Oecologia (1999) 120:563–574

Eeva-Stiina Tuittila · Veli-Matti Komulainen
Harri Vasander · Jukka Laine

Restored cut-away peatland as a sink for atmospheric CO_2

Received: 21 September 1998 / Accepted: 18 May 1999

Abstract In a field study, we examined the relationship between vegetation, abiotic factors and the CO_2 exchange dynamics of a cut-away peatland 20 years after production had ended. The main objective was to determine the effect of rewetting on the CO_2 exchange dynamics, measured separately in *Eriophorum vaginatum* tussocks and intertussocks (almost non-vegetated surfaces) using closed-chamber techniques, one growing season before and three growing seasons after the rewetting treatment. Rewetting lowered total respiration (R_{TOT}) and increased gross photosynthesis (P_G), which resulted in a higher incorporation of CO_2 into the system. The seasonal CO_2 balance for the almost continuously submerged section of the rewetted site became positive 2 years after rewetting (9.1 g CO_2-C m^{-2}), and it was still higher in the 3rd year (64.5 g CO_2-C m^{-2}), i.e. the system accumulated carbon. In the driest section of the rewetted site the seasonal balance increased strongly, but the balance was still negative during the 3 years following rewetting with losses from the system of 44.1, 26.1, 38.3 g CO_2-C m^{-2} in 1995, 1996 and 1997 respectively. At the control site seasonal balance during 1995–1997 varied between ecosystem C losses of 41.8 and 95.3 in an area with high *Eriophorum* cover and between 52.1 and 109.9 g CO_2-C m^{-2} with lower cover. Simulation of a cut-away peatland with dense *Eriophorum* vegetation (*Eriophorum* cover 70%) showed that if the water level (WT) is low, the seasonal CO_2 balance of the ecosystem can reach the compensation point of no net C change ($P_G = R_{TOT}$) only if weather conditions are favourable, but with a high WT the seasonal CO_2 balance would be positive even under varying weather conditions. It can be concluded that with dense *Eriophorum* vegetation a restored cut-away peatland acts as a functional mire and becomes a sink for atmospheric CO_2.

Key words Cut-away peatland · CO_2 exchange · *Eriophorum vaginatum* · Restoration · Water level

Introduction

Pristine peatlands act as long-term sinks for atmospheric carbon due to an unbalanced ratio of primary production and decomposition, i.e. a small proportion of the primary production is deposited under anaerobic conditions and accumulated as peat (e.g. Clymo 1984). In peat harvesting this accumulated biomass storage is utilized in horticulture or energy production.

Industrial peat production is concentrated mainly in Europe (including Russia) and North America (Lappalainen 1996). About half of the peat produced is used for fuel and the other half is used as growing media, soil conditioning or litter, and as an absorbent in environmental protection (Nyrönen 1996). Ireland, the Nordic countries and the former Soviet Union are the largest users of energy peat (Asplund 1996). In Germany, Great Britain, Canada and the United States almost all peat produced is used as horticultural peat and gardening products (Lappalainen 1996).

During peat harvesting peatlands are drained efficiently and divided into convex fields, and vegetation is completely removed (Frilander et al. 1996). After about 20–50 years of peat production the peatland is abandoned (Nyrönen 1996). After abandonment the mean water level remains well below the surface, and water level fluctuations can be larger than in pristine mires (Schouwenaars 1993). Cut-away peatlands do not have viable seed banks (Curran and MacNaeidhe 1986; Salonen 1987; Huopalainen et al. 1998) and the fields remain without vegetation cover for a long period, because plant colonization under such extreme conditions is very slow (Salonen 1992; Campeau and Rochefort 1996; Lavoie and Rochefort 1996). Thus, on non-vegetated

E.-S. Tuittila (✉) · V.-M. Komulainen · H. Vasander · J. Laine
Department of Forest Ecology,
P.O. Box 24,
FIN-00014, University of Helsinki,
Finland
e-mail: eevastiina.tuittila@helsinki.fi, Fax: +358-9-1917605

cut-away peatlands there is no carbon fixation into the ecosystem, but increased aeration in the surface peat significantly enhances organic matter oxidation and CO_2 emission (Billings et al. 1982, 1983; Peterson et al. 1984; Silvola et al. 1985, 1996; Glenn et al. 1993; Funk et al. 1994; Martikainen et al. 1995; Nykänen et al. 1995). Average respiration rates during the warmest summer period have been measured as between 4.2 and 4.8 g CO_2 m^{-2} day^{-1} (Silvola and Alm 1992).

The objective of peatland restoration is to bring back a naturally functioning mire ecosystem (e.g. Wheeler and Shaw 1995). To achieve this, the first steps in restoration consist of raising the water table level by blocking the drainage ditches and, in case of minerotrophic sites, reestablishing the predrainage inflow by leading ground water to the area. Soil respiration is expected to decrease after rewetting, and CO_2 fixation is expected to begin after recolonization of mire species. Finally, in a successful restoration the carbon accumulation processes are assumed to begin again (e.g. Heikkilä and Lindholm 1995; Wheeler and Shaw 1995). Restoration is becoming more and more common, e.g. in Germany restoration is the dominant after-use of cut-away peatlands (Blankenburg and Kuntze 1986), and in Canada restoration is now a peatland management priority (Rubec 1996). Restoration and consequent recolonization of cut-away peatland have been studied in Europe (Meade 1992; Roderfeld et al. 1993, 1996; Salonen and Laaksonen 1994; Grosvernier et al. 1995; Wheeler and Shaw 1995) and in North America (Campeau and Rochefort 1996; Ferland and Rochefort 1997), but the potential of the cut-away peatlands as soil CO_2 sinks awaits further study.

The aims of this study were (1) to examine the relationship between the ecosystem CO_2 exchange dynamics, vegetation and abiotic factors on a cut-away peatland and the impact of restoration thereon, and (2) to create a model for CO_2 exchange components in order (3) to simulate the effects of restoration on CO_2 balance.

Material and methods

Study site and rewetting arrangements

The study was carried out in 1994–1997 on a cut-away peatland, Aitoneva, Kihniö (62°12′N, 23°18′E) in southern Finland. The study site is situated in the transitional zone between the southern and middle boreal coniferous forest zones (Ahti et al. 1968) in the raised bog region (Ruuhijärvi 1982). The long-term annual mean temperature of the region is 3.5°C and the mean annual precipitation is *c.* 700 mm. The average effective growing season is 160 days and the cumulative temperature sum (threshold value +5°C) is 1100 degree days.

Peat harvesting at this location ended in 1975 and the residual peat layer thickness after abandonment was 1 m on average. The residual peat was highly decomposed *Sphagnum-Eriophorum* peat, with an average bulk density of 0.198 ± 0.028 g cm^{-3} ($n=48$). The area of the field was 3.5 ha and it was divided into 20-m-wide strips by ditches. The drainage system was still partly functioning in 1994. The dominant plant species was cottongrass, *Eriophorum vaginatum* L.; however, 20 years after abandonment bare surfaces still occupied a major part of the field.

A 2-ha area that was rewetted in autumn 1994 is hereafter referred to the rewetted site (R), and the rest of the field is called the control site (C). Both sites were divided into a relatively dry part in the upper section of the site (R1, C1) and a moister part in the lower section (R2, C2). Restoration of the rewetted site was achieved by blocking the drainage ditches with peat dams. In addition, a feeder ditch was excavated to the upper section of the rewetted site to lead ground water to the site from surrounding areas. During the calibration period (growing season 1994) CO_2 exchange dynamics and vegetation were studied before restoration in order to quantify the relationships between the properties of rewetted and control sites. The effect of rewetting was studied during the growing seasons of 1995–1997.

Measurements of CO_2 fluxes

Eight CO_2 sample plots were established on different surfaces representing variations in vegetation of the study site. Four CO_2 sample plots were established on mature *E. vaginatum* tussocks, two on the rewetted site (plots 3 and 10) and two on the control site (plots 12 and 13). Four CO_2 sample plots were established on almost bare peat surfaces, hereafter referred to intertussocks (a term also used by Poole and Miller 1982; Johnson et al. 1996): three on the rewetted site (plots 2, 4 and 5) and one on the control site (plot 11). Their vegetation consisted mostly of a few *E. vaginatum* seedlings (Table 1). The plots were established in 1994, except for sample plot 10, which was established in 1995. The CO_2 sample plots were surrounded with 0.36-m^2 (60 × 60 cm) aluminium collars which were inserted into the peat to a depth of 30 cm. The collars were equipped with grooves which were filled with water before gas flux measurements to provide an airtight seal between the chamber and the collar. Boardwalks were built around the sample plots to avoid disturbance during measurements.

