

Carbon sink function of sedge and *Sphagnum* patches in a restored cut-away peatland: increased functional diversity leads to higher production

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Summary

1. Cut-away peatlands devoid of vegetation form a persistent source of carbon (C) to the atmosphere. The restoration of the C sink function in such areas can be facilitated by raising the water table. Planting vascular plants and *Sphagnum* may hasten the restoration process further. However, little is known about the effects of different species on the restoration process.

2. We studied carbon dioxide (CO₂) exchange in stands of different plants in a restored cut-away site over two growing seasons to quantify their ability to form a C sink. We sampled five different types of stand: monocultures of *Eriophorum vaginatum* and *Carex rostrata* (pure plots), mixtures of *Eriophorum* or *Carex* and *Sphagnum* mosses (mixed plots) and control plots without vegetation. We applied the closed chamber technique to gather CO₂ exchange data for modelling of gross photosynthesis (P_G) and ecosystem respiration (R_E). Finally, we used the models to reconstruct the seasonal net CO₂ exchange of the stands formed by different plants.

3. While the control plots without vegetation were sources of 20–71 g CO₂-C m⁻², all the vegetated plots acted as C sinks during both growing seasons. The monostands of *E. vaginatum* and *C. rostrata* created sinks of 23–114 g CO₂-C m⁻², while the mixtures of sedge and *Sphagnum* mosses resulted in larger sinks of 75–186 g CO₂-C m⁻². The larger sinks of the mixed patches were due to the lower respiration/photosynthesis ratio.

4. To eliminate the effect of differences in water table and the abundance of sedges between the patches, we reconstructed the CO₂ exchange for constant water table and vascular leaf area for all plots. The simulation further supported our result: the mixtures of sedge and *Sphagnum* mosses were clearly more efficient in sequestering CO₂ than pure sedge stands.

5. *Synthesis and applications.* The increased functional diversity in a cut-away peatland site resulted in higher net ecosystem exchange. When restoring cut-away peatlands, reintroduction of *Sphagna* is recommended after the colonization of vascular plants to hasten the formation of a sink for C.

Key-words: carbon dynamics, *Carex*, CO₂, ecosystem functioning, ecosystem respiration, *Eriophorum*, photosynthesis, RECIPE, restoration

Introduction

In pristine peatlands the high water table leads to a situation where the primary production exceeds the rate of decomposition; therefore they accumulate peat and act as a store for atmospheric carbon (C). In many countries the accumulated peat is used for horticultural purposes and for energy production. Prior to industrial harvesting the area is drained and the living vegetation removed (Frilander, Leinonen &

Alakangas 1996). These activities change the hydrology, microclimate and ecology of the entire ecosystem (Waddington & Price 2000; Waddington, Rotenberg & Warren 2001). Peat harvesting, and the lowering of the water table that accompanies this process, leads to oxidation of the peat and changes the area to a source for atmospheric C (Alm *et al.* 1997; Tuittila *et al.* 1999, 2000; Waddington *et al.* 2001).

Although some cut-away peatlands do regenerate spontaneously after industrial-scale harvesting (Girard, Lavoie & Thériault 2002), the regeneration process in general is slow (Salonen & Laaksonen 1994; Tuittila, Vasander &

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Laine 2000) unless hastened by human intervention through restoration. The first step in the restoration process is to raise the water table, which is the precondition for the peat-forming key species, *Sphagnum* mosses and sedges, to recolonize the area (Schouwenaars 1993; Tuittila *et al.* 2000; Girard *et al.* 2002; Van Seters & Price 2002; Rochefort *et al.* 2003). Both *Eriophorum vaginatum* L. and *Carex rostrata* Stokes are able to colonize restored areas rapidly (Tuittila *et al.* 2000; Lavoie *et al.* 2003; Lavoie *et al.* 2005) and may facilitate the colonization of mosses (Grosvernier *et al.* 1995; Tuittila *et al.* 2000). As the colonization of the key species is the limiting factor in the restoration (Salonen & Setälä 1992; Cobbaert, Rochefort & Price 2004), the process can be hastened by reintroduction or planting that can increase both the number of individuals and their coverage (Cobbaert *et al.* 2004). Restoration can also be speeded up by fertilization, by tilling or by adding straw mulch to protect *Sphagnum* L. diaspores from desiccation (Salonen & Laaksonen 1994; Rochefort *et al.* 2003).

The restored areas are normally small and thus do not form an important C sink in a global scale. However, the restoration process is important because it ends the oxidation of the residual peat and thus the fast decay and release of CO₂ to the atmosphere (Tuittila *et al.* 1999; Waddington *et al.* 2001). In general, the carbon sink function of restored areas has been found to be very efficient compared to pristine peatlands at the beginning of the process, i.e. a few years after raising the water table (Tuittila *et al.* 1999; Bortoluzzi *et al.* 2006), although contrasting results have been reported (Marinier, Glatzel & Moore 2004). The formation of strong C sinks seems to be related to mass colonization of sedge species (Tuittila *et al.* 1999; Bortoluzzi *et al.* 2006), but little is known about the effect of reintroduced *Sphagnum* on carbon balance. Although *Sphagnum* are the most important peat-forming species, they may restrict the growth and photosynthesis of other plants (Van Breemen 1995), which may result in declining C sink strength. Thus, in the long term, the carbon sink strength of restored peatlands may be declining (Glatzel, Basiliko & Moore 2004; Yli-Petäys *et al.* 2007). What happens in the shorter term is unclear, as is the role of different species in the formation of C sinks in restored areas.

When planning restoration we need to understand the roles of different plant species in ecosystem C dynamics and the conditions favouring their functioning. In this study we quantify the role of two sedge species, *Carex rostrata* and *Eriophorum vaginatum*, and *Sphagnum* mosses in the CO₂ balance of a restored cut-away peatland and their responses to the water table.

