

Carbon balance of a European mountain bog at contrasting stages of regeneration

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Summary

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Received: 10 March 2006

Accepted: 29 June 2006

- Carbon dioxide and methane (CH₄) fluxes were measured in a cutover bog of the Jura Mountains (France) together with biotic and abiotic variables for two entire vegetation periods in order to compare the carbon balance of the bog at three stages of regeneration.
- Among all factors, air temperature and vegetation index (including leaf area of vascular plants, bryophyte density and bryophyte desiccation) were the two main determinants of ecosystem respiration and gross photosynthesis at light saturation.
- During 2004 and 2005, the vegetated plots acted as carbon sinks. Net carbon exchange ranged between 67 and 166 g C m⁻² yr⁻¹ for the *Eriophorum*-dominated plots and between 93 and 183 g C m⁻² yr⁻¹ for the *Sphagnum*-dominated plots. The bare peat plots represented a net carbon source (between -19 and -32 g C m⁻² yr⁻¹). Methane fluxes accounted for a very small part of the total carbon efflux (< 2%).
- The recovery of vegetation in our naturally regenerating bog was beneficial for the carbon sequestration after the relatively short period of 20 yr.

Key words: carbon balance, carbon dioxide (CO₂), ecosystem respiration, methane (CH₄), net ecosystem exchange, peat bog, photosynthesis, regeneration.

New Phytologist (2006) **172**: 708–718

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doi: 10.1111/j.1469-8137.2006.01859.x

Introduction

Peat bogs are widespread ecosystems in many climatic areas of the world and provide services of global significance such as, for those of northern countries, a long-term storage of about one-quarter of the world's pool of soil organic carbon and ongoing sequestration of *c.* 1.2% of anthropogenic emissions of CO₂ (Gorham, 1991; Oechel *et al.*, 1993, 2000; Moore, 2002).

In recent decades the human impact on wetlands has been very strong, especially in densely populated areas (Bragg *et al.*, 1992). In Central Europe, for example, only a very small proportion of peatlands (originally millions of hectares) are still in a pristine state (Succow & Jeschke, 1986). The human exploitation of peat for horticulture and fuel modifies the

carbon balance consequently (Armentano & Menges, 1986; Price, 1996; Moore, 2002). Once drained and harvested, a peat bog may become for a long time a carbon source with CO₂ and methane (CH₄) losses (Silvola *et al.*, 1996; Waddington *et al.*, 2002). Their rehabilitation as a carbon sink is a considerable challenge in the context of climate change and environmental issues such as capability of ecosystems for carbon sequestration and reduction in net emissions of greenhouse gases. It has already been shown that the re-establishment of specific bog vegetation – particularly the keystone *Sphagnum* moss – is essential for accumulating organic matter (Clymo, 1984; Rydin & McDonald, 1985; Kuhry *et al.*, 1993; Gerdol *et al.*, 1996) and the *Sphagnum*-dominated bogs have, indeed, the greatest peat (thus carbon) accumulation potential of all peatlands. Some drained wetlands have

been restored, and the development of a mire vegetation and peat accumulation have started on top of the old dry peat (Grosvernier *et al.*, 1995, 1997; Tuittila *et al.*, 2000). Ecological conditions required for bare peat revegetation have been investigated by several authors (Grosvernier *et al.*, 1997; Buttler *et al.*, 1998; Rochefort, 2000; Girard *et al.*, 2002; Chapman *et al.*, 2003). The re-establishment of biogeochemical soil processes takes a considerable amount of time, and a successful regrowth of *Sphagnum* might, indeed, not be a good enough indicator that ecosystem functions as a carbon sink. The modelling of carbon fluxes is the next step to quantify the carbon balance in such harvested bogs (Komulainen *et al.*, 1999; Tuittila *et al.*, 1999; McNeil & Waddington, 2003).

The amount of carbon that is annually sequestered in peatlands depends on the balance between photosynthetic carbon fixation (gross primary production), respiration and decomposition of plant material. Changes in plant species composition may have important effects on this balance because species differ greatly in productivity and decomposability. *Sphagnum* litter is more recalcitrant than litter from vascular plants and decomposes slowly (Coulson & Butterfield, 1978; Clymo & Hayward, 1982; Thormann & Szumigalski, 1999). Important regulating factors are temperature, the groundwater level and nutrient status (Moore & Dalva, 1993; Nykänen *et al.*, 1998; Bellisario *et al.*, 1999; Aurela *et al.*, 2001; Laurila *et al.*, 2001). Taking into account the multiplicity of the post-harvesting states on a single site, as shown in recent studies on northern peatlands (Tuittila *et al.*, 1999; Waddington *et al.*, 2001; McNeil & Waddington, 2003), vegetation density and species composition might also affect gas exchanges at local scale.

Our work takes place in a more southern context, in a bog of the Jura Mountains, where most of the mires have been at least partly harvested, leaving patches dominated by various species (Grosvernier *et al.*, 1995). The aim of our study was to report on and to discuss the carbon balance of a cut-over bog at contrasting stages of regeneration. This was achieved by means of an intensive field measurement campaign including CO₂ and CH₄ fluxes and various biotic and abiotic variables and by the building of an empirical model.

Materials and Methods

Site characteristics

The study site, one of the sites of the European project RECIPE (reconciling commercial exploitation of peat with biodiversity in peatland ecosystems), is a bog of 27 ha in the Jura Mountains (Sur les Seignes, Frambouhans-Les Ecorces, France, 47°18'N, 6°79'E) at an altitude of 867 m above sea level. The long-term annual mean temperature of the region is 6.6°C. Monthly means are -1.4°C and 15.2°C for January and July, respectively. Mean annual precipitation is 1417 mm.

The snow cover is variable among years, with an average of 50 d yr⁻¹. The exploitation of the peat for horticultural

purposes ended in 1984 and the harvested surface covers 2 ha, leaving various topographic levels of exploitation. The drainage system was partly functioning until 2003.