Gas flux measurements were started in late May or early June and continued until late September or early November (13 June–20 September 1994, 31 May–8 November 1995, 4 June–23 October 1996 and 6 June–29 September 1997). Flux measurements were taken at 1- to 3-week intervals, most frequently from late June to mid-August.

A vented and thermostated transparent plastic chamber (0.112 m^3) was used in the CO_2 exchange measurements. The CO_2 concentration in the chamber was measured with a portable infrared gas analyser (ADC, LCA 2, Analytical Development Company Ltd., UK) equipped with vacuum pump (suction from the headspace 150–180 ml air min^{-1}). Analyser readings in parts per million (ppm) were recorded at intervals of 30 s after closing the chamber. The net CO_2 exchange (P_N) was measured with the chamber uncovered and exposed to ambient illumination for 60–120 s. On days with high irradiation levels, P_N values were also measured under lower irradiation levels, achieved by shading, in order to better establish the relationship between photosynthesis and irradiation. After each measurement period the chamber was removed for a while to allow stabilization of the gas concentration in the plot. After P_N measurements the total respiration rate (R_{TOT}) was measured with the chamber covered with an opaque lid made of 1-mm aluminium plate, under temperature and moisture conditions similar to those for P_N measurements. For this method see also Tuittila and Komulainen (1995) and Alm et al. (1997, 1999).

In connection with CH_4 measurements (results not given here), R_{TOT} was also measured with an opaque aluminum chamber technique (as modified by Martikainen et al. 1992) in sample plots 2, 3, 4, 11, 12 and 13. The chamber (0.108 m^3) was placed onto the collar and a series of air samples was taken from the chamber with 60-ml plastic syringes 5, 15, 25 and 35 min after closing the chamber. CO_2 concentrations in the samples were determined in the laboratory by gas chromatography (HP 5890 Series II, for the analytical method see Nykänen et al. 1995) within 24 h of sampling. No differences were found between the two methods and the data were combined for further analysis.

Monitoring vegetation and abiotic factors

Twelve circular vegetation-sampling plots, each 2 m^2, were placed systematically on the upper and lower section of the rewetted and the control site within which the vegetation change was monitored. The percentage cover class (scale 0.01, 0.02,...0.09, 0.1, 0.2,...0.9, 1, 2,...9, 10, 15, 20,...95, 96,...99, 100%) of each species was estimated, both for the CO_2 sample plots and for the vegetation sampling plots at the same time of each year between late July and early August, in order to minimize seasonal variation. If an *E. vaginatum* tussock was larger than the CO_2 sample plot, its cover was recorded as $>100\%$ because the whole tussock was placed inside the chamber during gas exchange measurements. Seedlings and living tussocks of *E. vaginatum* were recorded separately. Nomenclature follows Moore (1982) for vascular plants and Koponen et al. (1977) for bryophytes.

Simultaneously with each CO_2 measurement, air temperature inside the chamber, water level and soil temperature at peat profiles were measured in order to relate the gas flux to prevailing environmental conditions. Solar irradiation (PAR) was measured every 30 s with a quantum sensor during P_N measurements.

Water level of each vegetation plot was monitored throughout the growing season in ground water tubes next to each plot. Beginning in autumn 1995, water level was also monitored hourly with pressure sensors situated in the central part of upper and lower sections of the sites. Converted data from pressure sensors were used in the reconstruction of CO_2 fluxes for the summers of 1996 and 1997 after calculating the linear relationships between means of the water level tubes ($n=12$) and the values obtained from the pressure sensors of upper and lower sections of the sites.

Because continuous weather data were not available before autumn 1995, soil temperatures needed for CO_2 simulations were estimated using linear regressions of the 1996 data separately for the control site and upper and lower sections of the rewetted site ($r^2 > 0.93$ for all regressions). Soil temperature for the summer of 1994, prior to rewetting, was obtained using regression for control site. Soil temperature at 5 cm depth was used as dependent and ambient air temperature, and mean temperatures during the previous 6, 12, 24, 48, 72 and 96 hour periods as independent variables.

A time series for solar irradiation and air temperature was obtained from the Lakkasuo weather station (61°47′N, 24°18′E). A time series of solar irradiation (measurements taken with LI-COR pyranometer sensor LI-200SZ, unit W m^{-2} s^{-1}) was converted to quantum sensor units (LI-190SB, mol m^{-2} s^{-1}) using a quadratic relationship ($r^2=0.983$) between the pyranometer and the quantum sensor readings.

Modeling CO_2 exchange

CO_2 flux (P_N, R_{TOT}) rates were calculated from the linear change of CO_2 concentration as a function of time. P_N can be either positive or negative. We obtained positive values when the flux of CO_2 from the atmosphere into the vegetation exceeded total respiration from vegetation and soil. Although R_{TOT} represents a loss of C from the system, it was set to positive values. Gross CO_2 assimilation in photosynthesis (P_G) was estimated as the sum of P_N and R_{TOT} values (Alm et al. 1997).

Response functions for total respiration (R_{TOT}) and gross photosynthesis (P_G) with *E. vaginatum* cover (EV), solar irradiation (I), surface soil temperature (T_{-5}), water level (WT) and effective temperature sum index (ETI) as independent variables were constructed for the mosaic of *Eriophorum* tussocks and intertussock surfaces. ETI was calculated as a quotient of cumulative temperature sum (threshold 5°C) and the number of temperature sum days. Calculation of cumulative temperature sum was started when the 5-day moving average was over 5°C. The number of temperature sum days increased only on those days when the cumulative temperature sum was increasing.

The functions take the form

$$P_G = Q \cdot I/(I+k) \cdot \mathrm{EV} \cdot \mathrm{ETI} \cdot T_{-5} \qquad (1)$$

$$\ln R_{TOT} = b0 + b1 \cdot \mathrm{EV} + b2 \cdot T_{-5} + b3 \cdot \mathrm{WT} + b4 \cdot \mathrm{ETI} + b5 \cdot \mathrm{EV} \times \mathrm{WT} \qquad (2)$$

The dependence of P_G on irradiation (I) in Eq. 1 has the form of a rectangular hyberbola with coefficients Q (asymptotic maximum) and k (half-saturation constant), where the asymptotic maximum was dependent on *E. vaginatum* cover (EV), effective temperature sum index (ETI) and surface soil temperature (T_{-5}). The multiplicative structure was adapted from Kettunen (1998). Equation 1 was constrained to $P_G=0$ when T_{-5} was <0°C, i.e. in cases where the statistical model would have resulted in negative photosynthesis. Coefficients for the environmental variables (biotic and abiotic) in the functions were estimated using linear (ln R_{TOT}) or non-linear (P_G) regression technique. The net CO_2 exchange (P_N) was calculated for every hour as:

$$P_N = P_G - R_{TOT} \qquad (3)$$

and integrated over the growing season. All the calculations were made using the SYSTAT software package (SYSTAT 1996).

Results

Water table level and vegetation

During the calibration period in 1994, the upper section of the rewetted site R1 was driest (mean water level −39 cm) and the lower section R2 moistest (mean −30 cm). Both sections of the control site C1 and C2 were intermediate (Fig. 1a). The water table level at both sites was deeper than during the 3 following years (Fig. 1). The water table level of R2 was similar to that

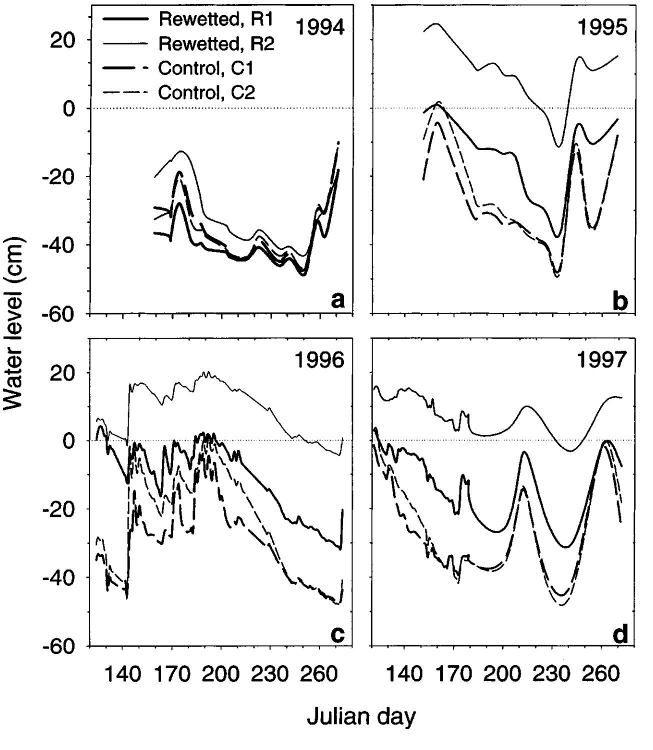

Fig. 1a–d Water level at upper (R1, C1) and lower sections (R2, C2) of rewetted and control sites during growing seasons 1994–1997. Year 1994 was a calibration period

of a pristine bog hummock in that year (Alm et al. 1999).