Materials and methods

STUDY SITE

The study was carried out during the 2003 and 2004 growing seasons in Aitoneva (62°12' N, 23°18' E), Kihniö, southern Finland. Aitoneva is one of the European RECIPE (Reconciling commercial exploitation of peat with biodiversity in peatland ecosystems) sites and is situated in the south boreal zone (Ahti, Hämet-Ahti & Jalas 1968).

The long-term annual mean temperature of the area is 3.5 °C and the mean precipitation 700 mm. The average growing season is 160 days, with a cumulative temperature sum (threshold value + 5 °C) of 1100 degree days. The study site itself was an old peat harvesting area, which was abandoned in 1975. The residual peat before the restoration was approximately 1 m thick and was fairly decomposed *Eriophorum-Sphagnum* or partly sedge-*Sphagnum* peat. The area was restored in 1994 by blocking the drainage ditches with peat dams and excavating a feeder ditch to bring water from the surrounding areas into the study site (Tuittila *et al.* 2000). Thereafter, the area was allowed to revegetate spontaneously; only minor planting of *Sphagnum* was carried out in a close-by area, which should not have affected the study area.

To compare CO₂ dynamics in the different vegetation types characteristic of the restored site we established a total of 19 sample plots in four types of vegetation stands along a moisture gradient at the site: monocultures consisting of either *E. vaginatum* L. ($n = 8$) or *C. rostrata* Stokes ($n = 3$) (referred to hereafter as pure stands) and mixtures of *Eriophorum* ($n = 3$) or *Carex* ($n = 5$) with *Sphagnum* spp. (mixed stands). Additionally, we laid out three bare control plots where any vegetation was removed; the control plots were chosen where possible on bare peat to avoid the effects of removing the vegetation. The area was divided into three according to depth of the water table and the sample plots were situated along this gradient. Three *Eriophorum* plots, two control plots and one *Carex* plot were situated in the upper, dry area; two *Eriophorum* plots and a control plot were situated in the middle part; and the remaining plots in the lower, wetter part. All the mixed plots were situated in the lower, wetter area because *Sphagnum* did not grow in the drier area. The sample plots for all pure stands and mixed *Carex* stands were established at the beginning of the 2003 growing season. The mixed *Eriophorum* stands were added a year later, at the beginning of the growing season 2004 when *Sphagnum* had spread sufficiently to form mixed stands with *Eriophorum*. For CO₂ exchange measurement, the sample plots were surrounded with aluminium collars (60 × 60 cm) inserted into the peat. The collars had water channels which were filled with water during the measurements to make an airtight seal between the chamber and air. Boardwalks were constructed to access the study site to avoid disturbance during the measurements.

VEGETATION MONITORING

To relate the spatial and temporal variation in CO₂ exchange to the vegetation type, we monitored vascular green area (VGA) development in the 19 sample plots over the growing seasons. We estimated the VGA as a product of leaf number and the average size of the leaves. From each sample plot the number of leaves was counted monthly and the size of the leaves was measured on permanently marked individuals of *Carex* and *Eriophorum* ($n = 3$) outside the sample plots every 3–4 weeks. To obtain a daily estimate of the total VGA in each sample plot we fitted a log-normal curve to the VGA observations separately for each plot using the Julian day as an explanatory variable. In the VGA development of *Eriophorum*, we observed a smaller VGA peak in the spring compared to the mid-summer maximum. It is typical for *E. vaginatum* to grow up to four cohorts every year (Silvan *et al.* 2004); this pattern was described by fitting a curve for the spring and the summer (autumn data were modelled separately). The VGA method is described in detail by Wilson *et al.* (2007). In contrast to the studies by Drösler *et al.* (2005) and Bortoluzzi *et al.* (2006), the coverage of *Sphagnum* was not taken into account in the models, although it was estimated on a percentage scale from every sample plot.

A two-way analysis of variance (ANOVA) was performed on the VGA data to examine the possible differences between the two vascular plant species and the 2 study years in the timing of the maximum VGA.

To relate the variation in the vegetation patches to moisture we established 19 additional sample plots (60 × 60 cm) along the water table (WT) gradient, which were located systematically at a 120 cm distance from the selected sample plots. We described species composition in the sample plots by estimating the projected cover for each species. We applied canonical correspondence analysis (CCA) to quantify compositional change along the WT gradient using the Canoco software package (Ter Braak & Šmilauer 2002).

MEASUREMENTS OF CO₂ FLUXES

CO₂ exchange measurements commenced at the end of May or in early June and were carried out biweekly until September. Before the measurements, the channel in the collar was filled with water to ensure an airtight seal between the collar and the chamber. The net ecosystem CO₂ exchange (NEE) was measured at different irradiation levels [photosynthetically active photon flux density (PPFD) μmol m⁻² s⁻¹] and in the dark using a transparent plastic chamber (60 × 60 × 30 cm) and a portable infra-red gas analyser (PP Systems UK EGM 2). Whenever possible, the measurements were performed at different irradiation levels using cloud cover or artificial shade to lower the radiation after the measurement in full daylight. Between measurements the chamber was removed to stabilize the gas concentration. At the end of the measurement series, the chamber was covered with an opaque hood to measure NEE in the dark, which provided an estimate for ecosystem respiration (R_E). During every measurement the CO₂ concentration in the chamber was recorded every 15 s over a 2–3 min measurement period. The chamber was equipped with an air circulating fan and a cooling coil to keep the temperature inside the chamber ambient. The method has been described previously by Alm *et al.* (1999, 2007) and Tuittila *et al.* (1999). 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; for the ecosystem exchange of CO₂ and CH₄, we use positive values when the ecosystem is gaining carbon from the atmosphere and negative values when the ecosystem is losing carbon.

