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Restoring
vegetation and carbon dynamics
in a cut-away peatland

Eeva-Stiina Tuittila

Academic dissertation

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EEVA-STIINA TUUTTILA

Pristine mire is a peat accumulating wetland ecosystem that is sustained by a high water level. Peat accumulated in mires is commonly harvested for energy and horticultural purposes. After harvesting, the cut-away sites are vegetationless and act as sources for CO₂. Because plant colonization of these harsh environments is slow, human measures are needed for promoting regeneration of the functional mire ecosystem. Although peatland restoration aims to regenerate a carbon accumulating ecosystem, so far there has been little if any research on the carbon dynamics of these sites.

The vegetation and carbon dynamics of a cut-away peatland were studied one year before and four years after rewetting, and compared to the restoration success of *Sphagnum* re-introduction.

Before rewetting, the cut-away site was a mosaic of *Eriophorum vaginatum* tussocks and almost vegetationless intertussocks developing towards closed dry ombrotrophic vegetation. *Eriophorum* facilitated the colonization of other plant species that find a variety of microsites around tussocks. The dry cut-away site generally was a source of carbon into the atmosphere, but the individual *Eriophorum* tussocks fixed CO₂ to the ecosystem and decreased the loss of carbon. The tussocks acted as a source for methane while the intertussocks were net consumers. The tussocks seemed to facilitate colonization of methanogenic microbes by releasing organic substrates into the rhizosphere.

Raising the water table level above or close to the soil surface promoted development of wet minerotrophic vegetation and some *Sphagna* were found. However, the most important impact of rewetting on the ecosystem's function was an increase in the cover of existing *Eriophorum* tussocks and a rapid development of new seedlings. The rise of the water table level decreased CO₂ emission and increased CH₄ emission from the ecosystem by lowering the oxidation of peat and CH₄. However, the expansion of *Eriophorum* was a driving force in transforming the carbon dynamics of the cut-away peatland towards a mire ecosystem. In high water level conditions the higher CO₂ flux into the ecosystem caused an increase in seasonal CO₂ balance and net CH₄ flux. In a cut-away site with 3000–7000-year-old peat, new photosynthates seem to be even more important for carbon dynamics than in other peatland ecosystems.

In conditions where the water table level was raised close to the soil surface, the ecosystem's seasonal CO₂ balance rose within three years after rewetting to the level necessary for long-term carbon accumulation of Finnish bogs. The functional change towards a mire ecosystem when the site was not

yet fully colonized showed that it is not possible to separate different phases in the restoration process.

The re-introduction of *Sphagnum angustifolium* by moss material with capitula showed a high potential for the rapid formation of a closed *Sphagnum* carpet if the moss material did not suffer from floodings. *Sphagnum* re-introduction increased carbon binding on the site, but *Sphagnum* surfaces had a lower seasonal balance than *Eriophorum* tussocks. Because of the sensitivity of the *Sphagnum* photosynthesis to variations in the water table level, the restoration of cut-away sites to peat accumulating mire ecosystems is likely to benefit from the presence of vascular plants.

Key words: CO₂, CH₄, *Eriophorum vaginatum*, facilitation, *Sphagnum*, restoration, succession, water table level

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1. INTRODUCTION

1.1 Vegetation and carbon dynamics in mire ecosystems

Northern mires, or pristine peatlands, are wetland ecosystems sustained by a humid climate and a high water level. Consequently, hydrology is dominant factor for mire development, ecology and distribution. Mire vegetation consists of plant species adapted to wet conditions with low oxygen availability (Ingram 1983, Tallis 1983). Ombrotrophic mires receive water and chemical elements from atmospheric deposition only, but minerotrophic mire ecosystems also receive them from the surrounding catchment area (Ingram 1983, Clymo 1984). Production level is dependent on nutrient level as well as on species composition and environmental factors: moisture, light, and temperature (Harley et al. 1989, Murray et al. 1989, Alm et al. 1997, 1999b, Bubier et al. 1998, Frohking et al. 1998). In ombrotrophic mires in particular, the most important vegetation component is the moss genus *Sphagnum* L. Contrary to *Sphagna*, vascular plants growing in lawn or hollow levels, like species of *Eriophorum* L. and *Carex* L. genera, have aerenchymatic roots as adaptation for water logged conditions and their biomass is mainly located below-ground (Sjörs 1991, Saarinen 1996). Therefore, although all vegetation is involved in the primary production of the ecosystem, *Sphagnum* mosses are responsible for the height growth of the mire (Laine et al. 2000).

Mires act as long-term sinks for atmospheric carbon because of an unbalanced ratio of decomposition to primary production. While most of the carbon bound in photosynthesis is released back to the atmosphere as CO₂, a small proportion of the primary production is deposited under anoxic conditions below water table and accumulated as peat (Fig. 1) (Clymo 1998). The actual rate of aerobic decomposition is controlled by water table level and

temperature (Kim & Verma 1992, Silvola et al. 1996, Bubier et al. 1998, Christensen et al. 1998), but also by the species composition, because the resistance to decay is species specific (Johnson et al. 1990, Buttler et al. 1994, Verhoeven & Toth 1995, Szumigalski & Bayley 1996, Aerts et al. 1999).

Part of the accumulated organic material is further decomposed in anoxic conditions (Fig. 1) (Cao et al. 1996). The slow anoxic decomposition releases carbon as CH₄, which diffuses through peat into the atmosphere along a concentration gradient. Part of the CH₄ produced is oxidized by methanotrophic bacteria in the aerobic layer, and released as CO₂ (Sundh et al. 1995). The thickness of the aerobic peat layer above the water table controls the ratio of production to oxidation (Whiting & Chanton 1993, Sundh et al. 1995), which is usually shown as decreasing emissions with deepening water levels (Roulet et al. 1993). Pristine peatlands typically act as a source of methane into the atmosphere (Harris et al. 1985, Crill et al. 1988, Moore & Knowles 1990, Bartlett et al. 1992, Bubier et al. 1993b, Bubier et al. 1995, Nykänen et al. 1998).

Although both production and oxidation processes are influenced by temperature, CH₄ oxidation has been found to be less sensitive to temperature variation (Moosavi & Crill 1998, Saarnio & Silvola 1999). The ecosystem's methane production is associated with its primary production capacity (Schimel 1995). Plants stimulate microbial activities by releasing organic substrates into the rhizosphere through litter and root exudation (Schütz et al. 1991, Whiting & Chanton 1993, Thomas et al. 1996, Huang et al. 1997a, b), and deep rooting species can supply organic material into anoxic layers even when the water table is deep. Vascular plants with aerenchymatic tissues also influence CH₄ flux by offering a route for its transport through root-shoot pathways (Schimel 1995, Thomas et al. 1996, Huang et al. 1997a, b). This transportation from

anoxic layers to the atmosphere is not only faster than the diffusion but also more efficient, because methane oxidation may be avoided inside the plant (Conrad 1989, Frenzel & Rudolph 1998). Spatial variation in methane emissions has also been connected to plant species composition,

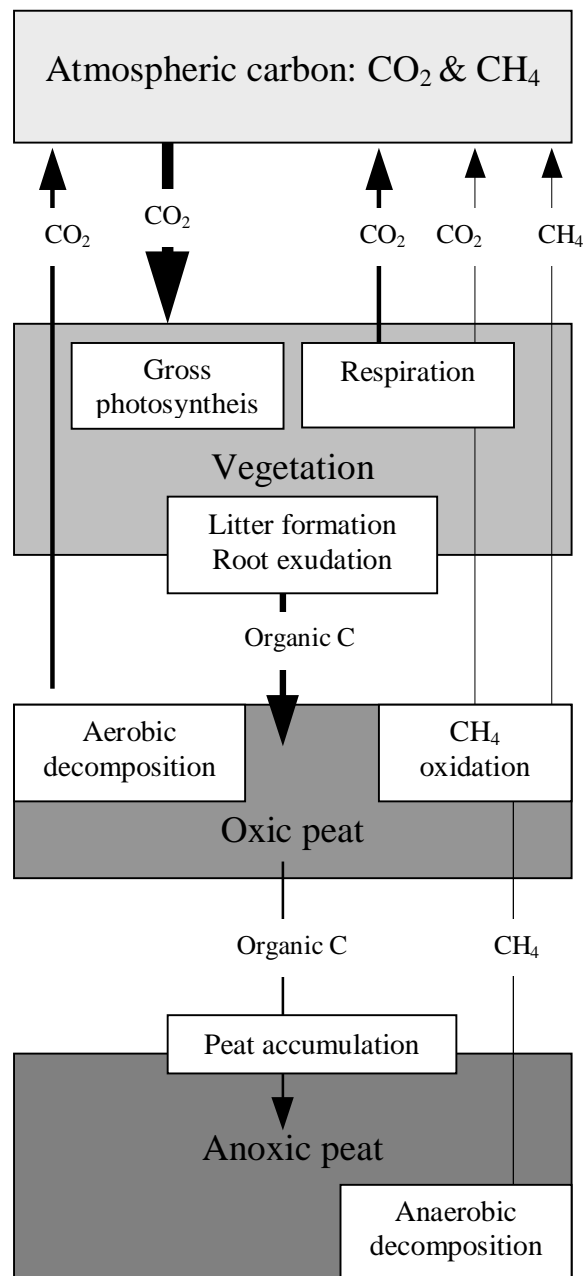


Fig. 1. Gaseous carbon cycle, typical of a pristine mire ecosystem.

microtopography, nutritional status, substrate concentration, the acidity of soils, and their microbial characteristics (Svensson & Rosswall 1984, Moore & Knowles 1989, Bubier et al. 1993a, Bubier 1995, Schimel 1995, Saarnio et al. 1997, Bergman et al. 1998).

1.2 Northern peat resources and their use

Northern mires form a carbon storage of $273 \cdot 10^{15}$ (Turunen et al. 2000) to $455 \cdot 10^{15}$ g (Gorham 1991), with an annual sink estimate of $0.096 \cdot 10^{15}$ g (Gorham 1991) or $0.07 \cdot 10^{15}$ g (Clymo et al. 1998). During the Holocene epoch, Finnish mires have sequestered carbon annually at the mean rate of 22.5 ± 0.4 (S.E.) g C m⁻², while the rate has varied between 2.8 and 88.6 g C m⁻² (Tolonen & Turunen 1996). The optimal conditions for peat formation are in areas with an annual mean temperature between 5 and 10 °C (Clymo et al. 1998).