Prior to rewetting, the vegetation consisted of a mosaic of *E. vaginatum* tussocks and bare peat surfaces (intertussocks). In the summer of 1994, C1 had the highest cover of *Eriophorum* (mean 34%) and R1 the lowest (mean 11%) (Fig. 2a). Some other plant species, e.g. *Betula* spp., *Calluna vulgaris* and *Vaccinium uliginosum*, were also found in the field layer, but their total cover was less than 1%. An exception was R2, where *Carex rostrata* occurred with a mean cover of 4% and *Empetrum nigrum* with a cover of 1.5%. The bottom-layer species occurred almost exclusively in the vicinity of tussocks. The dominant species was *Dicranella cerviculata*, with mean cover of 8% in C1. Other bryophyte species found were *Pohlia nutans*, *Polytrichum commune*, *P. strictum*, *Polytrichastrum longisetum* and *Warnstorfia fluitans*.

After rewetting, the mean water level in R1 was 26 cm higher during summer of 1995 than in the previous year (Fig. 1). R2 was almost continuously under water, with a mean water level more than 40 cm higher than during the calibration period. At the control site the median water level was also about 10 cm higher in the summer of 1995 than in 1994. The variation between years was large, and during the summer of 1997 the water level was lower than during the 2 previous years at both sites (Fig. 1).

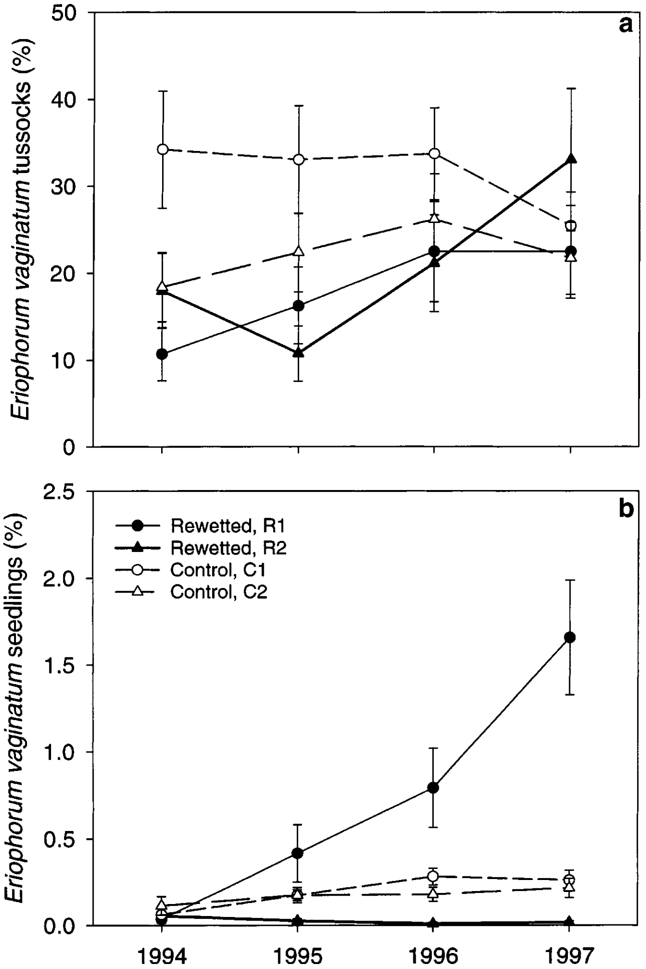

Fig. 2 The mean cover of *Eriophorum vaginatum* **a** tussocks and **b** seedlings from 1994 to 1997 at upper (R1, C1) and lower sections (R2, C2) of rewetted and control sites ($n = 12$). *Bars* indicate SEM

The effect of rewetting on *Eriophorum* tussocks was most obvious in R2, which after rewetting was almost continuously submerged. There, the *Eriophorum* cover decreased in the 1st year following rewetting but in the subsequent years the increase in the cover of the tussocks was rapid (Fig. 2). In R1, where the water level rise was moderate, the cover of *Eriophorum* tussocks increased evenly from 1994 to 1996 (Fig. 2). In C2 there was a steady increase in the cover of *Eriophorum* tussocks until 1996 but a decrease in 1997 to the level of the summer of 1995. In C1, with the densest vegetation, no change in tussock cover was observed until a decrease in 1997 (Fig. 2). The moderate rise in the water level at R1 clearly favoured the development of *Eriophorum* seedlings, as their cover increased exponentially from 1994 to 1997 while there were no change in the wettest area, R2 (Fig. 2). *Dicranella cerviculata* remained dominant in the bottom layer in both rewetted and control sites.

The vegetation change in CO_2 exchange plots followed the trend in the vegetation sample plots (Table 1). After rewetting, sparse *Eriophorum* vegetation developed in non-submerged intertussock spaces (Table 2). On the control site an intertussock sample plot (11) remained almost bare. The cover of *Eriophorum* tussocks increased from the summer of 1994 and was largest in 1996 both at the rewetted (plots 3 and 10) and the control site (plots 12 and 13).

Effect of rewetting treatment on CO_2 exchange

The CO_2 exchange components (P_G, R_{TOT}, P_N) were strongly related to the abundance of *E. vaginatum* (Figs. 3, 4, 5). During the calibration period, the mean R_{TOT} on tussocks (plots 3, 12 and 13) was approximately 3 times higher than on intertussocks (plots 2, 4, 5 and 11) (Fig. 3). After rewetting, the mean R_{TOT} strongly decreased on two intertussock plots (2 and 5), but on the driest plot (4) mean R_{TOT} remained at the same level as in 1994 (Fig. 3, Table 2). On the control site the mean R_{TOT} remained at the same level as in 1994 at two of the sample plots (11 and 12), but on tussock sample plot 13 the mean decreased from summer 1994 (Fig. 3).

As *Eriophorum* cover increased on the rewetted tussock sample plot (3) after rewetting, the potential P_G at PAR > 500 μmol m^{-2} s^{-1} also increased (Fig. 4). However, although the cover of *Eriophorum* was highest in the summer of 1996, the P_G was highest in 1995 as was effective temperature sum index (Fig. 6). Following rewetting, sparse *Eriophorum* vegetation developed on two intertussock plots (4 and 5) (Table 1) and their potential P_G rose steadily during the measurement years (Fig. 4c). The changes in P_N (Fig. 5) after rewetting largely followed those in P_G.

Table 1 Projection cover (%) of *Eriophorum vaginatum* in CO_2 sample plots representing different stages of vegetation succession of cut-away peatland during 1994–1997 (*Tu* tussock sample plots, *In* intertussock sample plots). Sample plots 2–10 were at the rewetted site (*R*) and 11–13 at the control site (*C*). Other ground layer species found at the sample plots were *Betula* spp. (plot 2: 1994, 3: 1994, 5: 1994, 10: 1997, 11: 1996–1997, 12: 1995–1997, 13: 1994–1997), *Dryopteris carthusiana* (13: 1994–1997), *Pinus sylvestris* (11: 1994–1996), *Salix phylicifolia* (2: 1997, 5: 1997, 10: 1997) and in bottom layer species found were *Aulacomnium palustre* (13: 1994–1997), *Cladonia* spp. (12: 1996–1997, 13: 1994–1997), *Dicranella cerviculata* (2: 1995, 3: 1995, 5: 1996–1997, 10: 1996–1997, 12: 1996–1997), *Dicranum polysetum* (13: 1994–1997), *Pleurozium schreberi* (12: 1996–1997, 13: 1994–1997), *Pohlia nutans* (3: 1994, 10: 1996–1997, 12: 1995–1997, 13: 1994–1997), *Polytrichastrum longisetum* (12: 1996–1997, 13: 1994–1997), *Polytrichum commune* (13: 1994–1997), *Sphagnum angustifolium* (13: 1994–1997), *S. russowii* (13: 1994–1997), *Warnstorfia fluitans* (13: 1994–1997)