The most disturbed area corresponds to a 0.2 ha area with a gentle slope, on which > 50 cm of peat were removed during peat harvesting. The spontaneous recolonization began 20 yr ago in the lowest part of this area with mostly cottongrass (*Eriophorum angustifolium* Honck.) and some tussocks of *Eriophorum vaginatum* L. A few patches of *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum magellanicum* Brid., *Sphagnum rubellum* Wils. and some *Polytrichum strictum* Brid. appeared under the cottongrass these last years and began to cover the highly decomposed peat horizon. Some bare peat surfaces were still present in the higher part of the scraped area. The least disturbed area is a drained area of 1.4 ha, that has been cleared but not scraped down. The highly decomposed peat horizon was covered with a 20 cm thick layer of *Sphagnum* litter. *S. fallax* is the dominant species with *Polytrichum strictum*, *Eriophorum vaginatum*, *Carex nigra* (L.) Reichard, *Calluna vulgaris* (L.) Hull., and *Vaccinium oxycoccus* L. as companion species.

Measurements of carbon fluxes

Eleven plots were installed in September 2003, and their locations were chosen so as to be representative of the vegetation in the three areas and to capture the variability for each of these situations. Three plots were established on the bare peat (bare peat plots), four plots with cottongrass as dominant species (*Eriophorum*-dominated plots), and four plots with *Sphagnum* as dominant species (*Sphagnum*-dominated plots). The three situations are not truly replicated because of the geographic localization of the plots but they represent typical stages of regeneration that are often observed on other regenerating bogs in the Jura Mountain. Each plot was equipped with a stainless steel collar (30 cm diameter and 10 cm high) that was inserted into the peat. Boardwalks were built around the plots to minimize disturbances. Flux measurements started on November 2003 and continued until November 2005, with breaks during the snow periods between December 2003 to March 2004 and between January and April 2005. During 2004, CO₂ fluxes were measured on 26 sunny days once a week except when the weather was too cloudy and every 3 wk, on 8 sunny days, during 2005.

The CO₂ fluxes were measured under a photosynthetic photon flux density (PPFD) higher than 1000 μmol m⁻² s⁻¹. Light response curves (see below) showed that light saturation was reached at PPFD *c.* 500 μmol m⁻² s⁻¹. A transparent chamber (surface area = 0.071 m²) was used, coupled with a portable infrared gas analyser, functioning in an open mode (CIRAS1; PP Systems, Hitchin, UK). The net CO₂ exchange of the ecosystem under saturating PPFD (EE_{Nsat}) was calculated every 10 s from the CO₂ difference between inlet and outlet

of the chamber and corrected for the vapour pressure difference between inlet and outlet. During data collection, the first 3 min were left for allowing CO₂ concentration to stabilize, and the next 3 min (30 measurements registered) were averaged. Then the chamber was darkened using an aluminium bag and, after a 2-min lag time, data recorded during the next 3 min were averaged to estimate ecosystem respiration (R_E). Gross photosynthesis under saturating photon flux density (P_{Gsat}) was calculated as the sum of EE_{Nsat} and R_E. Microbial CO₂ uptake was negligible on bare peat area.

Light response curves of net ecosystem exchange (EE_N) were obtained using artificial shading made with frames supporting plastic fly net. Depending on the number of net layers, five different PPF_D below the 500 μmol m⁻² s⁻¹ threshold were obtained in order to avoid underestimation of the apparent quantum yield (Burrows *et al.*, 2005). Those measurements were made during the year 2005 on different collars and at different seasons.

Methane fluxes (F_{CH₄}) were measured on the same collars as those used for CO₂ measurements on seven occasions in 2004 and 2005. Vented, closed chambers darkened with an aluminium cover preventing temperature increase were used. A septum on the top centre of the chambers enabled gas sampling with a syringe. The gas sample was immediately put in a 20-mL vacuum tube with a septum and stored in a cold and dark chamber for less than 1 wk until it was analysed by gas chromatography (CP 4900; Varian, Palo Alto, CA, USA). Three samples were taken after 15 min, 45 min and 75 min. The CH₄ fluxes were calculated from the slope of the linear increase of CH₄ concentration with time, knowing the chamber volume and the covered area.

Monitoring biotic and abiotic factors

The desiccation state of the *Sphagnum* carpet in each collar was characterized using a visual index that has been established on *S. fallax* during the very dry summer 2003 on the same site. The desiccation index (DI) was based on the colour of the first 4 cm of *Sphagnum* plants, which is related to their water content. This relationship was validated by measuring the water content of 20 plants of *S. fallax* collected randomly within each class of desiccation (Table 1). Collected plants were immediately transferred in Eppendorf tubes, and fresh and dry (after 48 h at 60°C) weighed. The differences of water content among each value of the index were statistically significant (nonparametric paired test of Mann–Whitney). If there were different states of desiccation on a single collar, a mean index was calculated according to the contributing surfaces.

During the CO₂ flux measurements, PPF_D inside the chamber was measured with a quantum sensor and air temperature (T_A) inside the chamber was measured with a thermocouple. In addition, soil temperature (T_S) at the depth of 5 cm, 10 cm and 50 cm was recorded in the vicinity of each

Table 1 Visual index of desiccation (DI) of *Sphagnum fallax* mosses and corresponding tissue water content

DI value	Visual desiccation	Colour	Water content (%)
1	Completely desiccated	Yellow	11 ± 7
2	Desiccated on top (1 cm)	Green pale	276 ± 90
3	Slightly hydrated	Green	889 ± 78
4	Well humidified	Deep green	1093 ± 78
5	Water saturated	Deep green	1413 ± 187
6	Flooded	Deep green	1996 ± 244

Values are mean ± SD; n = 20.

collar during CO₂ and CH₄ flux measurements. Depth of water table (WT) in perforated tubes located close to each collar was noted at the same time.

