1   Carbon sink function of sedge and *Sphagnum* patches in a restored cut-away peatland:

2   increased functional diversity leads to higher production?

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Abstract

26

27 **1.** Cut-away peatlands devoid of vegetation form a persistent source of carbon to the atmosphere.

28 The restoration towards carbon sink function in such areas can be facilitated by raising the water

29 level. Planting vascular plants and *Sphagnum* may further hasten the restoration process. However,

30 little is known about the effects of different species to the restoration process.

31 **2.** We studied carbon dioxide (CO_2) exchange in stands of different plants in a restored cut-away

32 site over two growing seasons to quantify their ability to form a carbon sink. We sampled five

33 different types of stands: monocultures of *Eriophorum vaginatum* and *Carex rostrata* (pure plots),

34 mixtures of *Eriophorum* or *Carex* and *Sphagnum* mosses (mixed plots) and control plots without

35 vegetation. We applied the closed chamber technique to gather CO_2 exchange data for modelling of

36 gross photosynthesis and ecosystem respiration. Finally we used the models to simulate the

37 seasonal net CO_2 exchange of the stands formed by different plants.

38 **3.** While the control plots without vegetation were sources of 20-71 g CO_2-C m^{-2}, all the vegetated

39 plots acted as carbon sinks during both growing seasons. The monostands of *Eriophorum*

40 *vaginatum* and *Carex rostrata* were sinks of 23-114 g CO_2-C m^{-2} while the mixtures of sedge and

41 *Sphagnum* mosses resulted in larger sinks of 70-186 g CO_2-C m^{-2}. The larger sinks of the mixed

42 patches were due to the smaller respiration/photosynthesis ratio.

43 **4.** To eliminate the effect of differences in water level and the abundance of sedges between the

44 patches, we simulated the CO_2 exchange for constant water level and vascular leaf area for all plots.

45 The simulation further supported our result: the mixtures of sedge and *Sphagnum* mosses were

46 clearly more efficient in binding CO_2 than pure sedge stands.

47 **5.** *Synthesis and application.* The increased functional diversity in the cut-away site resulted in

48 more productive ecosystem. When restoring cut-away peatlands re-introduction of *Sphagna* after

49 the colonization of vascular plants can increase the productivity and the efficiency of the ecosystem

50 and hasten the formation of a sink for carbon dioxide.

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 *Eripohorum* 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

76 a carbon dioxide sink and a source of methane cut-away peatlands emit CO_2 into the atmosphere

77 while they can oxidize atmospheric CH_4 (Alm *et al.* 1997; Tuittila *et al.* 1999; 2000).

78   In the restoration the aim is to bring back the functioning, peat accumulating ecosystem

79 (Gorham & Rochefort 2003). This will also restore the potential to function as a carbon sink. In the

80 formation of a functional peatland ecosystem *Sphagnum* mosses and sedges have a key role in

81 carbon sequestration and peat production as they are the major carbon sequesters and peat producers

82 (Clymo & Hayward 1982; Van Breemen 1995; Bubier *et al.* 2003). In restoration the first step is to

83 raise the water table, which is the precondition for these key species to re-colonize the area

84 (Schouwenaars 1993; Tuittila,Vasander & Laine 2000; Girard, Lavoie & Thériault 2002; Van Seters

85 & Price 2002; Rochefort *et al.* 2003). Both *Eriophorum vaginatum* and *Carex rostrata* are able to

86 rapidly colonize restored areas (Tuittila, Vasander & Laine 2000; Lavoie *et al.* 2003; Lavoie *et al.*

87 2005) and facilitate the colonization by mosses (Grosvernier *et al.* 1995; Tuittila,Vasander & Laine

88 2000). As the colonization of the key species is the limiting factor in the restoration (Salonen &

89 Setälä 1992; Cobbaert, Rochefort & Price 2004), the process can be hastened by plant re-

90 introduction or planting that can increase both the number of plant individuals and their coverage

91 (Cobbaert, Rochefort & Price 2004). Besides the planting, restoration can be hastened also by

92 fertilization, by tilling or by adding straw mulch to protect *Sphagnum* diaspores from desiccation

93 (Salonen & Laaksonen 1994; Rochefort *et al.* 2003).

94   When planning restoration to achieve rapid carbon sink formation, we need to understand

95 the roles of different plant species in ecosystem carbon dynamics and the conditions favoring their

96 functioning. However, so far little has been known about the effects of different plant communities

97 on the carbon gas balance of restored cut-away peatlands or about the differences between species

98 in their responses to different environmental variables. In this study we aimed to quantify (1) the

99 role of two sedge species, *Carex rostrata* and *Eriophorum vaginatum*, and *Sphagnum* mosses in the

100 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 (62º12'N, 23º18'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 ºC and the mean precipitation 700 mm. The average growing season is 160 days in length, with a cumulative temperature sum (threshold value + 5 ºC) 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 CO_2 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 CO_2 exchange measurement, the sample plots were surrounded with aluminium collars (60 cm $\times$ 60 cm), which were inserted to peat. Boardwalks were constructed to access the study site to avoid disturbance during the measurements.

