Influence of vascular plant photosynthetic rate on CH_4 emission from peat monoliths from southern boreal Sweden

Anna Joabsson, Torben Røjle Christensen & Bo Wallén

Peat monoliths taken from a boreal peatland system were incubated at two different light intensities to investigate the effect of the photosynthetic rate of vascular plants (*Eriophorum angustifolium*) on net CH_4 emission. The experimental set-up consisted of six replicate monoliths as controls and six where the photosynthetic active radiation (PAR) was reduced by 60%. NEP and total system respiration decreased significantly in response to reduced PAR. No significant changes in CH_4 emission were found, but two different trends were noted. Methane emissions from the shaded monoliths initially seemed to be higher than emissions from the controls. After approximately four weeks the trend was reversed. The pattern may have been caused by "leakage" of organic compounds from inactivated roots that fueled CH_4 production. It is suggested that a new balanced exchange of potential substrate carbon between the plants and the surrounding peat was established. Comparably less easily degradable carbon compounds would then become available for CH_4 production. The fact that there appeared to be an effect of decreased carbon flow on CH_4 emission is further supported by a tendency for lower concentrations of organic acids in porewater in the shaded monoliths at the end of the experiment. These results indicate a possible lagtime on the order of weeks before changes in photosynthesis rates and NEP have an effect on CH_4 emission rates. Nevertheless it confirms the linkage between CO_2 and CH_4 cycling in wetland ecosystems.

A. Joabsson & T. R. Christensen, Climate Impacts Group, Dept. of Ecology, Plant Ecology, Lund University, SE-223 62 Lund, Sweden; B. Wallén, Ecosystem and Population Ecology Group, Dept. of Ecology, Plant Ecology, Lund University, SE-223 62 Lund, Sweden.

Introduction

The contribution of CH_4 from wetlands to the atmosphere, on a global scale, is about 110 Tg per year (Matthews & Fung 1987; Fung et al. 1991; Bartlett & Harriss 1993); 10–20% originates from northern (>50°N), non-forested wetlands and tundra (Matthews & Fung 1987; Bartlett & Harriss 1993; Harriss et al. 1993; Cao et al. 1996; Christensen, Prentice et al. 1996). The total global CH_4 budget is thus greatly influenced by CH_4 emissions from these areas and vascular plants are considered to be a key factor controlling the rate of production and ultimately also emissions. This paper presents a laboratory experiment on peat monoliths with vascular plants. The purpose was to investigate the possible correlations between the photosynthetic rate of vascular plants and net emission of CH_4 from the monoliths.

Methane (CH_4) emissions from peatlands are subject to a number of environmental controls, of which moisture and temperature are considered to be among the most important (Torn & Chapin 1993; Sundh et al. 1994; Bubier 1995; Christensen, Jonasson et al. 1995). Vascular plants with root systems extending down into the anoxic peat horizons where methane production occurs have the potential to interfere with processes coupled to both the production of CH_4 and its transport out into the atmosphere (Chanton & Dacey 1991; Schütz et al. 1991; Whiting & Chanton 1992; Chanton & Whiting 1995; Schimel 1995; Shannon et al. 1996). Accumulated peat is composed of over 90% organic material. However, since it

becomes increasingly recalcitrant with depth (Hogg 1993; Christensen, Jonasson et al. 1999), the decomposition rates may be limited by the amount of labile carbon (Christensen, Jonasson et al. 1999). Easily degradable carbon may be provided by vascular plants as root exudates (e.g. as organic acids), by root turnover or litter fall. In this manner, the presence of vascular plants in peat-forming wetlands, where the prevailing waterlogged conditions are ideal for CH_4 production, may significantly increase the rate of methanogenesis. It has been suggested that the production rate of vascular plants influences the rate of methanogenesis, since carbon that has been recently fixed in photosynthesis is, to a large extent, translocated to below-ground organs and released into the rhizosphere (Saarinen et al. 1992; Chanton et al. 1995).

