

## Carbon gas exchange of a re-vegetated cut-away peatland five decades after abandonment

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Received 23 Jan. 2007, accepted 16 Mar. 2007 (Editor in charge of this article: Raija Laiho)

Yli-Petäys, M., Laine, J., Vasander, H. & Tuittila, E.-S. 2007: Carbon gas exchange of a re-vegetated cut-away peatland five decades after abandonment. *Boreal Env. Res.* 12: 177–190.

Only little is known about the long-term carbon dynamics related to peatland restoration. We studied CO<sub>2</sub> and CH<sub>4</sub> dynamics of spontaneously regenerated peat trenches five decades after peat harvesting had ceased. We used non-linear regression models and interpolation for simulating gas exchange of four regenerating plant communities during two growing seasons and one winter. The studied communities all acted as seasonal (June–September) sinks of CO<sub>2</sub> between 14 and 118 g C m<sup>-2</sup>, while the emissions of CH<sub>4</sub> ranged from –4.9 to –28.8 g C m<sup>-2</sup>. When the winter time losses of carbon and the estimated leaching were subtracted, the balance was very low or negative: between –67 and 31 g C m<sup>-2</sup>. The low or even negative annual carbon balance in all communities may suggest a decrease in carbon sink strength in the advanced regeneration after the previously observed strong sink in the first regeneration stages caused by mass colonization by *Eriophorum*.

### Introduction

Industrial peat harvesting either for horticultural or energy purposes is common throughout Europe and North America. In Finland, which currently is the largest peat producer in the world, peat is harvested over 56 000 hectares. Most of the harvested peat is used as fuel and approximately 6%–7% of the total energy consumption comes from peat (Sopo and Aalto 1996).

The impacts of peat harvesting on the peatland ecosystems are drastic. Living vegetation is removed during the harvesting and the hydrology of the peatland is completely altered. After cessation of peat harvesting the remaining cut-away surfaces are net sources of carbon to the atmosphere as the residual peat gradually

decomposes (Nykänen *et al.* 1996, Tuittila *et al.* 1999, Waddington *et al.* 2002). Thus, there is increased pressure to restore hydrological conditions favourable to the re-establishment of peatland vegetation which, according to Tuittila *et al.* (1999) and Bortoluzzi *et al.* (2006), can lead to rapid restoration of the sink function typical of pristine peatlands. However, restoring only the hydrology of the peatland is not always sufficient. The lack of seed bank delays peatland plant colonization from surrounding areas (Salonen 1987, Huopalainen *et al.* 1998, Campbell *et al.* 2003). More, the environmental conditions of a cut-away peatland are severe for plant establishment. Water table and temperature fluctuations may be very high (Schouwenaars 1993, van Seters and Price 2002), impeding mire

plant colonization (Salonen 1987).

The aim of restoration is to promote peatland vegetation establishment by altering factors hindering plant colonization and survival. There are examples of successful restoration of cut-away peatlands both in Europe and North America. In North America, diaspore introduction and mulching of vacuum harvested sites is a widely used method in the restoration of cut-away peatlands. This, combined with blocking of the drainage system, accelerates *Sphagnum* establishment (Rochefort *et al.* 2003). However, mulching appears to increase carbon loss from the ecosystem thus impeding recovery of the carbon sink function (Waddington *et al.* 2003). In Europe, restoration measures are often limited to hydrological management, while sowing or planting diaspores is rarely included. Salonen *et al.* (1992), Tuittila *et al.* (2000a) and Lavoie *et al.* (2005) noted that in suitable moisture conditions *Eriophorum vaginatum* or *Carex rostrata* rapidly colonize cut-away fields. Additionally, Tuittila *et al.* (1999) found that following mass colonization of *Eriophorum vaginatum*, a wet restored cut-away peatland in Finland very soon started acting as a sink for atmospheric CO<sub>2</sub>. On the other hand, sedge species, particularly *Eriophorum* species are often linked to high emissions of CH<sub>4</sub> from wetlands (e.g. Thomas *et al.* 1996, Greenup *et al.* 2000, Vasander and Kettunen 2006). Tuittila *et al.* (2000b) observed that following the colonization of *Eriophorum*, CH<sub>4</sub> emissions rose but stayed at lower levels than in pristine mires, and the CO<sub>2</sub> sink was large enough to compensate for the losses of carbon in CH<sub>4</sub>. In a similar Canadian study the carbon balance in patches of *Eriophorum* was very close to zero (Marinier *et al.* 2004), which may partly result from lower water tables as compared with those of the Finnish site. Both of the previously mentioned studies dealt with the carbon dynamics in the early plant colonization stage and the effects of rewetting during the following decades remained unknown.

Some implications of the carbon balance in later successional stages can be obtained by studying spontaneously regenerated peat cuttings/trenches such as Thorne Waste in England (Smart *et al.* 1989), Rivière-du-Loup and Shipagan peatlands in Canada (Robert *et al.* 1999) and Stormossen in Sweden (Soro *et al.* 1999).

Such sites are suitable for studying the development of carbon balance during the early decades after rewetting. Roderfeld *et al.* (1996) studied the biomass accumulation in such trenches in Isosuo, Finland, and found that it corresponded with that of geologically young pristine mires of western Finland (Tolonen and Turunen 1996). However, the results of Roderfeld *et al.* (1996) represented only the average accumulation after abandonment and it could not be quantified whether the regenerating peatland was presently acting as a sink or a source. Bortoluzzi *et al.* (2006) and E. Samaritani (unpubl. data) used the chamber method to study the CO<sub>2</sub> and CH<sub>4</sub> dynamics of regenerating peatlands in French and Swiss Jura Mountains. At both locations, the advanced regeneration stages were fairly large sinks of atmospheric carbon. Their results are very promising for ecologists and land managers but more research is still needed to clarify the long-term successional trend at restored sites.

The aim of this study was to determine whether the CO<sub>2</sub> and CH<sub>4</sub> dynamics of spontaneously regenerated peat trenches with closed *Sphagnum* carpets resemble those of pristine mires. In order to functionally resemble pristine mires with a long term sink function, the sequestration of new carbon into the system needs to compensate for the losses from the new organic matter and the residual peat layers. We carried out net CO<sub>2</sub> and CH<sub>4</sub> exchange measurements in field conditions over two different growing seasons and one winter in 2000 and 2001. We related gross photosynthesis and ecosystem respiration to environmental factors to achieve estimates for seasonal net CO<sub>2</sub> exchange. The emissions of CH<sub>4</sub> and CO<sub>2</sub> outside the growing season were estimated by interpolation.

## Materials and methods

### Study site

The study was carried out in a cut-away peatland, Aitoneva, in Kihniö, central Finland (62°12'N, 23°18'E). The study site, which is one of the European RECIPE sites (Chapman *et al.* 2003), lies in the transitional zone between southern-boreal and middle-boreal coniferous

forest zones. The long-term annual mean temperature is 3.5 °C and annual mean precipitation is approximately 700 mm. The average growing season is 160 days and the accumulative temperature sum (+5 °C) is 1100 degree-days.

The peat deposits of Aitoneva were surveyed in 1942. Originally the site had been a treeless bog with an average peat depth of 2.9 m. In the mire centre the highest peat depth was 6.6 m (Stén and Toivonen 1990). Unfortunately, no data on the original mire vegetation is available. Peat harvesting in the area started soon after the survey in 1942. The harvesting method used was block-cutting, which created several 3 to 4 metre deep trenches, surrounded by ca. 5-metre-wide dry baulks of peat. The harvesting method was rather uneconomical since large amounts of peat were left in the baulks; at the study site the harvesting was ceased in 1948. The drainage system was fairly inefficient and the trenches started to regenerate spontaneously soon after the harvesting had ceased.