VEGETATION MONITORING

5

125   To relate the spatial and temporal variation in CO_2 exchange to the vegetation type, we

126   monitored vascular green area (VGA) development in the 19 sample plots over the growing seasons.

127   We estimated the VGA as a product of leaf number and the average size of the leaves. From each

128   sample plot the number of the leaves was calculated monthly and the size of the leaves was

129   measured from permanently marked individuals of *Carex* and *Eriophorum* (n=3) outside the sample

130   plots every three to four weeks. To get a daily estimate of the total VGA in each sample plot we

131   fitted a log-normal curve to the VGA observations separately for each plot using the julian day as

132   an explanatory variable. In the VGA development of *Eriophorum* we observed a smaller VGA peak

133   in the spring besides the mid summer maximum. This pattern, typical for *Eriophorum vaginatum*

134   that can grow up to four cohorts every year (Silvan *et al*. 2004), was described by fitting a curve for

135   the spring and the summer – autumn data separately. The VGA method is described in detail by

136   Wilson *et al*. (2007).

137   A two-way ANOVA was performed on the VGA data to examine the possible differences

138   between the two vascular plant species and the two study years in the timing of the maximum VGA.

139   To relate the variation in the vegetation patches to moisture we established 19 additional

140   sample plots along the moisture gradient, which were systematically located at a 120 cm distance

141   from the selected sample plots. We described species composition in the sample plots by estimating

142   the projected cover for each species. We applied Canonical Correspondence Analysis (CCA) to

143   quantify compositional change along the water table level using the Canoco program package (Ter

144   Braak & Smilauer 2002).

145

146   MEASUREMENTS OF CO_2 FLUXES

147   CO_2 exchange measurements were started at the end of May or in early June and were carried

148   out biweekly until September. Before the measurements, the groove in the collar was filled with

149   water to ensure an air tight seal between the air and the chamber. The net ecosystem CO_2 exchange

150 (NEE) was measured in different irradiation levels (photosynthetically active photon flux density,

151 PPFD) and in the dark using a transparent plastic chamber and a portable infra-red gas analyzer (PP

152 Systems EGM 2). Whenever possible, the measurements were done in different irradiation levels

153 using cloud cover or artificial shade to lower the radiation after the measurement in full daylight.

154 Between measurements the chamber was removed to stabilize the gas concentration. At the end of

155 the measurement series, the chamber was covered with a plastic hood to measure NEE in the dark,

156 which allowed us to get an estimate for ecosystem respiration (R_E). In every measurement the gas

157 concentration in the chamber was recorded every 15 seconds during the two to three minute

158 measurement period. The chamber was equipped with an air circulating fan and a ventilator to keep

159 the temperature inside the chamber at the level of the ambient air temperature. The method has been

160 previously described by Alm *et al*. (1999) and Tuittila *et al*. (1999).

161 We recorded the temperature inside the chamber and the level of PPFD concurrently with gas

162 concentration. The temperature in the peat profile at depths of 5, 10 and 20 cm and the water table

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

164

165 MODELLING THE CO_2 EXCHANGE

166 Our aim was to estimate CO_2 exchange over the growing seasons in different vegetation

167 patches and to quantify their response to environmental variation. To achieve this we formed

168 models for gross photosynthesis (P_G) and ecosystem respiration (R_E) separately for each vegetation

169 type and bare peat. Models are adapted from and the response functions are discussed in more detail

170 in Tuittila, Vasander & Laine (2004).

171 We applied the Michaelis-Menten function to describe the saturating relationship between P_G

172 and PPFD. We used a Gaussian form of response to describe the unimodal dependence of P_G to air

173 temperature. We included VGA and *Sphagnum* in the model to describe the dependence on the

174 amount of photosynthesizing plant material. The P_G model got a form:

175     $P_G = P_{MAX(PPFD, T, VGA, S)} * (PPFD/(k_{PPFD} + PPFD)) * exp(-0.5((T_{air}-o)/t)^2) * (VGA/(k_{VGA}+VGA)) * S$ (1)

176   In the function $P_{MAX (PPFD, T, VGA, S)}$ denotes the photosynthesis that could be reached if the

177   amount of light (PPFD), photosynthesizing plant material (VGA, S) or temperature (Tair) did not

178   limit photosynthesis. Parameter k_{PPFD} denotes the PPDF level where half of the PPDF-saturated P_G

179   is reached, k_{VGA} denotes the VGA level where a half of the VGA saturated P_G is reached, o is the

180   optimum temperature for photosynthesis, t is temperature tolerance for photosynthesis and S is a

181   parameter applied to describe the photosynthetic potential of *Sphagnum* in relation to VGA. We

182   parameterized P_G model for the different stands separately. For *Carex* with had a remarkably lower

183   VGA than in *Eriophorum* we used linear form instead of the saturating VGA response. In mixed

184   *Eriophorum* stands the estimate for parameter S denoting *Sphagnum* photosynthesis did not

185   significantly differ from zero and was therefore excluded.