Methods

Sampling and treatments: Peat monoliths, 25 × 25 cm and 40 cm deep, were taken in 12 replicates from an ombrotrophic (weakly minerotrophic) bog lawn on the Åkhult mire in southern, boreonemoral Sweden (57°06′N, 14°33′E) at the end of the growing season. *Sphagnum magellanicum* dominated the moss layer and the only graminoid species present was *Eriophorum angustifolium*. Single specimens of *Narthecium ossifragum* and *Vaccinium oxycoccos* were also present. The sampling area has been thoroughly described by Malmer (1962). Aluminium frames were inserted into the ground while cutting around them with a sharp knife. The frames were then lifted up containing the peat monoliths. The monoliths were transported to the laboratory within six hours and incubated under constant light (220 μmol m^{-2} s^{-1}) and moisture conditions at 15°C for four months before the experiment began. The depth of the water table below the moss surface varied among the monoliths from 4 to 10 cm, which corresponded to the variation found in the field. Similar techniques of bringing in peat cores for laboratory CO_2 and CH_4 flux experiments have been used by Billings et al. (1982), Thomas et al. (1996) and Daulat & Clymo (1998), among others. Prior to the measurements, a shading treatment was established wherein six of the replicates were covered with sack cloth. The treatment reduced PAR by 60% (from 220 to 90 μmol m^{-2} s^{-1}) and the remaining available light was suboptimal for maintaining a maximum photosynthetic rate for the vascular plants. The remaining six replicates acted as controls.

Gas flux measurements: Carbon dioxide (CO_2) flux measurements were carried out using a PP System EGM-2 infrared gas analyser attached to a transparent plexiglass chamber with a volume of 13.7 L. For measurements of net ecosystem production (NEP), defined as the total system flux of CO_2 in light conditions, the chamber was installed on the aluminium frames with an airtight water seal and the change in CO_2 concentration within the chamber was continuously measured during 5 min. For measurement of total respiration in the system, the chamber was darkened during 5 min and the same measuring procedure as for NEP was carried out. For analysis of CH_4 emission, duplicate 10 ml syringe samples were taken during the NEP measurements at 0, 5 and 10 min after chamber installation. The CH_4 concentration in the samples was immediately analysed on a Shimadzu 17A gas chromatograph equipped with a flame ionization detector and a Porapak Q column. Injection/detection and column oven temperatures were 140°C and 70°C, respectively, and helium was used as carrier gas with a flow rate of 40 ml min^{-1}. CH_4 flux was calculated on basis of the change in concentration in the chamber over time, using the ideal gas law and correcting for the various total system volumes of the different replicates. Measurements with an r^2 of less than 0.8 in a linear regression of the concentration change with time were considered erroneous and were excluded.

Analysis of organic acids: Peat water was sampled once at the end of the experiment from all replicates at a depth of 7–8 cm below the water table. The samples were immediately analysed for organic acid content by ion chromatography, using a Varian 5000 HPLC to pump the eluent. A column system from Dionex was used with the analytical column, AS11 (4 mm, P/N 044076). The technique is described in detail by Ström et al. (1994).

Harvest: The above-ground living, green biomass of *E. angustifolium* and *N. ossifragum* was harvested after termination of the experiment. The samples were oven dried at 75°C for 72 hours before weighing.