At the time of this study, the microtopography of the trenches was fairly even and the vegetation consisted mainly of hollow and lawn vegetation. *Carex lasiocarpa*, *C. rostrata* and *Eriophorum vaginatum* were the dominant vascular plants in the field layer. In the bottom layer, *Sphagnum pulchrum* and, to a lesser extent, *S. lindbergii* dominated the hollows and *S. papillosum* and *S. riparium* the lawns.

## Sampling

We chose five regenerated trenches from the study site for further investigation. The trenches differed slightly regarding the time since the abandonment or regarding their vegetation composition. However, the exact time of the abandonment of each trench could not be ascertained. For vegetation and gas monitoring, we placed three sample plots in each trench in May 2000. We laid out the sample plots as a transect from the trench centre to its margin in each of the trenches in order to cover the variation of the vegetation in the study site.

For gas exchange measurements, all the sample plots were surrounded by 60 × 60 cm aluminium collars, which we inserted in the peat

to a depth of 30 cm. To avoid disturbance during the field work, boardwalks were built around the sample plots. Each sample plot was equipped with a dip well to allow repeated water table measurements.

We determined instantaneous CO<sub>2</sub> exchange rates in the plots using the transparent closed chamber method described in Alm *et al.* (2007). For measuring CO<sub>2</sub> concentration in the air-sealed chamber, we used an infrared gas analyzer (PP Systems, EGM-2) for a two or three minute period in 15 second intervals. To establish variation in the irradiation levels, we repeated measurements under artificially shaded conditions after a measuring period in full light. Shades made of thin mosquito net were placed on a rack standing approximately 50 cm above the chamber. Finally, to get an estimate of the instantaneous ecosystem respiration rate ( $R_E$ ) of the sample plot, we carried out the measurement with the chamber covered with an opaque hood. The temperature inside the chamber and photosynthetically active radiation (PPFD) were recorded during the measurements. During the winter, we measured  $R_E$  under the snow using aluminium chambers, which we inserted randomly in places where the snow was cleared away before the measurement. Since winter CO<sub>2</sub> fluxes are very low and the cold conditions would have caused problems for the use of the gas analyzer, we took a series of samples in syringes from the chamber headspace at 5, 15, 25 and 35 minute intervals. The CO<sub>2</sub> concentrations in the syringes were then analyzed in the laboratory using the EGM-2 gas analyzer.

We started growing season CO<sub>2</sub> flux measurements in the beginning of June 2000 and May 2001. Measurements were continued until late September 2000 and late August 2001 and we carried them out in two to three week intervals. During the winter 2001 three measurement campaigns were carried out in late January and at the beginning and end of March.

Three CH<sub>4</sub> flux measurement campaigns during the growing season in 2000 and four in 2001 were conducted at the study site using static chambers. During the winter, concentrations of CH<sub>4</sub> were also determined from the same field samples that we used for determining the CO<sub>2</sub> fluxes. All the analyses were made using a gas chromatograph equipped with a FI detector.

We calculated carbon gas flux rates from the linear change of gas concentrations as a function of time (Alm *et al.* 2007). Similarly to Alm *et al.* (2007), we follow the sign convention used traditionally by ecosystem ecologists, which differs from the common conventions recently suggested by Chapin *et al.* (2006). For the net ecosystem exchange of CO<sub>2</sub> (NEE) and CH<sub>4</sub>, we use positive values when the ecosystem is gaining carbon from the atmosphere and negative when the ecosystem is losing.

Simultaneously with the gas exchange measurements, we recorded manually peat temperature at 5, 10 and 20 cm depths and the water table depth. An automated micrometeorological station was placed in the study area measuring solar irradiance (PPFD), temperatures at 5, 10 and 20 cm depths and precipitation.

We recorded the projection cover (%) of each plant species in the sample plots at the end of July or at the beginning of August during the study years. Additionally, the vascular plant green area (Wilson *et al.* 2007) in the sample plots was determined. In 2000, we counted the number of leaves for each species at the end of June, July and September. We recorded the leaf length and width of five randomly chosen individuals of each species at two to three week intervals.

In 2001, we estimated the number of vascular plants' leaves in the sample plots using five 8 × 8-cm subplots which were located in each corner and at the centre of the sample plots. We counted the number of leaves in subplots monthly from June to August. We identified the species dominating in the subplots and measured the growth biometry of three randomly selected and marked individuals outside the sample plots at two week intervals. The average leaf size dynamics of non-dominating species we obtained from previous year's data and from literature (Hämet-Ahti *et al.* 1998).

## Data analyses

### Spatial variation in vegetation and hydrology

To link the variation in CO<sub>2</sub> fluxes to spatial variation in plant communities and their hydrological

conditions we grouped sample plots in two steps. Firstly, we classified sample plots according to their plant-species composition. A cluster analysis using the Bray-Curtis similarity measure was performed with the PAST package (Hammer and Harper 2002). Secondly, we formed a constrained ordination (Canonical Correspondence Analysis, CCA) using the vegetation classes obtained from the cluster analysis and water table variables as explaining variables (ter Braak and Šmilauer 2002). We selected CCA, which fits unimodal response of species to constrained axes, since the variation in the vegetation data was rather large (3.9 SD units, based on DCA using Hill's scaling and detrending by segments). We included three groups representing the extreme ends of the cluster analysis as dummy variables. For the water-level variables we chose the ones that best explained variation in the vegetation, namely minimum water table and the third quartile of the water level range. After including these two, none of the other water table variables improved the model. The resulting CCA ordination showed four groups of sample plots, namely Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*), that we named after their dominant *Sphagnum* species and used for presenting the variation in CO<sub>2</sub> fluxes.

### Vascular Green Area (VGA) index

We calculated the green area of each vascular plant species (VGA) in the sample plots as the product of leaf size and number of leaves. We used a rectangular shape to describe the leaf area. Since the measurements in 2000 were started quite late in the season, the green area at the beginning of the season was estimated by comparing the green area ratio of the sample plots during the high season of both study years. Then, we estimated the VGA in the early season of 2000 on the basis of this ratio assuming that it stayed constant throughout the growing season.

To model the seasonal development of the VGA in the sample plots, we fitted a log normal curve between measured VGA and day number of both study years (Wilson *et al.* 2006). As a result of a short night frost period at the begin-

ning of August 2001, the leaf area in many sample plots decreased rapidly causing poor fit of any regression function. In such cases, we estimated the VGA for the rest of the season by interpolation between the remaining data.

## CO<sub>2</sub> exchange models

We used data collected from June 2000 to November 2001 in the CO<sub>2</sub> model constructions. In model construction we followed the approach and functions as presented in Tuittila *et al.* (2004).

Gross photosynthesis ( $P_G$ ) model uses a saturating response to photosynthetically active radiation (PPFD) where the maximum light saturated photosynthesis ( $P_{\text{MAX(PPFD, VGA)}}$ ) is linearly related to VGA:

$$P_G = P_{\text{MAX(PPFD, VGA)}} \times \text{PPFD} / (k + \text{PPFD}) \times (d \times \text{VGA}). \quad (1)$$

The change in the method of estimating VGA for sample plots between the two years resulted in different responses in  $P_G$  to VGA. To take this into account we applied a correction parameter  $b$  to make VGA between the years comparable.

