of each of the carbon flux components
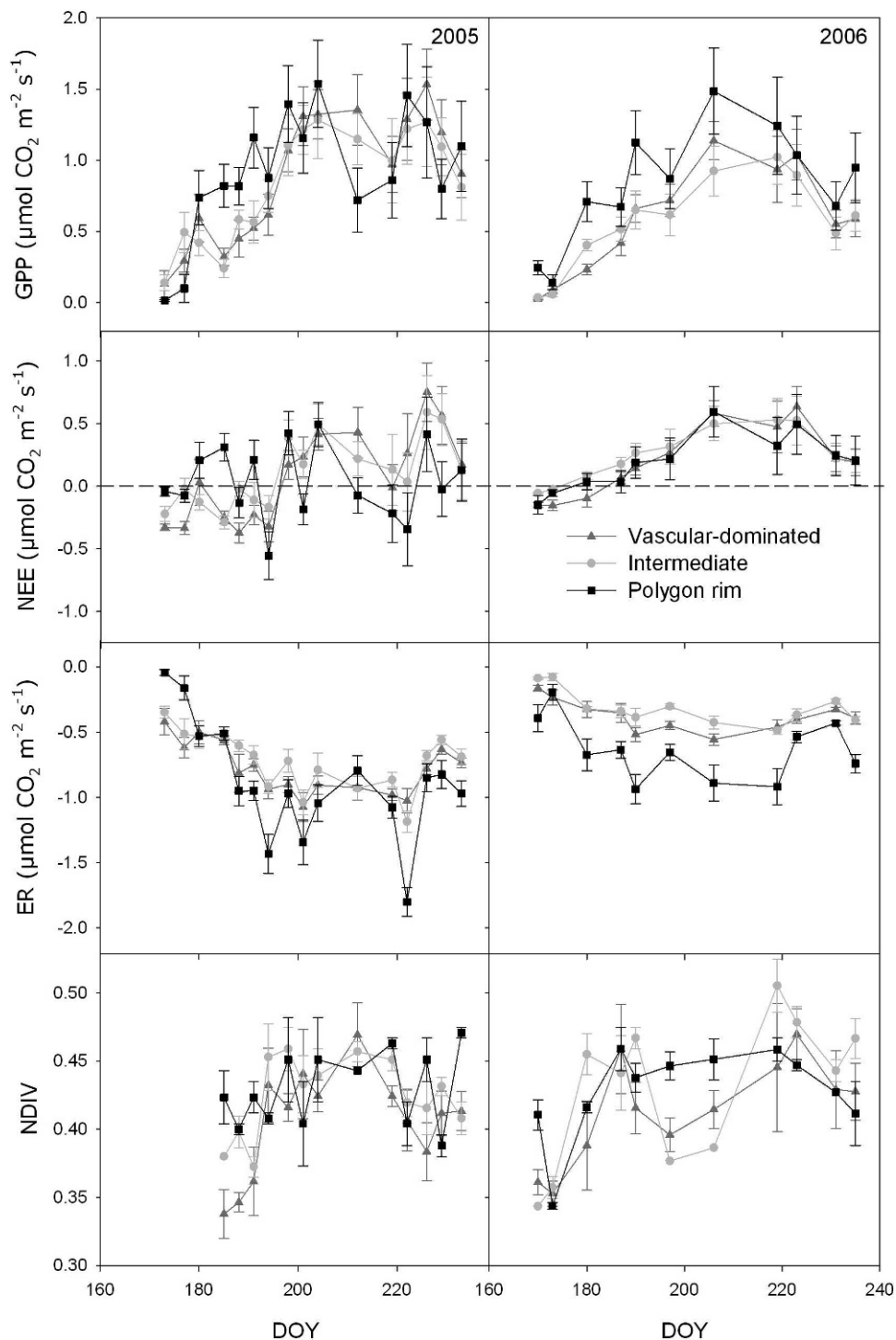
FIGURE 3. Seasonal CO$_2$ flux components for 2005 and 2006 separated by microtopographic category. Gross primary production (GPP), net ecosystem exchange (NEE), ecosystem respiration (ER), normalized difference vegetation index (NDVI), and day of year (DOY). CO$_2$ fluxes presented using ecosystem perspective where positive values represent CO$_2$ uptake. Error bars represent ± one standard error of the mean.

within each category suggest that any differences in relative elevation with respect to water table will affect the CO$_2$ balance. In general, during wet years, low areas (vascular-dominated) will generally experience the highest reduction in ER followed by intermediate areas, despite possibly greater thaw depths and soil temperatures. In low elevation microsites and wet years, GPP is likely to also be negatively affected as a result of temporary submersion of the moss layer and vascular leaf area. If high water persists, soil anoxia may cause stress in plants and microbes (Gebauer et al., 1995), reducing productivity and nutrient turnover.