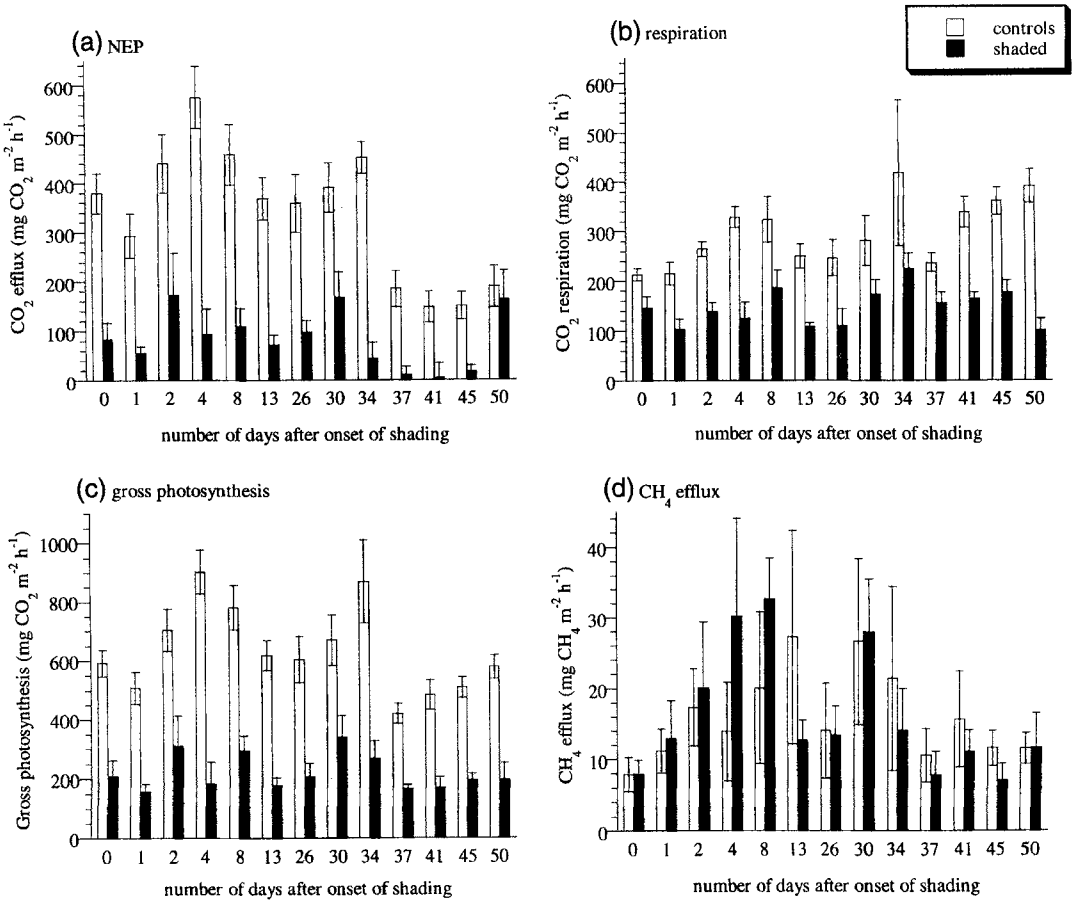

Fig. 1. (a) Mean net ecosystem productivity (NEP), defined as total system flux of CO_2 in light conditions (mg CO_2 m^{-2} h^{-1}) in transparent chambers; (b) mean total system respiration rates (mg CO_2 m^{-2} h^{-1}) in dark chambers; (c) mean gross photosynthesis (sum of NEP and total system respiration) (mg CO_2 m^{-2} h^{-1}); and (d) mean CH_4 emission rates (mg CH_4 m^{-2} h^{-1}) during the experimental period of 50 days. Open bars represent controls (n = 6) and closed bars represent shaded monoliths (n = 6). Error bars indicate standard errors.

Data treatment: The effect of shading on NEP, respiration rate and CH_4 emission was analysed statistically by one-way repeated ANOVAs and effects on biomass and gas flux time dependencies by one-way ANOVAs. The difference between treatments in organic acid concentration was analysed by Kruskal-Wallis one-way ANOVA.

Results

CO_2 fluxes: All light chamber CO_2 fluxes (NEP) decreased significantly ($F = 27.816$, $P < 0.001$) in response to shading (Fig. 1a). The mean NEP across the measuring period ranged between 147 and 574 mg CO_2 m^{-2} h^{-1} in the controls and between 5 and 166 mg CO_2 m^{-2} h^{-1} in the shaded monoliths. A significant variation of NEP over time in the unshaded monoliths was also found ($F = 8.279$, $P < 0.001$).

The shading treatment resulted in a significant decrease in dark chamber respiration ($F = 72.263$, $P < 0.001$) in all measurements across the experimental period (Fig. 1b). Fluxes in the controls ranged from 213 to 417 mg CO_2 m^{-2} h^{-1} and from 100 to 225 mg CO_2 m^{-2} h^{-1} in the shaded monoliths.

