

VARIATIONS OF CO₂ EXCHANGE AMONG VASCULAR PLANT COMMUNITIES IN A TEMPERATE OMBROTROPHIC PEATLAND

Derrick Y.F. Lai,^{1,2,*} Nigel T. Roulet,^{1,2} Tim R. Moore,^{1,2} Elyn R. Humphreys,³ Mike Dalva¹

¹Department of Geography, McGill University, Montreal, Quebec, Canada

²Global Environmental and Climate Change Centre, McGill University, Montreal, Quebec, Canada

³Department of Geography and Environmental Studies, Carleton University, Ottawa, Ontario, Canada

*Department of Geography, McGill University, 805 Sherbrooke Street West, Montreal, Quebec, Canada H3A 2K6. E-mail: yukfo.lai@mail.mcgill.ca

SUMMARY

We measured CO₂ fluxes at half-hourly intervals with automatic chambers in three vascular plant communities at the Mer Bleue bog in 2009 to compare the responses of gross ecosystem production (GEP) and ecosystem respiration (ER) to changing environmental and biotic conditions among communities. Based on the parameterized GEP models, we detected a significant decrease in effective quantum yield in the order of *Eriophorum* > *Chamaedaphne* > *Maianthemum/Ledum* community, indicating the most efficient photosynthetic activity in sedges at low light levels. The rate of linear increase in GEP with vascular green area index was considerably lower in the *Maianthemum/Ledum* community, probably related to the high specific leaf area of forb foliage. The ER model parameters (R_{10} , E_0) were significantly different among communities, with the highest temperature sensitivity of ER in the *Eriophorum* community. The observed significant difference in the overall parameterized GEP and ER models among all three communities implies that modelling of CO₂ fluxes in this bog should take into account the functionally different plant communities separately.

KEY WORDS: Autochamber, CO₂ exchange, ecosystem respiration, gross ecosystem production

INTRODUCTION

An understanding of the magnitude and controls of CO₂ exchange at smaller spatial scales is needed to improve the parameterization of peatland C models and estimation of C fluxes under various natural and anthropogenic perturbations. Distinct plant growth forms (e.g. evergreen and deciduous shrubs, graminoids, forbs) have morphologically different plant traits that could lead to differences in ecosystem functions such as biomass production and litter decomposition within peatland ecosystems (Dorrepaal, 2007). As a result, plant communities dominated by different species or growth forms could vary widely in their CO₂ exchange behaviour even within a single peatland (e.g. Laine *et al.*, 2007). Most studies of the controls of peatland C exchange at the plant community level are based on manual chambers, which are limited by the frequency of flux measurements that can be made and potential bias in the estimation of GEP model parameters owing to fluxes not being measured at naturally varying light levels (Burrows *et al.*, 2005). Yet, we are unaware of any studies that employ

automatic chambers to measure CO₂ fluxes in an ombrotrophic peatland at natural light conditions with a high temporal resolution.

Determining the appropriate functional unit is crucial for modelling and reconstructing peatland CO₂ exchange since a scale too small would require huge data inputs for model parameterization while a scale too large might fail to capture the spatial heterogeneity (Laine *et al.*, 2009). It has recently been shown in a northern patterned fen that four different plant communities could be classified into two distinct functional groups based on similarities in their photosynthetic and respiratory responses (Maanavilja *et al.*, 2011), but explicit comparison of the CO₂ exchange response among plant communities in an ombrotrophic bog is lacking. The objective of our study is to investigate the temporal controls of community level CO₂ fluxes and compare the GEP and ER responses to changing environmental and biotic conditions among plant communities.

MATERIAL AND METHODS

This study was conducted at the Mer Bleue peatland, a 28 km² ombrotrophic bog located near Ottawa, Canada (45.41°N, 75.52°W) with a cool, continental climate. Nine autochambers were installed within a 15-m radius, with three replicates each representing plant communities dominated by sedge *Eriophorum vaginatum*, evergreen shrub *Chamaedaphne calyculata*, and a mix of shrub *Ledum groenlandicum* and forb *Maianthemum trifolium*, respectively. The system was operated from 22 May to 30 November in 2009, with one measurement of net ecosystem exchange of CO₂ made for each chamber every half-hour. Details of the autochamber system and data treatment protocol can be found in Lai *et al.* (2012). We also measured peat temperature at 10 cm depth and water table position at each chamber location, as well as air temperature and photosynthetically active radiation (PAR) at the site at half-hourly intervals. We determined the vascular plant area index (VGA) over time for each chamber following the method of Wilson *et al.* (2007).

