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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Word count: 6546
Abstract

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

2. We studied carbon dioxide (CO$_2$) exchange in stands of different plants in a restored cut-away site over two growing seasons to quantify their ability to form a carbon sink. We sampled five different types of stands: 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 CO$_2$ exchange data for modelling of gross photosynthesis and ecosystem respiration. Finally we used the models to simulate the seasonal net CO$_2$ exchange of the stands formed by different plants.

3. While the control plots without vegetation were sources of 20-71 g CO$_2$-C m$^{-2}$, all the vegetated plots acted as carbon sinks during both growing seasons. The monostands of *Eriophorum vaginatum* and *Carex rostrata* were sinks of 23-114 g CO$_2$-C m$^{-2}$ while the mixtures of sedge and *Sphagnum* mosses resulted in larger sinks of 70-186 g CO$_2$-C m$^{-2}$. The larger sinks of the mixed patches were due to the smaller respiration/photosynthesis ratio.

4. To eliminate the effect of differences in water level and the abundance of sedges between the patches, we simulated the CO$_2$ exchange for constant water level 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 binding CO$_2$ than pure sedge stands.

5. *Synthesis and application*. The increased functional diversity in the cut-away site resulted in more productive ecosystem. When restoring cut-away peatlands re-introduction of *Sphagnum* after the colonization of vascular plants can increase the productivity and the efficiency of the ecosystem and hasten the formation of a sink for carbon dioxide.
Keywords: Carbon dynamics, Carex, CO₂, Ecosystem functioning, Ecosystem respiration, Eriophorum, Photosynthesis, RECIPE, Restoration

Introduction

In pristine peatlands the primary production exceeds the rate of decomposition; therefore they accumulate peat and act as a store for atmospheric carbon. In many countries this resource 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.

After peat harvesting the area is left bare. The dry dark surface acts as heat sink causing soil temperatures to rise to very high levels (Vasander & Roderfeld 1996). Lowering the water level during the harvesting leads to changes in soil properties and causes a large fluctuation of the water level (Van Seters & Price 2002). The fluctuating water level together with bare, dry surface makes the conditions difficult for plants to colonize (Salonen 1987). The old residual peat lacks a seed bank, therefore plants have to colonize from the surrounding areas (Salonen 1987; Huopalainen et al. 1998). Although some cut-away peatlands have been found to spontaneously regenerate after industrial large scale harvesting (Girard, Lavoie & Thériault 2002), the regeneration process in general is slow in the absence of human intervention (Salonen & Laaksonen 1994; Tuittila, Vasander & Laine 2000). The first species to colonize cut-away peatlands is in most cases the sedge Eriophorum vaginatum (Tuittila, Vasander & Laine 2000; Lavoie et al. 2003), which is adapted to live in oligotrophic conditions having efficient nutrient utilization (Wein 1973; Chapin et al. 1979; Silvan, Vasander & Laine 2004). By comparison with Eriophorum the colonization of Sphagnum mosses is generally slow in nature (Girard, Lavoie & Thériault 2002). Besides the slow colonization process, the water table positioned well below soil surface that leads to rapid oxidation of the peat partly alters the carbon gas fluxes of the area. Therefore, in contrast to pristine peatlands that act as
a carbon dioxide sink and a source of methane cut-away peatlands emit CO$_2$ into the atmosphere while they can oxidize atmospheric CH$_4$ (Alm et al. 1997; Tuittila et al. 1999; 2000).

In the restoration the aim is to bring back the functioning, peat accumulating ecosystem (Gorham & Rochefort 2003). This will also restore the potential to function as a carbon sink. In the formation of a functional peatland ecosystem *Sphagnum* mosses and sedges have a key role in carbon sequestration and peat production as they are the major carbon sequesters and peat producers (Clymo & Hayward 1982; Van Breemen 1995; Bubier et al. 2003). In restoration the first step is to raise the water table, which is the precondition for these key species to re-colonize the area (Schouwenaars 1993; Tuittila, Vasander & Laine 2000; Girard, Lavoie & Thériault 2002; Van Seters & Price 2002; Rochefort et al. 2003). Both *Eriophorum vaginatum* and *Carex rostrata* are able to rapidly colonize restored areas (Tuittila, Vasander & Laine 2000; Lavoie et al. 2003; Lavoie et al. 2005) and facilitate the colonization by mosses (Grosvernier et al. 1995; Tuittila, Vasander & Laine 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 plant re-introduction or planting that can increase both the number of plant individuals and their coverage (Cobbaert, Rochefort & Price 2004). Besides the planting, restoration can be hastened also by fertilization, by tilling or by adding straw mulch to protect *Sphagnum* diasporas from desiccation (Salonen & Laaksonen 1994; Rochefort et al. 2003).