In addition, air and soil temperature, rain events (P) and global radiation (R_g) were permanently recorded on the site over the whole period of 2 yr. Air temperature was measured every 10 min and averaged for half an hour. Peat temperature at 5 cm and 30 cm were measured every hour (Hobo H8 pro series; Onset Computer Corporation, Bourne, MA, USA). Global radiation was measured every 30 s using 33-cm-long linear radiometers (INRA Versailles, France) and averaged for half an hour (CR510 datalogger, Campbell Scientific, Courtaboeuf, France). A technical problem on the sensor led to missing data in April and May 2004, which were then reconstructed with the global radiation data recorded at the nearest weather station (Météo France, Pontarlier, 43 km). The R_g values obtained outside the chamber were converted to PPF_D within the chamber that was used as a driving variable for gross photosynthesis. A linear regression between both variables (PPFD = 58.9 R_g, r² = 0.99) was established by simultaneously recording PPF_D within the chamber and R_g on several days.

The bryophyte index (BI) in each collar was obtained by summing the product of covered area on a relative scale by the density of each species (recorded in three subplots with a total surface of 50.1 cm² per collar) relatively to the highest density observed. The BI was estimated three times during the growth period.

Leaf area index (LAI) in each collar was calculated by summing the leaf areas of the main vascular plant species. Leaf area of sedges (*E. angustifolium*, *E. vaginatum* and *C. nigra*) was estimated monthly in two steps. The mean length per leaf was measured using five marked plants close to the collar in each plot. For each species, leaf area was predicted by a power function of the leaf length obtained on a subset of leaves (*E. angustifolium*, R² = 0.95; *E. vaginatum*, R² = 0.93; *C. nigra*, R² = 0.93; data not shown). The total leaf area for a given species in a collar was obtained by multiplying the number of leaves of this species in the collar by the mean leaf area inferred

from the calibration curve and the measured leaf length of marked plants. For *Vaccinium oxycoccos* present in two collars, the leaves were counted three times during the vegetation period on three subplots of 50.1 cm², and 130 randomly selected leaves were scanned to obtain an average leaf area.

For each collar, a vegetation index (VI) ranging from 0 to 1 was calculated as followed:

$$VI = \frac{\left(LAI + BI \times \left(\frac{DI}{DI_{\max}} \right) \right)}{(LAI_{\max} + BI_{\max})} \quad \text{Eqn 1}$$

with LAI, the leaf area index, BI, the bryophyte index and DI, the desiccation index. LAI_{max} was set at 1.4 m² m⁻², a value just above the highest leaf area index recorded on all the collars; BI_{max} was set at 1 (BI is a relative value) and DI_{max} was set at 6, the highest value of the desiccation index (see Table 1).

Data analysis

Relationships between carbon fluxes and biotic and abiotic variables were fitted for each group of collars within each kind of vegetation using nonlinear regression curves (SIGMAPLOT 3.0; SPSS Inc., Chicago, IL, USA) for CO₂ fluxes and linear regression curves (JMPIN 3.2.1; SAS Institute Inc., Cary, NC, USA) for CH₄ fluxes. Criteria for a valid model were a minimum root mean squared errors (rmse) and no bias in the distribution of the residuals. The annual carbon balance was built for each collar by summing EE_N calculated every half hour using half-hour values of temperature and global radiations, the daily values of the depth of the water table, LAI, BI and DI were linearly interpolated between each date of measurements.

Relationships between CO₂ fluxes and biotic and abiotic factors

The R_E increased with increasing temperature. The best fit was obtained using a power function with air temperature as the driving variable.

On bare peat plots, the residuals of the power function were linearly related to the level of the water table:

$$R_E = \left(a \times \frac{WT}{WT_{\text{ref}}} + c \right) \times \left(\frac{(T_A - T_{\min})}{(T_{\text{ref}} - T_{\min})} \right)^b \quad \text{Eqn 2}$$

The reference depth for water table, WT_{ref}, was set at -0.4 m, a value just under the lowest observed water table. the minimum temperature at which a positive respiration occurred, T_{min}, was set at -5°C. The reference air temperature, T_{ref}, was set at 15°C. Coefficient *b* accounts for temperature sensitivity of R_E. Coefficients *a* and *c* are two fitted empirical parameters.

On vegetated plots, residuals of the power function increased with increasing vegetation index. In such conditions,

$$R_E = \left[\left(d \times \frac{WT}{WT_{\text{ref}}} \right) + (e \times VI) \right] \times \left(\frac{(T_A - T_{\min})}{(T_{\text{ref}} - T_{\min})} \right)^b \quad \text{Eqn 3}$$

Coefficients *d* and *e* are two fitted empirical parameters.

The relationship between gross photosynthesis under saturating photosynthetic photon flux density (P_{Gsat}) and T_A was well-described using the normal distribution function as suggested by June *et al.* (2004) for photosynthetic electron transport. The rmse were strongly reduced by adding a linear function of VI.

$$P_{G\text{sat}} = f \times VI \times e^{-\left(\frac{T_A - g}{b} \right)^2} \quad \text{Eqn 4}$$

(*f* is gross photosynthesis at saturation PPFD, at optimum temperature (*g*) and for a vegetation index of 1; *b* is temperature sensitivity factor).

Finally, the following equation was fitted to EE_{Nsat} values using fixed parameter values for respiration (Table 2a):

$$EE_{N\text{sat}} = f \times VI \times e^{-\left(\frac{T_A - g}{b} \right)^2} - \left[\left(d \times \frac{WT}{WT_{\text{ref}}} \right) + (e \times VI) \right] \times \left(\frac{(T_A - T_{\min})}{(T_{\text{ref}} - T_{\min})} \right)^b \quad \text{Eqn 5}$$

The value of P_G varied also with photosynthetic photon flux density. Rectangular hyperbolas were fitted to EE_N values using fixed parameter values for respiration (Table 2a) and for gross photosynthesis at saturation PPFD (Table 2b):

$$EE_N = \left(\frac{i \times \text{PPFD} \times P_{G\text{sat}}}{P_{G\text{sat}} + i \times \text{PPFD}} \right) - R_E \quad \text{Eqn 6}$$

(*i* is the initial slope of the rectangular hyperbola at low light levels – also called the apparent ecosystem quantum yield).