Ecosystem respiration ( $R_E$ ) was described using the exponential relationship of respiration

to temperature inside the chamber ( $T_{\text{AIR}}$ ) and linear response to the water table (WT).

$$R_E = a \times \exp(b \times T_{\text{AIR}}) + c \times \text{WT}. \quad (2)$$

We parameterized  $P_G$  and  $R_E$  models separately for each sample plot to improve the sensitivity of the models to environmental variables (Tables 1 and 2). In Ripa 2, consisting solely of *Sphagnum* mosses, only light response was used in the  $P_G$  model. Due to only minor variations in the water table in four sample plots (PaPu 1, PaPu 2, Pulc 1 and Pulc 2), these had no detectable dependence of  $P_G$  on WT.

## Carbon balance

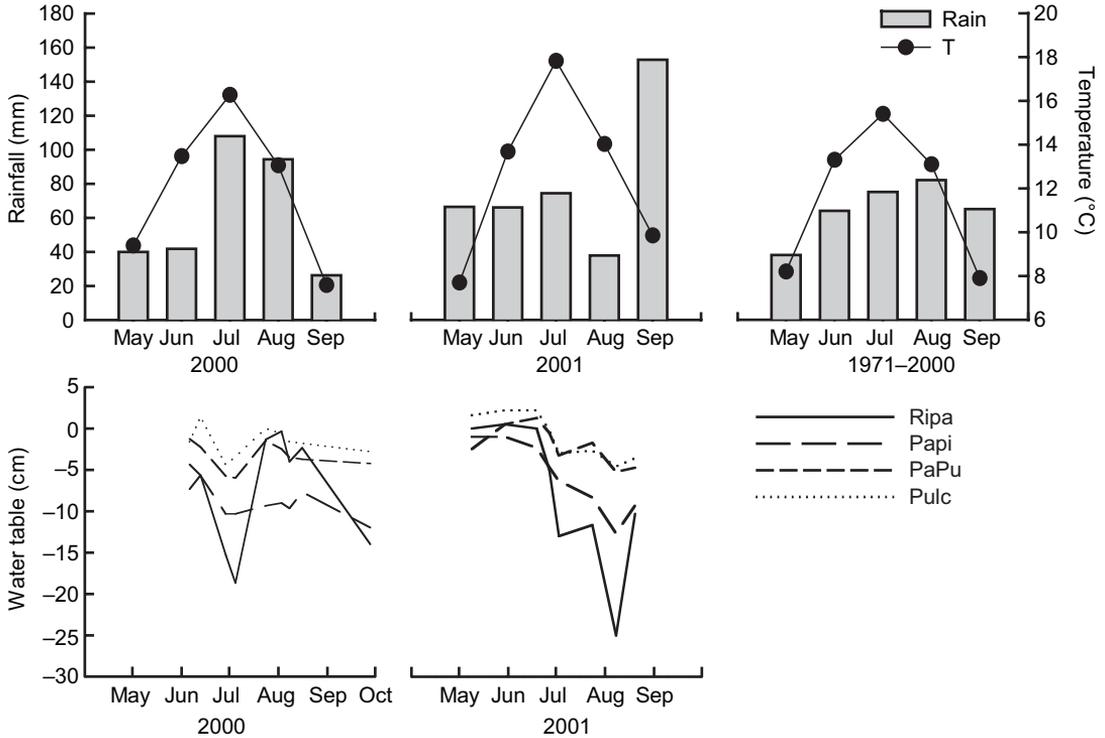
We used the plot-specific CO<sub>2</sub> model equations in reconstruction of hourly  $P_G$  and  $R_E$  for each sample plot over the two growing seasons. The equations were integrated with continuous weather data from Aitoneva from the beginning of June to the end of September. The actual growing season started earlier in May in both years but due to limited data from the early growing periods, we decided not to extrapolate the models outside the main period of measurements. We calculated NEE as the difference between  $P_G$  and  $R_E$ .

**Table 1.** Model parameters and their standard errors for  $P_G$  models for each sample plot. Ripa = *S. riparium*, Papi = *S. papillosum*, PaPu = *S. papillosum* with *S. pulchrum*, and Pulc = *S. pulchrum*.

Plot	$P_{\text{MAX}}$	$k$	$d$
Ripa1	694 ± 100	265 ± 83	–
Ripa2	1436 ± 261	251 ± 89	1.46 ± 0.15
Ripa3	16725 ± 4167	690 ± 224	0.86 ± 0.10
Papi1	935 ± 76	247 ± 53	2.50 ± 0.17
Papi2	1146 ± 108	326 ± 89	1.63 ± 0.13
Papi3	1437 ± 134	487 ± 105	1.86 ± 0.12
PaPu1	1229 ± 89	223 ± 47	1.66 ± 0.11
PaPu2	2073 ± 200	276 ± 72	1.04 ± 0.10
PaPu3	4249 ± 448	418 ± 100	0.59 ± 0.04
PaPu4	3895 ± 351	254 ± 67	0.95 ± 0.07
Pulc1	635 ± 70	366 ± 93	3.22 ± 0.29
Pulc2	708 ± 60	192 ± 51	2.90 ± 0.24
Pulc3	6839 ± 1288	218 ± 102	0.38 ± 0.07
Pulc4	3129 ± 288	362 ± 88	0.93 ± 0.08
Pulc5	3644 ± 318	312 ± 71	0.67 ± 0.05

**Table 2.** Model parameters and their standard errors for  $R_E$  models for each sample plot. Ripa = *S. riparium*, Papi = *S. papillosum*, PaPu = *S. papillosum* with *S. pulchrum*, and Pulc = *S. pulchrum*.

Plot	$a$	$b$	$c$
Ripa1	17.09 ± 18.50	0.14 ± 0.06	-7.79 ± 3.24
Ripa2	32.31 ± 24.35	0.11 ± 0.04	-10.17 ± 2.65
Ripa3	25.00 ± 12.37	0.10 ± 0.02	-8.78 ± 2.05
Papi1	34.68 ± 21.24	0.08 ± 0.02	-9.96 ± 4.76
Papi2	32.58 ± 23.77	0.09 ± 0.03	-6.47 ± 5.89
Papi3	28.81 ± 18.61	0.09 ± 0.03	-4.03 ± 4.18
PaPu1	49.05 ± 17.78	0.08 ± 0.01	–
PaPu2	12.04 ± 11.51	0.13 ± 0.04	–
PaPu3	6.59 ± 10.07	0.15 ± 0.06	-20.55 ± 10.00
PaPu4	78.11 ± 36.72	0.03 ± 0.03	-35.80 ± 7.37
Pulc1	19.55 ± 11.25	0.13 ± 0.02	–
Pulc2	45.06 ± 9.26	0.08 ± 0.01	–
Pulc3	25.77 ± 18.19	0.11 ± 0.03	9.63 ± 9.64
Pulc4	28.13 ± 12.92	0.10 ± 0.02	-11.39 ± 4.36
Pulc5	1.70 ± 1.53	0.19 ± 0.03	-18.54 ± 5.07



**Fig. 1.** Mean air temperature and monthly precipitation (top panel) and measured water table fluctuations (bottom panel) at Aitoneva from May to September in 2000, 2001 and as 30-year average. The long term data and the data for May 2000 were obtained from Ähtäri weather station 50 km northeast of the study site (Helminen *et al.* 2000–2001). Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*).

Since we only had a very limited amount of data on the  $\text{CH}_4$  emissions, model construction was not possible. Instead, we used the seasonal median values for each community separately for interpolating  $\text{CH}_4$  emissions over the growing season.