When planning restoration to achieve rapid carbon sink formation, we need to understand the roles of different plant species in ecosystem carbon dynamics and the conditions favoring their functioning. However, so far little has been known about the effects of different plant communities on the carbon gas balance of restored cut-away peatlands or about the differences between species in their responses to different environmental variables. In this study we aimed to quantify (1) the role of two sedge species, *Carex rostrata* and *Eriophorum vaginatum*, and *Sphagnum* mosses in the CO$_2$ balance of a restored cut-away peatland and (2) their responses to water level.
Material and methods

STUDY SITE

The study was carried out during the growing seasons 2003 and 2004 in Aitoneva (62°12’N, 23°18’E), in the commune Kihniö, in southern Finland. Aitoneva, which is one of the European RECIPE sites, 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 in length, 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. It 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, Vasander & Laine 2000).

To compare CO₂ dynamics in different vegetation types characteristic to the restored site we established altogether 19 sample plots in four types of patches along a moisture gradient at the site: monocultures consisting of only either Eriophorum vaginatum L. or Carex rostrata Stokes (here after referred as pure stands) and mixtures of Eriophorum or Carex with Sphagnum L. (mixed stands). Additionally, we laid out three bare control plots where any vegetation was removed. The sample plots for all pure stands and mixed Carex stands were established in the beginning of the growing season 2003. The mixed Eriophorum stands were added a year later, in 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 cm × 60 cm), which were inserted to peat. Boardwalks were constructed to access the study site to avoid disturbance during the measurements.

VEGETATION MONITORING
To relate the spatial and temporal variation in CO$_2$ 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 the leaves was calculated monthly and the size of the leaves was measured from permanently marked individuals of *Carex* and *Eriophorum* (n=3) outside the sample plots every three to four weeks. To get 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 besides the mid summer maximum. This pattern, typical for *Eriophorum vaginatum* that can grow up to four cohorts every year (Silvan et al. 2004), was described by fitting a curve for the spring and the summer – autumn data separately. The VGA method is described in detail by Wilson et al. (2007).

A two-way ANOVA was performed on the VGA data to examine the possible differences between the two vascular plant species and the two 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 along the moisture gradient, which were systematically located 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 water table level using the Canoco program package (Ter Braak & Smilauer 2002).

MEASUREMENTS OF CO$_2$ FLUXES

CO$_2$ exchange measurements were started at the end of May or in early June and were carried out biweekly until September. Before the measurements, the groove in the collar was filled with water to ensure an air tight seal between the air and the chamber. The net ecosystem CO$_2$ exchange
(NEE) was measured in different irradiation levels (photosynthetically active photon flux density, PPFD) and in the dark using a transparent plastic chamber and a portable infra-red gas analyzer (PP Systems EGM 2). Whenever possible, the measurements were done in 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 a plastic hood to measure NEE in the dark, which allowed us to get an estimate for ecosystem respiration ($R_E$). In every measurement the gas concentration in the chamber was recorded every 15 seconds during the two to three minute measurement period. The chamber was equipped with an air circulating fan and a ventilator to keep the temperature inside the chamber at the level of the ambient air temperature. The method has been previously described by Alm et al. (1999) and Tuittila et al. (1999).

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 water table level (WL) in relation to the peat surface were measured.