186   In the R_E model for vegetation stands we used exponential form to describe the dependence of

187   ecosystem respiration on temperature. We parameterized the R_E model separately for the different

188   vegetation patches. We applied linear response of R_E on VGA to describe the dependence of

189   ecosystem respiration on the amount of living plant material. The R_E model got a form:

190     $R_E = b_1 * exp(b_2 * T_{air}) + (b_4 * VGA)$ (2)

191   In the R_{PEAT} model for bare peat surfaces we included water level response in the model in

192   negative exponential form to describe the dependence of soil respiration on the thickness of oxic

193   layer. The model got a form:

194     $R_{PEAT} = b_1 * exp(b_2 * T_{air}) * exp(-b_3 * WT)$ (3)

195

196   COMPARING THE CO_2 EXCHANGE IN DIFFERENT VEGETATION PATCHES

197   To compare the P_G of *Eriophorum* and *Carex* in their optimal conditions we used P_G models

198   to calculate the maximal potential P_G per unit of VGA separately for each group. To take into

199   account the hyperbolic nature of P_G to PPFD, where the P_G asymptotically increases towards the

200 theoretical maximum with increasing light, we used 90% of the maximum PPDF saturated P_G as the

201 realized maximal potential P_G.

202 Using the models with hourly weather data we estimated P_G and R_E for all the sample plots

203 over the both growing seasons between the beginning of June and the end of September. CO_2

204 balances in sample plots were calculated by summing the hourly P_G and R_E from the whole period.

205 PPFD and air temperature data came from Lakkasuo weather station ($61°47'N$; $24°18'E$), which is

206 situated 100 km south-east from Aitoneva.

207 Finally, we compared CO_2 exchange between the four groups without the effect of different

208 VGA and water levels between the plots. We used the R_{PEAT} model to calculate the hourly peat

209 respiration for all the vegetated plots, which was then subtracted from the balances of the vegetated

210 plots. The residual implies plant derived NEE (P_N) without the effect of water level controlled soil

211 respiration. Similarly the plant derived respiration (R_{PLANTS}) was calculated by subtracting the

212 estimated soil respiration from the estimated R_E of the vegetated sample plots. To compare the

213 groups without the effect of different VGA P_G, R_{PLANTS} and P_N are expressed per one VGA unit.

214 Only three out of the five mixed plots of *Carex* were used for this analysis because of the much

215 lower VGA values of the other two plots.

216 All the calculations were done using SPSS 12.0.1 for Windows.

217

218 **Results**

219 VARIATION IN VEGETATION

220 The two vascular plant species studied differed in their timing of the maximum vascular green

221 area (VGA) (species effect: P=0.000). While *Eriophorum* reached its maximum VGA in late July or

222 early August, the timing of the maximum VGA of *Carex* was approximately a week earlier in

223 general and in some cases happened in the beginning of July (Fig. 1). Both species reached their

224 maximum VGA about a week later in the warmer growing season of 2003 than in the colder 2004

225   (year effect: P=0.003). The pattern between the years did not differ between the species

226   (species*year effect: P=0.959)

227   Plant species showed a clear pattern in their distribution along the water level (Fig. 2 a & b).

228   *Eriophorum* had its highest abundance in the drier end of the water level gradient while the wetter

229   conditions favoured *Carex* and *Sphagna* (Fig 2a). *Eriophorum* and *Carex* differed also in their

230   tolerance to water level variation. *Eriophorum* seems to be a generalist that could grow also in the

231   higher water level conditions, but the abundance of *Carex* dramatically decreased towards the dry

232   end of the gradient. The *Sphagnum* species, as a group, favoured wetter conditions (Fig 2a).

233   However, within *Sphagna* there was a turnover of species along the gradient. While most of the

234   *Sphagnum* species had their optimum WL in wet conditions, *S. fallax* had its optimum WL in

235   similar water level conditions to *Eriophorum* (Fig. 2b).