During years of decreased water availability, we expect an increase in ER and a decrease in GPP in the plots located on polygon rims as a result of desiccation of the moss layer. If the

moss layer dries completely, ER may also decline as respiration of mosses and surface layer microbes become negligible. Plots located in vascular-dominated and intermediate conditions will likely experience a large increase in ER as a result of exposure of normally submerged labile carbon to oxygen. However, the carbon losses could be offset by an increase in GPP as a result of faster turnover of the organic matter, and higher nutrient availability (Chapin et al., 1995; Hobbie and Chapin, 1998). Bhatt et al. (2010) found considerable changes in the greenness of the areas along the Chukchi and Bering seas associated with an increase in the summer land temperatures. The increase of the greenness of these areas of the Arctic suggests an increase in productivity and a potential change in species composition.
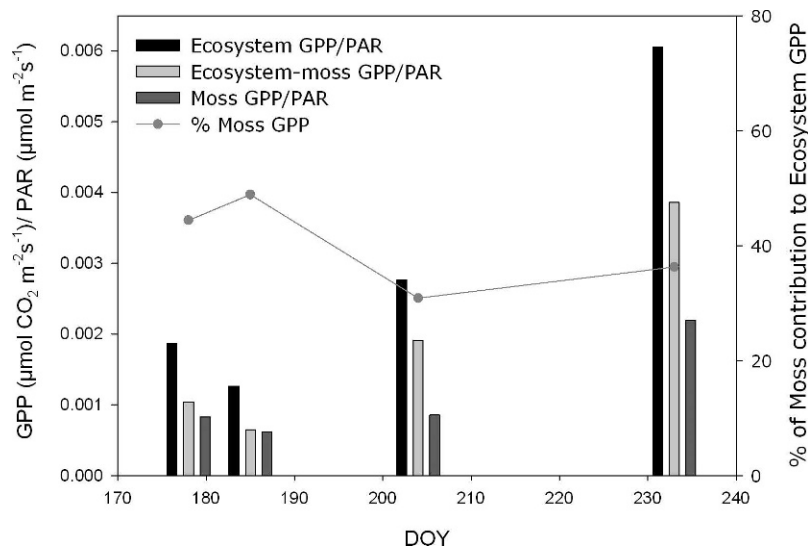
P. C. OLIVAS ET AL. / 263

FIGURE 4. Contribution of mosses to the ecosystem gross primary production (GPP). Columns present mean values of GPP for the ecosystem, GPP for the ecosystem with moss removed, and GPP of the moss. GPP was normalized by photosynthetically active radiation (PAR). The line shows the percent of ecosystem GPP contributed by moss. In the horizontal axis is day of the year (DOY).

Additionally, the increase of the summer temperature in the Arctic will most likely affect the hydrological regime and the integrity of the permafrost (Schuur et al., 2008). In the long term, the degree to which soil carbon is lost, the magnitude of the offset by GPP (especially of vascular plants), and how mosses will adapt to changes in the hydrological regimes remain large uncertainties.

MOSS CONTRIBUTION TO ECOSYSTEM FLUXES

Moss removal treatments suggest that mosses contribute up to 48% of the daily rates and ~33% of the seasonal average of the ecosystem GPP, with the greatest proportion during the periods when the vascular photosynthetic tissue is developing or senescing. Douma et al. (2007) found that the contribution of non-vascular plants to the ecosystem carbon uptake in moss-dominated areas varied considerably depending on the presence of a vascular canopy, 14% under high vascular cover and 96% under low vascular cover. These results suggest that the contribution of mosses to the ecosystem carbon uptake might change considerably throughout the growing season in response to vascular canopy development. Campioli et al. (2009), in a subarctic heath, found that the highest contribution (25%) of the non-vascular plants to the ecosystem net primary productivity occurred late in the growing season. Similarly, we found that the moss contribution to the ecosystem GPP was higher at the beginning and end of the growing season (Fig. 4).