MODELLING THE CO$_2$ EXCHANGE

Our aim was to estimate CO$_2$ exchange over the growing seasons in different vegetation patches and to quantify their response to environmental variation. To achieve this we formed models for gross photosynthesis ($P_G$) and ecosystem respiration ($R_E$) separately for each vegetation type and bare peat. Models are adapted from and the response functions are discussed in more detail in Tuittila, Vasander & Laine (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. We included VGA and Sphagnum in the model to describe the dependence on the amount of photosynthesizing plant material. The $P_G$ model got a form:
\[ P_G = P_{\text{MAX}(\text{PPFD}, T, \text{VGA}, S)} \cdot (\frac{\text{PPFD}}{k_{\text{PPFD}} + \text{PPFD}}) \cdot \exp(-0.5((T_{\text{air}} - o)/t)^2) \cdot (\frac{\text{VGA}}{k_{\text{VGA}} + \text{VGA}}) \cdot S \]  (1)

In the function \( P_{\text{MAX}(\text{PPFD}, T, \text{VGA}, S)} \) denotes the photosynthesis that could be reached if the amount of light (PPFD), photosynthesizing plant material (VGA, S) or temperature (T_{\text{air}}) did not limit photosynthesis. Parameter \( k_{\text{PPFD}} \) denotes the PPFD level where half of the PPFD-saturated \( P_G \) is reached, \( k_{\text{VGA}} \) denotes the VGA level where a half of the VGA saturated \( P_G \) is reached, \( o \) is the optimum temperature for photosynthesis, \( t \) is temperature tolerance for photosynthesis and \( S \) is a parameter applied to describe the photosynthetic potential of \textit{Sphagnum} in relation to VGA. We parameterized \( P_G \) model for the different stands separately. For \textit{Carex} with had a remarkably lower VGA than in \textit{Eriophorum} we used linear form instead of the saturating VGA response. In mixed \textit{Eriophorum} stands the estimate for parameter \( S \) denoting \textit{Sphagnum} photosynthesis did not significantly differ from zero and was therefore excluded.

In the \( R_E \) model for vegetation stands we used 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 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 got a form:

\[ R_E = b_1 \cdot \exp(b_2 \cdot T_{\text{air}}) + (b_4 \cdot \text{VGA}) \]  (2)

In the \( R_{\text{PEAT}} \) model for bare peat surfaces we included water level response in the model in negative exponential form to describe the dependence of soil respiration on the thickness of oxic layer. The model got a form:

\[ R_{\text{PEAT}} = b_1 \cdot \exp(b_2 \cdot T_{\text{air}}) \cdot \exp(-b_3 \cdot \text{WT}) \]  (3)

**COMPARING THE CO\(_2\) EXCHANGE IN DIFFERENT VEGETATION PATCHES**

To compare the \( P_G \) of \textit{Eriophorum} and \textit{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. To take into account the hyperbolic nature of \( P_G \) to PPFD, where the \( P_G \) asymptotically increases towards the
theoretical maximum with increasing light, 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 the both growing seasons between the beginning of June and the end of September. CO$_2$ balances in sample plots were calculated by summing the hourly $P_G$ and $R_E$ from the whole period. PPFD and air temperature data came from Lakkasuo weather station (61°47’N; 24°18’E), which is situated 100 km south-east from Aitoneva.

Finally, we compared CO$_2$ exchange between the four groups without the effect of different VGA and water levels 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 implies plant derived NEE ($P_N$) without the effect of water level controlled soil respiration. Similarly the plant derived respiration ($R_{PLANTS}$) was calculated by subtracting the estimated soil respiration from the estimated $R_E$ of the vegetated sample plots. 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 out of the five mixed plots of Carex were used for this analysis because of the much lower VGA values of the other two plots.

All the calculations were done using SPSS 12.0.1 for Windows.

Results

VARIATION IN VEGETATION

The two vascular plant species studied 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, the timing of the maximum VGA of Carex was approximately a week earlier in general and in some cases happened in the beginning of July (Fig. 1). Both species reached their maximum VGA about a week later in the warmer growing season of 2003 than in the colder 2004
Plants showed a clear pattern in their distribution along the water level (Fig. 2a & b). *Eriophorum* had its highest abundance in the drier end of the water level gradient while the wetter conditions favoured *Carex* and *Sphagna* (Fig. 2a). *Eriophorum* and *Carex* differed in their tolerance to water level variation. *Eriophorum* seems to be a generalist that could grow also in the higher water level conditions, but the abundance of *Carex* dramatically decreased towards the dry end of the gradient. The *Sphagnum* species, as a group, favoured wetter conditions (Fig. 2a).

However, within *Sphagna* there was a turnover of species along the gradient. While most of the *Sphagnum* species had their optimum WL in wet conditions, *S. fallax* had its optimum WL in similar water level conditions to *Eriophorum* (Fig. 2b).