236

237   MOMENTARY CO_2 FLUXES AND THEIR RESPONSE TO ENVIRONMENTAL

238   VARIABLES IN DIFFERENT GROUPS

239   The seasonal variation in the measured net CO_2 exchange (NEE) of the pure *Eriophorum* plots

240   was smaller than the variation of the other three groups (Fig. 3). The measured NEE values were

241   generally larger in the *Eriophorum* plots than in the *Carex*, especially in the spring and autumn. The

242   difference in the measured NEE was in good agreement with the difference in VGA between the

243   species (Fig. 1). Additionally, the measured NEE values in the mixed plots of *Carex* and *Sphagnum*

244   were larger than in the pure *Carex* plots and the difference was similarly more pronounced in the

245   early and late growing season. In contrast to the *Carex* plots, measured NEE values were larger in

246   the pure *Eriophorum* plots than in the mixed plots of *Eriophorum* and *Sphagnum* where the GA of

247   *Eriophorum* was smaller than in the pure plots (Fig. 3).

248   The efficiency of P_G differed between the sedge species (Fig. 4). The half saturation constant

249   in both *Eriophorum* models was clearly higher than in the *Carex* models (parameter k_{PAR} in Table 1,

250 Fig. 4) indicating higher light use efficiency in *Eriophorum*. In the pure vascular plant plots,

251 *Eriophorum* had slightly higher maximal potential P_G (light saturated P_G per 1 unit of VGA in

252 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}

253 VGA m^{-2}, respectively. As a result of the larger amount of photosynthesizing plant material in the

254 mixed plots containing sedges and *Sphagnum*, their maximal potential P_G exceeded the pure sedge

255 plots. The mixed *Eriophorum* plots had higher maximal potential P_G than the mixed *Carex* plots,

256 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

257 variation in P_G, which was not related to the amount of light and the light use efficiency, was

258 associated with the variation in VGA (Fig. 4). In both *Eriophorum* models (Table 1) the response of

259 P_G to VGA typified saturation while in *Carex* P_G increased linearly with the increasing VGA. The

260 difference in the form of response between the species agreed with their amount of VGA. The VGA

261 up to 3 m^2 m^{-2} in the *Eriophorum* plots is likely to cause intensive self-shading, in contrast to rather

262 low VGA in the *Carex* plots where the VGA was around at its largest 1 m^2 m^{-2}. The inclusion of air

263 temperature in the P_G models did not greatly improve their explanatory power in terms of r^2 due to

264 the large tolerance of P_G to variation in temperature in all groups (Table 1, Fig. 4) and due to the

265 autocorrelation between temperature and VGA. However, the inclusion of temperature made

266 parameter values more ecologically meaningful and decreased the standard error of the estimates.

267   In *Eriophorum* plots the large variation in VGA explained most of the seasonal and spatial

268 variation in respiration (R_E). In *Carex*, however, a lower variation in VGA meant that most of the

269 variation in R_E was related to the variation in temperature (Fig. 5). The parameter values in R_E

270 models were of the same magnitude between the groups (Table 2).

271

272 THE CO_2 BALANCES OF THE GROWING SEASONS

273   The simulated seasonal net CO_2 exchange (June - September) was positive in both years in all

274 the vegetated plots, *ie*. they all acted as net sinks for atmospheric CO_2 (Fig. 6). The seasonal NEE

275 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

276 and 133 g CO_2-C m^{-2} in the pure and mixed *Carex* and *Eriophorum* plots, respectively. The *Carex*

277 plots with *Sphagnum* had significantly higher seasonal NEE than the pure sedge plots (P=0.031)

278 resulting from the higher seasonal P_G (P=0.008). In contrast to the *Carex* plots, the seasonal NEE of

279 the pure and mixed *Eriophorum* plots were of the same magnitude, in spite of the trend towards

280 higher seasonal R_E in the mixed plots (P=0.074). Differences in the seasonal fluxes between the two

281 growing seasons were small (Fig. 6). The control plots acted as seasonal sources of 20-71 g CO_2-C

282 m^{-2} into atmosphere (Fig. 6).

283   When the P_G and R_E of the groups were proportioned to the VGA and the estimated peat

284 respiration was subtracted, it became even more obvious that the mixed plots with *Sphagnum* were

285 more efficient sinks than the pure vascular plant plots (Fig. 7). The seasonal P_N when seasonal

286 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

287 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

288 the pure and mixed *Carex* and *Eriophorum* plots, respectively. The difference was uniform over the

289 whole growing season rather than seasonal during the spring or autumn, when the difference in

290 VGA between the species was largest. The plant derived respiration (R_{PLANT}) per VGA unit was at

291 the same level in all the groups and varied between 119 and 216 g CO_2-C m^{-2} VGA m^{-2}; the

292 differences in the P_G was responsible for the difference between the pure and mixed plots. The P_G

293 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

294 clearly higher, between 306 and 588 g CO_2-C m^{-2} VGA m^{-2}.

295

296 **Discussion**

297 FACTORS INFLUENCING REVEGETATION

298   In order to promote carbon sink function it is essential to maximise vegetation cover of the

299 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* occured 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_2O 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

350   carbon balance of the whole study site one has to consider that in the area there are still totally non-

351   vegetated peat surfaces, which must be taken account when the greenhouse gas balance is

352   considered.