We recorded the temperature inside the chamber and the level of PPFD concurrently with gas concentration. The temperature in the peat profile at depths of 5, 10 and 20 cm and the WT, in relation to the peat surface, was also measured.

MODELLING THE CO₂ EXCHANGE

To estimate CO₂ exchange over the growing seasons in different vegetation patches and to quantify their response to environmental variation, we formed models for gross photosynthesis (P_G) and ecosystem respiration (R_E) separately for each vegetation type and bare peat (R_{PEAT}). Models are adapted from, and the response functions are discussed in Tuittila *et al.* (2004).

We applied the Michaelis–Menten function to describe the saturating relationship between P_G and PPFD. We used a Gaussian form of response to describe the unimodal dependence of P_G to air temperature (T_{air}). We included VGA and *Sphagnum* in the model to describe the seasonal variation in photosynthesizing plant material. The P_G model had the form:

$$P_G = P_{\text{MAX(PPFD,T,VGA,S)}} \times [\text{PPFD}/(k_{\text{PPFD}} + \text{PPFD})] \times \text{VGA}/(k_{\text{VGA}} + \text{VGA}) \times \exp(-0.5[(T_{\text{air}} - o)/t]^2) \times (S) \quad \text{eqn 1}$$

The function $P_{\text{MAX(PPFD,T,VGA,S)}}$ denotes the level of photosynthesis that could be reached if the amount of light (PPFD), photosynthesizing plant material (VGA, S) or temperature (T_{air}) did not limit photosynthesis. The parameter k_{PPFD} denotes the PPFD level where half the PPFD-saturated P_G is reached, k_{VGA} denotes the VGA level where half of the VGA saturated P_G is reached, T_{air} is air temperature, o is the optimum air temperature for photosynthesis, t is air temperature tolerance for photosynthesis and S is a parameter applied to describe the photosynthetic potential of *Sphagnum* in relation to VGA. We parameterized the P_G model for the different stands separately. For *Carex*, which had a lower VGA than *Eriophorum* and was probably less self-shading with more available nutrients, we used a linear form instead of the saturating VGA response. The parameter S , denoting *Sphagnum* photosynthesis, was used only for mixed *Carex* stands.

R_E originates from both autotrophic and heterotrophic respiration and thus the vegetated plots and control plots had different models for R_E. In the R_E model for vegetation stands we used an exponential form to describe the dependence of ecosystem respiration on temperature. We parameterized the R_E model separately for the different vegetation patches. We applied a linear response of R_E on VGA to describe the dependence of ecosystem respiration on the amount of living plant material. The R_E model had the form:

$$R_E = b_1 \times \exp(b_2 \times T_{\text{air}}) + (b_4 \times \text{VGA}) \quad \text{eqn 2}$$

In the R_{PEAT} model for bare peat surfaces we included WT response in the model in a negative exponential form to describe the dependence of soil respiration on the thickness of oxic layer. The model had the form:

$$R_{\text{PEAT}} = b_1 \times \exp(b_2 \times T_{\text{air}}) \times \exp(-b_3 \times \text{WT}) \quad \text{eqn 3}$$

COMPARING THE CO₂ EXCHANGE IN DIFFERENT VEGETATION PATCHES

To compare the P_G of *Eriophorum* and *Carex* in their optimal conditions we used P_G models to calculate the maximal potential P_G per unit of VGA separately for each group. This was performed by setting VGA to 1.0 and air temperature to the optimum for every group according to the parameters from the models. To take into account the hyperbolic nature of P_G to PPFD, we used 90% of the maximum PPFD saturated P_G as the realized maximal potential P_G.

Using the models with hourly weather data we estimated P_G and R_E for all the sample plots over both growing seasons between the beginning of June and the end of September. Seasonal CO₂ balances in sample plots (NEE_{SEASON}) were calculated by summing the hourly P_G and R_E from the whole period. Due to malfunctioning of the weather station at Aitoneva, PPFD, air temperature data were obtained from Lakkasuo weather station (61°47' N; 24°18' E), which is situated 100 km south-east from Aitoneva. Both areas are situated in the south boreal zone and thus the climatic conditions are comparable; also, because the data were used for counting CO₂ balances for the whole growing seasons, any error was assumed to be marginal.

Finally, we compared CO₂ exchange between the four groups without the effect of different VGA and WT between the plots. We used the R_{PEAT} model to calculate the hourly peat respiration for all the vegetated plots, which was then subtracted from the balances of the vegetated plots. The residual defines plant-derived net photosynthesis (NEE_{PLANTS}) without the effect of WT controlled soil respiration. Similarly, the plant-derived respiration (R_{PLANTS}) was calculated by

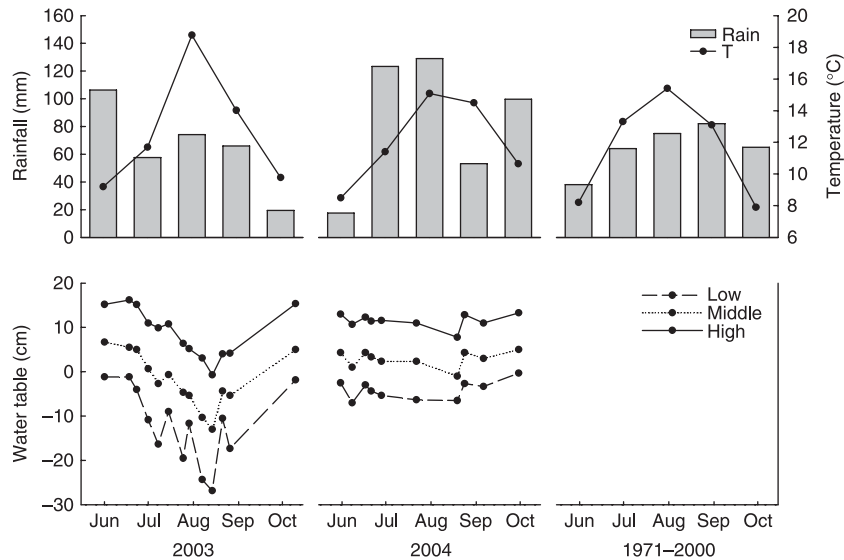


Fig. 1. Mean monthly rainfall, air temperature and water level in the study area compared to a 30-year average. Water table is shown for different moisture regimes of the study site. The study pots were situated along the water table gradient.