The estimation of gross ecosystem photosynthesis, based on the sum of NEP and the total

ecosystem respiration, resulted in a significantly lower ($F = 66.245$, $P < 0.001$) mean CO_2 assimilation rate across the experimental period in the shaded monoliths (ranging from 159 to 339 mg CO_2 m^{-2} h^{-1}) as compared to the controls (ranging from 420 to 868 mg CO_2 m^{-2} h^{-1}) (Fig. 1c).

CH_4 fluxes: Mean CH_4 fluxes ranged from 8 to 27 mg CH_4 m^{-2} h^{-1} in the controls and from 7 to 33 mg CH_4 m^{-2} h^{-1} in the shaded monoliths. No significant differences between treatments were found across the experimental period ($F = 0.002$, $P > 0.05$), but two contrasting trends can be discerned (Fig. 1d). Early in the experiment, between days 1 and 8, mean CH_4 effluxes were highest from the shaded monoliths, while the reverse situation with higher mean effluxes from the controls was found between days 34 and 45. However, the large variability makes these differences non-significant.

Gas fluxes in relation to biomass: No significant difference in living vascular plant biomass (*E. angustifolium* and *N. ossifragum*) between treatments was found. The photosynthetic efficiency in terms of CO_2 assimilation per unit dry biomass decreased as a result of the shading treatment (Fig. 2). Any correlation between photosynthetic rate of the vascular plants and net CH_4 emission can thus be attributed to changes in NEP and not to a secondary effect of lower biomass in the shaded monoliths.

Gas fluxes in relation to organic acid content: In the monoliths, the ranges of organic acid concentrations were as follows: lactate + acetate ranged from 48.2 to 372.4 µM and 20.3 to 344.6 µM; formate from 0.5 to 14.0 µM and 0 to 1.0 µM; malate + succinate from 0 to 124.8 µM and 0 to 123.4 µM; oxalate from 0.4 to 0.6 µM and 0.4 to 0.5 µM in the controls and shaded monoliths, respectively. Due to large variation among the monoliths and a nonparametric distribution of the organic acid exudation as dependent on vascular plant photosynthetic rate, a Kruskal-Wallis one-way ANOVA was used for the analysis of differences in organic acid concentrations between the two treatments. As shown in Table 1 no significant differences between treatments were found for any of the detected organic acids. The rank sums were, however, consistently higher in the controls compared to the shaded monoliths, pointing towards a tendency for a larger exudation of organic acids in the monoliths that had the highest rate of photosynthesis.

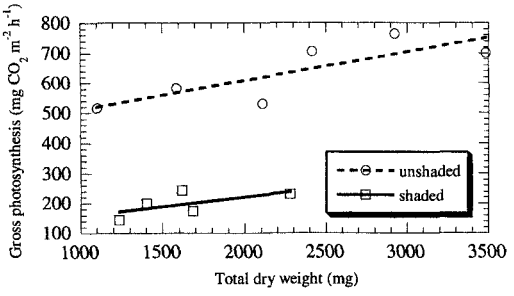

Fig. 2. Gross assimilation of CO_2 (mg CO_2 m^{-2} h^{-1}) per unit dry total biomass of *Eriophorum angustifolium* and *Narthecium ossifragumi* (mg) in the peat monoliths. One replicate from the shading treatment was excluded from the analysis due to anomalies.

Table 1. Kruskal-wallis one-way ANOVA on the effect of shading on organic acid concentration in the peat monoliths. Numbers in parenthesis are the number of replicates (n).