353   When the seasonal P_N estimates per VGA unit were compared between the stands, the mixed

354   stands appeared to be more efficient. Tuittila, Vasander & Laine (2004) measured a NEE of 94 g

355   CO_2-C m^{-2} for *Sphagnum* in the same study area under optimal conditions. Accordingly, most of the

356   bigger NEE of the mixed plots is explained by the photosynthesis of *Sphagnum*. However, it does

357   not explain the difference entirely and it seems that the enhanced functional diversity leads to

358   increased productivity. According to our study the combination of the two components appears to

359   be more efficient that the sum of the individual components. Growth in productivity with increasing

360   functional diversity has been found also in other ecosystems (e.g. Tilman *et al.* 1997; Kaye *et al.*

361   2000).

362   The control plots formed a source of CO_2 during both growing seasons. The measured values

363   in this study, -20 to 71 g CO_2-C m^{-2}, were much smaller than measured by Waddington *et al.* (2002)

364   from non-restored cut-away peatland. They had values of -363 g C m^{-2} in a dry year and -112 g C

365   m^{-2} in a rainy year. However, compared to the study of Tuittila *et al.* (1999), made in the same

366   study area immediately following the restoration, the non-vegetated plots have the same or slightly

367   smaller respiration values. It seems that the restoration has also decreased the respiration of the non-

368   vegetated areas. McNeil & Waddington (2003) measured a value of -84 g C m^{-2} from a bare peat

369   surface in a spontaneously revegetated area, which is of the same magnitude as the values in our

370   study.

371   In conclusion, when restoring a cut-away peatland it would be useful to encourage both

372   *Eriophorum vaginatum* and *Carex rostarata* to colonize the area, either naturally or by planting,

373   because these species are at their most efficient during different time of the growing season and at

374   different water levels. The reintroduction of *Sphagna* following vascular plant colonization would

375   further enhance the productivity and the efficiency of the ecosystem.

376

386

Literature cited

388   Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern

389   Europe. *Annales Botanici Fennici*, **5**, 169-211.

390   Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H. & Martikainen,

391   P. J. (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen,

392   Finland. *Oecologia*, **110**, 423-431.

393   Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P.J. & Silvola, J. (1999) Carbon

394   balance of a boreal bog during a year with an exceptionally dry summer. *Ecology*, **80**, 161-174.

395   Aurela, M., Laurila, T. & Tuovinen, J.-P. (2001) Seasonal CO_2 balances of a subarctic mire.

396   *Journal of Geophysical Research*, **106**, 1623-1637.

397   Bernard, J. M. & Hankinson, G. (1979) Seasonal changes in standing crop, primary production and

398   nutrient levels in a Carex rostrata wetland. *Oikos*, **32**, 328-336.

399   Bubier, J., Crill, P., Mosedale, A., Frolking, S. & Linder, E. (2003) Peatland responses to varying

400   interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical*

401   *Cycles*, **17**, 1-15.

402   Chapin, F. S. III, Cleve, K. V. & Chapin , M. C. (1979) Soil temperature and nutrient cycling in the

403   tussock growth form of Eriophorum vaginatum. *Journal of Ecology*, **67**, 169-189.

404   Clymo, R.S. & Hayward, P.M. (1982) The ecology of Sphagnum. *Bryophyte Ecology*. (ed. A.J.E.

405   Smith) 229-291.Chapman & Hall, London,

406   Cobbaert, D., Rochefort, L. & Price J. S. (2004) Experimental restoration of a fen plant community

407   after peat mining. *Applied Vegetation Science*, **7**, 209-220.

408   Frilander, P., Leinonen, A. & Alakangas, E. (1996) Peat production technology. *Peatlands in*

409   *Finland* (*ed.* H. Vasander), 99-106. Finnish Peatland Society, Helsinki.

410   Girard, M., Lavoie, C. & Thériault, M. (2002) The regeneration of a highly disturbed ecosystem: A

411   mined peatland in southern Québec. *Ecosystems*, **5**, 274-288.

412   Gorham, E. & Rochefort L. (2003) Peatland restoration: A brief assessment with special reference

413   to Sphagnum-bogs. *Wetlands Ecology and Management*, **11**, 109-119.

414   Griffis, T.J., Rouse.T.R., Waddington, J.M. (2000) Interannual variability of net ecosystem CO_2

415   exchange at a subarctic fen. *Global Biogeochemical Cycles*, **14**, 1109-1121.