subtracting the estimated soil respiration from the reconstructed R_E of the vegetated sample plots. Plant CO_2 balances for the whole growing season in sample plots were calculated by summing the hourly NEE_{PLANTS} and R_{PLANTS} from the whole period. To compare the groups without the effect of different VGA, P_G , R_{PLANTS} and P_N are expressed per one VGA unit. Only three of the five mixed plots of *Carex* were used for this analysis because of the very low VGA values of the other two plots.

All the calculations were performed using spss version 12.0.1 for Windows using the Levenberg–Marquardt estimation procedure.

Results

VARIATION IN VEGETATION

The two vascular plant species differed in their timing of the maximum vascular green area (VGA) (species effect: $P = 0.000$). While *Eriophorum* reached its maximum VGA in late July or early August, that of *Carex* was approximately a week earlier and in some cases at the beginning of July (see Supplementary material, Fig. S1). Both species reached their maximum VGA about a week later in the warmer and drier growing season of 2003 (Fig. 1) compared to the colder, wetter growing season of 2004 (year effect: $P = 0.003$). The pattern between the years did not differ between the species (species \times year effect: $P = 0.959$).

Plant species showed a clear distribution pattern along the WT gradient (Fig. 2a,b). *Eriophorum* was most abundant in the drier end of the gradient while the wetter conditions favoured *Carex* and *Sphagnum* (Fig. 2a). *Eriophorum* and *Carex* also differed in their tolerance to WT variation. *Eriophorum* seemed to be a generalist that could also grow in higher WT conditions, but the abundance of *Carex* decreased dramatically towards the dry end of the gradient. The *Sphagnum* species, as a group, favoured wetter conditions (Fig. 2a), although species changed along the gradient. While the optimal WT for most of the *Sphagnum* species occurred in wet conditions, the optimum for *S. fallax* was in similar WT conditions to that of *Eriophorum* (Fig. 2b).

INSTANTANEOUS CO_2 FLUXES AND THEIR RESPONSE TO ENVIRONMENTAL VARIABLES IN DIFFERENT GROUPS

The seasonal variation in the measured CO_2 fluxes (NEE and R_E) of the pure *Eriophorum* plots was smaller than the variation among the other three groups (Fig. 3). The measured values were generally larger in the *Eriophorum* plots than in the *Carex* plots, especially in the spring and autumn. The difference in the measured fluxes was in good agreement with the difference in VGA between the species (see Supplementary material, Fig. S1). Additionally, the measured flux values in the mixed plots of *Carex* and *Sphagnum* were larger than in the pure *Carex* plots especially in the early and late growing season. In contrast, measured flux values were larger in the pure *Eriophorum* plots than in the mixed plots of *Eriophorum* and *Sphagnum*, whereas the VGA of *Eriophorum* was smaller than in the pure plots (Fig. 3).

The half saturation constant in both *Eriophorum* models was clearly higher than in the *Carex* models (parameter k_{PAR} in Table 1; see Supplementary material, Fig. S2), indicating greater light use efficiency in the dense tussocks of *Eriophorum*. In the pure vascular plant plots, *Eriophorum* had slightly higher maximal potential P_G (light saturated P_G per 1 unit of

Table 1. The parameters and standard errors for the whole models in P_G models for pure and mixed *Eriophorum* and *Carex* stands. SE: standard error

Parameter	EV	CR	EV \pm S	CR \pm S
P_{max} (mg)	4588 \pm 816	986 \pm 73	4836.9 \pm 1874	813 \pm 81
k_{PPFD} (μ mol)	316 \pm 58	135 \pm 52	513 \pm 228	130 \pm 41
k_{VGA} (m^{-2})	3.4 \pm 0.8		1.0 \pm 0.5	
s				0.46 \pm 0.1
o ($^{\circ}C$)	16.6 \pm 2.5	29.8 \pm 4.5	22.0 \pm 3.3	22.1 \pm 1.2
t ($^{\circ}C$)	17.5 \pm 3.2	17.5 \pm 6.8	15.1 \pm 6.3	13.6 \pm 2.8
SE of estimate	236.9	192.2	220.6	238.7