Treatment and plot number	Vegetation	Cover (%)			
		1994	1995	1996	1997
RIn 2	*E. vaginatum* seedling	0.04	0	0.01	0.1
RTu 3	*E. vaginatum* tussock	95	99	115	60
	Eriophorum litter	10	2	20	100
RIn 4	*Eriophorum vaginatum* seedling	0.03	0.5	0.7	2
RIn 5	*E. vaginatum* seedling	1	3	7	2
	E. vaginatum tussock	0	0	0	7
	Eriophorum litter				2
RTu 10	*E. vaginatum* seedling	–	0.2	0.3	0
	E. vaginatum tussock	–	90	85	55
	Eriophorum litter	–	1	70	70
CIn 11	*E. vaginatum* seedling	0.01	0.1	0	0.1
CTu 12	*E. vaginatum* seedling	0.01	0.1	0	0.1
	E. vaginatum tussock	70	80	95	70
	Eriophorum litter	10	20	70	90
CTu 13	*E. vaginatum* tussock	40	45	60	30
	Eriophorum litter	40	40	70	70

Seasonal variation in CO_2 exchange

Variation in gross photosynthesis (P_G) and total respiration rate (R_{TOT}) during the growing season followed the seasonal distribution of solar irradiation, soil temperature, and effective temperature sum index, as well as the seasonal fluctuations of the water level (Figs. 1, 6, 7). The highest P_G in all tussock plots was 2450 mg CO_2 m^{-2} h^{-1} at the rewetted site (Fig. 4a) and 1934 mg CO_2 m^{-2} h^{-1} at the control site (Fig. 4b). On the rewetted site the measured R_{TOT} values during 1995–1997 varied between 76 and 1324 and −6 and 470 mg CO_2 m^{-2} h^{-1} in tussocks and intertussocks, respectively. At the control site the corresponding values were 48–1249 and 55–430 mg CO_2 m^{-2} h^{-1}.

In tussocks temporal variation in net CO_2 exchange (P_N) during the growing seasons followed the variation in P_G (Fig. 7b, c). However, because R_{TOT} and P_G reached their maximum at the same time, the increasing trend of P_N towards July–August and decreasing trend towards autumn were weaker than that of P_G (Fig. 7). In the intertussocks where P_G was low, the seasonal pattern in P_N during the growing seasons was the inverse of that in tussocks (Fig. 7). In the intertussocks P_N was highest at the beginning and the end of the study periods and lowest in July–August, when the water table was at its lowest level and the soil temperature highest.

R_{TOT} and P_G models

Model 1, which uses the Michaelis-Menten function for describing the saturating response of photosynthesis to irradiation (PAR) and linear dependence of maximal photosynthesis on the cover of *Eriophorum* (EV), effective temperature sum index (ETI) and soil temperature

Table 2 The mean seasonal water table level (WT, cm) and its standard deviation (SD) at CO_2 sample plots during weeks 24–38 (*Tu* tussock sample plots, *In* intertussock sample plots). Sample plots 2–10 were at the rewetted site (*R*) and 11–13 at the control site (*C*). Number of measurements (*n*) also given

Treatment and plot number	1994			1995			1996			1997		
	WT	SD	*n*	WT	SD	*n*	WT	SD	*n*	WT	SD	*n*
RIn 2	−31.3	8.6	11	0.7	5.9	16	3.0	6.1	13	–	–	–
RTu 3	−31.2	8.2	12	0.1	5.3	17	2.8	5.9	20	–	–	–
RIn 4	−41.4	6.0	11	−17.3	10.3	23	−19.1	11.3	14	–	–	–
RIn 5	−33.6	1.9	6	−10.4	9.0	16	−12.9	11.3	9	−9.1	7.2	8
RTu 10	–	–	–	−17.3	9.7	6	−12.0	10.9	13	−14.9	9.2	8
CIn 11	−45.8	6.2	10	−32.2	12.8	21	−36.0	12.8	14	–	–	–
CTu 12	−42.7	7.5	10	−27.6	15.6	21	−33.7	13.5	17	–	–	–
CTu 13	−26.2	3.9	5	−9.5	11.7	20	−12.5	8.1	16	–	–	–

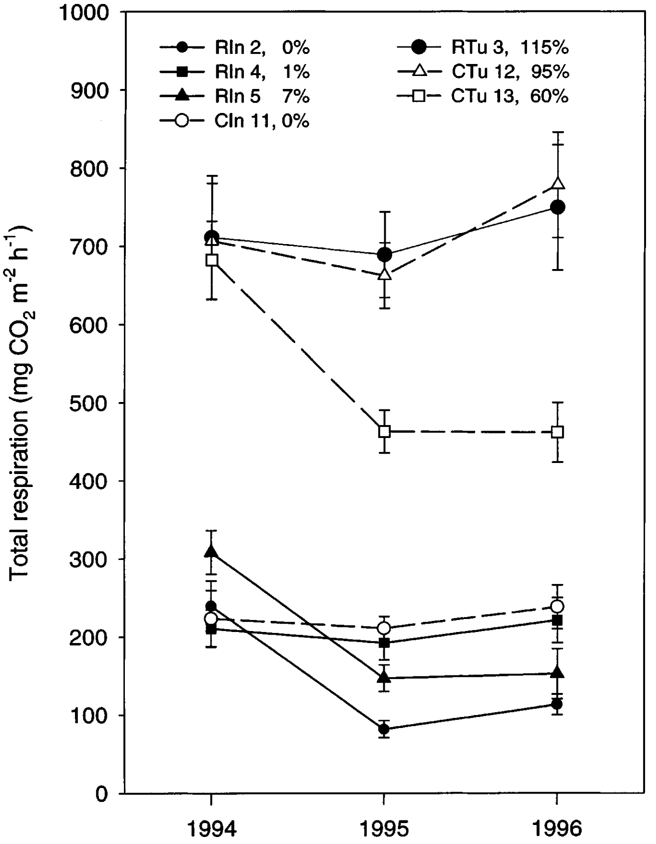

Fig. 3 The mean rates of total respiration during weeks 24–38 in 1994, 1995 and 1996 at CO_2-exchange sample plots (*RTu 3* tussock sample plot at the rewetted site, *RIn 2*, *4*, *5* intertussock sample plots at the rewetted site, *CTu 12*, *13* tussock sample plots at the control site, *CIn 11* intertussock sample plot at the control site). *Small bars* indicate SEM. The percentage for each plot refers to the *E. vaginatum* cover in 1996

(T_{-5}), explained 89% of the variation in P_G (Table 3). The linear model with EV alone explained 62% of variation in photosynthesis, and the distribution of residuals indicated that the linear dependence was valid.

The R_{TOT} model (model 2), where respiration was log-linearly related to the cover of *Eriophorum* (EV), temperature (T_{-5}), effective temperature sum index (ETI) and water level (WT) explained 84% of the variation in total respiration (Table 4). Because the processes involved in R_{TOT} are more heterogeneous than photosynthetic processes, lower explanatory power was to be expected. Variation in EV alone explained 46% of the variation in respiration. WT had a negative coefficient in the model: the lower the water level the deeper is the oxic layer and therefore the higher the soil respiration. The interaction term between WT and EV was positive (Table 4).