416   Grosvernier, P., Matthey, Y. and Buttler A. (1995) Microclimate and physical properties of peat:

417   new clues to the understanding of bog restoration processes. *Restoration of Temperate Wetlands*

418   (*eds.* B. D. Wheeler, S.C. Shaw,W.J. Fojt & R.A. Robertson), 435-450. John Wiley & Sons

419   Chicester, UK.

420   Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (*eds.*) (1998) *Retkeilykasvio* (Field Flora of

421   Finland), 4th edn. 656 pp. Finnish Museum of Natural History, Botanical Museum, Helsinki.

422   Huopalainen, M., Tuittila, E.-S., Laine, J. & Vasander, H. (1998) Seed and spore bank in a cut-

423   away peatland twenty years after abandonment. *International Peat Journal*, **8**, 42-51.

424   Kaye, J. P., Resh, S. C., Kaye, M. W. & Chimner, R. A. (2000) Nutrient and carbon dynamics in a

425   replacement series of Eucalyptus and Albizia trees. *Ecology*, **81**, 3267-3273.

426   Lavoie, C., Grosvernier, P., Girard, M. & Marcoux, K. (2003) Spontaneous revegetation of mined

427   peatlands: An useful restoration tool? *Wetlands Ecology and Management*, **11**, 97-107.

428   Lavoie, C., Marcoux, K., Saint-Louis, A. & Price, J.S. (2005) The dynamics of a cotton-grass

429   (Eriophorum vaginatum L.) cover expansion in a vacuum-mined peatland, Southern Quebec,

430   Canada. *Wetlands*, **25**, 64-75.

431   McNeil, P. & Waddington, M. (2003) Moisture controls on Sphagnum growth and CO_2 exchange

432   on a cutover bog. *Journal of Applied Ecology*, **40**, 354-367.

433   Money, R. (2004) Optimising conditions for wetland restoration. *Guidelines for wetland restoration*

434   *of peat cutting areas.* Results of the BRIDGE-PROJECT, (eds. Blankenburg, J. & Tonnis W),60 pp.

435   Bremen.

436   Rochefort, L., Quinty, F., Campeau, S., Johnson, K. & Malterer, T. (2003) North American

437   approach to the restoration of Sphagnum dominated peatlands. *Wetlands Ecology and Management*,

438   **11**, 97-107.

439   Rydin, H. & McDonald, A.J.S. (1985). Photosynthesis in *Sphagnum* at different water contents.

440   *Journal of Bryology*, **13**, 579-584.

441   Salonen, V. (1987) Relationship between the seed rain and the establishment of vegetation in two

442   areas abandoned after peat harvesting. *Holarctic Ecology*, **13**, 171-174.

443   Salonen, V. & Laaksonen, M. (1994) Effects of fertilization, liming, watering and tillage on plant

444   colonization of bare peat surfaces. *Annales Botanici Fennici*, **31**, 29-36.

445   Salonen, V. & Setälä, H. (1992) Plant colonization of bare peat surface – relative importance of

446   seed availability and soil. *Ecography*, **15**, 199-204.

447   Schouwenaars, J. M. (1993) Hydrological differences between bogs and bog-relicts and

448   consequences for bog restoration. *Hydrobiologia*, **265**, 217-224.

449   Silvan, N., Vasander, H. & Laine, J. (2004) Vegetation is the main factor in nutrient retention in a

450   constructed wetland buffer. *Plant and Soil*, **258**, 179-187.

451   Silvan, N., Tuittila, E.-S., Vasander, H. & Laine, J. (2004) Eriophorum vaginatum plays a major

452   role in nutrient immobilisation in boreal peatlands. *Annales Botanici Fennici*, **41**, 189–199.

453   Soegaard, H. & Nordström, C. (1999) Carbon dioxide exchange in a high arctic fen estimated by

454   eddy covariance measurements and modeling. *Global Change Biology*, **5**, 547-562.

455   Ström, L., Mastepanov, M. & Christensen, T.R. (2005) Species-specific effects of vascular plants

456   on carbon turnover and methane emissions from wetlands. *Biogeochemistry*, **75**, 65-82.

457   Svensson, B. M. (1995) Competition between Sphagnum fuscum and Drosera rotundifolia: a case

458   of ecosystem engeneering? *Oikos*, **74**, 205-212.

459   Ter Braak, C.J.F. & Šmilauer, P. (2002) *Canoco reference manual and CanoDraw for Windows*

460   *user's guide: Software for canonical community ordination (version 4.5).* Microcomputer Power,

461   Ithaca, NY, USA.

462   Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of

463   functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

464   Tuittila, E.-S., Komulainen, V.-M., Vasander, H. & Laine J. (1999) Restored cut-away peatland as a

465   sink for atmospheric CO_2. *Oecologia*, **120**, 563-574.

466 Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Nykänen, H., Martikainen, P. J. & Laine, J. (2000)

467 Methane dynamics of a restored cut-away peatland. *Global Change Biology*, **6**, 569-581.

468 Tuittila, E-S., Vasander, H. & Laine, J. (2000) Impact of rewetting on the vegetation of a cut-away

469 peatland. *Applied Vegetation Science*, **3**, 205-212.

