Short-term carbon dioxide exchange and environmental factors in a boreal fen

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Introduction

Northern peatlands are important contributors to the global carbon cycle. In cold and moist climatic conditions, boreal peatlands have sequestered large amounts of atmospheric carbon during the past few thousand years (GORHAM 1991). The carbon balance in mires depends on the rates of photosynthesis and respiration which are affected by both the long-term and the short-term variations in environmental factors. So far, more emphasis has been put on the annual carbon balance of mires, and short-term dynamics have received less attention. However, a relationship between the carbon dioxide and methane cycling has been proposed as newly photosynthesized carbon provides substrates for methanogenesis substrates and promotes methane emissions (WHITING & CHANTON 1993). To analyze the connection between green plant photosynthesis and methane emissions, we need to analyze the short-term dynamics of carbon dioxide exchange. Consequently, we use earlier data (ALM et al. 1997) to study the diurnal patterns and calculate the daily carbon dioxide balances in different microsites of a boreal fen.

Materials and methods

The net CO_2 exchange, P_n, and the total dark respiration, R_{tot}, were measured using the chamber technique in 17 study plots in a Finnish low-sedge *Sphagnum papillosum* pine fen during the summer season 1993 (for details see ALM et al. 1997). Photosynthetically active radiation (PAR), temperature (T) and water table (WT) series were also measured to analyze the dependence of photosynthesis and respiration rates on environmental variables.

Based on vegetation and microtopography, the study plots were first classified into four microsite types: hummocks, *Carex* lawns, *Eriophorum* lawns, and flarks (minerotrophic hollows). *E.* lawns covered about 86% and hummocks 14% of the mire surface, while the proportion of the other microsites was very small. Carbon exchange data analysis revealed that CO_2 dynamics in the wettest *E.* lawns differed from those in dryer *E.* lawns, and hence we moved the two wettest *E.* lawns into a class called 'wet *E.* lawns' and the five dryer *E.* lawns remained in a class called 'dry *E.* lawns'. Later, it also turned out that data from dry *E.* lawns, *C.* lawns and hummocks could be grouped together into a class hereafter referred to as 'dry microsites'. Thus, we ended up with three classes: dry microsites, wet *E.* lawns and flarks. For the gross CO_2 exchange, P_g, we used an estimate $P_g = P_n + R_{tot}$. The dependencies of the photosynthesis and respiration rates on environmental variables were analyzed separately for each microsite class.

We started with the commonly used Michaelis–Menten-type relationship for the light dependence of photosynthesis rates:

$$P_g = P_{g\,max}PAR/(PAR + k)$$

(see, e.g., BUBIER et al. 1998, FROLKING et al. 1998), where P_g is the gross CO_2 exchange, PAR is the photosynthetically active radiation, the parameter $P_{g\,max}$ is the maximal photosynthesis rate, and the parameter k is the PAR value for which P_g reaches half of its maximum. However, both in this study and in previous studies (ALM et al. 1997, BUBIER et al. 1998, FROLKING et al. 1998), the dependence of gross CO_2 exchange on PAR has been found to dynamically change over the season, apparently due to the seasonal cycle of plants. Different ways have been used to describe the seasonal dynamics of P_g in relation to PAR. BUBIER et al. (1998) and FROLKING et al. (1998) divided the growing season into three periods for which the parameters of the model $P_g = P_{g\,max}PAR/(PAR + k)$ were estimated separately. ALM et al. (1997) added linear terms including different environmental factors to the basic Michaelis–Menten model, resulting in the model:

$$P_g = P_{g\,max}PAR/(PAR + k) + a_0 + a_1(ETI) + a_2(WT) + a_3(WT)^2 + a_4T$$

where P_g is the gross CO_2 exchange, PAR is the photosynthetically active radiation, ETI is the effective temperature sum index which was calculated by dividing the cumulative effective temperature sum (threshold of 5 °C) by the number of days (where May 17th was given the number 1, as it was the first day in the simulation), WT is the water table, T is the peat surface temperature, and $P_{g\,max}$, k, a_0, a_1, a_2, a_3 and a_4 are the model parameters. It is not easy to give any ecological interpretation to the six model parameters in the model of Alm et al. (1997). Furthermore, the additive form of the model of Alm et al. (1997) can result in non-reasonable model outputs, e.g. non-zero photosynthesis when PAR = 0. To avoid these problems, we chose the following multiplicative model:

$$P_g = a_1 T(ETI)(PAR)/(PAR + k_1) \qquad (1)$$

where P_g is the gross CO_2 exchange, T is the peat surface temperature, ETI is the effective temperature sum index calculated as in Alm et al. (1997), PAR is the photosynthetically active radiation, and a_1 and k_1 are the model parameters. The parameter k_1 is the PAR value for which P_g is half of its maximum. The parameter a_1 is related to the maximal photosynthesis rate so that $P_{g\,max} = a_1 T(ETI)$ is reached when both T and ETI are maximal.