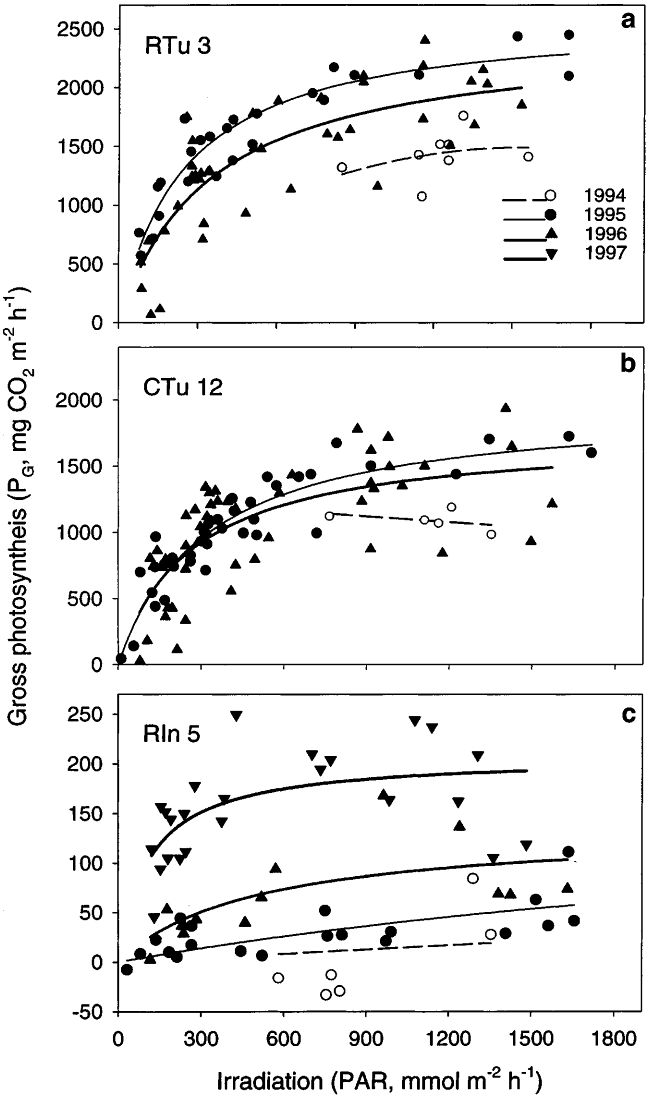

Fig. 4 Gross photosynthesis in sample plots during July–August (weeks 27–34) by photosynthetic radiation (PAR). **a** RTu 3 tussock sample plot at the rewetted site, **b** CTu 12 tussock sample plot at the control site, **c** RIn 5 intertussock sample plot at the rewetted site, in 1994–1997. In 1997 P_G was not measured in plots 3 and 12

Reconstructed CO_2 balance at the rewetted site and the control site

During the calibration period in 1994, the seasonal estimates (mid-May to end of September) of the CO_2 balance were all negative and very low, i.e. the system lost carbon to the atmosphere. The seasonal CO_2 balance was highest (−111.8 g CO_2-C m^{-2}) in C1 with largest *Eriophorum* cover, and lowest (−164.4 g CO_2-C m^{-2}) in R1 (Fig. 8a).

During the 3 years of restoration, the high water level together with increasing *Eriophorum* cover increased the seasonal net CO_2 influx of the rewetted site when compared with the situation at the control site (Fig. 8a). This difference between the rewetted and the control site became especially clear in 1997, when the *Eriophorum* cover decreased at the control site. R2 with the highest water level reached a positive seasonal CO_2 balance of 9.1 g CO_2-C m^{-2} 2 years after rewetting and it was still higher and reached 64.5 g CO_2-C m^{-2} during the 3rd year. In R1, with a moderate rise in water level, the

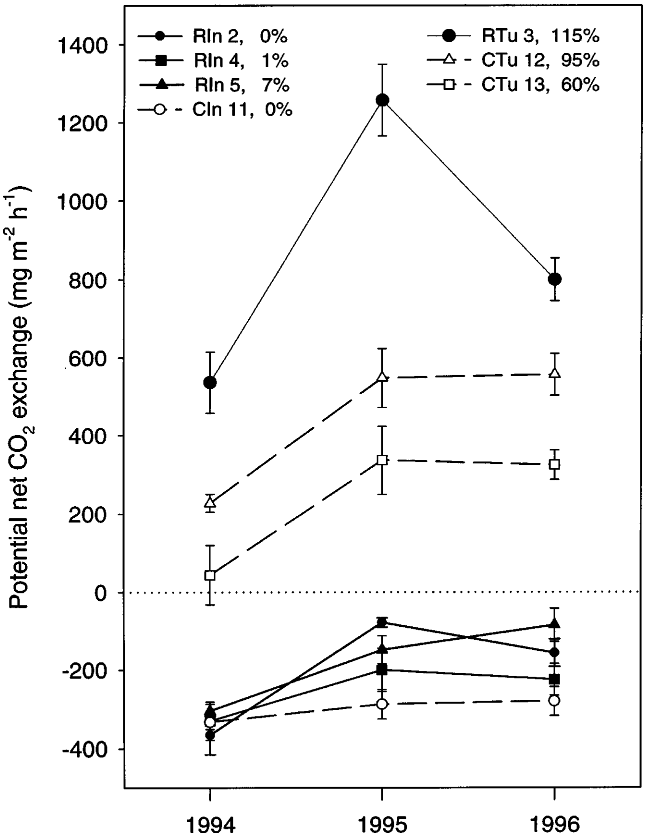

Fig. 5 The mean rates of potential net CO_2 exchange (PAR > 500 µmol m^{-2} s^{-1}) of sample plots during July–August (weeks 27–34) (*RTu 3* tussock sample plot at the rewetted site, *RIn 2*, *4*, *5* intertussock sample plots at the rewetted site, *CTu 12*, *13* tussock sample plots at the control site, *CIn 11* intertussock sample plot at the control site). *Small bars* indicate SEM. The *percentage* for each plot refers to the *E. vaginatum* cover in 1996

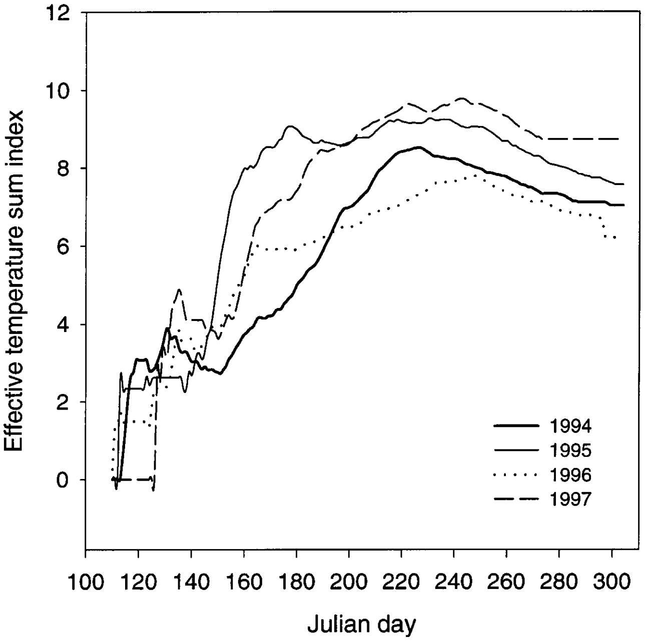

Fig. 6 Effective temperature sum index (ETI) over the growing seasons of 1994–1997

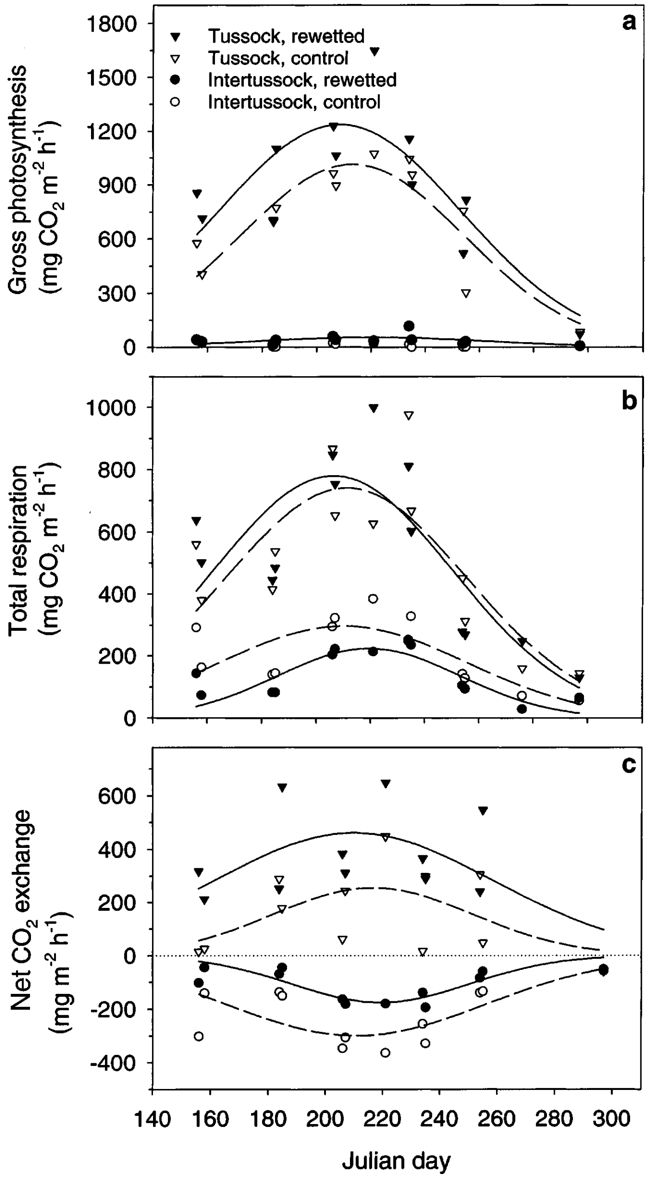

Fig. 7a–c Seasonal patterns of CO_2-exhange components during 1996: average values from tussock and intertussock sample plots at rewetted and control sites. **a** Gross photosynthesis (P_G). **b** Total respiration (R_{TOT}). **c** Net CO_2 exchange (P_N)

seasonal balance had already reached the level of C1 (greatest *Eriophorum* cover) in the 1st year after rewetting. However, the seasonal balance in R1 remained negative during the 3-year study period (−44.1, −26.1, −38.3 g CO_2-C m^{-2} in 1995, 1996 and 1997, respectively).