We used a process-based modelling approach to investigate the GEP and ER response of plant communities to changing environmental conditions similar to that of Tuittila *et al.* (2004). The GEP model had a multiplicative form shown below:

$$GEP = \left(\frac{\alpha * PAR * P_{max}}{\alpha * PAR + P_{max}} \right) * \exp \left(-0.5 * \left(\frac{T - T_{opt}}{T_{tol}} \right)^2 \right) * (s + VGA)$$

where α is the apparent quantum yield, P_{max} is the VGA-dependent maximum gross photosynthesis when PAR and temperature are not limiting, T is air temperature, T_{opt} is the optimum temperature for GEP, T_{tol} is the temperature tolerance (deviation from the optimum at which GEP was 60% of its maximum), and s is an estimate of the *Sphagnum* moss green area.

The overall ER model form was as follows:

$$ER = R_{10} * \exp \left(E_0 * \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0} \right) \right) * \exp(-b * WT) + v * VGA$$

where R_{10} is the respiration rate at 10°C when water table is not limiting and VGA is zero, E_0 is a parameter related to the activation energy, T_{ref} is a reference temperature (283.15 K), T_0 is the temperature at which ER becomes zero (227.13 K), T_{soil} is the peat temperature at 10 cm depth, b is the initial slope of the water table response function, WT is the water table depth, and v is the change in respiration rate per VGA unit.

RESULTS

All five estimated parameters of the GEP model were significantly different among the three plant communities ($p < 0.01$), except for T_{tol} between the *Eriophorum* and *Chamaedaphne* communities ($p = 0.93$, Table 1). PAR was the most dominant factor governing GEP, alone explaining 49-60% of the variations in the three communities. We obtained the highest apparent quantum yield in the *Eriophorum* community and lowest in the *Maianthemum/Ledum* community with 0.015 and 0.006 $\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ PAR}$, respectively. We found P_{max} values (expressed in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ VGA unit}^{-1}$) decreasing significantly in the order of *Chamaedaphne* (8.4) > *Eriophorum* (7.8) > *Maianthemum/Ledum* community (3.3) (Table 1).

Table 1. Parameter estimates of the GEP model for three vascular plant communities at the Mer Bleue bog.

Plant community	α ($\mu\text{mol CO}_2$ $\mu\text{mol}^{-1} \text{ PAR}$)	P_{max} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$ VGA unit ⁻¹)	T_{opt} (°C)	T_{tol} (°C)	s ($\text{m}^2 \text{ m}^{-2}$)	R^2	SEE	N
<i>Eriophorum</i>	0.015 a (0.0002)	7.80 a (0.138)	14.4 a (0.31)	19.2 a (0.46)	0.49 a (0.016)	0.77	1.94	11605
<i>Chamaedaphne</i>	0.013 b (0.0002)	8.42 b (0.150)	15.8 b (0.37)	19.3 a (0.58)	0.25 b (0.015)	0.76	2.26	12209
<i>Maianthemum/Ledum</i>	0.006 c (0.0001)	3.28 c (0.061)	18.2 c (0.14)	13.3 b (0.22)	1.54 c (0.036)	0.69	2.06	12582

Different letters denote significant difference in parameter estimate between plant communities ($p < 0.05$).

Values in parentheses are standard errors of the parameter estimates.

R^2 : Coefficient of determination, SEE: standard error of estimate, N : Number of data points.

Green area was another important factor controlling the photosynthetic activity of plant community. Inclusion of VGA improved the R^2 of GEP model by 0.15-0.21 compared to the one based solely on PAR. The rate of linear increase in GEP with VGA was considerably lower in the *Maianthemum/Ledum* community with a slope of 2.55, compared to 5.93 and 6.21 in the other two communities, given a PAR of 2000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ and air temperature of 20 °C. Moreover, the estimated parameter s (in $\text{m}^2 \text{ m}^{-2}$) increased in the order of *Chamaedaphne* (0.25) < *Eriophorum* (0.49) < *Maianthemum/Ledum* (1.54), implying a significantly greater contribution of moss to GEP in the latter community (Table 1).