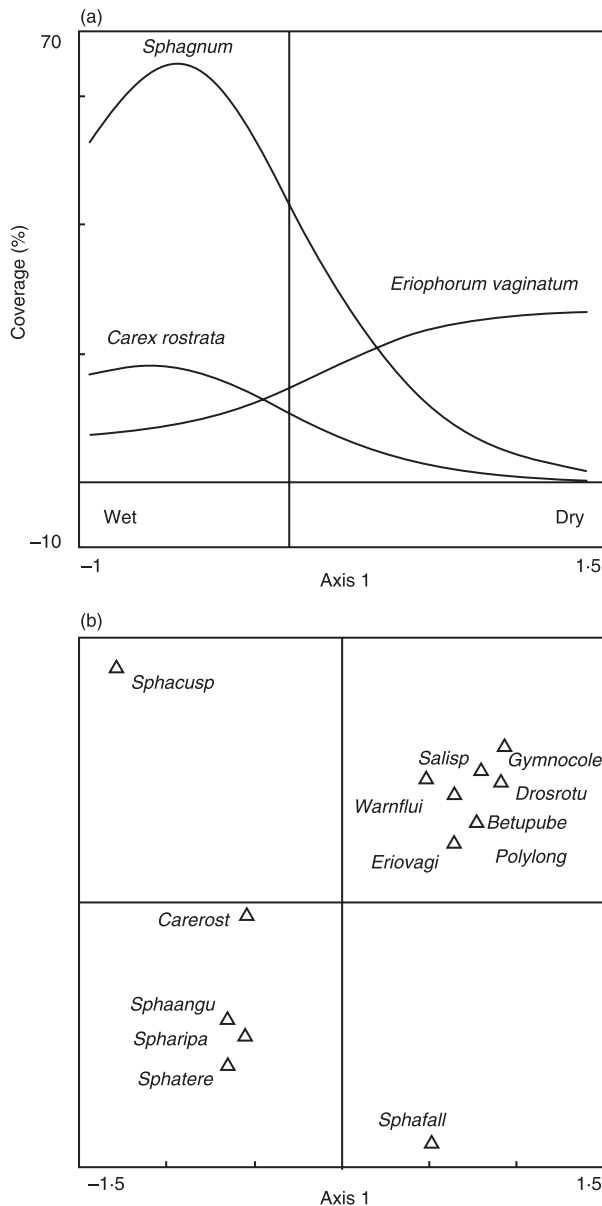


Fig. 2. Distribution of the studied species along the moisture gradient. (a) Projection cover of the dominant plant species along the moisture gradient, first canonical correspondence analysis (CCA) axis. Water table (WT) is closer to the surface along the axis from right to left. (b) Distribution of plant species in CCA ordination space, where the first axis is related to WT. The following abbreviations are used: Betupube = *Betula pubescens*, Carerost = *Carex rostrata*, Drosrotu = *Drosera rotundifolia*, Eriovagi = *Eriophorum vaginatum*, Gymnocole = *Gymnocolea* sp., Polylong = *Polytrichastrum longisetum*, Salisp = *Salix* sp., Sphaangu = *Sphagnum angustifolium*, Sphacusp = *S. cuspidatum*, Sphafall = *S. fallax*, Spharipa = *S. riparium*, Sphatere = *S. teres*, Warnflui = *Warnstorfia fluitans*.

VGA in optimal temperature conditions) than *Carex*, 934 mg CO₂ h⁻¹ m⁻² VGA⁻¹ and 887 mg CO₂ h⁻¹ m⁻² VGA⁻¹, respectively. The mixed *Eriophorum* plots had higher maximal potential P_G than the mixed *Carex* plots, 2152 mg CO₂ h⁻¹ m⁻² VGA⁻¹ and 1067 mg CO₂ h⁻¹ m⁻² VGA⁻¹, respectively. Most of the

variation in P_G, which was not related to the amount of light and efficiency of use, was associated with the variation in VGA (see Supplementary material, Fig. S2). In both *Eriophorum* models (Table 1) the response of P_G to VGA indicated saturation, while in *Carex* P_G increased linearly with the increasing VGA. The difference in the form of response between the species was consistent with the amount of VGA. The VGA up to 3 m² m⁻² in the *Eriophorum* plots is likely to cause intensive self-shading, in contrast to the rather low VGA in the *Carex* plots of around 1 m² m⁻² at its greatest. The inclusion of air temperature in the P_G models did not improve their explanatory power greatly due to the large tolerance of P_G to variation in temperature in all groups (Table 1; see Supplementary material, Fig. S2) and due to the obvious autocorrelation between temperature and VGA. However, the inclusion of temperature made the models ecologically more meaningful and decreased the standard error of the model parameters.

In *Eriophorum* plots the large variation in VGA explained most (35%) of the seasonal and spatial variation in respiration (R_E). In *Carex*, however, most (51%) of the variation in R_E was related to temperature fluctuations (see Supplementary material, Fig. S3). The parameter values in the R_E models were of the same magnitude between the groups (Table 2).

THE CO₂ BALANCES OF THE GROWING SEASONS

The reconstructed NEE_{SEASON} (June–September) was positive in both years in all the vegetated plots, i.e. they all acted as net sinks for atmospheric CO₂ (Fig. 4). The mean NEE_{SEASON} varied between 45 and 98 g CO₂-C m⁻², 75 and 186 g CO₂-C m⁻², 23 and 114 g CO₂-C m⁻², and 101 and 181 g CO₂-C m⁻² in the pure and mixed *Carex* and *Eriophorum* plots, respectively. The *Carex* plots with *Sphagnum* had significantly higher seasonal balance than the pure plots ($P = 0.031$) resulting from the higher seasonal P_G ($P = 0.008$). In contrast, the seasonal P_G of the pure and mixed *Eriophorum* plots were of the same magnitude, with a tendency towards higher seasonal R_E in the pure plots ($P = 0.074$). Thus, the mixed plots of *Eriophorum* had significantly higher seasonal balance ($P = 0.012$) than the pure plots. Differences in the seasonal fluxes between the two growing seasons were small (Fig. 4). The control plots acted as seasonal sources from -20 to -71 g CO₂-C m⁻² into atmosphere (Fig. 4).