470 Tuittila, E-S., Vasander, H. & Laine, J. (2004) Sensitivity of C sequestration in reintroduced

471 Sphagnum to water-level variation in a cutaway peatland. *Restoration Ecology*, **12**, 483-493.

472 Van Breemen, N. (1995) How *Sphagnum* bogs down other plants? *TREE*, **10**, 270-275.

473 Van Seters, T. & Price, J. S. (2002) Towards a conceptual model of hydrological change on an

474 abandoned cutover bog, Québec. *Hydrological processes*, **16**, 1695-1981.

475 Vasander, H. & Roderfeld, H. (1996) Restoration of peatlands after peat harvesting. *Peatlands in*

476 *Finland* (ed. H.Vasander), pp.143-147. Finnish Peatland Society, Helsinki.

477 Waddington, J. M., Warner, K. D. & Kennedy, K. W. (2002) Cutover peatlands: A persistent source

478 of atmospheric CO_2. *Global Biogeochemical Cycles*, **16**, doi:10.1029/2001GB001398.

479 Wein, R. W. (1973) *Eriophorum vaginatum* - Biological flora of the British Isles. *Journal of*

480 *Ecology*, **61**, 601-615.

481 Wilson, D., Alm, J., Riutta, T., Laine, J., Kenneth, B.A., Farrell, E.P. & Tuittila, E.-S. (2007) A

482 high Resolution green Area index for Modelling CO_2 exchange in Vascular Plant Peatland

483 Communities. *Plant Ecology*, in press.

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

486

Parameter	EV	CR	EV+S	CR+S
P_{max} (mg)	4587.9 ± 815.6	985.8 ± 73.1	4872.6 ± 1679.7	813.4 ± 81.1
k_{PPFD} (µmol)	316.2 ± 58.3	134.7 ± 52.0	452.1 ± 184.6	130.2 ± 41.2
k_{VGA} (m^{-2})	3.4 ± 0.8		1.1 ± 0.47	
s				0.46 ± 0.1
o (ºC)	16.6 ± 2.5	29.8 ± 4.5	24.3 ± 1.2	22.1 ± 1.2
t (ºC)	17.5 ± 3.2	17.5 ± 6.8	10.5 ± 2.3	13.6 ± 2.8

494 Table 2. The parameters and their standard errors in R_E models for pure and mixed *Eriophorum* and
495 *Carex* stands.
496

Parameter	EV	CR	EV+S	CR+S	Control
b1	49.79±14.6	32.57±17.7	18.53±11.8	12.11±8.4	12.23±3.6
b2	0.044±0.01	0.065±0.01	0.086±0.02	0.085±0.02	0.069±0.01
b3	133.31±11.9	108.78±43.6	173.83±47.1	199.57±20.7	
b4					0.055±0.005