The ER model parameterized using the available nighttime CO_2 flux and environmental data had an R^2 of 0.70-0.72 in the three plant communities (Table 2). Peat temperature was the single most dominant factor governing the rate of ecosystem respiration at the Mer Bleue bog, alone explaining 64-69% of the variations. ER increased exponentially with peat temperature, with the highest sensitivity seen in the *Eriophorum* community. *Chamaedaphne* community had a significantly higher R_{10} and lower E_0 than the other two communities ($p < 0.05$). Moreover, when compared to the *Eriophorum* community, the *Maianthemum/Ledum* community had a significantly lower R_{10} but no significant difference in E_0 value.

Table 2. Parameter estimates of the ER model for three vascular plant communities at the Mer Bleue bog.

Plant community	R_{10} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	E_0 (K)	b (cm^{-1})	v ($\mu\text{mol m}^{-2} \text{s}^{-1}$ VGA unit ⁻¹)	R^2	SEE	N
<i>Eriophorum</i>	0.56 a (0.022)	392.3 a (4.36)	0.023 a (0.0011)	0.36 a (0.033)	0.72	0.25	7812
<i>Chamaedaphne</i>	0.64 b (0.021)	321.8 b (2.93)	0.014 b (0.0007)	-0.10 b (0.025)	0.70	0.20	7980
<i>Maianthemum/Ledum</i>	0.36 c (0.008)	401.8 a (4.64)	0.025 a (0.0008)	0.27 c (0.008)	0.71	0.11	8024

Different letters denote significant difference in parameter estimate between plant communities ($p < 0.05$).

Values in parentheses are standard errors of the parameter estimates.

R^2 : Coefficient of determination, SEE: standard error of estimate, N : Number of data points.

Results of F-test show that both the GEP and ER models were significantly different among the three communities ($p < 0.01$), further confirming that the three sets of parameter values generated different overall curves.

DISCUSSION

Temporal variation of GEP in northern peatlands is often predominantly controlled by PAR. At Mer Bleue, PAR alone explained 49-60% of the variability of GEP through a rectangular hyperbolic relationship. We obtained significantly different apparent quantum yields between each of the three communities, with the highest and lowest values in the *Eriophorum* and *Maianthemum/Ledum* communities, respectively (Table 1). This suggests that the rate of increase in CO₂ uptake with PAR at low light levels is greatest in the *Eriophorum* community, which agrees with previous finding that sedge is highly efficient in photosynthetic activity (Leppälä et al., 2008).

While all communities at Mer Bleue demonstrated a positive relationship between VGA and GEP, we observed a much lower rate of increase in *Maianthemum/Ledum* than the other two communities under selected environmental conditions. This suggests that VGA plays an important role in controlling the seasonal variations of GEP within community, but is less capable of explaining the spatial variability of GEP across communities, in contrary to findings in the Arctic tundra that leaf area alone could account for 81% of the spatio-temporal variations in plot-level GEP (Street et al., 2007). The lower sensitivity of GEP to VGA in the *Maianthemum/Ledum* community might be related to the much higher specific leaf area of forb leaves. Even with a modest increase in leaf nitrogen concentration by mass over time, the substantial increase in the area of *M. trifolium* leaves could lead to a lower foliar nitrogen content on an areal basis, thus posing a constraint on the photosynthesis rate per unit leaf area (Street et al., 2007). This can potentially explain the very low photosynthetic efficiency of herbs per unit leaf area, but high efficiency per unit foliar biomass observed in northern peatlands (Bubier et al., 2003).

Peat temperature at 10 cm depth was the single most dominant control of ecosystem respiration, explaining 64-69% of the variability in the three plant communities. We found from our parameterized ER models a significantly higher R_{10} and significantly lower E_0 in the

Chamaedaphne community (Table 2). This resulted in the lowest temperature sensitivity of ER in this shrub-dominated community, while the response of ER to peat temperature especially at the higher range was strongest in the *Eriophorum* community due to the combination of moderate R_{10} and E_0 values. The higher rate of ER increase with temperature in the *Eriophorum* community might at least be partly related to the enhanced plant production and hence turnover of recent photosynthate, with CO₂ emission arising from root exudation and mineralization shown to be much greater in peatland cores with sedge than with shrub (Crow & Wieder, 2005).