More than 90% of peatlands are located in the boreal and temperate vegetation zones (Immirzi et al. 1992), where peat accumulated in mires has commonly been utilised as a fuel or for horticultural purposes (Göttlich et al. 1993). Nowadays the largest harvesting areas are found in Russia (about 90 000 km²), Ireland (1 100 km²), Belarus (1 090 km²), Finland (526 km²), Germany (325 km²), Latvia (261 km²) and Canada (160 km²) (Lappalainen 1996). Although energy use accounts for only about half of the total amount of harvested peat, the major share of peat in countries such as Ireland and Finland is used for energy production (Asplund 1996).

Currently the main harvesting method is milling, which needs effective drainage because heavy machinery is used and because milled peat is dried on the surface of the strips from a gravimetric moisture content of 85-92% to 35-55%. Prior to harvesting, the mire is ditched, the vegetation completely removed and strips between the ditches made slightly convex (Frilander et al. 1996). Extensive areas are

usually involved because a layer of only 1-2 cm of peat is removed at a time. After about 20-50 years of peat production the peatland is abandoned. Because large scale industrial production only began in the late 1960s, harvesting is coming to an end over extensive areas (Nyrönen 1996).

1.3 Cut-away peatland as an ecosystem

After abandonment, cut-away peatlands have no propagule bank (Salonen 1987b, Poschlod 1995, Huopalaïnen et al. 1998) and the distance from propagule sources might restrict colonization from surrounding areas (Campbell 2000). The lack of plant cover strengthens the drying effect of the wind on the uppermost peat layer (Salonen 1987b). The low albedo of the dark peat surface and low heat conductance in dry peat causes high fluctuations in daily temperature. In spite of the deep mean water table level, large water table fluctuations characterise cut-away peatlands because of low water storage capacity in relatively high bulk density (Joosten 1992, Schouwenaars 1993, Price 1996). Thus, on non-vegetated cut-away peatlands there is no carbon fixation in the ecosystem, but, as results from tundra (Billings et al. 1982, 1983, Peterson et al. 1984) and peatland ecosystems indicate (Silvola et al. 1985, 1996, Glenn et al. 1993, Funk et al. 1994, Martikainen et al. 1995, Nykänen et al. 1995), a deep water table level favours organic matter oxidation resulting in CO₂ emissions (Fig. 2). Without human activities promoting the regeneration of the mire ecosystem, i.e. restoration, plant colonization of these areas has been found to be very slow due to harsh hydrological and microclimatic conditions (Famous et al. 1991, Joosten 1995, Pfadenhauer & Klötzli 1996, Price 1996).

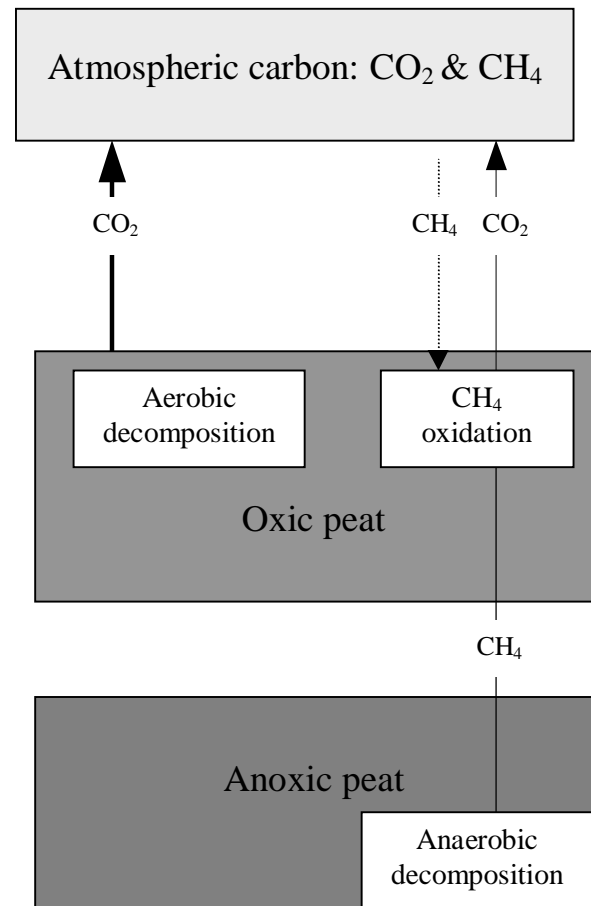


Fig. 2. Gaseous carbon cycle, typical of a vegetationless cut-away peatland.

There is evidence that facilitation may be an important succession mechanism in the colonization of cut-away peatlands. Thus, *Sphagnum* colonization of cut-away peatlands has been found under leaves of *Eriophorum vaginatum* L. in the Swiss Jura Mountains (Grosvernier et al. 1995) and *Eriophorum angustifolium* Honck. was found to facilitate *Sphagnum* establishment in a re-introduction experiment in Canada (Ferland & Rochefort 1997). On boreal and temperate cut-away peatlands with a thick residual peat layer, *Eriophorum vaginatum* is a typical dominant in early succession (Gimingham 1960, Smart et al. 1989, Meade 1992, Salonen 1992, Cooper & McCann 1995, Lavoie & Rochefort 1996) because of its ability to colonize bare peat surfaces (Gardner et al. 1986).

More humid microclimate has been observed under *Eriophorum vaginatum* tussocks where shading reduces the drying effect of wind and solar irradiation (Grosvernier et al. 1995, Sliva 1997). Sliva (1997) has documented the gradient in exposure by observing daytime temperatures, which are lower near the base of tussocks than farther away. He also observed the highest daily temperature maxima and fluctuations in the southern direction of the tussock and the lowest temperature fluctuations in the northern direction. It is not known, however, how variations in tussock characteristics and in the location of microsites relative to the tussock affects spatial variation in colonizing vegetation.

Carbon dynamics between mire ecosystems and the atmosphere involves the dynamics of CO₂ and CH₄, both of which contribute to atmospheric warming by absorbing the infrared energy reflected from the earth's surface. Therefore, the changes in peatland carbon dynamics affect climate (Blunier et al. 1995, Franzen et al. 1996). The use of peat changes the balance, not only by liberating carbon accumulated in mires into the atmosphere, but by diminishing the size of the carbon sink, and also the size of the methane source.

1.4 Restoration of cut-away peatland to a mire ecosystem

Peatland restoration aims to bring back a naturally functioning, self-sustaining ecosystem (Wheeler and Shaw 1995), or re-initiate the peat forming processes (Pfadenhauer & Klötzli 1996). The first restoration attempts of cut-away peatlands, carried out in Germany, the United Kingdom and the Netherlands, included the rewetting of peat deposits by filling or blocking drainage ditches. Kuntze & Eggelmann (1981) have presented a theoretical model of the restoration process for cut-away peatlands after rewetting that distinguishes various phases. In the model the Colonization Phase following rewetting is estimated to take from years to decades. This is followed by the Renaturation Phase

when the acrotelm is formed and the plant, animal, and microbe communities start to resemble those in pristine peatlands. In the final phase, Regeneration, which might be reached after centuries, the carbon dynamic resemble those in pristine peatland; the ecosystem becomes a sink of carbon and accumulates peat.

Up to now restoration studies have dealt only with the first phase of restoration process; Colonization. Firstly, vegetation composition in cut-away peatlands has been studied in Europe (Curran & MacNaeidhe 1986, Salonen 1987a, 1990, 1992, Poschlond 1992, Salonen & Setälä 1992, Salonen et al. 1992, Cooper & McCann 1995, Grosvernier et al. 1995) and North America (Elling & Knighton 1984, Desrochers et al. 1998, Bérubé & Lavoie 2000). Studies of restoration by rewetting and the consequent recolonization of cut-away peatlands have followed (Meade 1992, Roderfeld et al. 1993, Salonen & Laaksonen 1994, Wheeler & Shaw 1995, Sliva 1997, Sliva & Pfadenhauer 1999). However, results of monitored plant colonization and vegetation succession are still rare (Meade 1992) and improved knowledge of vegetation patterns and succession mechanisms, eg. facilitation, is needed for a better understanding of how a certain peatland area can be manipulated to become a functional mire ecosystem.

Promotion of the colonization by *Sphagnum* re-introduction to has been studied in the laboratory (Poschlod & Pfadenhauser 1989, Rochefort et al. 1995, Sagot & Rochefort 1996, Grosvernier et al. 1997) and in field conditions in Europe (Money 1995, Sliva 1997, Sliva & Pfadenhauer 1999) and North America (Campeau & Rochefort 1996, Bugnon et al. 1997, Ferland & Rochefort 1997, Rochefort & Campeau 1997, Price et al. 1998). In spite of the aim to restore the carbon cycle typical to mire ecosystems, thus far little if any research has been done on carbon dioxide and methane dynamics in these ecosystems, and the impacts of

restoration by rewetting or *Sphagnum* re-introduction cannot be quantified.

1.5 The aims of the study

This study aimed to assess the major biotic and abiotic factors controlling the vegetation and carbon dynamics of a cut-away peatland ecosystem. Instead of an extensive study over a variety of cut-away peatland sites, a process orientated approach was used in studying the change in the dynamics of the ecosystem following rewetting as well as *Sphagnum* re-introduction in order to test the theoretical model of the restoration process (Kuntze & Eggelmann 1981). More specifically the aims were:

- (i) to reveal how facilitation by *Eriophorum vaginatum* affects the colonization pattern in cut-away peatland (I)
- (ii) to connect the variation in vegetation to variation in abiotic factors (II)
- (iii) to assess the impact of rewetting on vegetation succession (II)
- (iv) to evaluate *Sphagnum* recolonization success in dry and wet conditions (V)
- (v) to quantify factors controlling carbon dynamics of cut-away peatland (III, IV, V)
- (vi) to assess the impact of rewetting and the following vegetation change, as well as *Sphagnum* re-introduction, on carbon dynamics of cut-away peatland (III, IV, V)

2. MATERIALS AND METHODS

2.1 Study site and experimental design

The study was carried out in a cut-away peatland, Aitoneva, (62°12'N, 23°18'E), in Kihniö, in southern Finland. The study site was situated on the transition between the southern and middle boreal coniferous forest zones (Ahti et al. 1968) in the eccentric raised bog region (Ruuhijärvi 1982). The long-term annual mean temperature of the area is 3.5°C, and the mean annual precipitation is c. 700 mm. The average growing season is 160 days, and the accumulative temperature sum (threshold value +5°C) is 1100 degree days. Since Aitoneva is the oldest industrially harvested peat production area in Finland, peat production fields, cut-away peatlands of different ages, and spontaneously regenerated old peat pits surrounded the study site.