Simulated effect of water level and *Eriophorum* on seasonal CO_2 balance

The seasonal (mid-May to end of September) CO_2 balance was simulated for conditions on bare peat surface (Fig. 8b) and for closed *Eriophorum* vegetation on cutaway peatland (Fig. 8c). Environmental data from the

Table 3 Estimated parameter values for models used to reconstruct hourly gross photosynthesis (P_G). The dependence of P_G on irradiation (I) (Eq. 1) has the form of a rectangular hyberbola with coefficients Q (asymptotic maximum) and k (half-saturation constant), where the asymptotic maximum was dependent on *E. vaginatum* cover (EV), effective temperature sum index (ETI) and surface soil temperature (T_{-5}) (*ASE* asymptotic standard error, df_{reg}, df_{res} degrees of freedom for regression and residuals, respectively)

Gross photosynthesis ($P_G = Q \cdot I/(I + k) \cdot \mathrm{EV} \cdot \mathrm{ETI} \cdot T_{-5}$)

Parameter	Estimate	ASE	Wald confidence interval, 95%	
			Lower	Upper
Q	0.16	0.0037	0.15	0.16
k	249.01	18.06	213.52	284.49
r^2 adj. (%)	89.0			
df_{reg}, df_{res}	2,494			

rewetted and control sites were used but EV cover was set to be zero or 70%, the latter being assumed to represent a fully closed surface layer vegetation.

The simulation for the calibration period 1994 showed that even quite small differences in water level affected the seasonal CO_2 balance. In the bare peat surface stage, seasonal estimated CO_2 balance for the driest conditions with a mean water table level of −39 cm was about 30 g CO_2-C m^{-2} deeper than for the moistest situation with a mean water level of −30 cm (Fig. 8b). In the *Eriophorum* vegetation the difference between the driest and the moistest conditions was even larger, reaching 51 g CO_2-C m^{-2} (Fig. 8c).

The simulation showed that by raising the water level moderately the CO_2 emission from bare peat surfaces was lowered by about 30%, and by raising the water level to or above the peat surface CO_2 emission was reduced by over 50%. Therefore the simulated seasonal CO_2 balance for the bare peat surface with moderate rise of water level was almost 1.5 times higher than for the drier conditions of the control site, and with high rise of the water level it was over twice as high (Fig. 8b).

The simulation for cut-away peatland with closed vegetation of *Eriophorum* showed that when the water table is low the seasonal CO_2 balance of the ecosystem can reach the compensation point ($P_G = R_{TOT}$), but only if weather conditions are favourable (Fig. 8c). At the rewetted site the simulated seasonal CO_2 balance was positive in each year 1995–1997. When the water table was high the CO_2 balance was 2–3 times higher than when it was moderate (Fig. 8c).

Discussion

The relationship between gross photosynthesis and biotic and abiotic factors

Because the single species *E. vaginatum* dominated at the study site, the dependence of the P_G rate on abiotic factors included only relations that affected this one species. Rewetting had no direct effect on P_G. This was as expected because *Eriophorum* is a deep-rooting species (Bliss 1956) and therefore it can transfer water from deeper soil layers and keep its stomata open even during periods of low water level. However, rewetting indirectly increased P_G by promoting an increase in the cover of *Eriophorum* tussocks and seedlings. This is in accordance with previous findings that growth of *E. vaginatum* is improved in flooded soils by increased tillering (Gebauer et al. 1995).

The seasonal variation in the activity of *Eriophorum* is a consequence of the sequential leaf development characteristic of this species (Robertson and Woolhouse 1984; Jonasson and Chapin 1985; Defoliart et al. 1988). The growth of leaves formed late in the previous season continues early in the spring, and simultaneous initiation of the first cohort of new leaves enables *Eriophorum* to develop near maximal potential for photosynthesis early in the season. This potential is maintained throughout most of the season because new leaves with high photosynthetic capacity gradually replace the overwintered leaves with decreased capacity (Robertson and Woolhouse 1984; Defoliart et al. 1988). The effective temperature sum index (ETI), which was used in the model to explain the seasonal variation in the photosynthetic capacity of *Eriophorum*, rapidly increased at the beginning of the season and reached its highest values in August, when also maximal P_G was reached in most years (Figs. 6, 7a). The moderate decrease in ETI at the end

Table 4 Estimated parameter values for models used to reconstruct total respiration (R_{TOT})

Respiration ($\ln R_{TOT} = b0 + b1 \cdot \mathrm{EV} + b2 \cdot T_{-5} + b3 \cdot \mathrm{WT} + b4 \cdot \mathrm{ETI} + b5 \cdot \mathrm{EV} \times \mathrm{WT}$)

	Parameter	Estimate	SD	P
	$b0$	2.70	0.12	< 0.01
EV	$b1$	0.018	0.00055	< 0.01
T_{-5}	$b2$	0.095	0.0038	< 0.01
WT	$b3$	−0.021	0.0015	< 0.01
ETI	$b4$	0.053	0.013	< 0.01
EV × WT	$b5$	0.00012	0.00002	< 0.01
r^2 adj. (%)	84.1			
df_{reg}, df_{res}	5, 412			

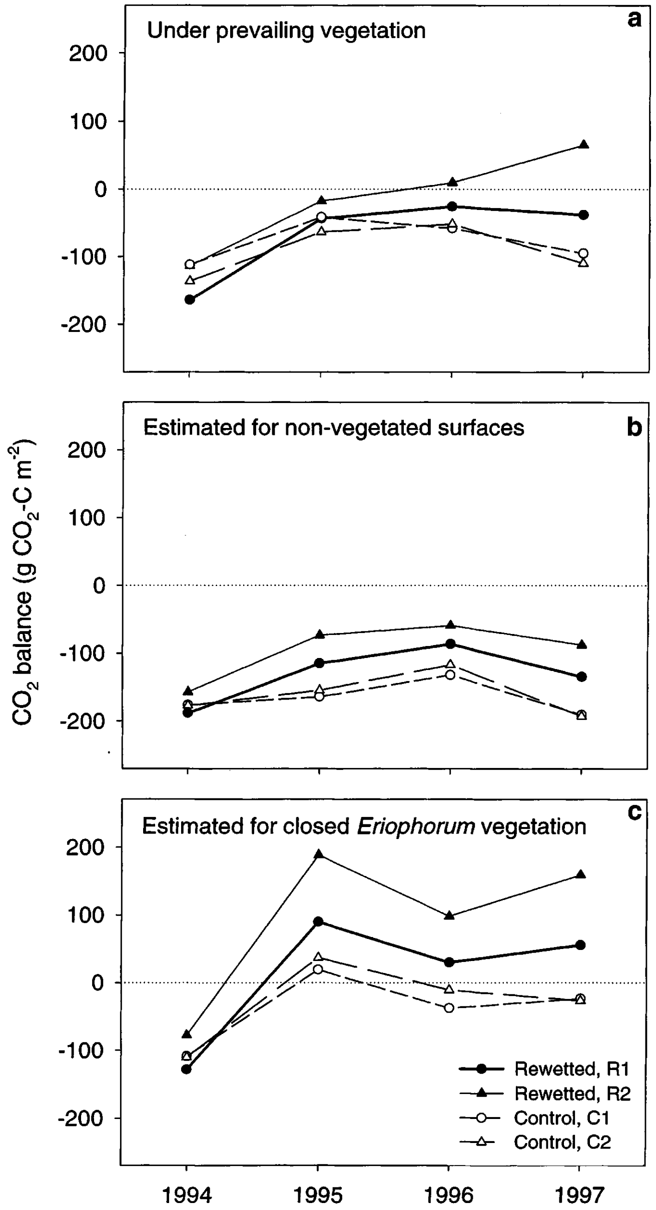

Fig. 8 Development of CO_2 balance from 1994 to 1997 at upper (R1, C1) and lower sections (R2, C2) of rewetted and control sites for **a** prevailing vegetation, and estimated for **b** non-vegetated peat surfaces and **c** closed *Eriophorum* vegetation (EV 70%) using environmental data from R1, R2, C1, and C2 during 1994–1997. Year 1994 was a calibration period

of the season was closely mirrored by the decrease in P_G which was caused mostly by lowered irradiation and temperature. This was in accordance with seasonal patterns found in other peatland ecosystems (Bubier et al. 1998).