Relationships between methane fluxes and biotic and abiotic factors.

Methane fluxes followed the seasonal variation in the water table for the bare peat plots.

$$F_{\text{CH}_4} = j \times WT \quad \text{Eqn 7}$$

(*j* is the slope of the linear relation between F_{CH₄} and WT. F_{CH₄} was not related to the water table level but was linearly linked with the leaf area index for *Eriophorum*-dominated plots and for *Sphagnum*-dominated plots.

$$F_{\text{CH}_4} = k \times LAI \quad \text{Eqn 8}$$

(*k* is the slope of the linear relation between F_{CH₄} and LAI).

Table 2 Root mean square errors (rmse) and adjusted model parameters (\pm standard errors) for ecosystem respiration (R_E), as fitted against R_E data (Eqns 2 and 3), gross photosynthesis at light saturation (P_{Gsat}), as fitted against EE_{Nsat} data (Eqn 5), light response of gross photosynthesis (P_G), as fitted against light response curves of EE_N (Eqn 6), and methane fluxes (F_{CH_4}), as fitted against F_{CH_4} data (Eqns 7 and 8) in bare peat plots (three collars), *Eriophorum*-dominated plots (four collars) and *Sphagnum*-dominated plots (four collars)

	Bare peat	<i>Eriophorum</i> -dominated	<i>Sphagnum</i> -dominated
Respiration (R_E)			
rmse	0.23	0.57	0.87
a	0.4 \pm 0.1 (+3%; -3%)		
b	2.7 \pm 0.4 (+2%; -3%)	1.8 \pm 0.1 (-2%; 1%)	1.9 \pm 0.2 (-3%; 2%)
c	0.08 \pm 0.02 (+8%; -7%)		
d		1.2 \pm 0.2 (7%; -7%)	0.9 \pm 0.2 (5%; -5%)
e		2.3 \pm 0.2 (13%; -13%)	3.2 \pm 0.3 (14%; -14%)
Gross photosynthesis at light saturation (P_{Gsat})			
rmse	1.23		1.59
f	19.7 \pm 0.6 (-24%; 23%)		28 \pm 0.6 (-26%; 26%)
g	35.1 \pm 2.1 (48%; -50%)		32.5 \pm 0.9 (78%; -75%)
h	23.9 \pm 3.9 (-30%; 24%)		17.7 \pm 1.5 (-42%; 37%)
Light response of gross photosynthesis (P_G)			
rmse	0.77		1.28
i	0.032 \pm 0.002 (-7%; 6%)		0.058 \pm 0.005 (-4%; 3%)
Methane fluxes (F_{CH_4})			
rmse	1.2	15	4.2
j	-24.6 \pm 4.3 (0%; 0%)		
k		27.5 \pm 5.67 (0%; 0%)	19.9 \pm 2.4 (0%; 0%)

Sensitivity of net carbon exchange (relative change in percentage) in response to a 10% decrease or increase in the value of each model parameter for a typical collar of each station in 2005 is given under bracket. Absolute values of net carbon exchange in 2005 were -19 g C m⁻² yr⁻¹ for the collar on bare peat, 111 g C m⁻² yr⁻¹ for the *Eriophorum*-dominated collar and 122 g C m⁻² yr⁻¹ for the *Eriophorum*-dominated collar.

Results

Seasonal trends

The fluctuation of T_A (Fig. 1a) was important all over the seasons and from one day to another. During summer, absolute values often reached 30°C at midday, but with low temperatures, near to 0°C during night. Annual

precipitations were different between both years with 1633 mm in 2004 and 1335 mm in 2005 (Fig. 1b). The water table level (WT) fluctuated during the seasons mainly following the precipitations. The water table remained quite low in early summer 2005 in all plots, from day 530–544 (Fig. 1c). The variation in the desiccation index (DI) of the bryophytes followed the fluctuation of the water table (Fig. 2a). The averaged leaf area index (LAI) differed among plots because of the different dominant species of vascular plants (Fig. 2b). *Eriophorum vaginatum* in *Sphagnum*-dominated plots had more photosynthetically active leaves at the beginning of spring and at the end of autumn than *E. angustifolium* in *Eriophorum*-dominated plots, but *E. angustifolium* reached higher leaf area values during summer. For all plots, the LAI values were higher in 2005 than in 2004. The bryophyte density was greater in *Sphagnum*-dominated plots than in *Eriophorum*-dominated ones in both years (Fig. 2c).

In 2004, R_E increased from snowmelt (Day 100) until the middle of August up to 4.6 \pm 0.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *Sphagnum*-dominated plots and 3 \pm 1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *Eriophorum*-dominated plots (Fig. 3a). On bare peat plots, the highest R_E values of 1.45 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was on day 178. The R_E values decreased during autumn and reached very low values just before the snow period (0.02, 0.08 \pm 0.04 and 0.14 \pm 0.12 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, for bare peat plots, *Eriophorum*-dominated plots and *Sphagnum*-dominated plots on the day 344). Similarly low values were obtained the previous winter (data not shown). In summer 2005, R_E reached higher values than in summer 2004, with 6.7 \pm 1.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *Sphagnum*-dominated plots and 5.4 \pm 0.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *Eriophorum*-dominated plots. By contrast, R_E was slightly lower in 2005 than in the previous year in bare peat plots with 1.05 \pm 0.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

In 2004, light-saturated net ecosystem CO_2 exchange (EE_{Nsat}) reached maximum values in the middle of August (7.5 \pm 1.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Sphagnum*-dominated plots and 4.6 \pm 1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots), and exhibited positive values throughout the snow-free period (Fig. 3b). In 2004, calculated P_{Gsat} values were maximal in late summer (10.7 \pm 1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the *Sphagnum*-dominated plots and 6.5 \pm 1.8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots) and then decreased until the snow period with the lowest flux of 0.27 \pm 0.12 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Sphagnum*-dominated plots and 0.28 \pm 0.19 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots (Fig. 3c). At the end of June, in 2005, the average EE_{Nsat} fell near to 0 (-0.01 \pm 0.93 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Sphagnum*-dominated plots and 0.58 \pm 0.78 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots) with negative values in some collars. This occurred during the driest period when bryophytes were strongly desiccated and this was related to a drop of P_{Gsat} and a concomitant increase in R_E .