**MOMENTARY CO$_2$ FLUXES AND THEIR RESPONSE TO ENVIRONMENTAL VARIABLES IN DIFFERENT GROUPS**

The seasonal variation in the measured net CO$_2$ exchange (NEE) of the pure *Eriophorum* plots was smaller than the variation of the other three groups (Fig. 3). The measured NEE values were generally larger in the *Eriophorum* plots than in the *Carex*, especially in the spring and autumn. The difference in the measured NEE was in good agreement with the difference in VGA between the species (Fig. 1). Additionally, the measured NEE values in the mixed plots of *Carex* and *Sphagna* were larger than in the pure *Carex* plots and the difference was similarly more pronounced in the early and late growing season. In contrast to the *Carex* plots, measured NEE values were larger in the pure *Eriophorum* plots than in the mixed plots of *Eriophorum* and *Sphagna* where the GA of *Eriophorum* was smaller than in the pure plots (Fig. 3).

The efficiency of P$_G$ differed between the sedge species (Fig. 4). The half saturation constant in both *Eriophorum* models was clearly higher than in the *Carex* models (parameter $k_{PAR}$ in Table 1,
Fig. 4) indicating higher light use efficiency in *Eriophorum*. In the pure vascular plant plots, *Eriophorum* had slightly higher maximal potential $P_G$ (light saturated $P_G$ per 1 unit of VGA in optimal temperature conditions) than *Carex*, 934 mg CO$_2$ h$^{-1}$ m$^{-2}$ VGA m$^{-2}$ and 887 mg CO$_2$ h$^{-1}$ m$^{-2}$ VGA m$^{-2}$, respectively. As a result of the larger amount of photosynthesizing plant material in the mixed plots containing sedges and *Sphagnum*, their maximal potential $P_G$ exceeded the pure sedge plots. The mixed *Eriophorum* plots had higher maximal potential $P_G$ than the mixed *Carex* plots, 2133 mg CO$_2$ h$^{-1}$ m$^{-2}$ VGA m$^{-2}$ and 1067 mg CO$_2$ h$^{-1}$ m$^{-2}$ VGA m$^{-2}$, respectively. Most of the variation in $P_G$, which was not related to the amount of light and the light use efficiency, was associated with the variation in VGA (Fig. 4). In both *Eriophorum* models (Table 1) the response of $P_G$ to VGA typified saturation while in *Carex* $P_G$ increased linearly with the increasing VGA. The difference in the form of response between the species agreed with their amount of VGA. The VGA up to 3 m$^2$ m$^{-2}$ in the *Eriophorum* plots is likely to cause intensive self-shading, in contrast to rather low VGA in the *Carex* plots where the VGA was around at its largest 1 m$^2$ m$^{-2}$. The inclusion of air temperature in the $P_G$ models did not greatly improve their explanatory power in terms of $r^2$ due to the large tolerance of $P_G$ to variation in temperature in all groups (Table 1, Fig. 4) and due to the autocorrelation between temperature and VGA. However, the inclusion of temperature made parameter values more ecologically meaningful and decreased the standard error of the estimates.

In *Eriophorum* plots the large variation in VGA explained most of the seasonal and spatial variation in respiration ($R_E$). In *Carex*, however, a lower variation in VGA meant that most of the variation in $R_E$ was related to the variation in temperature (Fig. 5). The parameter values in $R_E$ models were of the same magnitude between the groups (Table 2).

THE CO$_2$ BALANCES OF THE GROWING SEASONS

The simulated seasonal net CO$_2$ exchange (June - September) was positive in both years in all the vegetated plots, *ie.* they all acted as net sinks for atmospheric CO$_2$ (Fig. 6). The seasonal NEE
varied between 45 and 98 g CO$_2$-C m$^{-2}$, 75 and 186 g CO$_2$-C m$^{-2}$, 23 and 114 g CO$_2$-C m$^{-2}$, and 70 and 133 g CO$_2$-C m$^{-2}$ in the pure and mixed Carex and Eriophorum plots, respectively. The Carex plots with Sphagnum had significantly higher seasonal NEE than the pure sedge plots (P=0.031) resulting from the higher seasonal P$_G$ (P=0.008). In contrast to the Carex plots, the seasonal NEE of the pure and mixed Eriophorum plots were of the same magnitude, in spite of the trend towards higher seasonal R$_E$ in the mixed plots (P=0.074). Differences in the seasonal fluxes between the two growing seasons were small (Fig. 6). The control plots acted as seasonal sources of 20-71 g CO$_2$-C m$^{-2}$ into atmosphere (Fig. 6).