The carbon balance outside the model-estimated period between October 2000 and June 2001 was interpolated using the median values of measured NEE,  $R_E$  and  $\text{CH}_4$  flux data. For the snow-free period from October to November and in May, we used the median NEE for estimating the net  $\text{CO}_2$  exchange during daylight hours and the median  $R_E$  for estimating the respiration during the dark. For the snow-covered period from December to April, we used only the median  $R_E$ .

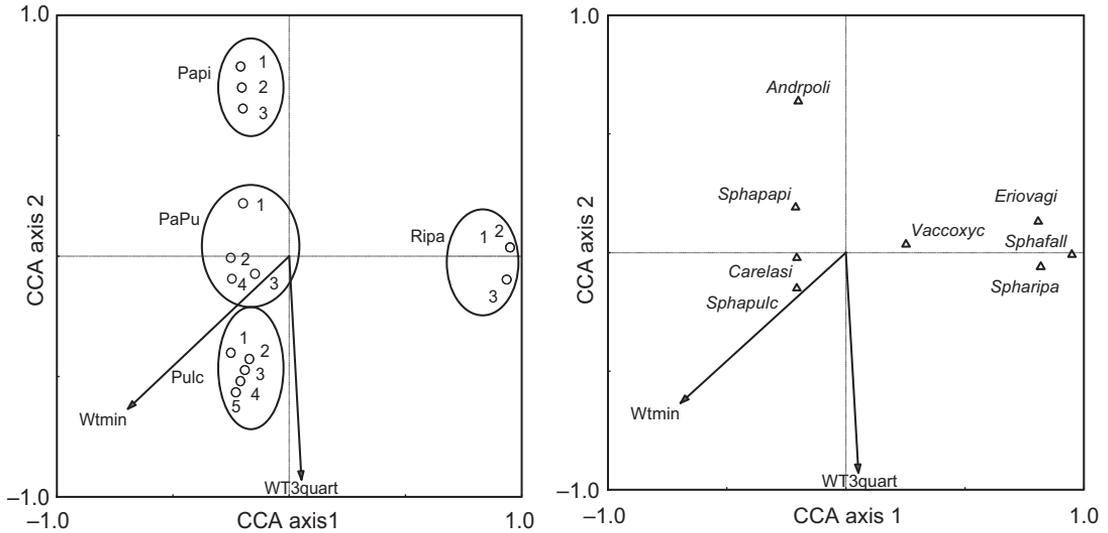
The statistical data analyses were performed using Excel 2002, SigmaPlot ver. 8.0 (SPSS Inc.), and SYSTAT 9 (SPSS Inc.) software. The Kolmogorov-Smirnov normality test was

employed for all the modeled data sets. As the data generally was not normally distributed, we used the non-parametric Kruskal-Wallis test to study differences between the selected data.

## Results

### Weather conditions during the study period

The thermal growing season started in early May in 2000 and at the end of April in 2001 (Helminen *et al.* 2000–2001). Day temperatures at the end of April and in early May in central Finland in both years were exceptionally high and reached as high as 23 °C, but also severe frosts (temperature minimum  $>-4$  °C) occurred during many nights at the beginning (2000) and at the end of May (2001). The mean summer temperatures (June–August) in Aitoneva (Fig. 1) were slightly lower



**Fig. 2.** CCA sample-environment (left-hand-side panel) and species-environment (right-hand-side panel) biplot revealing the environmental relationship of the samples and species along the axes. Ellipses were drawn around four clusters of sample plots, which were named according to their dominant *Sphagnum* species, Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*).

(13.4 °C in 2000) or higher (14.6 °C in 2001) than the long term average of 13.9 °C (1971–2000) in that area (Drebs *et al.* 2002). Similarly, cumulative precipitation (June–August) was above (244 mm in 2000) and below (178 mm in 2001) the long term average of 221 mm.

**Vegetation**

The sample plots were distributed quite clearly into four groups on the CCA axes (Fig. 2). Three sample plots dominated by *Eriophorum vaginatum* and *Sphagnum riparium* (Ripa) were separated on the first axis from the rest of the sample plots consisting of vegetation typical to poor fen communities: *Carex lasiocarpa*, *C. rostrata*, *Sphagnum papillosum* and *S. pulchrum*. The poor fen communities were oriented along a water table gradient from relatively dry (Papi) to very wet conditions (Pulc). The dominance of *S. papillosum* was replaced by *S. pulchrum* along the gradient. An intermediate community (PaPu) was found in transitional water table conditions.

The maximum vascular green area was rather low and varied between 0.24 and 1.13 m<sup>2</sup> m<sup>-2</sup> (Table 3). The variation of VGA among the communities was rather similar in both years,

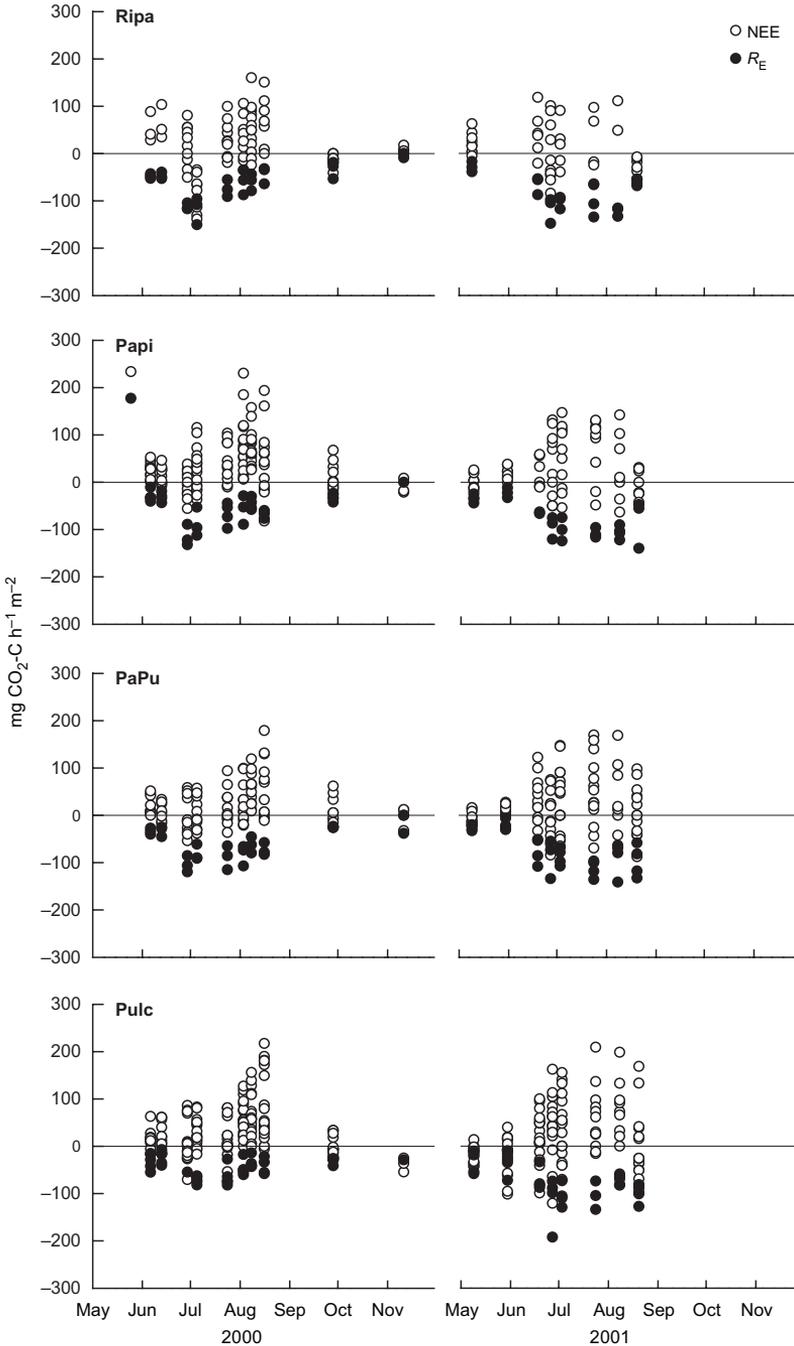
but generally VGA showed to be higher in 2001 in all the communities (*p* = 0.059) although the difference between the two years was not significant.