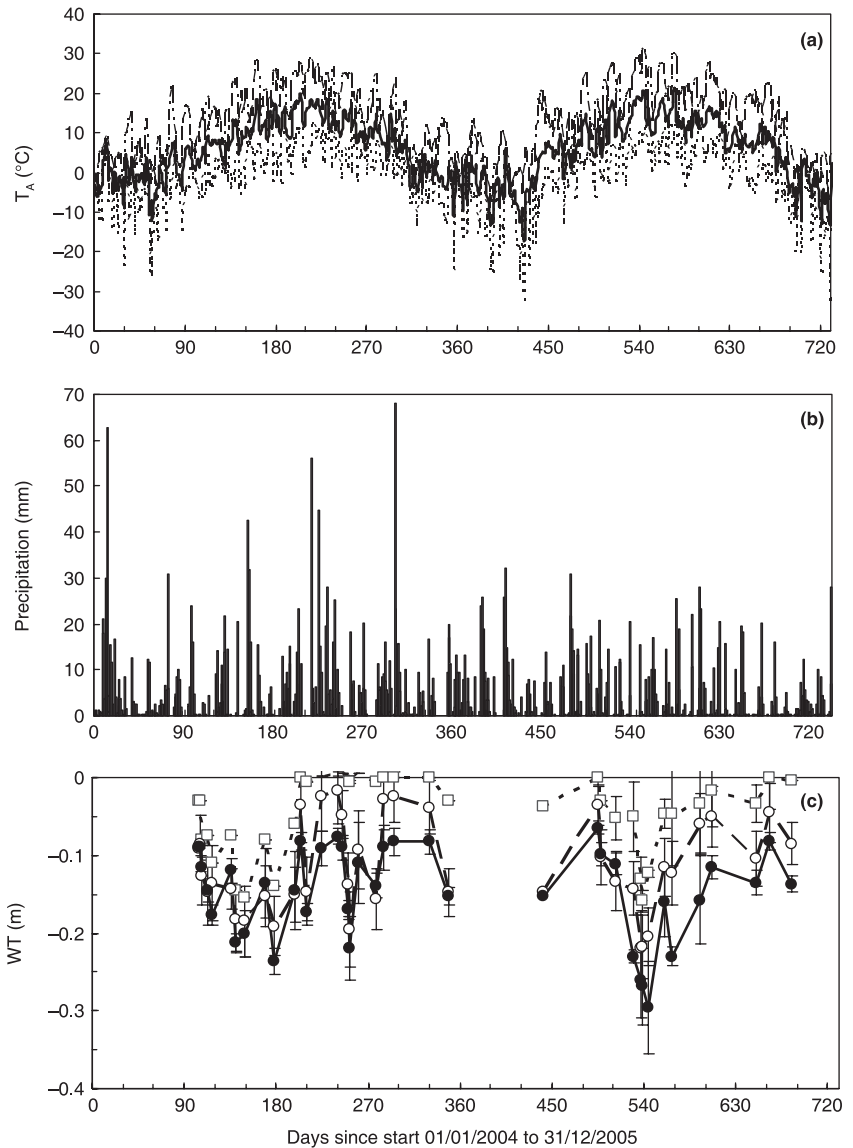


Fig. 1 Seasonal courses (days of years 2004–05) of: (a) daily average (thick line), daily minimum (dotted line) and daily maximum (thin line) air temperature (T_A); (b) daily precipitation (mm); (c) average depth of the water table (WT) in bare peat plots (squares and fine dotted line, $n = 3$), *Eriophorum*-dominated plots (open circles and large dotted line, $n = 4$) and *Sphagnum*-dominated plots (closed circles and unbroken line, $n = 4$). Vertical bars are standard deviations.

Throughout the two years, the CH_4 fluxes measured in *Eriophorum*-dominated plots were higher than the fluxes in *Sphagnum*-dominated plots and the lowest fluxes were observed on bare peat plots (Fig. 4). There were large variations among collars, as highlighted by high values of standard deviations. The fluxes were slightly higher in 2005 than in the previous year. The greatest fluxes were found in May 2005, with a mean value of $30.5 \pm 31.4 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots, $8.7 \pm 5.8 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for *Sphagnum*-dominated plots and $2.1 \pm 1.7 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for the bare peat plots. The lowest values were recorded at the beginning of the winter 2004 with a mean value of $3.6 \pm 2.1 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots, $2.4 \pm 2.2 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for *Sphagnum*-dominated plots and $0.5 \pm 0.3 \text{ nmol CH}_4 \text{ m}^{-2} \text{ s}^{-1}$ for the bare peat plots.

Predicted model parameters and sensitivity analysis

Predicted model parameters from Eqns 2–8 and associated rmse values are given in Table 2. There was a close agreement between predicted and observed values of R_E , $EE_{N_{\text{sat}}}$ and EE_N except for the highest R_E values, which were slightly underestimated. The sum ($a + c$) is equal to R_E at T_{ref} and WT_{ref} for bare peat plots, and the sum ($d + e$) is equal to R_E at T_{ref} , WT_{ref} and for a VI of 1 for vegetated plots. These sums were, respectively, 0.48 , 3.5 and $4.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for bare peat plots, *Eriophorum*-dominated plots and *Sphagnum*-dominated plots. Gross photosynthesis at saturation PPFD and at optimum temperature and for a vegetation index of 1 (i.e. the f parameter) were, respectively, 19.7 and $28.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *Eriophorum*-dominated plots and for