Originally the study site had been a wet treeless mire, but no information of the mire site type was available. The site was first ditched in 1938. From 1944 to 1951, sod peat was produced, and milled peat from 1951 to 1975. During the last years of harvesting, pumping was also used to drain the site. The site was abandoned in 1975 when drainage was no longer economically feasible; therefore the average residual peat layer was unusually thick by Finnish standards, approximately one metre. The residual surface peat was highly decomposed *Sphagnum-Eriophorum* peat.

The size of the study site was 3.5 ha and it was divided into 20-m-wide convex strips by ditches. In 1994 the drainage system was still partially functioning. A two hectare area, rewetted in the autumn of 1994, was referred to as the rewetted site (R), and the remainder of the field was called the control site (C). The strips sloped down and formed a moisture gradient from a drier upper (R1, C1) to a wetter lower section (R2, C2).

Rewetting of the site was achieved by blocking the drainage ditches with peat dams in the autumn of 1994. In addition, a

feeder ditch was excavated to the upper section of the rewetted site to restore the ground water flow to the site from surrounding areas.

2.2. Vegetation monitoring and analysis

2.2.1 *Sampling and analysing vegetation around Eriophorum vaginatum tussocks*

In order to determine how the variation in *Eriophorum vaginatum* tussock characteristics and the location of microsites relative to the tussock affect the spatial variation in colonizing vegetation, the vegetation around the tussocks was studied during summer 1994 before rewetting (I).

Seventy two tussocks located on one peat strip were randomly selected. At each tussock, four 30 cm long transects, one in each cardinal direction, were established in order to detect changes in vegetation as a function of distance from the base of the tussock. Each transect consisted of six adjoining 5*5 cm sample plots, with the first one next to the tussock's leaf sheath bundle (Fig. 1 in I). The percentage cover in sample plots was estimated for each plant species. The cases where a neighbouring tussock was closer than 30 cm were omitted from the statistical analyses, and the total number of sample plots used was 1665.

The diameter and height of each tussock and the diameter and height of the tussock's leaf sheath bundle were measured (Fig. 1 in I). A variable shade index was calculated by multiplying the diameter of the tussock by the height of the tussock's leaf sheath bundle. The proportion of the tussock's living leaves was estimated. The distances from the tussock's base in the four cardinal directions were used to describe the degree of exposure. The mean water table level of tussocks was estimated as described in I.

The effects of the tussock characteristics and the distance and orientation of a sample plot on the vegetation composition around tussocks were analysed with Partial

Canonical Correspondence Analysis (CCA) (Ter Braak 1988). The effect of water table level was omitted by treating it as a co-variable.

The response of five frequent species and variable "presence of any species" to variation in tussock characteristics, the distance and orientation of a sample plot in relation to tussock, and water table level, were modelled using logit regression analysis (Hoemer & Lemenshaw 1989). The response model is described in detail in I.

2.2.2 *Studying vegetation of a cut-away peatland before and after rewetting*

To assess vegetation developed in cut-away peatland after abandonment, and the impact of rewetting on vegetation succession, the change in vegetation was monitored from permanent sample plots between 1994 and 1998 (II). Before rewetting in 1994, a group of twelve circular vegetation sample plots of 2 m² each were established on the upper and lower section of the rewetted and control sites. Sample plots were placed systematically in three lines over one and a half strips at seven-metres distance from each other. The percentage cover class of each species was estimated by the same person at the same time each year: between late July and early August.

The water level of each vegetation plot was monitored throughout the growing season in ground water tubes next to each plot, and the depth of the peat layer in each sample plot was measured. Undisturbed surface (0-10 cm) peat samples (593 cm³) were taken next to each plot in 1994. Dried (105°C) and weighed peat samples were ground to pass a 2 mm sieve. The total carbon and nitrogen concentrations were measured on a Leco CHN 600 analyser. The concentrations of other elements were measured on an ICP analyser (ARL 358) after HNO₃-H₂SO₄-HClO₄ digestion at 200°C.

Detrended correspondence analysis (DCA) (ter Braak 1987) was used to ana-

lyse the variation in vegetation and its correlation with environmental variables in the plant community data collected in 1994, prior to rewetting. DCA was also used to analyse the change in vegetation during 1994-1998, and to compare the change in the rewetted site to the succession in the control site.

The diversity index of each sample plot was calculated each year using the Shannon formula $H' = -\sum p_i \ln p_i$ (Shannon & Weaver 1948), where p_i is the proportion of the total cover contributed by each species.

2.2.3 Studying recolonization success of re-introduced *Sphagnum*

In order to study the recolonization success of *Sphagnum angustifolium* (Russ.) C. Jens. using material consisting of stems and branches and material including capitula, living *Sphagnum angustifolium* material (top 10 cm layer) was collected from an *Eriophorum vaginatum* pine bog in southern Finland (61°51'N, 24°17'E) in September, 1994. Living moss material was cut into 2-3 cm fragments, and divided into (1) material consisting of stems and branches and (2) material including capitula.

Ten sample plots, each 60*60 cm, were set up at the lower and upper ends of one peat strip forming two moisture treatments at the study site. Moss material was spread into the sample plots and an even covering layer was formed by hand, after randomising five sample plots for stem material and five for capitulum material in both sections.

Five randomised *Sphagnum* individuals were picked from each sample plot at the end of August, 1995-1997, and their total length was measured. The mean of the annual measurements was used to represent the *Sphagnum* length of a plot for each year. The cover of *Sphagnum* capitula was recorded annually at the end of August during 1995-1998. In each sample plot, a circular subplot with a diameter of 10 cm was mapped in transparent plastic film.

The area covered by capitula on these maps was measured with a digitizing pad. In 1998, when the sample plots in the lower section were continuously inundated, the cover was visually estimated.

The effect of the moss material treatment (stem or capitula material) and the moisture level treatment on the cover of *Sphagnum* capitula during 1995-1998, and on the moss length during 1995-1997 was analysed separately using ANOVA of repeated measures. The linearity of the moss cover development and length development in time were tested separately using the Polynomial Test of Order 1 (SYSTAT 1998).

2.3 Carbon gas studies

2.3.1 CO₂ and CH₄ flux measurements

Ten sample plots were established for gas flux measurements on different surfaces representing variations in the vegetation of the study site, i.e. the mosaic of *Eriophorum vaginatum* tussocks and almost vegetationless intertussocks (a term also used by Poole & Miller 1982, Johnson et al. 1996) (III, IV). Six of the *Sphagnum* re-introduction plots were selected for gas flux measurements, and two bare peat sample plot was established among the moss sample plots in order to compare the carbon dynamics of *Sphagnum* re-introductions with that of bare peat surfaces (V). All these plots were surrounded by aluminium collars with a groove for airtight water sealing during gas flux measurements.

Gas flux measurements were started in late May or early June and continued until late September or early November. Flux measurements were done at 1 to 3 week intervals, most frequently from late June to mid August. CO₂ flux measurements in tussocks - intertussock sample plots were carried out during 1994-1997 and CH₄ flux measurements during 1994-1996. In *Sphagnum* re-introduction plots CO₂ flux measurements were carried out during

1995-1998 and CH₄ flux measurements were made in 1996 and 1997.

Each instantaneous CO₂ exchange measurement series consists of a couplet of net CO₂ exchange (P_N) and total respiration measurement (R_{TOT}) (III, IV). P_N, sometimes referred to as NEE in literature, is a difference between the CO₂ fixed by plants in gross photosynthesis (P_G) and CO₂ released in respiration of plants, soil animals, and microbes that decompose organic carbon and oxidise methane, i.e. R_{TOT}. A vented and thermostated transparent plastic chamber (0.106 m³) was used in measurements (Alm 1997). The CO₂ concentration in the chamber was measured with a portable infrared gas analyser. P_N was measured with the chamber uncovered and exposed to ambient illumination. After P_N measurements R_{TOT} was measured with the chamber covered with an opaque lid, under temperature and moisture conditions similar to those for P_N measurements.

CH₄ measurements were carried out using the dark, static chamber technique: the chamber (0.108 m³) was placed onto the collar and a series of gas samples was drawn from the chamber headspace (IV, V). The samples' CH₄ concentrations were determined in the laboratory with a gas chromatograph within 24 hours of sampling.

In connection with gas sampling, air temperature inside the chamber, water table level, and a peat temperature profile were measured. Solar irradiation (PAR) was measured simultaneously with P_N measurements. Similarly to permanent vegetation sample plots, the projection cover class of each species at gas sample plots was estimated each year.

Gas flux rates were calculated by regression from the linear change of concentration in the chamber headspace as a function of time, base area, chamber volume, and the molar volume of CO₂ or CH₄ at chamber air temperature. Positive P_N values were used when the CO₂ flux from the atmosphere into the vegetation

exceeded total respiration from vegetation and soil, i.e. the site was a sink for atmospheric CO₂. An estimate of gross photosynthesis (P_G) was calculated as the sum of P_N and R_{TOT} values. Positive values were used for CH₄ emission from the site, and negative values when the site acted as a sink for atmospheric CH₄.

2.3.2 Modelling CO₂ and CH₄ fluxes

In order to quantify factors controlling carbon dynamics of cut-away peatland, response functions for gross photosynthesis (P_G), total respiration (R_{TOT}), and CH₄ flux were constructed (III, IV, V). Modelling was based on simultaneous measurements of gas exchange fluxes and environmental variables.

In the P_G model for the mosaic of *Eriophorum* tussocks and intertussock surfaces (Eq.2 in III), photosynthesis was assumed to have a saturating response to irradiation (PAR), which was described by the Michaelis-Menten function with parameters Q (asymptotic maximum) and k (half saturation constant). Maximal photosynthesis (Q) was assumed to be linearly dependent on the cover of *Eriophorum* (EV), effective temperature sum index (ETI), and soil temperature (T₋₅). Variable ETI (Alm et al. 1997), a quotient of cumulative temperature sum (threshold 5°C) and the number of temperature sum days, was formed to describe seasonality. The parameter values for Q and k were estimated using a non-linear regression technique.