**CO<sub>2</sub> balance**

The mean measured NEE for Ripa, Papi, PaPu and Pulc was 18, 26, 30 and 31 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-2</sup>, and *R<sub>E</sub>* in the dark 70, 67, 64 and 63 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-2</sup>, respectively (Fig. 3). Both fluxes were generally higher in 2001.

**Table 3.** Simulated average maximum green area (VGA, m<sup>2</sup> m<sup>-2</sup>) and its SD, of vascular plant species in the four different plant communities in 2000 and 2001. Ripa = *S. riparium*, Papi = *S. papillosum*, PaPu = *S. papillosum* with *S. pulchrum*, and Pulc = *S. pulchrum*.

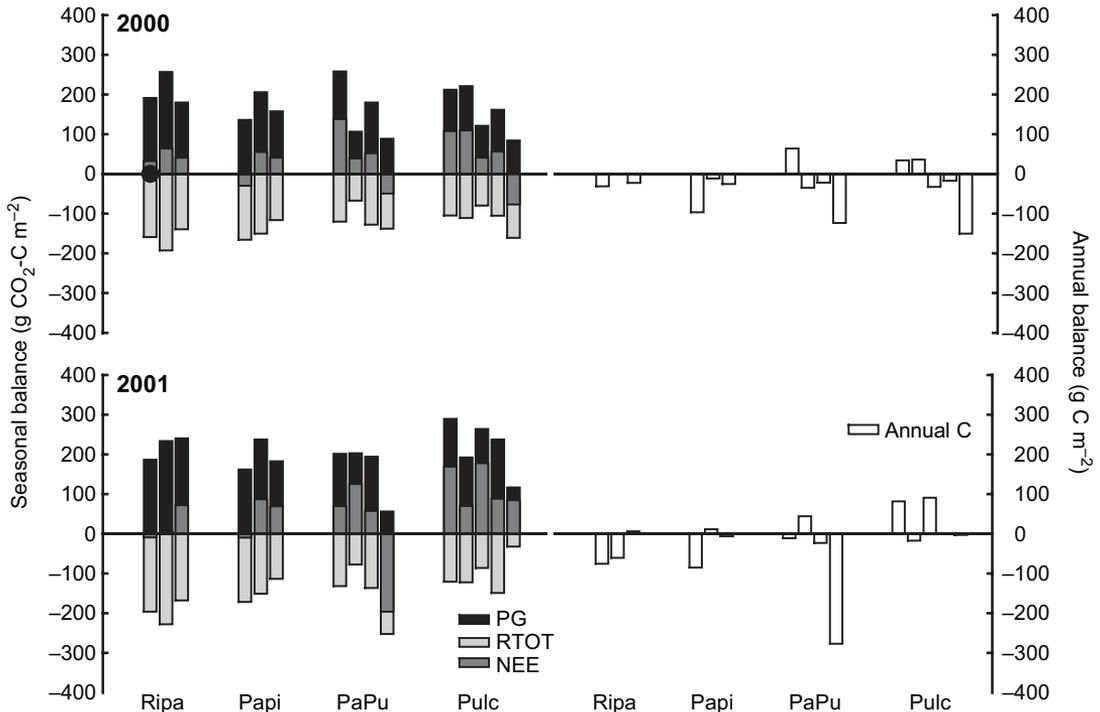
	2000		2001	
	Mean	SD	Mean	SD
Ripa	0.25	0.26	0.81	0.65
Papi	0.37	0.14	1.05	0.16
PaPu	0.33	0.15	0.57	0.33
Pulc	0.34	0.16	1.14	1.22



**Fig. 3.** Measured instantaneous net  $\text{CO}_2$  exchange ( $\text{NEE}$  and  $R_E$ ) of the studied communities in 2000 and 2001, Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*).

On average, all the four communities showed a positive seasonal net balance based on reconstructions with models and weather data, i.e. they were acting as sinks for  $\text{CO}_2$  (Fig. 4). The wettest community Pulc (Fig. 2) was the most productive. The reconstructed mean net balances for PaPu, Ripa, Papi, and Pulc were

30, 34, 36, and 83  $\text{g CO}_2\text{-C m}^{-2}$ , respectively. All the communities showed rather large differences between the two years, but neither year was more favorable for all the communities. The two communities Ripa and PaPu with lowest net production had higher mean seasonal net balance in 2000, (46 and 23, 45 and 14  $\text{g CO}_2\text{-C m}^{-2}$ , in



**Fig. 4.** Simulated seasonal  $\text{CO}_2\text{-C}$  exchange (left-hand-side axes) and the estimated annual carbon balance (right-hand-side axes) of the studied communities in 2000 and 2001, Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*).

2000 and 2001 respectively) while summer 2001 was more favorable for the other two (Papi: 22 and 49, Pulc: 47 and 118  $\text{g CO}_2\text{-C m}^{-2}$  in 2000 and 2001, respectively). There was no clear trend in seasonal gross photosynthesis between communities and the significant differences in ecosystem respiration ( $p = 0.007$ ) were thus responsible for the differences in the seasonal net balances. On average, seasonal  $R_E$  estimated for Ripa, Papi, PaPu and Pulc was 180, 145, 131 and 107  $\text{g CO}_2\text{-C m}^{-2}$ , the Ripa with unstable water levels having the highest and the continuously wettest Pulc having the lowest respiration.

The estimated  $\text{CO}_2$  emission for the period from October to May in all plots was 44  $\text{g C m}^{-2}$ . When this was subtracted from the estimated growing season balance in 2000, the communities Ripa, PaPu and Pulc became very small sinks of 1–3  $\text{g CO}_2\text{-C m}^{-2}$  and Papi a small source of 22  $\text{g CO}_2\text{-C m}^{-2}$  during the whole year period. In 2001, using the same estimate for the winter fluxes, Ripa and PaPu acted as sources of 21 and 30  $\text{g CO}_2\text{-C m}^{-2}$  and Papi and Pulc as sinks of 5 and 74  $\text{g CO}_2\text{-C m}^{-2}$ , respectively (Table 4).

### $\text{CH}_4$ balance

In contrast to the  $\text{CO}_2$  balance,  $\text{CH}_4$  emissions varied significantly between the communities ( $p < 0.001$ ) and growing seasons ( $p = 0.011$ ) (Table 5). The estimated seasonal fluxes ranged from 4.9  $\text{g CH}_4\text{-C m}^{-2}$  in Ripa to 28.8  $\text{g CH}_4\text{-C m}^{-2}$  in Pulc (Table 4). The median  $\text{CH}_4$  fluxes in November 2000 and May 2001 were 50 and 70  $\text{mg CH}_4\text{-C m}^{-2} \text{d}^{-1}$ , and 3.5  $\text{mg CH}_4\text{-C m}^{-2} \text{d}^{-1}$  in the middle of the winter. Our estimation for the  $\text{CH}_4$  emission from October to May was 6.4  $\text{g CH}_4\text{-C m}^{-2}$ .