	Rank sum		
	Unshaded	Shaded	*P*
Lactate + acetate	47 (6)	31 (6)	0.2
Formate	41 (6)	25 (5)	0.36
Malate + succinate	11 (3)	10 (3)	0.83
Oxalate	42 (6)	36 (6)	0.63

Discussion

The presence of vascular plants is considered one of the key factors controlling the rate of CH_4 production and net CH_4 emission from northern peatlands (Bubier 1995). Transport of CH_4 from the waterlogged peat to the atmosphere through vascular plant aerenchyma tissue has been shown to greatly enhance net emissions of CH_4 (e.g. Whiting & Chanton 1992; Schimel 1995; Shannon et al. 1996). By providing substrate for methanogenesis, vascular plants also have the potential to influence the actual rate of CH_4 production (Schütz et al. 1991). A study using isotopic analysis of dissolved CH_4 in peat porewater suggested that 50–75% and 35–45% of the CH_4 produced in porewater in fens and bogs, respec-

tively, originated from recently fixed carbon (Chanton et al. 1995). The same study also showed a linear relation between CH_4 emission and CO_2 uptake under light conditions and CO_2 release under dark conditions. As CH_4 emission increased, the CH_4 became increasingly enriched in ^{13}C, which emphasizes the importance of living plant biomass in controlling CH_4 emission. Inputs of labile carbon by roots would increase the importance of acetate fermentation which produces CH_4 that is ^{13}C enriched relative to the CO_2 reduction pathway (Tyler et al. 1997). It is thus likely that vascular plants with relatively higher CO_2 fixation rates have the potential to provide more labile carbon to the methanogens, via e.g. increased root exudation, leading to increased CH_4 production.

In response to the shading treatment in this study, both NEP and the total system respiration decreased significantly. Mire plants generally have a high root:shoot ratio (Saarinen et al. 1992; Saarinen 1996) and it is likely that decreased carbon fixation would result in less plant-derived, labile carbon being released into the rhizosphere. Potentially, this could lead to decreased CH_4 production and ultimately also emission. In this experiment, no significant changes in CH_4 emission rates followed the decrease in photosynthetic rate, but the results are not completely clear-cut. Efflux of CH_4 was initially highest from the shaded monoliths and this pattern was consistent for the first eight days of the experiment. As of day 34, the trend was reversed and comparably more CH_4 was emitted from the controls. This seemingly delayed response of decreased emission indicates that CH_4 transport through the aerenchymateous tissues of *E. angustifolium* was not influenced by decreased stomatal conductance in the shaded monoliths. If that had been the case, the CH_4 flux would have responded immediately to the shading treatment. It is instead likely that the observed pattern of CH_4 emission from the monoliths is a result of altered exchange of carbon compounds between the plants and the surrounding peat. Because *E. angustifolium* has a high root : shoot ratio, a sudden decrease in photosynthetic rate could result in reduced root growth and activity. The shading may thus initially have initiated a "leaking" of non-structural carbohydrates available as substrate for methanogenesis into the peat. Later in the experiment the plants seemed to have adjusted to the lower light situation, leading to a balanced carbon partitioning between roots and shoots with comparably less substrate carbon being released into the peat. A resulting decrease in CH_4 production and ultimately emission would then be expected to occur, which corresponds to the trend found in this experiment. The organic acid concentrations in the porewater support such a relationship, since all the detected acids from the shaded monoliths display lower rank sums than the controls (Table 1). Acetate, which was lower in concentration in the shade treatment, is one of the most important substrates for methanogenesis, but more complex organic structures can also be utilized after initial breakdown of other groups of microorganisms (Oremland 1988).

The water table in the monoliths was at no point during the experiment at or above the moss surface, suggesting that CH_4 oxidation in the surface peat layer might have had a damping effect on net CH_4 emission. A treatment effect of the lowered photosynthesis rate could thus possibly be hidden behind a relatively large oxidation of CH_4. This could partly explain why no significant response of the CH_4 flux to decreased photosynthetic rate was seen in this experiment. It also stresses the importance of aerobic CH_4 consumption as a controlling factor of net CH_4 flux. This accords with earlier results from boreal peatlands (Waddington et al. 1996) and high arctic tundra (Christensen, Friborg et al. in press).

In this experiment, a coupling between vascular plant photosynthetic rate and CH_4 emission is suggested. The shading treatment was applied over the monoliths when the roots and shoots of *E. angustifolium* were already fully developed. This may have caused the initial period of increased CH_4 production due to leakage of substrate carbon into the peat. The following trend of decreased CH_4 emission rate could, however, be linked to the lower photosynthetic rate in the shaded monoliths with a subsequent decreased supply of methanogenic substrate into the peat.

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