Similarly to the P_G of the mosaic of *Eriophorum* tussock and intertussock surfaces, the dependence of gross photosynthesis on irradiation in *Sphagnum* surfaces was assumed to have the form of rectangular hyperbola with coefficients Q and k , but the asymptotic maximum was assumed to be linearly dependent on *Sphagnum* capitula cover (SA) and unimodally dependent on water table level (WT) (Eq. 1 in V). The Gaussian form of response, where coefficient m is the maximum photosynthesis in optimal water table

level, coefficient u the optimum WT for photosynthesis, and coefficient t the tolerance, i.e. the measure of width in water table level amplitude, was used to describe the dependence of Q on water table level.

In the R_{TOT} model for the mosaic of *Eriophorum* tussocks and intertussock surfaces, statistical relationships were derived between log transformed total respiration and *Eriophorum vaginatum* cover (EV), surface soil temperature ($T_{.5}$), water level (WT), and effective temperature sum index (ETI) (Eq.2 in **III**). Parameter values for the coefficients of the environmental variables were estimated using a linear regression technique.

The dependence of R_{TOT} in *Sphagnum* surfaces on water table level (WT) was assumed to have a form of sigmoid, where the maximum respiration (a) was dependent on air temperature (T). Coefficient b was used to determine the speed and direction of change in R_{TOT} along the WT gradient, and c for the centre of the fastest change (Eq. 2 in **V**). Parameter values for the coefficients of the environmental variables were estimated separately for *Sphagnum* surfaces and bare peat surfaces using non-linear regression technique.

The net CO_2 exchange (P_N) was calculated as a difference between P_G and R_{TOT} .

A statistical response model for CH_4 flux in the mosaic of the *Eriophorum* tussocks and intertussocks at the study site was constructed using multiple linear regression. The strongest correlation was in the model where soil temperatures ($T_{.15}$ and $T_{.30}$), interaction between *Eriophorum* cover and effective temperature sum index (EV \times ETI), and interaction between *Eriophorum* cover and water level (EV \times WT), were used as independent variables (Eq. 1 in **IV**).

2.3.3 Simulating seasonal CO_2 and CH_4 fluxes

The effect of rewetting and *Sphagnum* re-introduction on the seasonal (mid May to the end of September) carbon gas balance

was assessed with reconstructions of seasonal CO_2 balance (sometimes referred to as NEP in the literature) and net CH_4 flux (**III**, **IV**, **V**). Reconstructions were based on the gas flux response functions (Eqs. 1-3 in **III**, Eq. 1 in **IV** Eqs. 1, 2 and 4 in **V**) and measured time series of environmental variables over the growing seasons; the fluxes were estimated for each hour of growing season and summed. Hourly environmental data was taken from the weather stations located on the study site and Lakkasuo mire (61°47'N, 24°18'E).

The equations (1-3 in **III** and 1 in **IV**) were used for estimating the hourly net CO_2 exchange (P_N), and CH_4 flux for the upper and lower sections of the rewetted (R1, R2) and control sites (C1, C2) that were integrated over the growing seasons 1994-1997. The equations (1, 2 and 4 in **V**) were used for estimating the hourly P_N in the *Sphagnum* stem and capitulum plots, and bare peat surfaces in drier and moister sections during the growing season 1996.

For the study, the direct effect of rewetting in closed vegetation, the seasonal CO_2 balance and net CH_4 flux were simulated for R1, R2, C1, using their measured environmental data but setting EV cover to 70%, here assumed to represent a fully closed ground layer vegetation (**III**, **IV**). In addition, the seasonal CO_2 balance for bare peat surfaces was similarly simulated, setting EV cover to 0% (**III**).

For the study of the highest potential CO_2 balance in *Sphagnum* surfaces, the seasonal CO_2 fluxes were simulated for a closed *Sphagnum* carpet at an optimal water table level using the measured irradiation and temperature data but setting *Sphagnum* capitula cover to 97% and water table level to -12 cm (**V**).

The temporal relationship between CH_4 and CO_2 dynamics in a tussock and a intertussock was studied in dry and wet conditions by reconstructing fluxes over the growing seasons. The hourly CH_4 flux, P_G and R_{TOT} for a tussock and intertussock sample plot in a rewetted and in a control area were estimated using equations (1-3 in

III and 1 in IV) and integrated over the growing seasons 1994-1997 (IV).

2.3.4 Analysing the effect of *Sphagnum* re-introduction on CH₄ fluxes

ANOVA of repeated measures were used in the analysis of 1996 and 1997 data (analysed separately) concerning the effect of *Sphagnum* re-introduction on CH₄ emission (V). The grouping factor, *Sphagnum* (bare peat surface, *Sphagnum* surfaces spread with moss material consisting of stems and branches, and *Sphagnum* surfaces spread with moss material including capitula), and the within factor, week, together with their interaction, were used in the analysis.

3. RESULTS

3.1 Vegetation before and after rewetting

3.1.1 Vegetation composition prior to rewetting

Nineteen years after the abandonment, the bare peat surfaces still constituted a major part of the field. The main variation in vegetation before rewetting was related to the variation in the amounts of main nutrients, the water table level, and the decomposition level of the peat (C:N, bulk density) (II). The moistest site with the highest nutrient level, the lower section of rewetted site (R2), had the highest total cover (51±7%) and diversity. The monodominance in R2 was remarkably lower than in other sites. *Eriophorum vaginatum* was the dominant of the field layer in all sites, but in R2 the minerotrophic species, *Carex rostrata* Stokes and *E. angustifolium*, also made a considerable contribution. In the bottom layer, *Dicranella cerviculata* (Hedw.) Schimp. and *Polytrichum strictum* Brid. were dominants. *Betula pubescens* Ehrh., together with *B. pendula* Roth and *Pinus*

sylvestris L., formed a shrub layer that was densest in R2.

3.1.2 Facilitation by *Eriophorum vaginatum* tussocks

Altogether 19 plant species or species groups were found around the *Eriophorum vaginatum* tussocks studied. Only a few of them, *Betula* spp. L., *Eriophorum vaginatum* seedlings and moss species *Dicranella cerviculata*, *Pohlia nutans* (Hedw.) Lindb., *Polytrichastrum longisetum* (Brid.) G.L. Sm. and *Polytrichum strictum*, were frequent.

Most of the species, e.g. *Drosera rotundifolia* L., *Vaccinium uliginosum* L. and seedlings of *Betula*, had their highest cover in the most shaded microsites, i.e. in the close vicinity of large tussocks with a high proportion of living leaves (Figs 3, 5 and 6 in I). These species had their optima in the northern and western directions. *Pohlia nutans* had the narrowest ecological amplitude. Its optimal sites were at the base of very large tussocks, in the northern direction. In contrast, *Calluna vulgaris* (L.) Hull, *Polytrichum* spp. Hedw., and *Eriophorum* seedlings had their optima in least shaded sites, i.e. in the southern direction further away from small tussocks with a low proportion of living leaves. The most frequent species *Dicranella cerviculata* seemed to be generalist.

3.1.3 Vegetation change following rewetting

The main gradient in the succession data was related to differences between drier ombrotrophic and wetter minerotrophic vegetation (Fig. 4 in II). The dry ombrotrophic end of the gradient was characterised by a dense shrub layer, dwarf shrubs, lichens, and forest bryophytes, while species typical to wet minerotrophic mires, like *Carex rostrata* and *Sphagnum riparium* Ångstr., were located at the other end. Rewetting promoted the development of the lower section of the rewetted site towards wet minerotrophic vegetation, while the others tended to develop into a

closed dry ombrothrophic plant community. However, in the fourth year after rewetting, the development of the upper section of the rewetted site diverged from the control sites and turned towards the community found in the lower section of the rewetted site prior to rewetting.

In the lower section of the rewetted site, where the water table rose above or close to the soil surface, diversity decreased at first because of the disappearance of hummock vegetation. Shrub layer vegetation died soon after rewetting. However, rapid increase of *Eriophorum vaginatum* and *Carex rostrata* had started by the second year. The bryophytes typical of wet habitats, like *Warnstorfia fluitans* (Hedw.) Loeske and *Sphagnum* species, started to colonize the site more slowly.

Moderate rewetting in the upper section of the rewetted site caused an immediate increase in the cover of *Eriophorum vaginatum* tussocks and seedlings, and the wet mire plant species *Drosera rotundifolia* and minerotrophic species *Carex canescens* L. and *Salix* sp. L. colonized the site. In the bottom layer a considerable increase began a year later. Bryophytes typical of disturbed peat surfaces, like *Dicranella cerviculata*, *Polytrichastrum longisetum*, and *Pohlia nutans*, were clearly favoured.

3.1.4 Growth of re-introduced *Sphagnum*

Moss material with capitula produced higher capitula cover and length than moss material without capitula (Fig 1 in V). One year after re-introduction, the *Sphagnum* capitula cover was similar in drier and wetter treatments, being 48% in the capitulum sample plots and 8% in stem plots. After the first year, the mean cover was always lower in the regularly flooded lower section than in the drier section. The *Sphagnum* surfaces were in a dynamic stage; i.e. there was a significant difference between years, and the development of cover was non-linear. In drier treatment, the length was significantly higher in capitulum plots than in stem plots in each

of the three measurement years. At both moisture levels, the moss length increased linearly during the three year period.

3.2 Carbon dynamics

3.2.1 CO₂ dynamics before and after rewetting

In the cut-away site characterized by the mosaic of tussocks and intertussocks the CO₂ exchange components (P_G , R_{TOT} , P_N) (III) were strongly related to the abundance of *Eriophorum vaginatum* (Figs. 3 & 4). Before rewetting, the mean R_{TOT} on tussocks was approximately three times higher than on intertussocks. After rewetting, the mean R_{TOT} strongly decreased on two intertussock plots, but not on the tussock or the driest intertussock plot (Fig. 3 in III). While rewetting caused an increase in the cover of *Eriophorum vaginatum* tussocks and promoted the development of seedlings (II), the potential P_G at PAR > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ also increased (Fig. 4 in III). The changes in P_N following rewetting were largely similar to those in P_G (Fig. 5 in III).