In our study P_G did not show saturation to irradiation in the measured range of PAR (Fig. 4). This seems realistic with respect to tussocks: in general, the upper leaves shade the lower ones and the saturation level is probably never reached. This is in contrast to the results of Limbach et al. (1982), who measured light saturation at 780 mol m^{-2} s^{-1} for *E. vaginatum* ssp. *spissum* tussocks in Alaska. However, this may be a result of differences in growth conditions or genotypic differences between subspecies (Johansson and Tieszen 1976; Robertson and Woolhouse 1984).

The relationship between respiration and biotic and abiotic factors

In intertussocks total respiration mainly consists of CO_2 released by aerobic decay of peat, but in *Eriophorum* tussocks it also includes dark respiration of plants and oxidation of dead plant material and root exudates. Comparison of intertussocks and tussocks suggests that most of the total respiration of tussocks is derived from recently fixed carbon. During the calibration period and in the control site the R_{TOT} in intertussocks was about 30% of that in tussocks, but in the rewetted site only 20%. The importance of new photosynthates in the carbon dynamics of peatlands has been emphasized in recent studies (Charman et al. 1994; Saarinen 1996; Komulainen et al. 1999). In cut-away peatland, where peat is up to thousands of years old and easily decomposable carbon compounds have already been used by microbes (Hogg et al. 1992), the decay rate of peat is slow and new carbon seems to be even more important than in other peatland ecosystems. Because the study site is a mosaic of almost non-vegetated intertussocks and *Eriophorum* tussocks, *Eriophorum* cover during the colonization period is the key factor in the total respiration of the ecosystem.

Our results for cut-away peatland indicate that water table level regulates peat oxidation. This is in accordance with results for various peatland ecosystems (Billings et al. 1982; Silvola et al. 1985, 1996; Moore and Knowles 1989; Freeman et al. 1993; Glenn et al. 1993; Moore and Dalva 1993; Funk et al. 1994; Martikainen et al. 1995). Rewetting lowered R_{TOT} rate in intertussocks, but not in tussocks (Fig. 3). Therefore it appears that respiration in *Eriophorum* tussocks is not directly influenced by water level: roots under water receive oxygen from leaves through aerenchyma. However, high water level can lower respiration derived from plants by decreasing the oxidation rate of root exudates and dead plant material. Interaction between *Eriophorum* cover and water table level was included in the R_{TOT} model to describe this effect. A similar interaction between *Eriphorum* and water regime was found by Johnson et al. (1996), who found that the respiration rate in tussock microhabitats was less affected by water regime than that of moss-dominated intertussocks.

ETI was used in the R_{TOT} model to explain the seasonal dynamics of *Eriophorum* and microbial population activity. R_{TOT} increased towards mid-season and decreased slightly towards the end of the season (Fig. 6), as has also been found for the biomass of leaves and roots of *Eriophorum* (Bliss 1956; Chapin et al. 1979;

Shaver et al. 1986; Kummerow et al. 1988). Similarly the bacterial biomass is known to increase early in the season but decrease relatively late towards the end of the season (Clarholm and Rosswall 1980). Without ETI, the model underestimated the R_{TOT} rate in the middle of the growing season.

Seasonal CO_2 balance

The water level during the calibration period in 1994 was deeper than during any of the 3 following years in the control area as well, and this was reflected in the very low, negative seasonal CO_2 balance (Figs. 1, 7a). Similarly, in 1994 the seasonal CO_2 balance of a pristine bog in eastern Finland was found to be negative (Alm et al. 1999). The net loss of CO_2 from our study sites was, however, over 2–3 times greater than the loss from the bog studied by Alm et al. (1999). The large annual variation of seasonal CO_2 balance at the control site (Fig. 8a) as well as the result of Alm et al. (1999) imply that the CO_2 exchange dynamics of peatlands are very sensitive to variations in environmental factors, e.g. water level and temperature, during the growing season.

The long-term annual carbon accumulation in Finnish bogs is on average 24 g C m^{-2} (Tolonen and Turunen 1996). Alm et al. (1999) estimated that the average active season P_N in the pristine bog must be at least 64–76 g CO_2-C m^{-2} in order to maintain this average accumulation. If the annual CH_4 emission, carbon leaching and winter-time R_{TOT} at a rewetted site were of the same magnitude as in the pristine bog, the rewetted site with high water level would have reached the average carbon accumulation level of Finnish bogs by the 3rd year after rewetting. It thus seems that, following successful restoration, cut-away peatlands can develop towards functioning peatland ecosystems within a reasonable time.

Restored cut-away peatland as a potential CO_2 sink

In Finland alone, which has the world's fourth largest peat harvesting area (Lappalainen 1996), the area of cut-away peatlands increases by 2000 ha annually (Selin 1996). If our simulations for bare peat surfaces are generalized to this area, the seasonal CO_2 emission without restoration can be estimated to be 2.5–3.8 Gg CO_2-C annually.

After rewetting and with dense *Eriophorum* vegetation the balance would turn positive with a net sink capacity similar to that of the pristine fen site of 108–160 g CO_2-C m^{-2} sequestered annually (Alm et al. 1997). Thus, after successful restoration the Finnish cut-away peatlands (3000 ha) would form a 1.4–3.4 Tg CO_2-C sink, and with a 2000-ha annual increase of area, the increase of the sink woud be 0.9–2.3 Tg CO_2-C $year^{-1}$. Because in boreal and temperate zones *E. vaginatum* has been found to be a typical dominant species in early succession in cut-away peatlands (Smart et al. 1989; Salonen 1992; Cooper and McCann 1995; Campeau and Rochefort 1996) due to its ability to colonize bare peat surfaces (Gardner et al. 1986), the importance of the species in the CO_2 dynamics of cut-away peatlands may be assumed to be a general phenomenon.

Acknowledgements We thank Tapio Aitolahti, Jouni Meronen and Anu Mälkönen for their assistance with the field work, Hannu Nykänen for help with gas measurements and Anu Kettunen for her valuable comments on the manuscript. Eeva-Stiina Tuittila was supported by the Finnish Cultural Foundation and Vapo Oy.

References

Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn 5:169–211

Alm J, Talanov A, Saarnio S, Silvola J, Ikkonen E, Aaltonen H, Nykänen H, Martikainen PJ (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. Oecologia 110:423–431

Alm J, Schulman L, Walden J, Nykänen H, Martikainen PJ, Silvola J (1999) Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80:161–174

Asplund D (1996) Energy use of peat. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyskä, pp 319–325

Billings WD, Luken JO, Mortensen DA, Peterson KM (1982) Arctic tundra: a source or sink for atmospheric carbon dioxide in changing environment. Oecologia 53:7–11

Billings WD, Luken JO, Mortensen DA, Peterson KM (1983) Increasing atmospheric carbon dioxide: possible effects on arctic tundra. Oecologia 58:286–289

Blankenburg J, Kuntze H (1986) Aspects of future utilization of cut over bogs in western Germany. In: International Peat Society, Socio-economic impacts of the utilization of peatlands in industry and forestry. International Peat Society, Finnish National Committee, Helsinki, pp 219–226

Bliss LC (1956) A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol Monogr 26:303–337

Bubier JL, Crill PM, Moore TR, Savage K, Varner RK (1998) Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. Global Biogeochem Cycles 12:703–714.