When the P_G and R_E of the groups were proportioned to the VGA and the estimated peat respiration was subtracted, it became even more obvious that the mixed plots with *Sphagnum* were more efficient sinks than the pure vascular plant plots, per unit of VGA (Fig. 5). The seasonal plant CO₂ balance (NEE_{PLANTS}) when seasonal maximal VGA was set to 1 unit varied between 62 and 121 g CO₂-C m⁻² VGA⁻¹, 140 and 371 g CO₂-C m⁻² VGA⁻¹, 50 and 149 g CO₂-C m⁻² VGA⁻¹ and 327 and 448 g CO₂-C m⁻² VGA⁻¹ in the pure and mixed *Carex* and *Eriophorum* plots, respectively. The difference in NEE_{PLANTS} was uniform over the whole growing season. The plant-derived respiration (R_{PLANT}) per VGA unit was similar

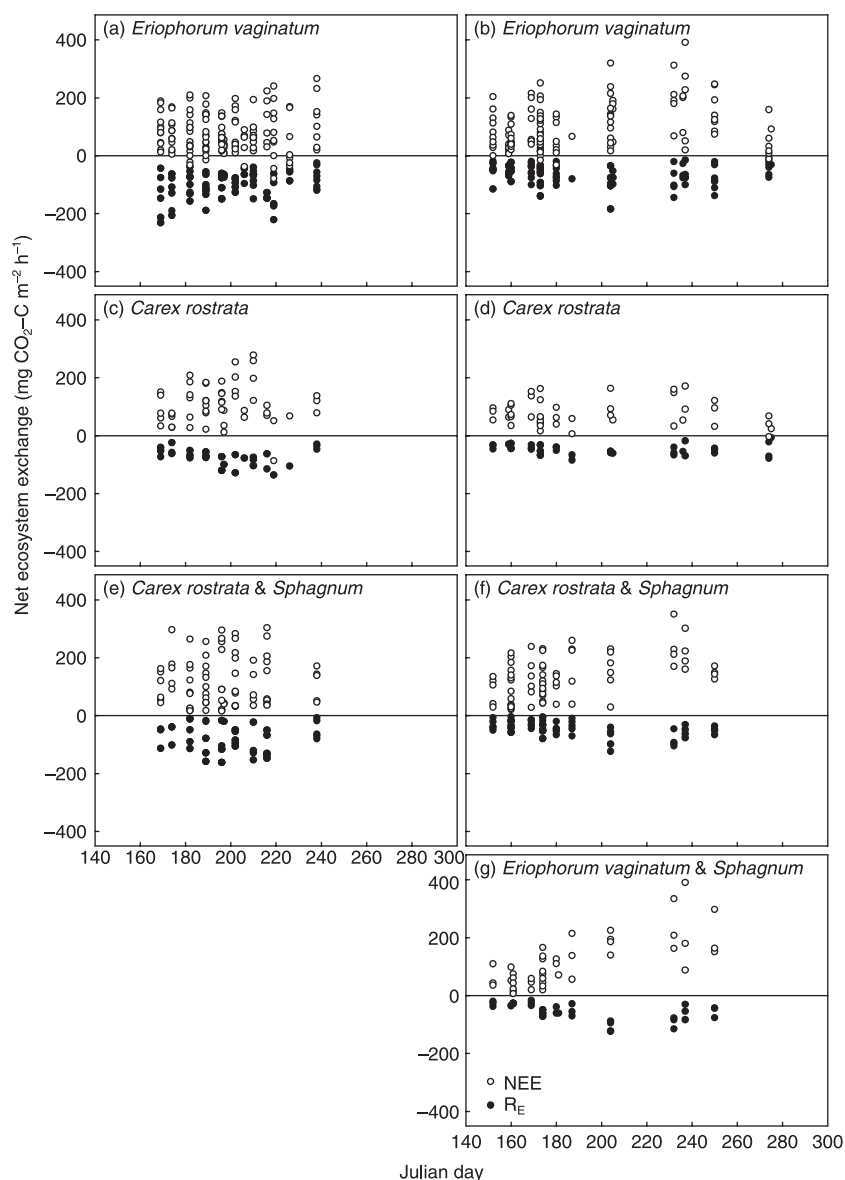


Fig. 3. The measured net ecosystem exchanges (NEE) of the different stands during the growing seasons 2003 (left) and 2004 (right) under various levels of light. The open circles are net ecosystem exchanges measured in light and closed circles are NEE values measured in dark. (a, b) *Carex rostrata*; (c, d) *C. rostrata* + *Sphagnum*; (e, f) *Eriophorum vaginatum*; (g) *E. vaginatum* + *Sphagnum*.

Table 2. The parameters and their standard errors in ecosystem respiration (R_E) models for pure and mixed *Eriophorum* and *Carex* stands. SE: standard error

Parameter	EV	CR	EV ± S	CR ± S	Control
b1	49.8 ± 14.6	32.6 ± 17.7	18.5 ± 11.8	12.1 ± 8.4	12.2 ± 3.6
b2	0.04 ± 0.01	0.07 ± 0.01	0.09 ± 0.02	0.09 ± 0.02	0.07 ± 0.01
b3	133.3 ± 11.9	108.8 ± 43.6	173.8 ± 47.1	199.6 ± 20.7	
b4					0.06 ± 0.01
SE of estimate	103.4	72.1	63.4	99.5	47.1

in all groups, varying between 119 and 216 g CO₂-C m⁻² VGA⁻¹; the differences in the P_G was responsible for the difference between the pure and mixed plots. The P_{G,SEASON} of the pure plots varied between 185 and 275 g CO₂-C m⁻² VGA⁻¹, while in the mixed plots it was clearly higher, between 306 and 617 g CO₂-C m⁻² VGA⁻¹.