The 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, and 7 in III). In tussocks, the temporal variation in net CO₂ exchange (P_N) during the growing seasons followed the variation in P_G (Fig. 7 in III). However, because R_{TOT} and P_G reached their maximum at the same time, the increasing trend of P_N towards July - August and the decreasing trend towards autumn were weaker than that of P_G . In the intertussocks with small P_G , the seasonal pattern in P_N during the growing seasons was inverse to the pattern in tussocks (Fig. 7 in III).

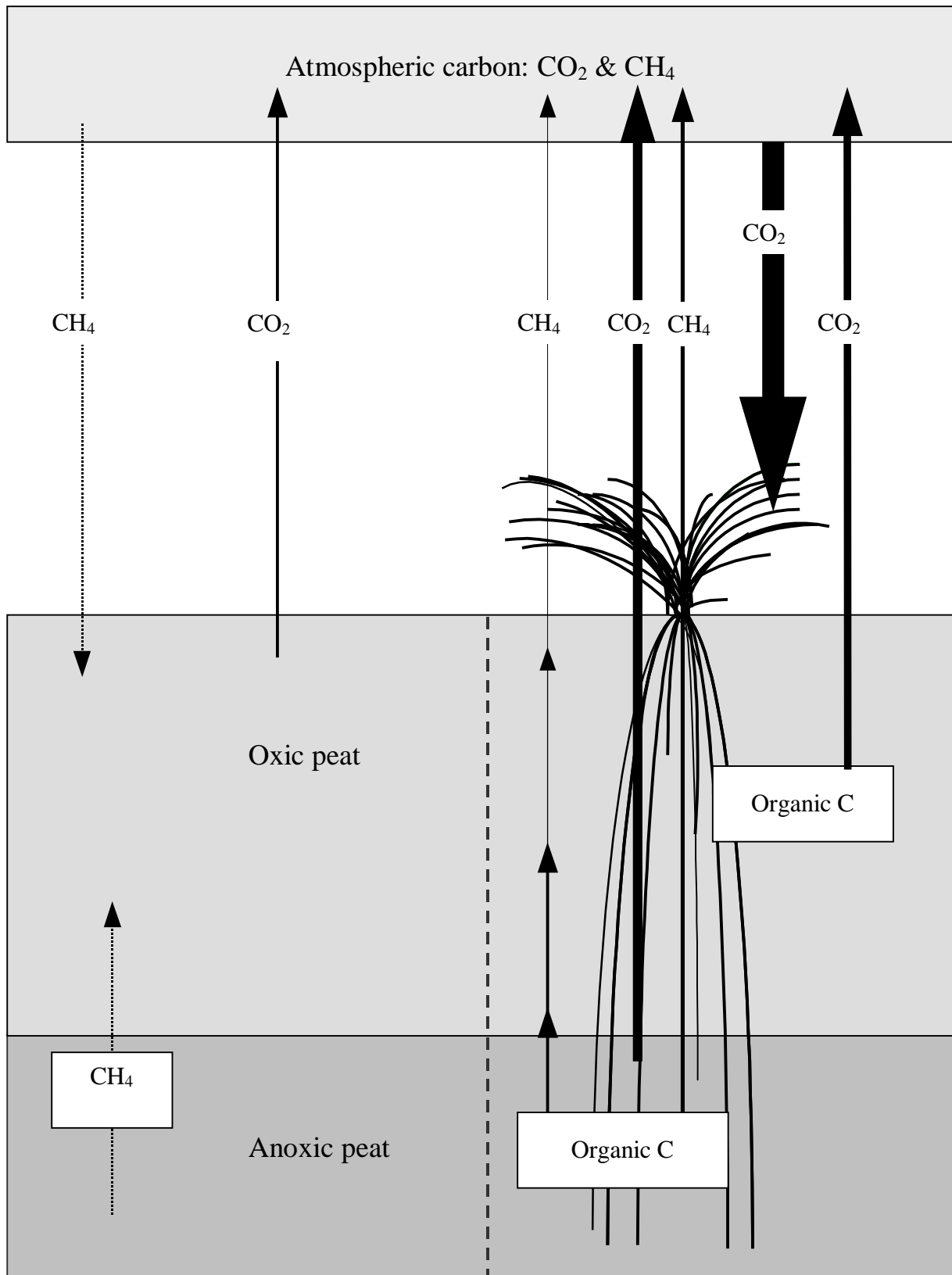


Fig. 3. Gaseous carbon cycle of a dry cut-away peatland.

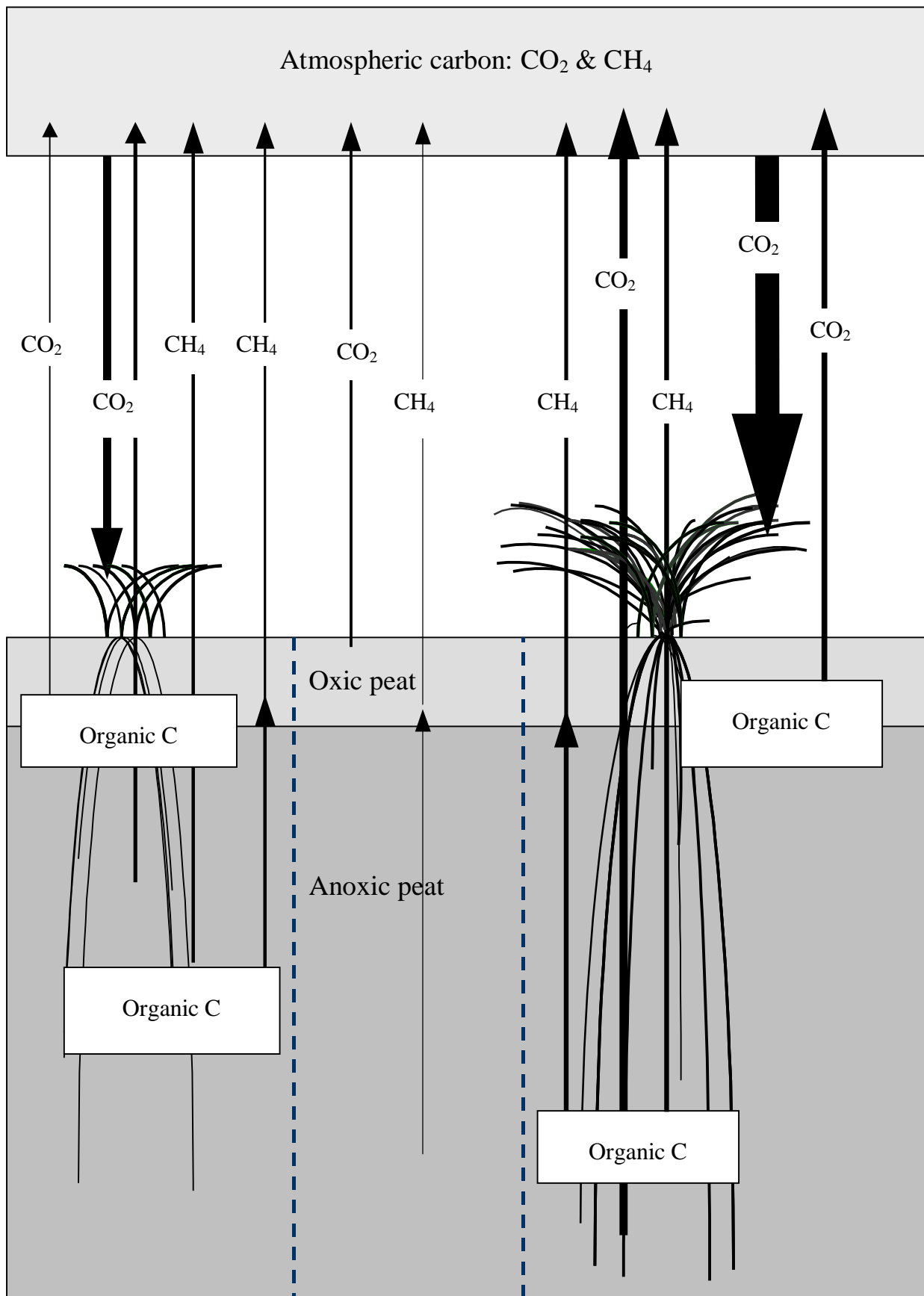


Fig. 4. Gaseous carbon cycle of a rewetted cut-away peatland.

3.2.2 CH₄ dynamics before and after rewetting

The measured CH₄ fluxes were generally low and the mean emissions from tussocks were significantly higher than those from intertussocks (Fig. 2 in **IV**). Before rewetting, all intertussocks consumed CH₄ (Fig. 3).

CH₄ emissions from all sample plots increased slightly after rewetting (Fig. 2 in **IV**). However, the emissions were significantly higher after rewetting only in the tussock sample plot, where a strong increase in *Eriophorum* cover was also observed (Fig. 4).

After the rise in water table level, the dynamics of the CH₄ fluxes in a rewetted tussock coincided with those of P_G until mid August (Fig. 4 in **IV**). However, while the P_G decreased at that time, the increase in CH₄ fluxes continued until mid September.

In the middle of the season, CH₄ emissions from intertussocks were at their lowest while the CH₄ fluxes into intertussocks were at their highest. The CH₄ flux from intertussocks resembled a mirror image of R_{TOT}, but after rewetting, the proportion of CH₄ in the carbon outflux was higher than it had been in 1994 (Fig. 6 in **IV**). The relative proportions of carbon emitted as CH₄ and CO₂ followed seasonal fluctuations in the water table level.

3.2.3 Seasonal CO₂ balance and CH₄ flux before and after rewetting

The seasonal estimates of the CO₂ balance for the calibration period in 1994, which had an exceptionally deep water table level, were all negative, i.e. the system was a net source of CO₂ into the atmosphere (Fig. 8a in **III**). The seasonal estimates for CH₄ fluxes at the study sites were very low (Fig. 7a in **IV**). The highest seasonal CO₂ balance was in the upper section of control site C1 (-111.8 g CO₂-C m⁻²), having the densest *Eriophorum* cover and the highest seasonal CH₄ emission (0.13 g CH₄-C m⁻²). The upper section of rewetted site R1, with the smallest *Eriophorum* cover and

the deepest water table level, had the lowest CO₂ balance (-164.4 g CO₂-C m⁻²), and it was a net consumer of CH₄ (-0.03 g CH₄-C m⁻²).