Respiration rates were exponentially related to peat surface temperatures and water tables, in a way similar to that in Alm et al. (1997):

$$\ln(R_{tot}) = b_0 + b_1(WT) + b_2 T \qquad (2)$$

where R_{tot} is the total dark respiration, WT is the water table, T is the peat surface temperature, and b_0, b_1 and b_2 are the model parameters.

Results and discussion

Our model (1) for the gross CO_2 exchange, P_g, and model (2) for the total dark respiration, R_{tot}, performed well (Table 1, Figs. 1a–f). For our data, the model (1) where the effective temperature sum index and the peat surface temperature were included was clearly better than the basic Michaelis–Menten model:

$$P_g = P_{g\,max}PAR/(PAR + k)$$

where only PAR is used as the independent variable. The goodness-of-fit values increased from 54%, 67% and 62% to 91%, 86% and 78% (Table 1) for flarks, wet *E.* lawns and dry microsites, respectively, when ETI and T were included. Our model (1) for P_g performs as well as the model used by Alm et al. (1997) with respect to goodness-of-fit even though our model has two parameters and the model of Alm et al. (1997) has six parameters. As the model of Alm et al. (1997) was constructed to analyze the annual carbon balance, it is natural that our model (1) describes better the diurnal and daily patterns. For example, our model (1) is not sensitive to small changes in the water table, while the model of Alm et al. (1997) is; this becomes important when analyzing short-term carbon balance. Furthermore, additive linear models for photosynthesis may predict non-zero photosynthesis even when PAR becomes zero, but thanks to its multiplicative structure, our model (1) never predicts non-zero photosynthesis for cases when PAR = 0.

As expected from the reasonable goodness-of-fit values, the predicted and observed values of P_n match well (Figs. 1a–f). For simplicity, Fig. 1 presents only *C.* lawns and dry and wet *E.* lawns but our model fits data from hummocks and flarks similarly. The difference between the predicted and observed values of P_n was in almost all cases less than 100 mg CO_2 m^{-2} h^{-1} (<20%). In a few cases, however, the values of the environmental variables in the hourly time

Table 1. Goodness-of-fits and parameter values for models (1) and (2). M, number of microsites; N, number of measurements. The maximal photosynthesis rate, Q_{max}, is calculated by multiplying the parameter a_1 by the maximal value of ETI and T. Dry microsites include hummock, dry *E.* lawn and *C.* lawn data.