Campeau S, Rochefort L (1996) *Sphagnum* regeneration on bare peat surfaces: field and greenhouse experiments. J Appl Ecol 33:599–608

Chapin FS III, Van Cleve K, Chapin MC (1979) Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. J Ecol 67:169–189

Charman DJ, Aravena R, Warner BG (1994) Carbon dynamics in a forested peatland in north-eastern Ontario, Canada. J Ecol 82:55–62

Clarholm M, Rosswall T (1980) Biomass and turnover of bacteria in a forest soil and a peat. Soil Biol Biochem 12:49–57

Clymo RS (1984) The limits to peat bog growth. Philos Trans R Soc Lond B 303:605–654

Cooper A, McCann T (1995) Machine peat cutting and land use change on blanket bog in Northern Ireland. J Environ Manage 43:153–170

Curran PL, MacNaeidhe FS (1986) Weed invasion of milled-over bog. Weed Res 26:45–50

Defoliart LS, Griffith M, Chapin FS III, Jonasson S (1988) Seasonal patterns of photosynthesis and nutrient storage in *Eriophorum vaginatum* L., and arctic sedge. Funct Ecol 2:185–194

Ferland C, Rochefort L (1997) Restoration techniques for *Sphagnum*-dominated peatland. Can J Bot 75:1110–1118

Freeman C, Lock MA, Reynolds B (1993) Fluxes of CO_2, CH_4 and N_2O from a Welsh peatland following simulation of water table draw-down: potential feedback to climatic change. Biogeochemistry 19:51–60

Frilander P, Leinonen A, Alakangas E (1996) Peat production technology. In: Vasander H (ed) Peatlands in Finland. Finnish Peatland Society, Helsinki, pp 99–106

Funk DW, Pullman ER, Peterson KM, Crill P, Billings DW (1994) Influence of water table on carbon dioxide, carbon monoxide, and methane fluxes from taiga bog microcosms. Global Biogeochem Cycles 8:271–278

Gardner BL, Chapin FS III, Shaver GR (1986) Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. J Ecol 74:1–18

Gebauer RLE, Reynolds JF, Tenhunen JD (1995) Growth and allocation of the arctic sedges *Eriophorum angustifolium* and *E. vaginatum*: effects of variable soil oxygen and nutrient availability. Oecologia 104:330–339

Glenn S, Heyes A, Moore T (1993) Carbon dioxide and methane emissions from drained peatland soils, southern Quebec. Global Biogeochem Cycles 7:247–258

Grosvernier P, Matthey Y, Buttler A (1995) Microclimate and physical properties of peat: new clues to the understanding of bog restoration processes. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Proceedings of the Ecological Society Mire Symposium, Sheffield. Wiley, Chichester, pp 435–450

Heikkilä H, Lindholm T (1995) The basis of mire restoration in Finland. In: Wheeler BD, Shaw SC, Fojt WJ, Robertson RA (eds) Restoration of temperate wetlands. Wiley, Chichester, pp 549–556

Hogg EH, Lieffers VJ, Wein RW (1992) Potential carbon losses from peat profiles: effects of temperature, drought cycles and fire. Ecol Appl 2:298–306

Huopalainen M, Tuittila E-S, Laine J, Vasander H (1998) Seed and spore bank in a cut-away peatland twenty years after abandonment. Int Peat J 8:42–51

Johansson S, Tieszen LL (1976) Aboveground biomass allocation, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. Oecologia 24:159–173

Johnson LC, Shaver GR, Giblin AE, Nadelhoffer KJ, Rastetter ER, Laundre JA, Murray GL (1996) Effects of drainage and temperature on carbon balance of tussock tundra microcosms. Oecologia 108:737–748

Jonasson S, Chapin FS III (1985) Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. Oecologia 67:511–518

Kettunen A (1998) The dependence of photosynthesis and respiration rates on environmental factors in different microsites from a boreal oligotrophic pine fen. In: Sopo R (ed) The spirit of peatlands – 30 years of the International Peat Society. Proceedings of the International Peat Symposium, Jyväskylä, Finland. International Peat Society, Helsinki, pp 234–236

Komulainen V-M, Tuittila E-S, Vasander H, Laine J (1999) Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO_2 balance. J Appl Ecol, in press

Koponen T, Isoviita P, Lammes T (1977) The bryophytes of Finland, an annotated checklist. Flora Fenn 6:1–77

Kummerow J, Mills JN, Ellis BA, Kummerow A (1988) Growth dynamics of cotton-grass (*Eriophorum vaginatum*). Can J Bot 66:253–256

Lappalainen E (1996) Global peat resources. International Peat Society, Jyskä

Lavoie C, Rochefort L (1996) The natural revegetation of a harvested peatland in southern Quebec: a spatial and dendroecological analysis. Ecoscience 3:101–111

Limbach WE, Oechel WC, Lowell W (1982) Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. Holarct Ecol 5:150–157

Martikainen PJ, Nykänen H, Crill P, Silvola J (1992) The effect of changing water table on methane fluxes at two Finnish mire sites. Suo 43:237–240

Martikainen PJ, Nykänen H, Alm J, Silvola J (1995) Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophy. Plant Soil 168–169:571–577

Meade R (1992) Some early changes following the rewetting of a vegetated cut-over peatland surface at Danes Moss, Cheshire, UK, and their relevance to conservation management. Biol Conserv 61:31–40

Moore DM (1982) Flora Europaea check-list and chromosome index. Cambridge University Press, Cambridge

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J Soil Sci 44:651–664

Moore TR, Knowles R (1989) The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Can J Soil Sci 69:33–38

Nykänen H, Alm J, Lång K, Silvola J, Martikainen PJ (1995) Emissions of CH_4, N_2O and CO_2 from a virgin fen and a fen drained for grassland in Finland. J Biogeogr 22:351–357

Nyrönen T (1996) Peat production. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyskä, pp 315–318

Peterson KM, Billings WD, Reynolds DN (1984) Influence of water table and atmospheric CO_2 concentration on the carbon balance of arctic tundra. Arct Alp Res 16:331–335

Poole DK, Miller PC (1982) Carbon dioxide flux from three arctic tundra types in north-central Alaska, U.S.A. Arct Alp Res 14:27–32

Robertson KP, Woolhouse HW (1984) Studies of the seasonal course of carbon uptake of *Eriophorum vaginatum* in a moorland habitat. II. The seasonal course of photosynthesis. J Ecol 72:685–700

Roderfeld H, Kuntze H, Schwaar J (1993) Vegetationsversuche mit Bunkerde – ein Beitrag zur Wiederbesiedlung teilabgetorfter Hochmoore mit hochmooretypischen Pflanzen (Vegetation trials on top-spits – a study concerning the revegetation of cutover raised bogs with typical mire plants). Telma 23:163–180

Roderfeld H, Vasander H, Tuittila E-S (1996) Ein abgetorftes Hochmoor im Regenerationsstadium im südlichen Finnland (A cut-over bog in the stage of regeneration in southern Finland). Telma 26:223–235

Rubec C (1996) The status of peatland resources in Canada. In: Lappalainen E (ed) Global peat resources. International Peat Society, Jyskä, pp 243–252

Ruuhijärvi R (1982) Mire complex types in Finland. In: Laine J (ed) Peatlands and their utilization in Finland. Finnish Peatland Society, Helsinki, pp 24–28

Saarinen T (1996) Biomass and production of two vascular plants in a boreal mesotrophic fen. Can J Bot 74:934–938

Salonen V (1987) Relationship between seed rain and establishment of vegetation in two areas abandoned after peat harvesting. Holarct Ecol 10:171–174

Salonen V (1992) Plant colonization of harvested peat surfaces. Biol Res Rep Univ Jyväskylä 29:1–29

Salonen V, Laaksonen M (1994) Effects of fertilization, liming, watering and tillage on plant colonization of bare peat surfaces. Ann Bot Fenn 31:29–36

Schouwenaars JM (1993) Hydrological differences between bogs and bog-relicts and consequences for bog restoration. Hydrobiologia 265:217–224

Selin P (1996) Many uses for peatland cut-away areas. In: Vasander H (ed) Peatlands in Finland. Finnish Peatland Society, Helsinki, pp 128–129

Shaver GR, Chapin F III, Gardner BL (1986) Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. J Ecol 74:257–278

Silvola J, Alm J (1992) Dynamics of greenhouse gases in virgin and managed peatlands. In: Kanninen M, Anttila P (eds) The Finnish research programme on climate change. Progress report. The Academy of Finland, Helsinki, pp 193–198

Silvola J, Välijoki J, Aaltonen H (1985) Effect of draining and fertilization on soil respiration at three ameliorated peatland sites. Acta For Fenn 191:1–32

Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996) CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J Ecol 84:219–228

Smart PJ, Wheeler BD, Willis AJ (1989) Revegetation of peat excavations in a derelict raised bog. New Phytol 111:733–748

SYSTAT (1996) Systat 6.0 for Windows: statistics. SPSS, Chicago

Tolonen K, Turunen J (1996) Accumulation of carbon in mires of Finland and implications for climatic change. Holocene 6:41–48

Tuittila E-S, Komulainen V-M (1995) Vegetation and CO_2 balance in an abandoned harvested peatland in Aitoneva, southern Finland. Suo 46:69–80

Wheeler BD, Shaw SC (1995) Restoration of damaged peatlands with particular reference to lowland raised bogs affected by peat extraction. University of Sheffield and Department of the Environment, London