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 (Fig. 7). The seasonal P$_N$ when seasonal maximal VGA was set to 1 unit varied between 62 and 121 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$, 140 and 371 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$, 50 and 149 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$ and 245 and 375 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$ in the pure and mixed Carex and Eriophorum plots, respectively. The difference was uniform over the whole growing season rather than seasonal during the spring or autumn, when the difference in VGA between the species was largest. The plant derived respiration (R$_{PLANT}$) per VGA unit was at the same level in all the groups and varied between 119 and 216 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$; the differences in the P$_G$ was responsible for the difference between the pure and mixed plots. The P$_G$ of the pure plots varied between 185 and 275 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$ while in the mixed plots it was clearly higher, between 306 and 588 g CO$_2$-C m$^{-2}$ VGA m$^{-2}$.

Discussion

FACTORS INFLUENCING REVEGETATION

In order to promote carbon sink function it is essential to maximise vegetation cover of the restored area (Tuittila et al. 1999; McNeil & Waddington 2003; Tuittila, Vasander & Laine 2004).
Satisfying the different habitat requirements of the studied species can hasten the revegetation in the different parts of the restored area. *Carex rostrata* can colonize parts with higher water levels (Fig. 2a) due to its ability to spread vegetatively over a distance of several meters (Bernard & Hankinson 1976). The vegetative spreading of *Eriophorum vaginatum* by contrast is limited to the formation of tussocks and the tillers of *Eriophorum vaginatum* can successfully only colonize bare peat surfaces (Wein 1973; Tuittila, Vasander & Laine 2000). Therefore it can only colonize areas with lower water levels (Fig. 2a). In addition, different *Sphagnum* species favour different water levels (Fig. 2b; Rydin & McDonald 1985), and this range enables *Sphagna* to potentially colonize the whole area, providing the species propagules are available. The maximum VGA of *Carex* and *Eriophorum* occurred at different times in the growing season during both test periods; therefore the combination of the two sedges with different seasonal patterns assures higher coverage of the field layer and the related carbon fixation over the growing season. While by planting it is possible to speed up the colonization process (Cobbaert, Rochefort & Price 2004), it is also possible to manipulate the vegetation towards the desired species composition (Money 2004). Reintroduction may be more crucial for *Carex* than *Eriophorum*, which has a higher ability to spontaneously colonize these areas (Tuittila, Vasander & Laine 2000; Lavoie *et al.* 2005).

**FACTORS INCREASING SINK STRENGTH IN A CUT-AWAY PEATLAND**

The larger measured net CO$_2$ exchanges of *Eriophorum* compared to *Carex* (Fig. 3), especially in the spring and autumn, were partly related to the timing of development of the different leaf cohorts (Silvan *et al.* 2004), which leads to bigger VGA of *Eriophorum* in the beginning and end of the growing season. Similarly to our results, in a laboratory experiment Ström, Mastepanov & Christensen (2005) also found *Eriophorum* to be more efficient than *Carex* in the spring and autumn. On the other hand in this study, *Carex* was at least as, or even more, efficient then *Eriophorum* during the midsummer. According to our study, the two vascular plants are
efficient compared to each other at different times of the growing season, and thus, to maximize the
photosynthesis for the whole growing season, it would be essential to get both species established in
restored areas. Promoting Sphagnum colonize in the restored area also increases the effectiveness of
the stands in spring and autumn, which was seen especially in the mixed plots of Carex (Fig. 3). On
the other hand, the colonization of Sphagnum can decrease the VGA of the vascular plants by
growing over them (Svensson 1995), which is likely what has happened in the mixed plots of
Eriophorum. This was also seen in the smaller VGA and NEE values of mixed Eriophorum plots
compared to pure plots (Fig. 1 and Fig. 3).