Microsite class	M	N	$R^2 (P_g)$	a_1	k_1	Q_{max}	$R^2 (R_{tot})$	b_0	b_1	b_2
Flarks	2	32	91%	4.5	130	764	72%	2.96	0.11	0.10
Wet *E.* lawns	2	60	86%	7.1	161	1207	75%	3.33	0.10	0.10
Dry microsites	13	323	78%	10.7	134	1829	76%	4.25	0.02	0.08
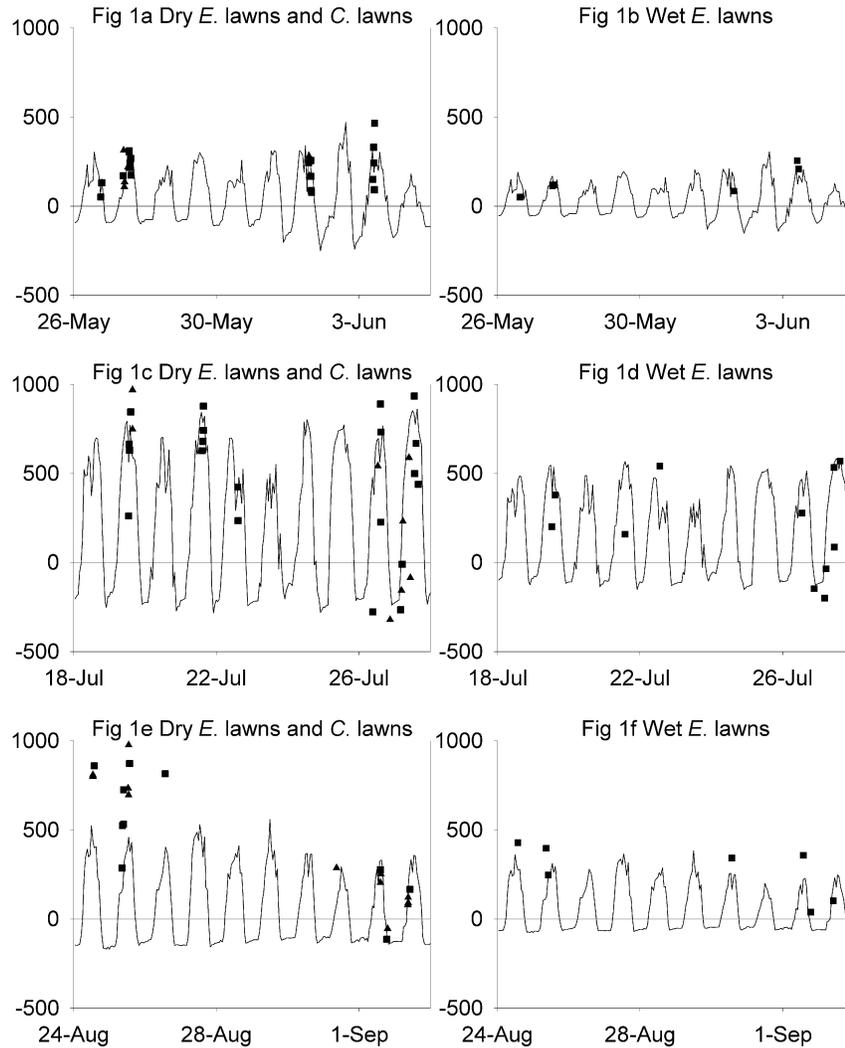
Fig. 1. The predicted (lines) and measured (squares for wet and dry *E.* lawns and triangles for *C.* lawns) net CO_2 exchanges (P_n in mg CO_2 m^{-2} h^{-1}) in two microsite classes for three typical 10-day periods.

series differed significantly from the values in the measured data, resulting in differences larger than 100 mg CO_2 m^{-2} h^{-1} between the predicted and observed values of P_n. For example, during the midday hours on August 24–26 (Fig. 1e), the PAR values used in the simulation remained below 300 µmol m^{-2} s^{-1}, while the measured PAR values ranged up to 900 µmol

m^{-2} s^{-1}, and, as a result, the model underestimates the P_n values in dry microsites in these exceptional cases.

During the early- (May–June, Figs. 1a, 1b) and late-summer (late August–September, Figs. 1e, 1f) seasons, P_n ranges between –300 and +300 mg CO_2 m^{-2} h^{-1}. The range increases during the mid-summer season (late July–early

August, Figs. 1c, 1d) when both PAR and T show high values, and P_n varies from –500 to +1000 mg CO_2 m^{-2} h^{-1}.

All microsites show a similar diurnal rhythm of binding carbon during the daytime when the rate of photosynthesis exceeds the rate of respiration, and losing carbon during the nighttime when photosynthesis ceases but respiration continues. During the nighttime, dry sites release more carbon than wet sites: R_{tot} hummock > R_{tot} dry $E.$ lawn and $C.$ lawn > R_{tot} wet $E.$ lawn > R_{tot} flark (Figs. 1a–1f). During the daytime, dry sites bind more carbon than wet sites: P_g dry microsites > P_g wet $E.$ lawn > P_g flark, probably due to the fact that most plants cannot grow efficiently in extremely wet sites with the water table at the peat surface.

Among the microsites, the net carbon dioxide exchange $P_n = P_g – R_{tot}$ was always highest in dry $E.$ lawns and $C.$ lawns. Interestingly, even though dry and wet $E.$ lawns could easily be classified in the same microsite class, based on vegetation and water table data, dry $E.$ lawns show much higher P_n values than wet $E.$ lawns. For example, in Figs. 1c and 1d, in dry $E.$ lawns the daytime P_n reaches 1000 mg CO_2 m^{-2} h^{-1}, while in wet $E.$ lawns it remains at about 500 mg CO_2 m^{-2} h^{-1}. Wet $E.$ lawns showed slightly higher P_n than flarks throughout the season. In hummocks P_n was below P_n in wet $E.$ lawns and flarks during the early season (May–June), but later during the summer hummocks showed higher P_n than the wet microsites.