The inability of mosses to regulate the water loss and low nutrient content of leaves and shoots (potentially affecting photosynthetic performance) implies that the absence of a protective overstory can reduce moss productivity during extended periods of high irradiance by increasing water losses and photoinhibition (Harley et al., 1989; Murray et al., 1993; Maseyk et al., 1999). We observed that some *Sphagnum* species in the study area with little or no vascular canopy exhibited red photoprotective pigmentation, whereas understory mosses tended to be green. Maseyk et al. (1999) observed light-saturated photosynthesis at higher light levels in brown mosses than in green mosses; however, the brown mosses also presented lower photosynthetic rates. The 31–48% contribution of mosses to the ecosystem GPP that we recorded represents the average percentage for mosses under different overstory conditions (Fig. 4). Although the sample size was not large enough to test for contribution of mosses with different topographic position/vascular cover to the ecosystem GPP, our data suggest that under the weather conditions of 2005

and 2006, mosses without a vascular overstory have higher photosynthetic rates than those of understory mosses. Although contradictory to previous findings (Maseyk et al., 1999), we conclude that irradiance was not high enough to negatively affect overstory mosses and that understory mosses suffered reduced light availability as a result of the protective canopy.

NDVI AND PRODUCTIVITY

A next step for these studies would be to scale up fluxes of different topographic positions to the landscape and regional level using remotely sensed indices. Prior studies in tundra have shown strong correlations between GPP and NDVI over the growing season (La Puma et al., 2007). In this study NDVI only explained 16% and 26% of the variation in GPP over the growing season for 2005 and 2006, respectively. Low correlations can result when environmental factors (low light, temperature, or soil moisture) lower GPP for a given green biomass value represented by NDVI (La Puma et al., 2007). Furthermore, the relationship between NDVI and GPP for vascular plants and mosses differs (Stow et al., 2004; Huemmrich et al., 2010), introducing variation depending on the relative contribution of mosses to ecosystem GPP. Reflectance of mosses is also affected by changes in water content (Harris, 2008; Huemmrich et al., 2010). NDVI was best correlated with GPP at the beginning and end of the growing season when mosses were moist and had the highest contribution to the ecosystem GPP, and at peak season when the vascular leaf area was fully developed (data not shown).

NDVI did not detect differences among microtopographic categories in 2005. During 2006, NDVI was able to detect differences between microtopographic categories; however, these differences were not consistent with significantly higher GPP rates. One issue is that in *Carex aquatilis,* one of the dominant vascular species at the study site, more than 70% of the leaves have angles over 60° (Dennis et al., 1978), and as a result of taking NDVI images vertically over steeply oriented leaves, differences in the vascular leaf area among the microtopographic positions may not have been detected (Huemmrich et al., 2010).

Conclusions

Estimates of the lake basin CO_2 uptake showed that the basin was a sink over the growing season in both years (17 vs. 64 g CO_2

m^{-2} season^{-1}, respectively). Polygon rims were close to CO_2 neutral in 2005, but relative high sinks in 2006 (5 vs. 53 g CO_2 m^{-2} season^{-1}, respectively). Intermediate plots were the strongest sinks of carbon for both seasons (22 vs. 71 g CO_2 m^{-2} season^{-1}), followed by the vascular-dominated plots (19 vs. 63 g CO_2 m^{-2} season^{-1}). The interannual difference in growing season NEE among plots was driven by differences in both GPP and ER, but ER was most responsive to interannual climate differences. Mosses accounted for ~33% of the seasonal mean daytime ecosystem GPP and as much as 48% of the daily daytime GPP.

We conclude that: (1) under the observed conditions (relatively dry and wet growing seasons), GPP of the polygon rim areas was significantly higher than the GPP of the vascular-dominated and intermediate areas (2006); (2) on average, ER of the polygon rim areas was significantly higher than that of the other microsites; and (3) the intermediate microsites presented the highest seasonal NEE on average, but differences were non-significant. In terms of the moss contribution to the ecosystem GPP we conclude that: (1) mosses contribute with up to 33% of the seasonal ecosystem GPP, and (2) this contribution is the highest at the beginning and end of the growing season.

Any difference in the level of the vegetation surface with respect to the water table will affect CO_2 flux components and their responses to climate variation. These differences can result from differences in the long-term vegetation properties that have developed in response to the long-term mean water level, or from short-term environmental differences such as moisture availability, temperature, and irradiance, and their interactions. Quantitatively predicting the CO_2 fluxes of coastal plain tundra will require further understanding of the water table and temperature thresholds on the carbon balance of different vegetation types and an in-depth understanding of the effects of water level and soil properties on soil thermal regimes.

Acknowledgments

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