During the three years after rewetting, there was an obvious increasing trend in the estimated seasonal net CO₂ influx into the rewetted site (Fig. 8a in **III**) as well as in the CH₄ emission from the rewetted site (Fig. 7a in **IV**). This increase followed the growth of the *Eriophorum* cover together with the rising water table. The lower section of the rewetted site with the highest water level, R2, reached a positive seasonal CO₂ balance two years after rewetting. During the third year it was still higher: 64.5 g CO₂-C m⁻². In the upper section of rewetted site R1, which had a moderate rise of the water level, the seasonal balance remained negative during the three-year study period, being -38.3 g CO₂-C m⁻² in the third year. In the third year following rewetting, the reconstructed seasonal CH₄ emission was 0.95 g CH₄-C m⁻² from R2, and 0.40 g CH₄-C m⁻² from R1.

3.2.4 Simulated effect of water level and *Eriophorum* on seasonal CO₂ balance and CH₄ flux

The seasonal CO₂ balance was simulated for conditions on bare peat surface. Environmental data from the rewetted and control sites were used but *Eriophorum* cover was set to zero. Similarly the seasonal CO₂ balance and CH₄ flux were simulated for closed *Eriophorum* vegetation on cut-away peatland, but *Eriophorum* cover was set to 70%, which was here presumed to represent fully closed surface layer vegetation.

The simulation for cut-away peatland with closed vegetation of *Eriophorum* showed that in conditions prevailing in a dry control site, the ecosystem can reach the compensation point (P_G = R_{TOT}), but only if weather conditions are favourable. According to CH₄ flux simulation, methane emission is low, also from *Eriophorum* vegetation, if the water table

remains deep below the surface (Fig. 7b in **IV**).

Moderate rises in water level (R1) lowered CO₂ emission from bare peat surface about 30%, and by raising the water level close to the surface (R2), the emission was reduced by over 50% (Fig. 8c in **III**). In dense rewetted *Eriophorum* vegetation, the simulated seasonal CO₂ balance was positive in each year 1995-1997 (Fig. 8c in **III**). The CO₂ balance was 2-3 times higher with a high rise in the water level than with a moderate rise in the water level.

Raised water table level increased the methane emissions from dense *Eriophorum* vegetation (Fig. 7b in **IV**). Moderate rewetting (R1) increased seasonal emissions to 1.5-1.9 fold, and a high rise in the water level (R2) to 2.6-3.4 fold in comparison to emissions from the *Eriophorum* vegetation having a deep water table.

3.2.5 Factors controlling CO₂ dynamics in *Sphagnum* re-introductions

The water table level and the amount of moss cover controlled how effectively the *Sphagnum* surfaces were able to use irradiation for gross photosynthesis (P_G) (Figs. 3 & 4 in **V**). Gross photosynthesis (P_G) of *Sphagnum* surfaces showed a unimodal response to water table level, which reached a maximum at a water table level of -12 cm (Fig. 3 in **V**). The form of the light response was saturating, but in the measured amplitude of PAR, the *Sphagnum* surfaces did not seem to reach the light saturation point (Fig. 4 in **V**).

The total respiration (R_{TOT}) level of *Sphagnum* and bare peat surfaces increased with increasing temperature and decreasing water table level (Fig. 5 in **V**). The R_{TOT} rate in *Sphagnum* surfaces was clearly higher than the R_{TOT} rate of bare peat surfaces when moisture conditions were favourable for photosynthesis.

The mean of measured net CO₂ exchange (P_N) of *Sphagnum* sample plots was always higher than that of bare peat

surfaces. While the difference in cover between capitulum and stem plots decreased after the first year (Fig. 1a in **V**), the P_N in the two moss material treatments started to resemble each other (Fig. 6 in **V**). The seasonal variation in net CO₂ exchange (Fig. 6 in **V**) followed the seasonal variation in water table level (Fig. 2 in **V**).

The reconstruction of CO₂ fluxes over the growing season 1996 demonstrate the sensitivity of carbon dynamics in *Sphagnum* plots to water table level variation. There was no CO₂ fixation in the drier upper section after the end of August, when the water table level fell below the lower tolerance limit (Fig. 7 in **V**). In contrast, the P_G in the lower section decreased in the beginning of July when the water table level rose clearly above the optimum. However, in conditions too dry for photosynthesis, P_N was also reduced by an increase in R_{TOT}, and the *Sphagnum* surfaces emitted more CO₂ into the atmosphere than the bare peat surfaces.

3.2.6 Seasonal CO₂ balance in *Sphagnum* surfaces

The seasonal estimate of CO₂ balance was positive (21 g CO₂-C) only in the capitulum plots of wetter moisture treatment, where the *Sphagnum* cover was over 90%. All the other plots lost CO₂ to the atmosphere (Fig. 8a,b in **V**). However, *Sphagnum* re-introduction in all plots had reduced the loss, i.e. the *Sphagnum* plots had 4 g and 68 g CO₂-C higher seasonal balances than bare peat surfaces with similar water table levels.

The simulation of a closed *Sphagnum* carpet in optimal water table conditions showed positive P_N over the whole growing season (Fig. 8c in **V**). The seasonal CO₂ balance, 95 g CO₂-C, was 4.5 times higher than the estimate for capitulum plots of wetter moisture treatment, although the *Sphagnum* cover used in the simulation was only slightly higher. In this optimal situation, the CO₂ balance was 159 g CO₂-C higher than in bare peat surfaces.

3.2.7 CH₄ dynamics of *Sphagnum* re-introductions in comparison to bare peat surfaces

The CH₄ fluxes from and to *Sphagnum* surfaces were generally low (Fig. 9 in V). In 1996, CH₄ fluxes measured from capitulum plots varied between -0.1 and 0.2 mg m⁻² h⁻¹, and from bare peat surfaces between -0.1 and 0.3 mg m⁻² h⁻¹. There was no significant difference in the CH₄ fluxes between *Sphagnum* plots and bare peat surfaces, and fluxes did not show any seasonal pattern (Fig. 9a in V). In 1997, when measurements were made only in *Sphagnum* plots, fluxes from capitulum plots into the atmosphere were on average slightly higher, -0.05 – 0.8 mg CH₄ m⁻² h⁻¹, than from stem plots, -0.1 – 0.4 mg CH₄ m⁻² h⁻¹ (Fig. 9b in V). In 1997, fluxes showed a significant seasonal pattern; emissions into the atmosphere were highest at the end of August.

4. DISCUSSION

4.1 Vegetation dynamics

4.1.1 Species composition prior to rewetting resembled dry heath community

Species composition found prior to rewetting supported the Grime's theory (Grime 1977): that perennials with features of stress-tolerants are typical dominant colonizers of nutrient-poor habitats. The finding was in accordance with the previous results of Salonen (1992). The dominant colonizers were typical of the hummock and lawn levels of ombrotrophic mires, such as *Polytrichum strictum* and *Eriophorum vaginatum* (Eurola et al. 1984) or bare peat surfaces, such as *Dicranella cerviculata* and *Polytrichastrum longisetum* (Smith 1978, Koponen 1986) (II).

The site was still in a colonization state, and resembled a dry heath-like vegetation or a secondary birch forest

community that has been described from cut-away peatlands and drained bogs in central Europe (e.g. Pfadenhauer & Klötzli 1996, Money & Wheeler 1999). Ditches isolated the site from the surrounding area and made the site functionally ombrotrophic; it received additional water and chemical elements only from atmospheric deposition. A pattern typical of pristine mires, higher diversity connected to higher nutrient level together with higher wetness (Söyrinki et al. 1977, Vasander 1987), was found on the sites.

4.1.2 Colonization of cut-away peatland was facilitated by *Eriophorum vaginatum*

The aggregation of most species close to *Eriophorum* tussocks with a high proportion of living leaves (I) indicated that *Eriophorum* influences plant colonization patterns. This may reflect the existence of a more humid microclimate under the tussock (Grosvernier et al. 1995, Sliva 1997). The positive interaction between distance from the base of the tussock and shade index (sheltering cavity around the tussock, Fig. 1 in I) found for all the species studied indicates that the smaller the tussock, the nearer the plants have to occur to find a microsite similar to that further away from the base of a larger tussock. This reflects the increasing gradient in exposure from near the base of the tussock to further away, as documented by Sliva (1997). The temperature gradient measured (Fig. 7 in I) supports this finding. The environmental differences between cardinal points from tussocks observed by Sliva (1997) were reflected in the species probability of presence. The probability of presence for all species studied was lower in the southern than in other directions. The smallest temperature fluctuation in the northern direction (Sliva 1997) may be the reason for the more even responses of species on the distance and shade index.

The species studied differed from each other according to their optimal microsites (Figs. 3, 5 and 6 in I). Therefore the char-

acteristic life cycle of *Eriophorum* tussocks (Fetcher & Shaver 1982) forms a temporal ecological gradient in the vicinity of tussocks and increases the number and variety of microsites for colonizers with varying ecological requirements.

4.1.3 Rewetting promoted development towards wet minerotrophic vegetation

This study provides evidence for the assumption (Schouwenaars 1988, Wheeler & Shaw 1995) that conditions wet enough for rapid succession towards closed mire vegetation are only reached by raising the water level so that it is close to the soil surface. In waterlogged conditions *Sphagnum* had established itself amongst *Eriophorum vaginatum* tussocks, but in the drier section, the bryophyte species characteristic of disturbed peat surfaces were spreading (II). Inundation, which caused the death of shrub layer vegetation, stopped the development towards "dry heath-like vegetation" or "secondary birch forest community". Earlier findings on successful *Sphagnum* colonization on or between tussock-building plants in wet conditions comes from the Netherlands (Joosten 1992) and the U.K. (Meade 1992).

The lower nutritional status of the drier rewetted section might also be the reason for the slower compositional change (II), although in this study it is not possible to clearly distinguish the effects of water table level and fertility. The rate of peatland vegetation succession after drainage (Laine et al. 1995) and after rewetting (Komulainen et al. 1999) have been shown to be dependent on the fertility of the site: the compositional change is more rapid in nutrient-rich than nutrient-poor sites.

4.1.4 *Sphagnum* re-introduction promoted the formation of moss carpet

Sphagnum re-introduction succeeded rather well, although the moisture conditions in our experiment did not resemble those typical of natural habitats of *Sphagnum angustifolium*: lawns or low hummocks of relatively dry oligotrophic

bogs and fens (Horton et al. 1979, Pakarinen 1979, Gignac & Vitt 1990). The capitulum cover in stem plots one year after re-introduction (Fig. 1 in V) was slightly higher than that found in short-term trials in Canada (Campeau & Rochefort 1996, Ferland & Rochefort 1997), and the ten-fold cover in capitulum plots showed high potential of capitula for the rapid development of *Sphagnum* carpet.