The daily balance which integrates the carbon binding during daytime and the release of carbon during the nighttime varied among the microsites (Fig. 2). Daily carbon dioxide balance was highest in dry $E.$ lawns and $C.$ lawns and lowest in hummocks throughout the season, as high respiration in hummocks lowers the daily estimate most. In wet $E.$ lawns, the daily carbon dioxide balance (daily values not shown) was lower than in dry $E.$ lawns and $C.$ lawns but higher than in flarks and hummocks throughout the season. In $E.$ lawns, $C.$ lawns and flarks, the daily carbon dioxide balance was almost always positive, resulting in a positive balance for the whole period. In hummocks,
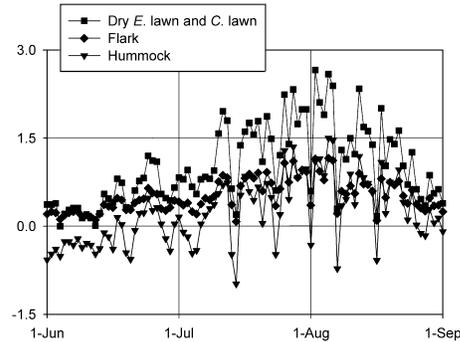
Fig. 2. The predicted daily carbon dioxide exchange (g CO_2-C m^{-2} day^{-1}) in three microsite classes during the summer period.

the continuously negative daily balances in June mean that hummocks show a net release of carbon in the early season, but later the balance turns positive, resulting in a positive carbon dioxide balance for the whole summer season. The summertime carbon dioxide exchange estimates were high for dry $E.$ lawns and $C.$ lawns (86 g CO_2-C m^{-2}), wet $E.$ lawns (67 g CO_2-C m^{-2}) and flarks (45 g CO_2-C m^{-2}), but hummocks had a small estimate (12 g CO_2-C m^{-2}). The whole mire carbon dioxide exchange estimate, 71 g CO_2-C m^{-2}, is above the average accumulation rate of about 30 g CO_2-C m^{-2} $year^{-1}$ for Finnish mires (TOLONEN & TURUNEN 1996), mainly due to the constantly high water tables and consequently low respiration rates during summer 1993. In addition, our estimates do not take into account the carbon losses in leaching, methane emissions and wintertime respiration, which could substantially lower the estimates (ALM et al. 1997, MAST et al. 1998).

The carbon dioxide balance in the microsites was most sensitive to changes in the parameters b_0 and a_1, and fortunately least sensitive to changes in the parameters k_1 and b_1 (these were the most difficult to estimate). P_n in flarks and wet E. lawns was less sensitive to model parameters than P_n in dry microsites, especially in hummocks where the percentage changes

become large as P_n shows low absolute values. Increases in b_0, b_1 and b_2 resulted in an increase in R_{tot} and a consequent decrease in P_n. P_g, and consequently also P_n, increased with increasing a_1 and decreasing k_1. A 10% increase/decrease in a_1 increased/decreased the daily P_n values by between 10 and 20% in most cases. The ±10% change in b_0 was strongly reflected in the daily P_n as the change was more than 20% in most cases. The daily P_n was affected by between 10 and 20% by a 10% change in b_2. The daily P_n changed by less than 10% and by less than 5% with 10% changes in k_1 and b_1, respectively.

Conclusion

The purpose of this study was to analyze the diurnal and daily dynamics of carbon dioxide balance in the microsite classes. Our model clearly is more appropriate for the analysis of short-term patterns than models designed to analyze the annual balance. In addition, our models seem to be applicable to annual levels as well, so that the approach works satisfactorily in predicting both short-term and long-term variations in carbon dioxide balance. Our results emphasize that carbon dioxide exchange is extremely sensitive to variations in environmental factors on a short-term time-scale, and, consequently, the annual estimates are also affected by short-term variations. Hence, short term patterns must be considered when analyzing the annual carbon balance.

Acknowledgement

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