All the vegetation patches appeared to be sinks for CO$_2$ in both growing seasons. The NEE
values in this study, 70-133 g CO$_2$-C during the growing season for Eriophorum and Sphagnum and
75-186 g CO$_2$-C for Carex and Sphagnum, are the same magnitude as in the study of Alm et al.
(1997) in pristine boreal peatland. In other studies the estimated balances for arctic and sub-arctic
fens have ranged from -20 g CO$_2$-C to 64 g CO$_2$-C (Soegaard & Nordström 1999; Griffis, Rouse &
Waddington 2000; Aurela, Laurila & Tuovinen 2001). In the study of Alm et al. (1999), where the
water table fell to as low as 48 cm below the peat surface during an extremely dry summer, the
studied plots in a pristine peatland became sources of carbon. In our study all the plots acted as
sinks for CO$_2$ even during the very dry growing season 2003. It seems that at the study site the
water table level is sufficiently higher even in the drier part to maintain the sink function.

When considering the results, one has to keep in mind that these data only represent the
carbon dioxide balances for the growing season. In order to establish the greenhouse gas balance for
the plots estimates for the whole year and/or the global warming potential one should take into
account the methane balance, respiration outside the growing season, runoff and N$_2$O balance. Alm
et al. (1999) estimated that during the growing season a NEE of 64-76 g CO$_2$-C m$^{-2}$ would be
needed to support the annual sink function for the peatland. Based on this assumption all the mixed
plots and a portion of the pure plots would provide annual sinks of carbon. When considering the
carbon balance of the whole study site one has to consider that in the area there are still totally non-vegetated peat surfaces, which must be taken account when the greenhouse gas balance is considered.

When the seasonal P\textsubscript{N} estimates per VGA unit were compared between the stands, the mixed stands appeared to be more efficient. Tuittila, Vasander & Laine (2004) measured a NEE of 94 g CO\textsubscript{2}-C m\textsuperscript{-2} for \textit{Sphagnum} in the same study area under optimal conditions. Accordingly, most of the bigger NEE of the mixed plots is explained by the photosynthesis of \textit{Sphagnum}. However, it does not explain the difference entirely and it seems that the enhanced functional diversity leads to increased productivity. According to our study the combination of the two components appears to be more efficient than the sum of the individual components. Growth in productivity with increasing functional diversity has been found also in other ecosystems (e.g. Tilman \textit{et al.} 1997; Kaye \textit{et al.} 2000).

The control plots formed a source of CO\textsubscript{2} during both growing seasons. The measured values in this study, -20 to 71 g CO\textsubscript{2}-C m\textsuperscript{-2}, were much smaller than measured by Waddington \textit{et al.} (2002) from non-restored cut-away peatland. They had values of -363 g C m\textsuperscript{-2} in a dry year and -112 g C m\textsuperscript{-2} in a rainy year. However, compared to the study of Tuittila \textit{et al.} (1999), made in the same study area immediately following the restoration, the non-vegetated plots have the same or slightly smaller respiration values. It seems that the restoration has also decreased the respiration of the non-vegetated areas. McNeil & Waddington (2003) measured a value of -84 g C m\textsuperscript{-2} from a bare peat surface in a spontaneously revegetated area, which is of the same magnitude as the values in our study.

In conclusion, when restoring a cut-away peatland it would be useful to encourage both \textit{Eriophorum vaginatum} and \textit{Carex rostarata} to colonize the area, either naturally or by planting, because these species are at their most efficient during different time of the growing season and at
different water levels. The reintroduction of *Sphagna* following vascular plant colonization would further enhance the productivity and the efficiency of the ecosystem.

### Acknowledgements

We thank Jouni Meronen and the whole peatland ecology field team at Hyytiälä Forestry Station for their help with the gas measurements. Niko Silvan, Pirita Soini, Heli Raiskinmäki and Eeva Putro have assisted in the field work. The data collection and analyses were supported by VAPO Ltd and a project “The green house gas balances of restored peatlands funded by the Finnish Ministry of Trade and Industry”. This study was a part of the RECIPE project funded by the European Commission, Directorate I, under the programme: “Energy, Environment and Sustainable Development” (n° EVK2-CT-2002-00154). We thank Lucy J. Sheppard and Kyle Devine for comments on the manuscript and for revising the language.

### Literature cited


Table 1. The parameters and standard errors in $P_G$ models for pure and mixed *Eriophorum* and *Carex* stands.