The higher capitula cover in the drier section (Fig. 1 in V), was contrary to the results from a greenhouse experiment, where *Sphagnum angustifolium* showed higher regeneration in a water level of -5 cm than in -15 and -25 cm (Campeau & Rochefort 1996). The weak success in the wetter section was a result of peat erosion and the disappearance of mosses due to periodical floodings. This was also observed by Money (1995) and Sliva & Pfadenhauer (1999). Sliva and Pfadenhauer (1999) found that vascular plants can stabilise the peat surface, and thus enhance the success of *Sphagnum* establishment.

4.2 Carbon dynamics

4.2.1 CO_2 and CH_4 dynamics was controlled by *Eriophorum vaginatum*

The rewetting had no direct effect on gross photosynthesis of *Eriophorum* (P_G) (III). This was because *Eriophorum* is a deep-rooting species (Metsävainio 1931, Bliss 1956) and therefore it can transfer water from deeper soil layers and keep its stomata open even during periods of low water levels. However, rewetting indirectly increased P_G of the site by promoting an increase in the cover of *Eriophorum* tussocks and seedlings (II & III). Results from experimental work in arctic tundra similarly showed that in flooded soils at high nitrogen availability the growth of *Eriophorum vaginatum* is improved by increased tillering (Gebauer et al. 1995).

In intertussocks, total respiration (R_{TOT}) is mainly composed of CO_2 released by aerobic decay of peat; but within *Eriophorum* tussocks, it also includes dark respiration of plants and oxidation of dead plant material and root exudates. A 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 only 20% in the rewetted site (III). 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 (Theander 1954, Hogg 1993), new carbon seems to be even more important than in other peatland ecosystems.

Even more clearly than total respiration, the spatial distribution of methane emissions at the sites was determined by the occurrence of *Eriophorum* tussocks (IV). The importance of vascular plants for CH_4 flux is also been shown in the studies of Schimel (1995), Granberg (1998), Verville et al. (1998), and Saarnio and Silvola (1999). In cut-away peatland the 3000-7000 year old peat appears to be an unsuitable substrate for methanogenesis. The extremely low CH_4 emissions measured from inter-tussocks - even when the water table had been raised close the soil surface (Fig. 2 in IV) - shows the importance of plants in producing new plant litter and root exudates in the rhizosphere, as the substrate for methanogenesis (Schütz et al. 1991, Whiting & Chanton 1993, Thomas et al. 1996, Huang et al. 1997a, b). The deep roots of *Eriophorum* (Metsävainio 1931, Bliss 1956) can channel organic substances into anoxic soil layers, even when the water table is low. The difference in methane emissions between tussocks and non-vegetated intertussocks

was higher in a cut-away site than between tussocks and moss dominated intertussocks in tussock tundra (Whalen & Reeburgh 1988, Johnson et al. 1996). Whalen and Reeburgh (1988) suggests that the difference in CH_4 emission level between tussocks and intertussocks is a result of more efficient transport inside the aerenchyma. Although the transportation through the aerenchyma pathway of *Eriophorum* is highly efficient due to the very low oxidation of methane (Frenzel & Rudolph 1998), the higher difference between tussock and intertussocks in a cut-away site indicates that the substrate availability for CH_4 production is more important than the rapidity of transport for CH_4 emissions from cut-away peatland.

The direct effect of raised water table on CH_4 emission from *Eriophorum* vegetation was shown in the simulation for closed *Eriophorum* vegetation (Fig. 7b in IV), where CH_4 emission from the moistest section was about three fold more than emission from the dry control area. In intertussocks, the direct effect of rewetting on CH_4 emission was weak. Similarly to CO_2 exchange dynamics, rewetting also had a strong indirect effect upon the CH_4 flux from the rewetted site via the expansion of *Eriophorum* (II, III, IV). A similar indirect effect of rewetting on CH_4 emission via the increase of *Eriophorum* has also been reported from a restored fen previously drained for forestry (Komulainen et al. 1998).

4.2.2 Seasonal variation in CO_2 and CH_4 dynamics was related to sequential leaf development of *Eriophorum vaginatum*

The seasonal variation in the photosynthetic activity of *Eriophorum* is a consequence of the sequential leaf development characteristic of this species (Robertson & Woolhouse 1984, Jonasson & Chapin 1985, Defoliart et al. 1988, Shaver & Laundre 1997). 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 through most of the season because new leaves with high photosynthetic capacity gradually replace the overwintered leaves with decreased capacity (Robertson & Woolhouse 1984, Defoliart et al. 1988). The effective temperature sum index (ETI), which was used in the model to explain the seasonal variation of *Eriophorum*'s photosynthetic capacity, rapidly increased in the beginning of the season and reached its highest values in August, when maximal gross photosynthesis (P_G) was also reached in most years (Figs 6 and 7a in **III**). The moderate decrease in ETI at the end of the season described well the decrease in P_G , which was caused mostly by lowered irradiation and temperature. The seasonal variation in P_G was controlled by the same factors as in mires: temperature, irradiation, and the resultant seasonal growth dynamics of plants. Therefore the seasonal pattern was similar to the variation found in pristine peatland ecosystems (Bubier et al. 1998).

A large part of the new carbon, sequestered by the plant itself, is released in respiration, as seen in similar seasonal variation in P_G and R_{TOT} (Fig. 4 in **IV**). During the period of high P_G and consequent high potential substrate levels for methanogenesis, CH_4 emission was also high, if the oxidation of substrate and methanotrophic consumption of CH_4 in the aerobic layer did not restrict it. In mid-August, when P_G started to decrease due to decreasing irradiation and R_{TOT} decreased due to rising water levels, the carbon fixed to plant material became available for methanogenesis via senescence. During the time of high carbon influx into the system, the substrate introduction to the anoxic layers may be higher than the decomposition capacity of the anaerobic processes. Therefore, in addition to dead plant material, the substrate storage accumulated during the season can maintain methanogenesis while the CO_2 influx into the sys-

tem decreases. This pattern, the loose relationship with lag between CO_2 influx and CH_4 emission, is in accordance with the seasonally increasing trend of potential CH_4 production until late autumn found in peat of a pristine fen and a pristine bog (Saarnio et al. 1997, Kettunen et al. 1999). The results of Huang et al. (1997b) also suggest that substrates produced during high season may be stored for the later methanogenesis because of the limited size of microbial population.

4.2.3 Seasonal CO_2 balance and net CH_4 flux increased after rewetting and following expansion of *Eriophorum vaginatum*

The water level before rewetting was deeper than during any of the three following years in the control area as well, and this was reflected in the very low, negative seasonal CO_2 balance (Figs 1, 7a in **III**) and low CH_4 emissions (Fig. 7a in **IV**). Similarly, a net loss of carbon was measured from a pristine bog in Finland (Alm et al. 1999b) and Sweden (Waddington & Roulet 2000). The net loss of gaseous carbon from the study sites was, however, over 2-3 times greater than the loss from the Finnish bog and 124-184 times greater than from the Swedish bog. The large annual variation of seasonal CO_2 balance at the control site (Fig. 8a in **III**) as well as the results of Alm et al. (1999b) and Waddington & Roulet (2000) 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 seasonal methane fluxes were at the same level as those from other northern drained peatlands with deep water table levels (Roulet et al. 1993, Roulet & Moore 1995, Nykänen et al. 1998).

In the seasonal balances of both gaseous forms of carbon there was an increasing trend following rewetting towards the dynamics typical of pristine peatlands. However, the change in CO_2 dynamics was much faster than in CH_4 (**III**, **IV**). Alm et

al. (1999b) estimate that an average seasonal CO_2 balance of $64\text{--}76 \text{ g C m}^{-2}$ is needed for the long-term average annual carbon accumulation in Finnish bogs, $24.0 \pm 0.5 \text{ g C m}^{-2}$ according to Tolonen & Turunen (1996). The rewetted site with a high water level had already reached this rate in the third year after rewetting (III). The seasonal CH_4 fluxes did not reach the level of seasonal emissions from pristine mires in the same area (southern and middle boreal Fennoscandia) (Saarnio et al. 1997, Nykänen et al. 1998, Waddington & Roulet 2000), or from pristine mires in Minnesota and Michigan (Crill et al. 1992, Dise et al. 1993, Shannon, R.D. & White 1994). The simulation for full *Eriophorum* cover in a rewetted environment (Fig. 7b in IV) also showed lower seasonal emissions, which were at a level measured from pristine bog under exceptionally dry summer conditions (Alm et al. 1999b). This is in accordance with the results from restoration experiments of peatlands drained for forestry in which the seasonal CH_4 emissions, although higher after rewetting, remained at a lower level than the seasonal emissions from pristine peatlands (Komulainen et al. 1998). Similarly lowered emissions with a high water table level following a long dry period have been observed in a pristine bog (Shannon & White 1994). In a laboratory experiment where peat columns were first dried and then rewetted, a similar phenomenon was also observed (Moore & Dalva 1993). It thus seems that following successful restoration, cut-away peatlands can develop towards carbon accumulating peatland ecosystems within a reasonable period of time, but at least during the first years CH_4 emissions could remain at a lower level than those from pristine peatlands.

One potential factor causing the low CH_4 emissions might be a reduced methanogenic population in dry peat, as discussed by Shannon & White (1994). According to a three-year study, they suggested that more than one year is needed to restore methane fluxes following a rela-

tively dry period in pristine peatland. As cut-away peatland has been dry for decades, it is possible that colonization and growth of a methanogenic population takes a considerably longer time than in pristine mires after a shorter dry period. Monitoring for a longer period than the two years covered in this study is needed to assess the CH_4 flux dynamics level of cut-away peatlands after restoration.

4.2.4 CO_2 dynamics in *Sphagnum* re-introductions was controlled by water table level

Water table level had a dual effect on total respiration (R_{TOT}) of *Sphagnum* re-introductions. The thickness of the aerobic layer above the water table regulated oxidation of peat and CH_4 , as was also seen in the results from the bare peat surfaces (III, IV, V). This is in accordance with results from various peatland ecosystems (eg. Peterson et al. 1984, Funk et al. 1994, Silvola et al. 1996, Bubier et al. 1998, Nieveen et al. 1998, Komulainen et al. 1999). Because the young *Sphagnum* re-introductions contained only a small amount of dead moss material, the difference between R_{TOT} of bare peat surfaces and re-introductions consists almost exclusively of the respiration of living moss material. This metabolic activity seemed to have a unimodal response to moisture (Fig. 5a in V) like P_G (Fig. 3 in V).