Previous studies have parameterized peatland CO₂ exchange models for botanically distinct plant communities due to differences in their photosynthetic and respiratory responses (e.g. Laine et al., 2009). Maanavilja et al. (2011) have specifically compared parameters of the GEP and ER models between four different plant communities in a northern patterned fen and identified two functional types, namely the ombrotrophic and minerotrophic components. They found that the three minerotrophic community types, including *Carex-Scorpidium* wet flark, *Trichophorum* tussock flarks and *Betula-Sphagnum* string margins, had similar responses of GEP and ER. Meanwhile, their minerotrophic communities had much lower moss coverage (5-54%) and higher mean water table (5 cm above to 16 cm below peat surface) than the bog communities at Mer Bleue. The three vascular plant communities in our study were functionally different with respect to their GEP and ER responses to environmental conditions, probably due to the dominance of different plant growth forms, namely shrub, sedge, and forb, in these communities.

REFERENCES

- Bubier, J. L., Crill, P. M., Mosedale, A., Frohling, S. and Linder, E. (2003). Peatland responses to varying interannual moisture conditions as measured by automatic CO₂ chambers. *Global Biogeochemical Cycles* **17**, 1066, doi:10.1029/2002GB001946.
- Burrows, E. H., Bubier, J. L., Mosedale, A., Cobb, G. W. and Crill, P. M. (2005). Net ecosystem exchange of carbon dioxide in a temperate poor fen: a comparison of automated and manual chamber techniques. *Biogeochemistry* **76**, 21-45.
- Crow, S. E. and Wieder, R. K. (2005). Sources of CO₂ emission from a northern peatland: the role of root respiration, root exudates, and organic matter. *Ecology* **86**, 1825-1834.
- Dorrepaal, E. (2007). Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology* **95**, 1167-1180.
- Lai, D. Y. F., Roulet, N. T., Humphreys, E. R., Moore, T. R. and Dalva, M. (2012). The effect of atmospheric turbulence and chamber deployment period on autochamber CO₂ and CH₄ flux measurements in an ombrotrophic peatland. *Biogeosciences Discuss.* **9**, 1439-1482.
- Laine, A., Byrne, K. A., Kiely, G. and Tuittila, E.-S. (2007). Patterns in vegetation and CO₂ dynamics along a water level gradient in a lowland blanket bog. *Ecosystems* **10**, 890-905.
- Laine, A., Riutta, T., Juutinen, S., Väliänta, M. and Tuittila, E.-S. (2009). Acknowledging the spatial heterogeneity in modelling/reconstructing carbon dioxide exchange in a northern aapa mire. *Ecological Modelling* **220**, 2646-2655.
- Leppälä, M., Kukko-Oja, K., Laine, J. and Tuittila, E. S. (2008). Seasonal dynamics of CO₂ exchange during primary succession of boreal mires as controlled by phenology of plants. *Ecoscience* **15**, 460-471.
- Maanavilja, L., Riutta, T., Aurela, M., Pulkkinen, M., Laurila, T. and Tuittila, E.-S. (2011). Spatial variation in CO₂ exchange at a northern aapa mire. *Biogeochemistry* **104**, 325-345.

- Street, L. E., Shaver, G. R., Williams, M. and Van Wijk, M. T. (2007). What is the relationship between changes in canopy leaf area and changes in photosynthetic CO₂ flux in arctic ecosystems? *Journal of Ecology* **95**, 139-150.
- Tuittila, E.-S., Vasander, H. and Laine, J. (2004). Sensitivity of C sequestration in reintroduced *Sphagnum* to water-level variation in a cutaway peatland. *Restoration Ecology* **12**, 483-493.
- Wilson, D., Alm, J., Riutta, T., Laine, J., Bryne, K. A., Farrell, E. P. and Tuittila, E.-S. (2007). A high resolution green area index for modelling the seasonal dynamics of CO₂ exchange in peatland vascular plant communities. *Plant Ecology* **190**, 37-51.