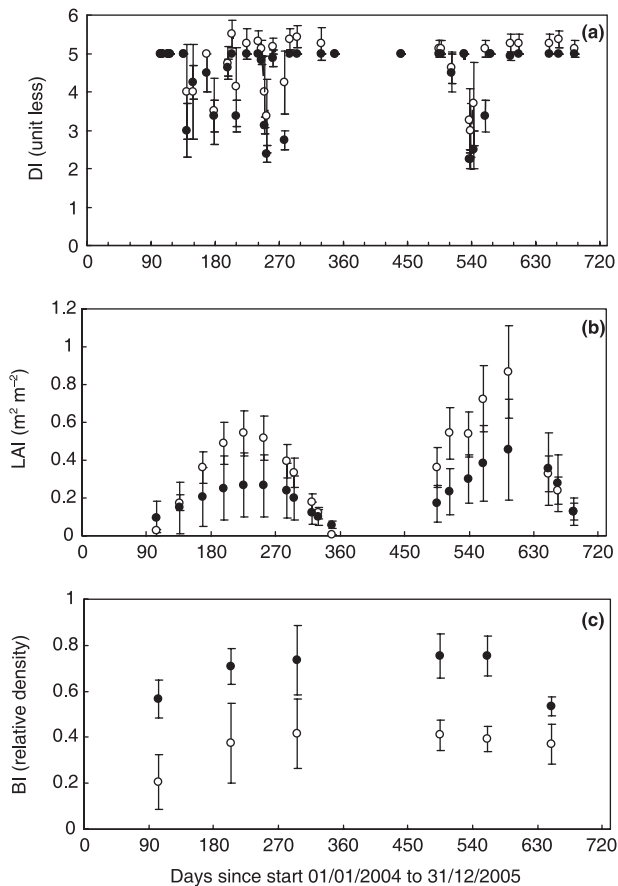


Fig. 2 (a) Average values of desiccation index of bryophytes (DI, from 1, completely desiccated, to 6, flooded); (b) average values of leaf area index (LAI); (c) average values of bryophyte index (BI, relative unit) in *Eriophorum*-dominated plots (open circles, $n = 4$) and *Sphagnum*-dominated plots (closed circles, $n = 4$). Vertical bars are standard deviations.

Sphagnum-dominated plots, and the optimum temperatures (g) were 35.1°C and 32.5°C , respectively. The apparent ecosystem quantum yields (i) were $0.032 \text{ mol CO}_2 \text{ mol photon}^{-1}$ and $0.058 \text{ mol CO}_2 \text{ mol photon}^{-1}$, respectively, for *Eriophorum*-dominated plots and for *Sphagnum*-dominated plots.

A sensitivity analysis was performed to assess how a 10% decrease and increase in each value of model parameters would affect our estimation of annual net carbon exchange. The same trends were observed for all collars and for the 2 yr. Then, only data for 2005 and for one collar per type of vegetation are presented in Table 2. Estimations of annual carbon exchanges were almost insensitive to a 10% change in parameters related to F_{CH_4} (parameters j and k) and were only slightly sensitive to a 10% change in parameters related to R_E (parameters a to e). Among parameters related to P_G , estimations of net carbon exchanges were especially sensitive to a 10% change in the temperature optimum for photosynthesis

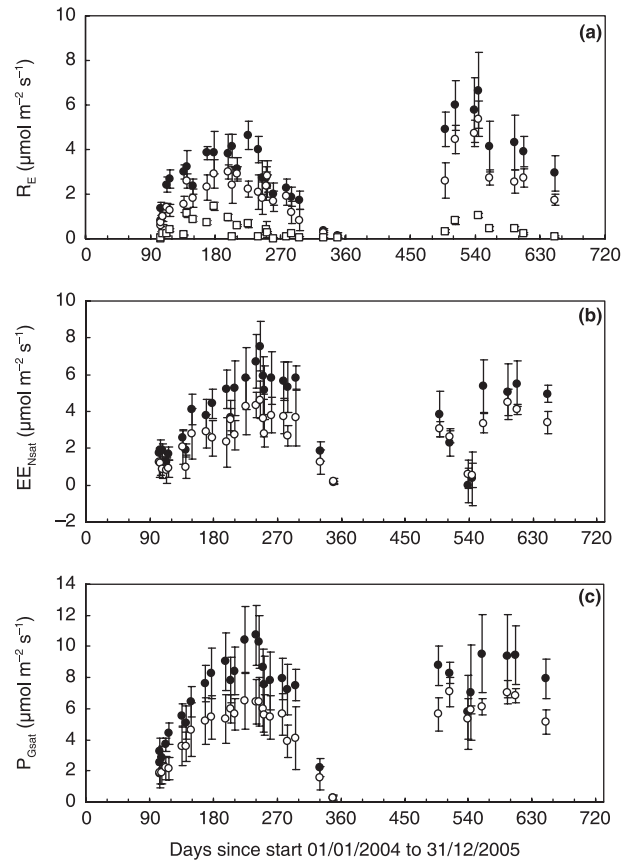


Fig. 3 Seasonal courses (days of years 2004–05) of: (a) ecosystem respiration (R_E); (b) net ecosystem CO_2 exchange under saturating photosynthetic photon flux density (PPFD > $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, EE_{Nsat}); (c) gross photosynthesis under saturating photosynthetic photon flux density (PPFD > $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, P_{Gsat}) in bare peat plots (squares, $n = 3$), *Eriophorum*-dominated plots (open circles, $n = 4$) and *Sphagnum*-dominated plots (closed circles, $n = 4$). Vertical bars are standard deviations.

(g) and to a 10% change in gross photosynthesis at saturation PPFD and at optimum temperature and for a vegetation index of 1 (f). It was less sensitive to a 10% change in the quantum yield for photosynthesis (i).

Annual carbon balance

The annual carbon fluxes were calculated for each collar, and ranges of values obtained for each type of vegetation are given in Table 3.