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<th>Parameter</th>
<th>EV</th>
<th>CR</th>
<th>EV+S</th>
<th>CR+S</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_{\text{max}}$ (mg)</td>
<td>4587.9 ± 815.6</td>
<td>985.8 ± 73.1</td>
<td>4872.6 ± 1679.7</td>
<td>813.4 ± 81.1</td>
</tr>
<tr>
<td>$k_{\text{PPFD}}$ (µmol)</td>
<td>316.2 ± 58.3</td>
<td>134.7 ± 52.0</td>
<td>452.1 ± 184.6</td>
<td>130.2 ± 41.2</td>
</tr>
<tr>
<td>$k_{\text{VGA}}$ (m$^{-2}$)</td>
<td>3.4 ± 0.8</td>
<td>1.1 ± 0.47</td>
<td>0.46 ± 0.1</td>
<td></td>
</tr>
<tr>
<td>$s$</td>
<td>0.46 ± 0.1</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>$t$ (°C)</td>
<td>16.6 ± 2.5</td>
<td>29.8 ± 4.5</td>
<td>24.3 ± 1.2</td>
<td>22.1 ± 1.2</td>
</tr>
<tr>
<td>$t$ (°C)</td>
<td>17.5 ± 3.2</td>
<td>17.5 ± 6.8</td>
<td>10.5 ± 2.3</td>
<td>13.6 ± 2.8</td>
</tr>
</tbody>
</table>
Table 2. The parameters and their standard errors in $R_E$ models for pure and mixed *Eriophorum* and *Carex* stands.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>EV (± SEM)</th>
<th>CR (± SEM)</th>
<th>EV+S (± SEM)</th>
<th>CR+S (± SEM)</th>
<th>Control (± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>b1</td>
<td>49.79±14.6</td>
<td>32.57±17.7</td>
<td>18.53±11.8</td>
<td>12.11±8.4</td>
<td>12.23±3.6</td>
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<td>b2</td>
<td>0.044±0.01</td>
<td>0.065±0.01</td>
<td>0.086±0.02</td>
<td>0.085±0.02</td>
<td>0.069±0.01</td>
</tr>
<tr>
<td>b3</td>
<td>133.31±11.9</td>
<td>108.78±43.6</td>
<td>173.83±47.1</td>
<td>199.57±20.7</td>
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</tr>
<tr>
<td>b4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.055±0.005</td>
</tr>
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</table>
Figure 1. The development of the vascular green area (VGA) of the different stands during growing seasons 2003 (left) and 2004 (right). Development in each sample plot is described by fitting a log-normal curve using the Julian day as an explaining variable. The VGA of *Eriophorum vaginatum* was described by fitting a curve for the spring and the summer – autumn data separately. A) and b) *Carex rostrata*, c) and d) *C. rostrata*+Sphagna, e) and f) *Eriophorum vaginatum*, g) *E. vaginatum*+Sphagna.
Figure 2. Distribution of the studied species along the moisture gradient. a) Projection cover of the dominant plant species along the moisture gradient, first CCA axis. Water level increases along the axis from right to left. b) Distribution of plant species in CCA ordination space, where the first axis is related to water level. The abbreviations: 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 fluviatilis.
Figure 3. The measured net ecosystem exchanges (NEE) of the different stands during the growing seasons 2003 (left) and 2004 (right) under various level of light. The open circles are net ecosystem exchanges measured in light and closed circles are NEE values measured in dark. A) and b) Carex rostrata, c) and d) C. rostrata+Sphagna, e) and f) Eriophorum vaginatum, g) E. vaginatum+Sphagna.
Figure 4. The measured gross photosynthesis ($P_G$) values against different environmental variables. The black circles are measured values with fitted curves for pure plots and the grey circles are measured values with fitted curve for the mixed plots.
Figure 5. The ecosystem respiration ($R_E$) values against different environmental variables. The black circles are measured values with fitted curves for pure plots and the grey circles are measured values with fitted curve for the mixed plots.
Figure 6. $P_G$, $R_E$ and CO$_2$ balance of the growing seasons for different groups in growing seasons 2003 and 2004. The mixed stands of *Eriophorum vaginatum* and *Sphagnum* were only measured in the growing season 2004.
Figure 7. The \( P_G \), \( R_{\text{plants}} \) and NEE of the four groups without the effect of peat respiration and VGA. For mixed plots of *Carex* only three plots out 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 \( P_G \) due to the linear relationship of \( P_G \) and VGA in the model and therefore do not have standard deviation.