Discussion

FACTORS INFLUENCING REVEGETATION

To promote the C sink function of restored peatland it is essential to maximize vegetation cover of the restored area

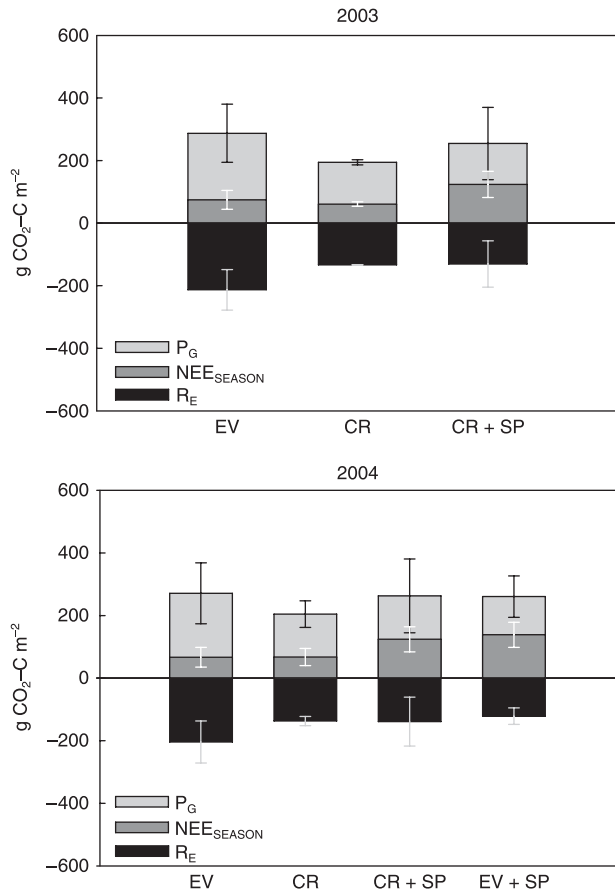


Fig. 4. Gross photosynthesis (P_G), ecosystem respiration (R_E) and balance of the growing seasons for different groups in growing seasons 2003 and 2004. The mixed stands of *Eriophorum vaginatum* and *Sphagnum* were measured only in the 2004 growing season.

(Tuittila *et al.* 1999, 2004; McNeil & Waddington 2003). Satisfying the different habitat requirements of the studied species can hasten revegetation. *Carex rostrata* can colonize areas of the peatland with a higher WT (Fig. 2a) due to its ability to grow well in waterlogged conditions (Visser *et al.* 2000) and to spread vegetatively over a distance of several metres (Bernard & Hankinson 1979). The vegetative spreading of *E. vaginatum*, by contrast, is limited to the formation of tussocks and its tillers can colonize only bare peat surfaces (Wein 1973; Tuittila *et al.* 2000) and hence areas with lower WT. Different *Sphagnum* species favour different levels of WT (Fig. 2b; Rydin & McDonald 1985), enabling *Sphagnum* to potentially colonize the whole area. The maximum VGA of *Carex* and *Eriophorum* occurred at different times in the growing season during both study years; therefore the combination of the two sedges with different seasonal patterns assures good coverage of the field layer and high rates of C fixation over the growing season. In addition, *Sphagnum* typically colonizes the spaces between vascular plants and thus increases the overall vegetation cover and the consequent C fixation.

By planting it is possible both to speed up the colonization process (Cobbaert *et al.* 2004) and to manipulate the vegetation

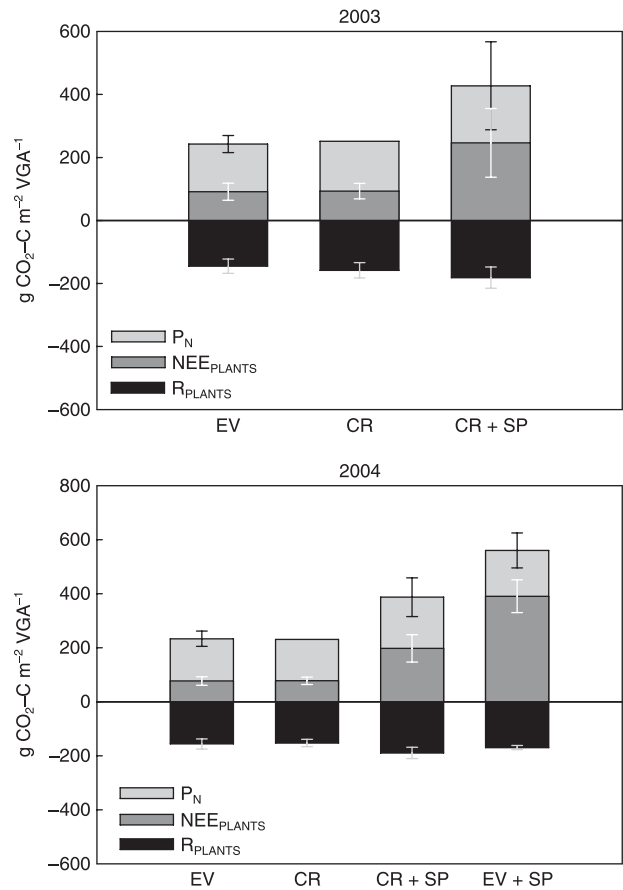


Fig. 5. The P_N , R_{plants} and plant CO₂ balance of the four groups without the effect of peat respiration and vascular green area (VGA). For mixed plots of *Carex* only three plots of five were used for this standardization due to very low VGA values in two of the plots. The pure *Carex* plots all have the same gross photosynthesis (P_G) due to the linear relationship of P_G and VGA in the model and therefore do not have standard deviation.

towards the desired species composition (Money 2004). Reintroduction may be more crucial for *Carex* and *Sphagnum* than *Eriophorum*, which has a high ability to colonize these bare areas spontaneously (Tuittila *et al.* 2000; Lavoie *et al.* 2005).