The *Eriophorum*-dominated plots and *Sphagnum*-dominated plots were net sinks of carbon for the years two studied. Annual net carbon exchange ($EE_{\text{N}} + F_{\text{CH}_4}$) ranged between 67 and $118 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2004 and between 78 and $166 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2005 for *Eriophorum*-dominated plots, while it ranged between 93 and $175 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2004 and between 122 and $183 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2005 for *Sphagnum*-dominated plots (Table 3). In 2005, all fluxes were higher

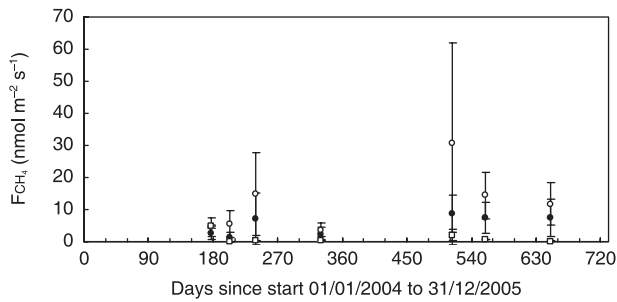


Fig. 4 Seasonal courses (days of years 2004–05) of methane fluxes (F_{CH_4}) in bare peat plots (squares, $n = 3$), *Eriophorum*-dominated plots (open circles, $n = 4$) and *Sphagnum*-dominated plots (closed circles, $n = 4$). Vertical bars are standard deviations.

than in 2004. Gross photosynthesis (P_G) and ecosystem respiration components (R_E) were higher for *Sphagnum*-dominated plots than for *Eriophorum*-dominated plots, while the reverse was true for methane efflux (F_{CH_4}). The bare peat plots represented a small carbon source during both years, with values ranging between -22 and $-32 \text{ g C m}^{-2} \text{ yr}^{-1}$. The methane fluxes had a very low contribution to the total carbon efflux ($F_{\text{CH}_4} + R_E$), between 1% and 2% for the bare peat plots and *Eriophorum*-dominated plots, and below 1% for *Sphagnum*-dominated plots.

Winter fluxes during the snow period were simulated with the peat temperature at 5 cm depth, assuming that with the protection of the snow cover, the respiration was better related to this temperature than to the air temperature because of the snow insulation effect. Those winter effluxes represented a very small part of the annual ecosystem respiration, $< 4\%$ for the vegetated plots and $< 3\%$ for the bare peat plots.

Discussion

The two areas with ongoing regeneration acted as sink for carbon during the two years of measurement, with a greater sink during the second year. Lower rates of net carbon exchange were estimated for an *Eriophorum* lawn in an ombrotrophic bog in Eastern Finland ($73 \text{ g C m}^{-2} \text{ yr}^{-1}$, Alm *et al.*, 1997) and for an ombrotrophic bog in Canada ($68 \text{ g C m}^{-2} \text{ yr}^{-1}$, Lafleur *et al.*, 2001). Twenty years after abandonment, a drained Finnish cutaway bog acted as a carbon source but 3 yr after rewetting, the seasonal carbon balance of the wet part became clearly positive (65 g C m^{-2}) with a dense cover of *Eriophorum vaginatum* (Tuittila *et al.*, 1999). Greater rates in our site (67 – $163 \text{ g C m}^{-2} \text{ yr}^{-1}$) could at least partly be explained by a more Southern location and/or by a less continental climate, and consequently by a longer growing season and a shorter period with snow cover.

Lower rates of net carbon exchange are expected for drier years. The drops of gross photosynthesis, which were observed during the short drought period in 2005 suggest that during extremely dry years, as in 2003 in Western Europe, the carbon

Table 3 Ranges of annual CO_2 and methane (CH_4) fluxes and net carbon exchange ($\text{g C m}^{-2} \text{ yr}^{-1}$) for bare peat plots (three collars), *Eriophorum*-dominated plots (four collars) and *Sphagnum*-dominated plots (four collars) for years 2004 and 2005

	Bare peat plots	<i>Eriophorum</i> -dominated plots	<i>Sphagnum</i> -dominated plots
2004			
P_G		197 to 306	284 to 474
R_E	-22	-121 to -207	-186 to -297
EE_N	-22	68 to 120	94 to 176
F_{CH_4}	-0.4	-1.5 to -2.8	-0.7 to -2.3
Net carbon exchange	-22	67 to 118	93 to 175
2005			
P_G	-	279 to 379	359 to 525
R_E	-19 to -31	-199 to -214	-233 to -340
EE_N	-19 to -31	80 to 169	122 to 185
F_{CH_4}	-0.2 to -0.6	-1.8 to -3.9	-0.5 to -2.7
Net carbon exchange	-19 to -32	78 to 166	122 to 183

sequestration could be much lower or even become negative, as reported for other sites by Alm *et al.* (1999) and Lafleur *et al.* (2003). This is in agreement with previous results showing that, for many *Sphagnum* species, net photosynthesis decreases with decreasing tissue water content below values corresponding to the level 3 of our visual desiccation index (Titus *et al.*, 1983; Schipperges & Rydin, 1998). Sedge (*Eriophorum*) species were probably less affected by the drop of water table, because these are deep-rooted species that can transfer water from deeper peat layers and therefore keep their stomata open even during dry periods (Tuittila *et al.*, 1999). Gross photosynthesis was less sensitive to summer drought in the *Eriophorum*-dominated area than in the *Sphagnum*-dominated area because collars in the *Eriophorum*-dominated area included fewer bryophytes and more vascular plants than did collars in the *Sphagnum*-dominated area.

Our vegetation index includes relative variations in leaf area of vascular plants (LAI), relative variations in moss density and covered area (BI) and the desiccation of bryophytes. This is well-adapted to the patchy situations we encountered in our site and to their potential impact in case of drought. Our approach differs from previous studies using vegetation index derived from leaf area of vascular plants only (Aurela *et al.*, 2001; Laurila *et al.*, 2001), or including an effective temperature sum index in the model for accounting for vegetation phenology (Alm *et al.*, 1997; Komulainen *et al.*, 1999; Tuittila *et al.*, 1999). It also differs from those of Bubier *et al.* (2003) where model parameters were first derived for each species on homogeneous collars, and then applied to more patchy ones. Our relative vegetation index was able to account for spatial variation in plant density and species composition among collars.