## Discussion

### Vegetation

The variation in vegetation was significantly related to the water table gradient (Fig. 2), also characteristic of pristine peatlands. The poor fen vegetation found in Aitoneva is rather atypical to the eccentric bogs of the region (Stén

**Table 4.** Components of the annual carbon budget (g C m<sup>-2</sup>) ± SD in four communities in 2000 and 2001, Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*). Seasonal balances are marked with s and wintertime balances with w. Leaching (L) was derived from Sallantaus (1992).

	2000				2001			
	Ripa	Papi	Papu	Pulc	Ripa	Papi	Papu	Pulc
NEEs	46 ± 16	22 ± 46	45 ± 77	48 ± 76	23 ± 43	49 ± 51	14 ± 143	118 ± 51
R <sub>E,w</sub>	-44	-44	-44	-44	-44	-44	-44	-44
CH <sub>4,s</sub>	-4.9 ± 2.6	-11.1 ± 4.8	-18.0 ± 10.6	-23.7 ± 15.4	-10.4 ± 8.7	-20.1 ± 11.3	-23.2 ± 14.4	-31.4 ± 21.1
CH <sub>4,w</sub>	-6.4	-6.4	-6.4	-6.4	-6.4	-6.4	-6.4	-6.4
L	-8	-8	-8	-8	-8	-8	-8	-8
Total	-18 ± 16	-44 ± 46	-29 ± 77	-26 ± 76	-43 ± 43	-27 ± 51	-67 ± 143	31 ± 5

and Toivonen 1990) but having rather a species composition more distinctive to northern aapa mires. *Sphagnum riparium* and *S. papillosum* in the driest microsites or microsites with an unstable water table and *S. pulchrum* dominating the wettest microsites, often accompanied by *S. lindbergii*, (Fig. 2) are common to the northern fens in Finland (Ruuhijärvi 1960). Quite similar to the findings of Soro *et al.* (1999), locally rare *Sphagnum* species have colonized the disturbed system. However, the area is one of the southernmost locations of aapa mires (Ruuhijärvi 1960), and it is possible that before the peat cutting, aapa mire features occurred there. Some fragments of the existing vegetation may have remained in the trenches but it is also possible that *Sphagnum* species, having great dispersal ability (Campbell *et al.* 2003), came from a longer distance. Long distance colonization may be a very general feature of spontaneous regeneration and it can be a positive force in restoration succession.

**Table 5.** Measured seasonal methane fluxes (mg CH<sub>4</sub>-C m<sup>-2</sup> d<sup>-1</sup>) and SD in 2000 (*n* = 3) and 2001 (*n* = 4–5) in four plant communities, Ripa (= *S. riparium*), Papi (= *S. papillosum*), PaPu (= *S. papillosum* with *S. pulchrum*), and Pulc (= *S. pulchrum*).

	2000		2001	
	Mean	SD	Mean	SD
Ripa	-39	-21	-85	-75
Papi	-91	-40	-165	-93
PaPu	-148	-87	-191	-118
Pulc	-194	-126	-257	-173

## Carbon balance

Neither the annual CO<sub>2</sub> balance between the communities nor that between the two growing seasons varied significantly and none of the communities was a superior sink. The differences between the balances of the communities were due to respiration, which was mostly related to the differences in relation to the water table. The differences in photosynthesis rates were small and likely to result from the dominance of the same sedge species in the field layer of most sample plots, as illustrated in the CCA ordination plot (Fig. 2). The importance of sedges in the photosynthesis of the whole community (Bubier *et al.* 2003) is likely to leave behind the role of different *Sphagnum* species in the ground layer. The replacement of different *Sphagnum* species along the water table gradient may also have leveled out some of the spatial differences in the seasonal balances due to the different tolerances for the water table (Schipperges and Rydin 1998).

The estimated one-year net CO<sub>2</sub>-C balance in the regenerated trenches was very low: close to zero or even clearly negative and the variability among the communities was large. Low seasonal production was not sufficient enough to exceed losses of winter time respiration, which may partly result from suboptimal weather conditions during the study period.

Pristine mires that are long term sinks for atmospheric carbon may undergo large interannual variations in the CO<sub>2</sub> balance (Alm *et al.* 1999a, Griffis *et al.* 2000, Aurela *et al.* 2002). Losses of carbon are often related to dry grow-

ing seasons but Griffis *et al.* (2000) also stressed the importance of environmental conditions in the early leafing period for the whole growing season. During the study period in Aitoneva, both of the early springs were in general exceptionally warm but some night frosts occurred. In 2000, the night frost period took place right after the start of the growing season, resulting in a low VGA of the vascular plants. Early season night frosts have been shown to decrease the annual production of dwarf shrubs by 50% (Lindholm and Vasander 1981). Without these kinds of night frosts the effect of spring on the annual carbon balance has been noticed to be very small in bogs dominated by dwarf shrubs (Moore *et al.* 2006).

Our estimate of the emissions outside the growing season was 47% higher than the 30 g CO<sub>2</sub>-C in Alm *et al.* (1999b) and 29 g CO<sub>2</sub>-C in Aurela *et al.* (2002). The winter temperatures in the region were clearly above the long-term average until the end of January 2001 (Helminen *et al.* 2001). The surface of the trenches did not freeze before February, which probably led to enhanced microbial peat decomposition. Thus, our estimate likely overrides average winter time emissions.

Snow free periods in late autumn and spring also form a source of uncertainty in our estimations. Due to limited data, especially our estimates of October 2000 and May 2001 CO<sub>2</sub> balance are rather unreliable. This may have led to larger uncertainty in the annual balance than the length of the period suggests; the large differences in spring time fluxes in fens can largely be responsible for the between-year differences in annual balance (Griffis *et al.* 2000, Aurela *et al.* 2001). Another possible error source might be the use of artificial shades in enlarging the range of photosynthetic radiation for  $P_G$  data. Burrows *et al.* (2005) observed reduced light use efficiency in shaded chambers when compared with unshaded automated chambers. That would cause an underestimation of the fluxes in low PPFD values. As opposed to Burrows *et al.* (2005) who omitted low PPFD values (< 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), we frequently measured gas exchange on cloudy days and 38% of our data was recorded at low PPFD values. As a consequence, we were likely able to catch the rapid

increase in the light response of photosynthesis at low light levels, which is reflected in the  $P_G$  model parameter  $k$  ( $\alpha$  in Burrows *et al.* 2005). Therefore, the light use efficiency of the communities should not be underestimated in our data. This, and the use of natural low PPFD values in our modelling, greatly reduce the error in our models as also seen in Riutta *et al.* (2007).

The estimated seasonal CH<sub>4</sub>-C balance in the communities was lowest in Ripa with values typical to bogs (Nykänen *et al.* 1998, Waddington and Roulet 2000), and highest in Pulc with emissions exceeding the mean values observed in northern fens (Saarnio *et al.* 1997, Nykänen *et al.* 1998). The emissions outside the growing season were similar to the values observed by Panikov and Dedysh (2000) in a Siberian patterned fen but more than twice as high as Alm *et al.* (1997) observed in an oligotrophic fen in Finland. The mild winter may have also promoted the high emissions of CH<sub>4</sub>. Without much doubt, the water level and the associated vegetation communities are the key factors in regulating oxic and anoxic decay at our study site. The importance of VGA on methane emissions is shown as the clear difference in emissions between the growing seasons. Despite the small amount of measured data and the lack of models, these results show how much carbon will be lost from the system as methane. More data and analyses would be needed for a detailed description of the CH<sub>4</sub> dynamics in the communities.