The Gaussian form of the response of the photosynthesis to water table level (Fig. 3 in V), which was used to describe environmental moisture similarly to Vourlitis et al. (2000), is in accordance with the response of P_G to moisture content found in earlier studies with the same species (Silvola & Aaltonen 1984, Murray et al. 1989, Silvola 1991). *Sphagnum angustifolium* (Silvola & Aaltonen 1984, Murray et al. 1989, Silvola 1991) as other *Sphagnum* species (Titus et al. 1983, Titus & Wagner 1984, Rydin & McDonald 1985, Gaberscik & Martincic 1987, Schipperges & Rydin 1998, Jauhiainen & Silvola 1999) has a unimodal response of

photosynthesis to the moisture content. Below the moisture optimum, photosynthesis is restricted by the lack of water for metabolic processes, but when mosses become water saturated, the gas (CO_2 , O_2) diffusion rate to and from chloroplasts limits CO_2 fixation (Proctor 1982, Williams & Flanagan 1996).

The measurements did not show light saturation of instantaneous P_G , even at an irradiation level of over $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$. This was in contrast with the results of Harley et al. (1989), who found light saturation for the net photosynthesis of *S. angustifolium* already below $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. This may be because, unlike in the earlier study, P_G rate was measured *in situ*. Inside the moss cover and close to the peat surface, where CO_2 concentration is markedly higher than ambient CO_2 concentration (Sonesson et al. 1992, Tarnawski et al. 1992, Hogg 1993), the availability of CO_2 is not likely to restrict *Sphagnum* photosynthesis as it has been found to do in ambient air CO_2 concentration (Jauhiainen & Silvola 1999). This indicates that a large number of *Sphagnum* photosynthesis studies where mosses have been taken out of the moss carpet, (eg. Skre & Oechel 1981, Gerdol et al. 1996, Potter et al. 1996, Schipperges & Rydin 1998), may underestimate the rate of photosynthesis in natural habitats of *Sphagna*.

4.3.5 *Sphagnum* re-introduction reduced carbon loss from cut-away peatland

In spite of the mainly negative mean P_N measured in *Sphagnum* plots during the four-year study, *Sphagnum* re-introduction caused a functional change and raised CO_2 balance to a higher level than that found in bare peat surfaces (Fig. 6 in V). The found high seasonal variation in the CO_2 dynamics is typical of pristine peatlands (Goodman & Perkins 1959, Bubier et al. 1998, Alm et al. 1999b). Desiccation of mosses in pristine peatlands can also reduce CO_2 balance; the maximum loss of CO_2 from *Sphagnum* plots was similar to the loss measured in *Sphagnum*

angustifolium lawns of a pristine boreal bog during an exceptionally dry summer (Alm et al. 1999b). However, the maximum P_N of lawns (Alm et al. 1999b) was twice as high as the maximum of capitulum plots, and five times higher than the maximum of stem plots. The reconstructed seasonal balance of capitulum plots in the wetter lower section, the only treatment with a positive balance (Fig. 8 in V), was only one third of the average seasonal CO_2 balance that Alm et al. (1999b) estimated as necessary for the long-term average annual carbon accumulation in Finnish bogs according to Tolonen & Turunen (1996).

The *Sphagnum* re-introduction experiments in Canada have shown that *Sphagnum* establishment success is related more to the humidity of microclimate rather than directly to water table level. An east-Canadian group (Quinty & Rochefort 1997, Rochefort & Campeau 1997) has created a restoration method in which a mulch cover reduces evaporation from re-introduced *Sphagna* and the soil surface, and favours the formation of a moss layer. The method alone, however, is not likely to lead to a regeneration of a carbon accumulating peatland ecosystem if oxic decomposition is not reduced by rewetting, as the CO_2 loss from well established but dry *Sphagnum* carpet showed (Fig. 8 in V). When combined with rewetting, the method is very promising; the water table level is higher and water table level fluctuation is more moderate than those of a rewetted site without mulch cover, because of the lowered evaporation (Price 1997, Price et al. 1998).

The 1996 results (Fig 9a in V), which showed no difference in CH_4 emissions between bare peat surfaces and *Sphagnum* plots, indicates that *Sphagnum* re-introduction does not generate new, easily decomposable substrate for methanogenesis. This is contrary to the results of Roura-Carol & Freeman (1999), who, in laboratory conditions, measured higher CH_4 fluxes in *Sphagnum* cores than in peat

cores from which the living *Sphagnum* had been removed. This contrast is surprising, because the difference in age between living *Sphagnum* and peat was much smaller in cores taken from a pristine mire (Roura-Carol & Freeman 1999) than in re-introductions (V). In 1997, capitulum cover had decreased from the previous year, and the plots contained dead *Sphagnum* material. The higher methane emission from capitulum plots with higher cover than from stem plots, might have been caused by methanogenesis promoted by the dead moss material. Because of the conflicting results, the lack of measurements in bare peat surfaces in 1997, and the small data, a larger study is needed to evaluate the importance of *Sphagnum* re-introduction to CH₄ dynamics of cut-away peatlands.

4.3.6 Restored cut-away peatland is a potential carbon sink and CH₄ source

In Finland alone, which has the world's fourth largest peat harvesting area (Lappalainen 1996), the area of cut-away peatlands is 3000 ha (Selin 1996). If the simulations for bare peat surfaces (III) are generalized for this area, the seasonal CO₂ emission without restoration can be estimated to be 3.8*10⁹ - 5.7*10⁹ g CO₂-C annually. If the winter CO₂ loss is 23% of the annual emission as found for a pristine bog (Alm et al. 1999a), the cut-away area would form an annual source for 4.9*10⁹ - 7.4*10⁹ g CO₂-C into the atmosphere. With a 2000 ha annual increase in cut-away area (Selin 1996), seasonal emission will be increasing by 2.5*10⁹ to 3.8*10⁹ g CO₂-C, or annual emission by 3.2*10⁹ - 4.9 *10⁹ g CO₂-C every coming year. In this area, however, there would be no methane emission from peat strips (IV).

After rewetting, and with dense *Eriophorum* vegetation, the balance would turn positive with an annual carbon accumulation of 31-105 g C m⁻² (III, IV) if the winter time CO₂ and CH₄ flux estimates for a pristine bog: 23% and 22% of annual CO₂ and CH₄ emissions (Alm et al.

1999a), are valid for cut-away peatlands. This positive carbon balance includes an annual 3 - 5 g C m⁻² methane emission into the atmosphere. Thus, after successful restoration, the Finnish cut-away peatlands (3000 ha) would form an annual sink of carbon for 0.9*10⁹ - 3.1*10⁹ g, and act as a methane source for 0.1*10⁹ g CH₄-C. With a 2 000 ha annual increase in area, the annual increase in the sink would be 0.6*10⁹ - 2.1*10⁹ g C a⁻¹. Because in boreal and temperate zones *Eriophorum vaginatum* has been found to be a typical dominant species during early-succession in cut-away peatlands (Smart et al. 1989, Salonen 1992, Cooper & McCann 1995, Campeau & Rochefort 1996), the importance of the species in the carbon dynamics of cut-away peatlands may be assumed to be a general phenomenon.

In optimal water level conditions for photosynthesis, the simulated seasonal CO₂ balance estimate for a closed *Sphagnum angustifolium* carpet was higher than the average for Finnish bogs (Tolonen and Turunen 1996; Alm et al. 1999b), and similar to the estimate in closed *Eriophorum* vegetation with a high water table level in the same growing season 1996 (III, V). However, according to what is known of the hydrology of cut-away peatlands (e.g. Schouwenaars 1993, Price 1997, Sliva & Pfenhauer 1999), a simulated situation in which the water table remains at an optimal level over the whole growing season is not easy or even possible to maintain in field conditions.

5. CONCLUSIONS

Although *Eriophorum vaginatum* is a typical bog species, Pfenhauer & Klötzli (1996) do not consider its mass establishment as an indicator of bog regeneration. If the formation of closed *Sphagnum* carpet or acrotelm (Pfenhauer & Klötzli 1996, Money & Wheeler 1999) is seen as the main indicator of successful restoration, neither of the sections of the rewetted site

had developed into a mire ecosystem during the four-year period after rewetting. However, the results showed that the wetter section of the site had become a net sink of atmospheric carbon during the third year after rewetting (III) and both had changed from a net methane sink to a source (IV). This functional change towards a mire ecosystem was mainly caused by the expansion of *Eriophorum vaginatum* following rewetting.

The relatively slow colonization of mire plant species, most of which were already present prior to rewetting (II), accords well with the time estimation of the colonization phase in the theoretical model of the restoration process for cut-away peatlands after rewetting (Kuntze & Eggelmann 1981). However, as found in this study (I, III, IV), the fact that the functional change towards a mire ecosystem happened when the site was not fully colonized shows that the phases in the restoration process (Kuntze & Eggelmann 1981) cannot be separated, since mire regeneration is a complex of dynamic and interactive processes.

If the restoration of minerotrophic vegetation is faster than that of ombrotrophic vegetation, as the results of study II and Komulainen et al. (1999) indicate, adding nutrients to these sites could enhance restoration. Furthermore, the fertilization experiments of Salonen & Laaksonen (1994), LeQuéré (1996), and Sliva & Pfohl (1999) show faster colonization and improved establishment of re-introduced *Sphagnum* and other mire species. This type of manipulation is in line with natural mire development where the minerotrophic phase comes before the ombrotrophic phase.

Similarly to the colonization of the vascular plants and bryophytes found in this study (I), *Sphagnum* regeneration from re-introduced fragments strongly benefits from the presence of vascular plants (Ferland & Rochefort 1997, Sliva 1997, Boudreau & Rochefort 1998, Sliva & Pfohl 1999). The results of this

study show that the carbon balance in peat surfaces with re-introduced *Sphagnum* is more sensitive to variation in water table (V) than the carbon balance in cut-away peatland dominated by *Eriophorum* (III). These results thus support the use of companion species together with *Sphagnum* re-introduction in order to more rapidly regenerate the carbon sink function of the ecosystem.

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