Annual carbon loss of bare peat areas ranged between -22 and $-32 \text{ g C m}^{-2} \text{ yr}^{-1}$ in our site and were smaller than those reported for a cutover bog in central Québec, Canada (-88 and $-112 \text{ g C m}^{-2} \text{ yr}^{-1}$, Waddington *et al.*, 2002). High water table in our site probably restricts carbon mineralization. Influence of water table fluctuation on ecosystem respiration has already been described (Alm *et al.*, 1999). Bare peat respiration was enhanced with the decrease in the water table level from the peat surface to 0.3 m depth. During a drier summer, the water table would probably go deeper, and the relationship should become nonlinear (Silvola *et al.*, 1996; Tuittila *et al.*, 2004). Unlike what was observed for bare peat area, the depth of the water table did not explain most of the variation in ecosystem respiration in the two other situations. The same trend was observed on an ombrotrophic bog in Canada, with a cool continental climate (Lafleur *et al.*, 2005). This suggests that not only peat but also vegetation contributes to R_E in vegetated plots. Plant respiration is known to account for as much as 35–90% of the ecosystem respiration in organic soils (Belkovsky & Reshetnik, 1981; Silvola *et al.*, 1996; Johnson *et al.*, 2000).

Temperature was the first explanatory factor, explaining most of the variations in ecosystem respiration, as underlined by Lafleur *et al.* (2005). On a newly restored Canadian bog, the CO_2 flux, which was predominantly soil respiration, was also strongly controlled by temperature fluctuations (Petronne *et al.*, 2001, 2003). The winter fluxes under snow, whose simulation remains uncertain, represented only 4% of the annual ecosystem respiration component. Compared with northern peatlands, with longer winters and lower temperatures, this percentage is rather small. Values as high as 13% and 28% were, respectively, reported for a fen in northern Finland (Aurela *et al.*, 2002) and for an ombrotrophic bog in eastern Finland (Alm *et al.*, 1997).

Sensitivity analysis showed a very small impact of the respiration parameters on the carbon balance. The carbon exchange was clearly more sensitive to adjusted parameters for gross photosynthesis linked to temperature. Adjusted optimal temperatures (g) were very similar in both types of vegetated plots (35.1°C and 32.5°C , respectively, for the *Eriophorum*-dominated plots and the *Sphagnum*-dominated plots), and were within the range of those reported for temperate vascular plants (Farquhar *et al.*, 1980; June *et al.*, 2004), but were much higher than those reported for *S. fallax* and *S. fuscum* (Titus & Wagner, 1984; Silvola, 1990). The optimal temperature was, indeed, set at 20°C in PCARS model for boreal ecosystems (Frolking *et al.*, 2002). Despite the wide range of acceptable values of this factor, it is the most sensitive to a 10% variation of its value but it does not change the trend of the balance.

A very small amount of carbon was lost as CH_4 when compared with the amount of carbon lost as CO_2 . The CH_4 efflux was 10 times smaller than those reported for an *Eriophorum* lawn in Finland (Alm *et al.*, 1999), for a

Canadian peatland (Bellisario *et al.*, 1999) and for a subarctic mire in Sweden (Bellisario *et al.*, 1999; Öquist & Svensson, 2002). However, it was in the same range as those included in the annual fluxes of carbon predicted by the PCARS model (Frolking *et al.*, 2002). In vegetated areas, CH_4 fluxes were related to the leaf area index of vascular plants. This is consistent with previous studies showing that CH_4 flux was in correlation with the number of vascular plants (Öquist & Svensson, 2002). This confirms that vascular plants play an important role in controlling CH_4 transfer from anaerobic horizon to the atmosphere (Bellisario *et al.*, 1999). For the bare peat plots, CH_4 fluxes increase with decreasing the depth of the water table. This is in agreement with data from Bellisario *et al.* (1999) but contrasted with those from Finnish peatlands (Nykänen *et al.*, 1998). We did not find any significant relationship between methane fluxes and temperature, as previously reported by Moore & Dalva (1993) and McKenzie *et al.* (1998). Seasonal fluctuations of the water table can be a confounding factor that would affect the relationship between peat temperature and methane production. Low CH_4 fluxes in our site where the peat was highly decomposed were in agreement with previous findings showing that dissolved CH_4 concentrations were negatively correlated to stage of peat decomposition (Buttler *et al.*, 1994).

No measurements of leaching of dissolved organic carbon (DOC) and emission of volatile organic carbon were available on our site but its contribution to peatland carbon balance is thought to be limited. For different Finnish bogs, the range of DOC values ranged between 2.6 and $8.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Alm *et al.*, 1997; Aurela *et al.*, 2002) and isoprene emission was one order of magnitude lower than methane emission (Haapanala *et al.*, 2006).

Conclusion

Air temperature and vegetation index account for most of the variation in both P_{Gsat} and R_E on vegetated plots while air temperature and the depth of the water table account for most of the variation in bare peat respiration. The same controls (i.e. temperature and vegetation index) can be applied across a range of sites differing in stage of revegetation and the same equations can be applied for two different years. This suggests that these equations can be applied across a wide range of restored peatland after calibrating the model parameters. The recovery of vegetation in cutover bogs is beneficial for the carbon sequestration and this was confirmed in our naturally restoring bog after the relatively short period of 20 yr. Options for active regeneration may consider that sites with more bryophytes tend to be first affected by summer drought, compared with sites with more vascular plants. However, vascular plants can 'pipe out' more methane from the peat, which has more impact on global change through its greater warming potential.

Acknowledgements

This work was carried out in the frame of the 5thFPRTD project RECIPE (reconciling commercial exploitation of peat with biodiversity in peatland ecosystems) of the European Union. We thank the RECIPE work team for helpful discussions about methods and results. We also thank J. D. Tissot for his technical help and Espace Naturel Comtois for having facilitated field work on the bog Sur les Seignes and for information on previous management.

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