When all the carbon fluxes including leaching (estimated based on Sallantausta 1992) are considered, the study site in Aitoneva would on average become a source of about 29 and 22 g C m<sup>-2</sup> in both study years 2000 and 2001. However, despite the high CH<sub>4</sub> fluxes, Pulc was able to remain as a sink of 31 g C m<sup>-2</sup> in 2001 (Table 4) and was the only community with a slightly positive two-year balance. The high productivity of Pulc may thus compensate the high losses of carbon as methane.

Unlike in the studies of Bortoluzzi *et al.* (2006) and E. Samaritani (unpubl. data), the advanced regeneration stage in Aitoneva did not represent a strong sink of CO<sub>2</sub> but showed high potential for CH<sub>4</sub> emissions. In general, the VGA in Aitoneva was very low, probably resulting in low primary production. Weather conditions

may have had an important role in the low C gain of the studied area during the study period. Glatzel *et al.* (2004) observed very high CO<sub>2</sub> and CH<sub>4</sub> production potentials at a similar site in Canada and related it to the weak decomposition grade of the fresh biomass. It is possible that the decomposition of the residual peat and the new accumulated organic layer in peat trenches is accelerated (Glatzel *et al.* 2003) in comparison to restored sites where peat was harvested using milled peat technique and the starting situation greatly differed (Tuittila *et al.* 1999). Our results may suggest a decreased carbon sink of restored sites after the observed *Eriophorum* peak (Tuittila *et al.* 1999) when competition of less productive species such as *Sphagnum* leads to a decrease in the abundance of *Eriophorum* or other sedges.

## Conclusions

Two growing seasons and one winter is a short period for estimating peatland carbon dynamics and a longer observation period would be needed for more conclusive results. Based on our findings, the carbon balance of the regenerated trenches falls within the range of annual variation in pristine mires but shows a smaller potential for being a large carbon sink as compared with recently restored cut-away sites.

*Acknowledgements:* We thank Jouni Meronen and the whole peatland ecology field team at Hyytiälä Forestry Station for their help with the gas measurements. The data collection and analyses were supported by VAPO Ltd., the Regional Council of South Ostrobothnia and the project “The green house gas balances of restored peatlands” funded by the Finnish Ministry of Trade and Industry. The study was a part of the RECIPE project funded by the European Commission, Directorate I, under the programme: “Energy, Environment and Sustainable Development” (no. EVK2-CT-2002-00154). We thank Dr. Stephen Chapman and Meeri Pearson for comments on the manuscript and for revising the language and an anonymous reviewer and the editor in charge of this issue, Dr. Raija Laiho, for very constructive comments on the manuscript.

## References

Alm J., Saarnio S., Nykänen H., Silvola J. & Martikainen P.J. 1999b. Winter CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes on some natural and drained boreal peatlands. *Biogeochemistry*

- 44: 163–186.
- Alm J., Schulman L., Walden J., Nykänen H., Martikainen P.J. & Silvola J. 1999a. Carbon balance of a boreal bog during a year with exceptionally dry summer. *Ecology* 80: 161–174.
- Alm J., Shurpali N.J., Tuittila E.-S., Laurila T., Maljanen M., Saarnio S. & Minkkinen K. 2007. Methods for determining emission factors for the use of peat and peatlands — flux measurements and modelling. *Boreal Env. Res.* 12: 85–100.
- Alm J., Talanov A., Saarnio S., Silvola J., Ikkonen E., Aaltonen H., Nykänen H. & Martikainen P.J. 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia* 110: 423–431.
- Aurela M., Laurila T. & Tuovinen J.-P. 2001. Seasonal CO<sub>2</sub> balances of a subarctic mire. *J. Geophys. Res.* 106: 1623–1637.
- Aurela M., Laurila T. & Tuovinen J.-P. 2002. Annual CO<sub>2</sub> balance of a subarctic fen in northern Europe: Importance of the wintertime efflux. *J. Geophys. Res.* 107: 1–17.
- Bortoluzzi E., Epron D., Siegenthaler A., Gilbert D. & Buttler A. 2006. Carbon balance of a European mountain bog at contrasting stages of regeneration. *New Phytologist* 172: 708–718.
- Bubier J., Crill P., Mosedale A., Frolking S. & Linder E. 2003. Peatland responses to varying interannual moisture conditions as measured by automatic CO<sub>2</sub> chambers. *Global Biogeochem. Cycles* 17: 1–15.
- Burrows E.H., Bubier J.L., Mosedale A., Cobb G.W. & Crill P.M. 2005. Net ecosystem exchange of carbon dioxide in a temperate poor fen: a comparison of automated and manual chamber techniques. *Biogeochemistry* 76: 21–45.
- Campbell D.R., Rochefort L. & Lavoie C. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Quebec. *J. Appl. Ecol.* 40: 78–91.
- Chapin F.S., Woodwell G.A., Randerson J.T., Rastetter E.B., Lovett G.M., Baldocchi D.D., Clark D.A., Harmon M.E., Schimel D.S., Valentini R., Wirth C., Aber J.D., Cole J.J., Goulden M.L., Harden J.W., Heiman M., Howarth R.W., Matson P.A., McGuire A.D., Melillo J.M., Mooney H.A., Neff J.C., Houghton R.A., Pace M.L., Ryan M.G., Running S.W., Sala O.E., Schlesinger W.H. & Schulze E.-D. 2005. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9: 1041–1050.
- Chapman S., Buttler A., Francez A.-J., Laggoun-Défarage F., Vasander H., Schloter M., Combe J., Grosvernier P., Harms H., Epron D., Gilbert D. & Mitchell E. 2003. Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. *Frontiers in Ecology and the Environment* 1: 525–532.
- Drebs A., Nordlund A., Karlsson P., Helminen J. & Rissanen P. 2002. *Climatological statistics of Finland 1971–2000*. Climatic Statistics of Finland 2002(1), Finnish Meteorological Institute.
- Glatzel S., Basiliko N. & Moore T. 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada.

*Wetlands* 24: 261–267.