FACTORS INCREASING SINK STRENGTH IN A CUT-AWAY PEATLAND

The larger measured net CO₂ exchanges of *Eriophorum* compared to *Carex*, especially in the spring and autumn, were related partly to the timing of development of the different leaf cohorts (Silvan *et al.* 2004), which leads to larger VGA of *Eriophorum* at the beginning and end of the growing season. Ström, Mastepanov & Christensen (2005) also found *Eriophorum* to be more efficient than *Carex* in the spring and autumn. In our study, *Carex* was at least as, or even more, efficient than *Eriophorum* during the midsummer. The two vascular plants are thus efficient at different times of the growing season, and therefore to maximize the photosynthesis for the whole growing season it would be essential to establish

both these species in restored areas. Promoting *Sphagnum* colonization in the restored area also increases the effectiveness of the stands in spring and autumn. On the other hand, the colonization of *Sphagnum* can decrease the VGA of the vascular plants by growing over them (Svensson 1995; Van Breemen 1995), as seen in the mixed plots of *Eriophorum*.

When the seasonal CO₂ balances of the groups were proportioned to VGA and the average peat respiration was subtracted, the sink strength of the mixed plots became even more pronounced. Tuittila *et al.* (2004) measured a balance of 94 g CO₂-C m⁻² for *S. angustifolium* in the same study area under optimal conditions. Accordingly, most of the higher NEE_{SEASON} of the mixed plots is explained by the photosynthesis of *Sphagnum*. However, it does not explain the difference entirely. There was an indication that the enhanced functional diversity of the patches leads to increased productivity per VGA unit similar to grassland ecosystems (Tilman *et al.* 1997). In the present study, the increase in the productivity per unit VGA is attributable partly to the longer assimilation period caused by *Sphagnum* (Fig. 3). It can also be due to a higher and more constant WT caused by *Sphagnum* that would benefit vascular plants (Schouwenaars 1993). Vascular plants may also provide a substrate-derived C source for *Sphagnum* through their respiration, thus increasing the carbon sink of the mixed plots (Lamers *et al.* 1999; Smolders *et al.* 2001). However, although the invasion of *Sphagnum* mosses seems to lead to higher carbon assimilation per VGA unit, it does not lead necessarily to an increase in the overall carbon sink function because of the decrease in GA of the vascular plants. Despite the lower VGA in *Eriophorum*, the carbon sink function remained high and the invasion of *Sphagnum* did not reduce the cover of *Carex*. Instead, *Sphagnum* filling the spaces between the individuals of *Carex* clearly increased the overall carbon sink function of the *Carex* patches.

The control plots formed a source of -20 to -71 g CO₂-C m⁻² during the two growing seasons, which is less than that observed by Tuittila *et al.* (1999) in the same study area immediately after the restoration. This may reflect reduced amounts of easily degradable carbon during the course of restoration succession. Bortoluzzi *et al.* (2006) measured values between -22 and -32 g C m⁻² year⁻¹ in a restored peatland, which may reflect a poor nutrient availability of *Sphagnum*-peat at that study site (Bortoluzzi *et al.* 2006). All these values are much lower than those reported by Waddington *et al.* (2002) from a non-restored cut-away peatland where they measured -363 g C m⁻² emission for a dry year and -112 g C m⁻² for a rainy year. This again highlights the fact that with restoration it is possible to stop the oxidation of the residual peat and turn the area into a sink of CO₂.

All vegetation patches were sinks for CO₂ in both growing seasons, as found in a restored cut-away peatlands in the French Jura Mountains by Bortoluzzi *et al.* (2006). Marinier *et al.* (2004) reported very low NEE_{SEASON} for *Eriophorum* tussocks in restored Canadian cut-away site with a low WT, and Alm *et al.* (1999) found pristine peatland to become a source of -4 to -157 g C m⁻² during an extremely dry summer, when the WT fell almost half a metre below the peat surface.

The present study represents the CO₂ balances for the growing season. In order to establish the greenhouse gas balance for the plot estimates for the whole year and/or the global warming potential, one should take into account the CH₄ balance, respiration outside the growing season, runoff and N₂O balance. During the first 3 years after the rewetting, the observed CH₄ emissions in the study site were much lower than in pristine mires in the area despite the rising trend during the study years (Tuittila *et al.* 2000). However, our preliminary results from the same area indicate that CH₄ emissions are now reaching the level of pristine mires with a rough estimate for the seasonal balance of 6.7 g CH₄-C m⁻² (Mika Yli-Petäys, Harri Vasander & Eeva-Stiina Tuittila, unpublished data) This is close to the observations of Saarnio *et al.* (1997) and Nykänen *et al.* (1998) from bogs in southern Finland. Alm *et al.* (1999) estimated that during the growing season a NEE of 64–76 g CO₂-C m⁻² would be needed to support the annual sink function for the peatland, whereas Roulet *et al.* (2007) concluded that ignoring CH₄ and the dissolved organic carbon (DOC) leads to an overestimation of the C sink by 16–23 g per m² year⁻¹. Based on these assumptions, all the mixed plots and a portion of the pure plots would provide annual sinks of C.

In conclusion, when restoring a cut-away peatland it would be beneficial to encourage both *Eriophorum vaginatum* and *Carex rostrata* to colonize the area, either naturally or by planting, due to the different timing of the most efficient carbon assimilation period and different adaptation to water level conditions. The reintroduction of *Sphagnum* following vascular plant colonization would enhance the productivity further and lengthen the active period of the year.

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Supplementary material

The following supplementary material is available for this article.

Fig. S1. The development of the vascular green area (VGA) of the different stands.

Fig. S2. The measured gross photosynthesis (P_G) values against different environmental variables.

Fig. S3. The measured ecosystem respiration (R_E) values against different environmental variables.

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