- Glatzel S., Kalbitz K., Dalva M. & Moore T. 2003. Dissolved organic matter and their relationship to carbon dioxide efflux from restored peat bogs. *Geoderma* 113: 397–411.
- Greenup A.L., Bradford M.A., McNamara N.P., Ineson P. & Lee J.A. 2000. The role of *Eriophorum vaginatum* in CH<sub>4</sub> flux from an ombrotrophic peatland. *Plant and Soil* 227: 265–272.
- Griffis T.J., Rouse T.R. & Waddington J.M. 2000. Interannual variability of net ecosystem CO<sub>2</sub> exchange at a subarctic fen. *Global Biogeochem. Cycles* 14: 1109–1121.
- Hämet-Ahti L., Suominen J., Ulvinen T. & Uotila P. (eds.) 1998. *Retkeilykasvio*, 4th ed., Finnish Museum of Natural History, Botanical Museum, Helsinki.
- Hammer Ø. & Harper D.A.T. 2002. *PAST, Palaentological Statistics*. Palaentological Museum, University of Oslo.
- Helminen J., Nordlund A. & Karlsson P. 2001. *Weather report 4/2000–10/2001*, Finnish Meteorological Institute. [In Finnish with English summary].
- Huopalainen M., Tuittila E.-S., Laine J. & Vasander H. 1998. Seed and spore bank in a cut-away peatland twenty years after abandonment. *International Peat Journal* 8: 42–51.
- Lavoie C., Marcoux K., Saint-Louis A. & Price J.S. 2005. The dynamics of a cotton grass (*Eriophorum vaginatum* L.) cover expansion in a vacuum-mined peatland, southern Quebec, Canada. *Wetlands* 25: 64–75.
- Lindholm T. & Vasander H. 1981. The effect of summer frost damage on the growth and production of some raised bog dwarf shrubs. *Annales Botanici Fennici* 18: 155–167.
- Marinier M., Glatzel S. & Moore T.R. The role of cotton grass (*Eriophorum vaginatum*) in CO<sub>2</sub> and CH<sub>4</sub> fluxes from restored peatlands, in eastern Canada. *Écoscience* 11: 141–149.
- Moore T.R., Lafleur P.M., Poon D.M.I., Heumann B.W., Seaquist J.W. & Roulet N.T. 2006. Spring photosynthesis in a cool temperate bog. *Global Change Biology* 12: 2323–2335.
- Nykänen H., Silvola J., Alm, J. & Martikainen P.J. 1996. Fluxes of greenhouse gases CH<sub>4</sub>, CO<sub>2</sub> and N<sub>2</sub>O on some peat mining areas in Finland. In: Laiho R., Laine J. & Vasander H. (eds.), *Northern peatlands in global climatic change, Proceedings of the international workshop held in Hyttälä, Finland, 8–12 October 1995. Publications of the Academy of Finland 1/96*, Helsinki, pp. 141–147.
- Nykänen H., Alm J., Silvola J., Tolonen K. & Martikainen P.J. 1998. Methane fluxes of different fertility and the effect of long-term experimental lowering of the water table on flux rates. *Global Biogeochem. Cycles* 12: 53–69.
- Panikov N.S. & Dedysh S.N. 2000. Cold season CH<sub>4</sub> and CO<sub>2</sub> emission from boreal peat bogs (West Siberia): Winter fluxes and thaw activation dynamics. *Global Biogeochem. Cycles* 14: 1071–1080.
- Riutta T., Laine J., Aurela M., Rinne J., Vesala T., Laurila T., Haapanala S., Pihlatie M. & Tuittila E.-S. 2007. Spatial variation at the plant community scale regulates carbon gas dynamics at the ecosystem scale in a boreal fen. *Tellus B* 59. [In press].
- Robert É.C., Rochefort L. & Garneau M. 1999. Natural revegetation of two block-cut mined peatlands in eastern Canada. *Can. J. Bot.* 77: 447–459.
- Rochefort L., Quilty F., Campeau S., Johnson K. & Malterer T. 2003. North American approach to the restoration of Sphagnum dominated peatlands. *Wetlands Ecology and Management* 11: 3–20.
- Roderfeld H., Vasander H. & Tuittila E.-S. 1996. Ein abgetorfte Hochmoor im Regenerationsstadium im südlichen Finnland. *Telma* 26: 223–235.
- Ruuhijärvi R. 1960. Über die regionale Einteilung der Nordfinnischen Moore. *Ann. Bot. Soc. Zool. Bot. Fen. Vanamo* 34: 1–360.
- Saarnio S., Alm J., Silvola J., Lohila A., Nykänen H. & Martikainen P.J. 1997. Seasonal variation in CH<sub>4</sub> emissions and production and oxidation potentials at microsites on an oligotrophic fen. *Oecologia* 110: 414–422.
- Sallantausta T. 1992. Leaching in the material balance of peatlands — preliminary results. *Suo* 43: 253–258.
- Salonen V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology* 10: 171–174.
- Salonen V., Penttinen A. & Särkkä A. 1992. Plant colonization of a bare peat surface: population changes and spatial patterns. *Journal of Vegetation Science* 3: 113–118.
- Schipperges B. & Rydin H. 1988. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. *Phytologist* 140: 677–684.
- Schouwenaars J.M. 1993. Hydrological differences between bogs and bog-relicts and consequences for bog restoration. *Hydrobiologia* 265: 217–224.
- Smart J., Wheeler B.D. & Willis A.J. 1989. Revegetation of peat excavations in a derelict raised bog. *New Phytologist* 111: 73–748.
- Sopo R. & Aalto A. 1996. A quarter century of efficient peat development. In: Vasander H. (ed.), *Peatlands in Finland*, Finnish Peatland Society, Helsinki, Finland, pp. 84–87.
- Soro A., Sundberg S. & Rydin H. 1999. Species diversity, niche metrics and species associations in harvested and undisturbed bogs. *Journal of Vegetation Science* 10: 549–560.
- Stén C.-G. & Toivonen T. 1990. *The peat resources and their potential use in Kihniö, Western Finland*. Turvetutkimus, turveraportti 236, Geological Survey of Finland, Espoo, Finland. [In Finnish with English summary].
- ter Braak C.J.F. & Šmilauer P. 2002. *Canoco reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, NY, USA.
- Thomas K., Benstead J., Davies K.L. & Lloyd D. 1996. Role of wetland plants in the diurnal control of CH<sub>4</sub> and CO<sub>2</sub> fluxes in peat. *Soil. Biol. Biochem.* 28: 17–23.
- Tolonen K. & Turunen J. 1996. Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene* 6: 171–178.
- Tuittila E.-S., Komulainen V.-M. & Laine J. 2000a. Impact of rewetting on vegetation of a cut-away peatland. *Applied*

- Vegetation Science* 3: 205–212.
- Tuittila E.-S., Komulainen V.-M., Vasander H. & Laine J. 1999. Restored cut-away peatland as a sink for atmospheric CO<sub>2</sub>. *Oecologia* 120: 163–174.
- Tuittila E.-S., Komulainen V.-M., Vasander H., Nykänen H., Martikainen P.J. & Laine J. 2000b. Methane dynamics of a restored cut-away peatland. *Global Change Biology* 6: 569–581.
- Tuittila E.S., Vasander H. & Laine J. 2004. Sensitivity of reintroduced Sphagnum to water-level variation in a cutaway peatland. *Restoration Ecology* 12: 483–493.
- van Seters T.E. & Price J.S. 2002. Towards a conceptual model of hydrological change on an abandoned cutover bog, Quebec. *Hydrological Processes* 16: 1965–1981.
- Vasander H. & Kettunen A. 2006. Carbon in boreal peatlands. *Ecological Studies* 188: 165–194.
- Waddington J.M., Greenwood M.J., Petrone R.M. & Price J.S. 2003. Mulch decomposition impedes net recovery of carbon sink. *Ecological Engineering* 20: 199–210.
- Waddington J.M. & Roulet N.T. 2000. Carbon balance of a boreal patterned peatland. *Global Change Biology* 6: 87–97.
- Waddington J.M., Warner K.D. & Kennedy G.W. 2002. Cutover peatlands: A persistent source of atmospheric CO<sub>2</sub>. *Global Biogeochem. Cycles* 16: 1002–1009.
- Wilson D., Alm J., Riutta T., Laine J., Byrne K.A., Farrell E.P. & Tuittila E.-S. 2007. A high resolution green-area index for modelling the seasonal dynamics of CO<sub>2</sub> exchange in vascular plant peatland communities. *Plant Ecol.* 190: 37–51.