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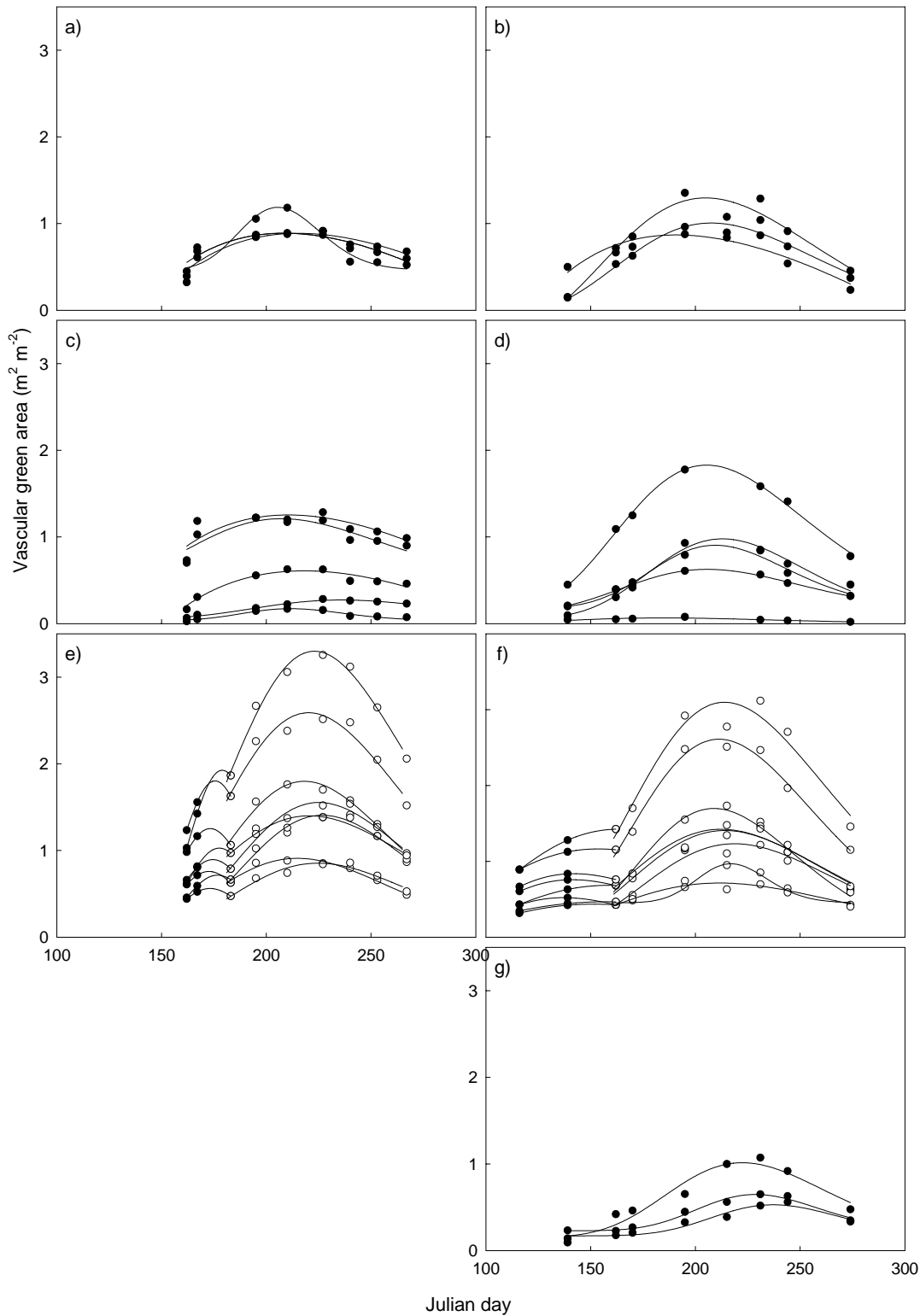
Figure 1. The development of the vascular green area (VGA) of the different stands during growing
seasons 2003 (left) and 2004 (right). Development in each sample plot is described by fitting a log-
normal curve using the Julian day as an explaining variable. The VGA of *Eriophorum vaginatum*
was described 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*

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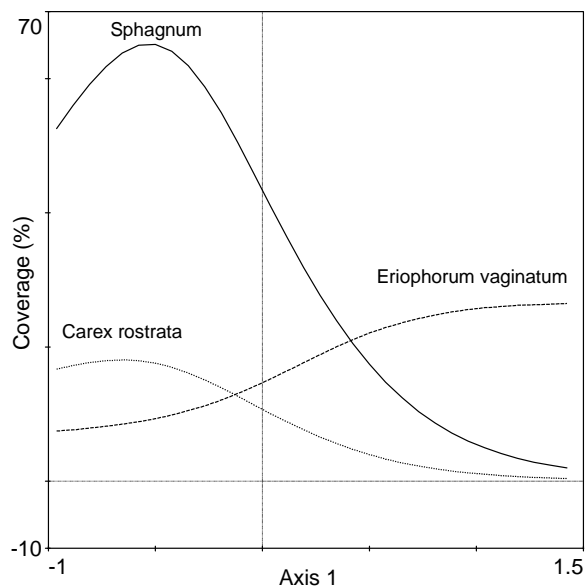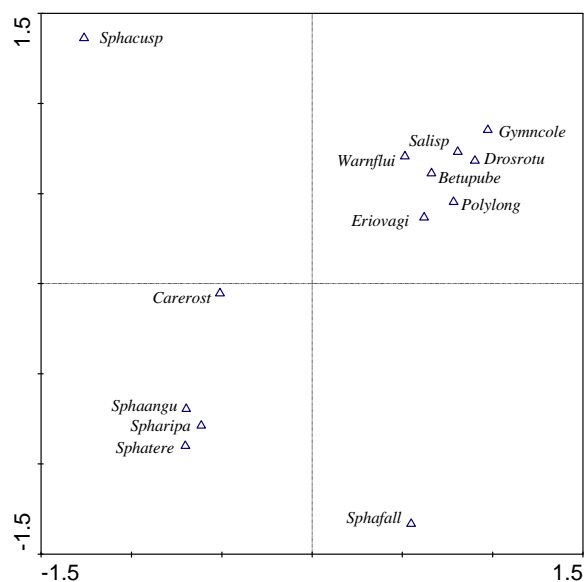
Figure 2. Distribution of the studied species along the moisture gradient. a) Projection cover of the dominant plant species along the moisture gradient, first CCA axis. Water level increases along the axis from right to left. b) Distribution of plant species in CCA ordination space, where the first 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 fluitans.*

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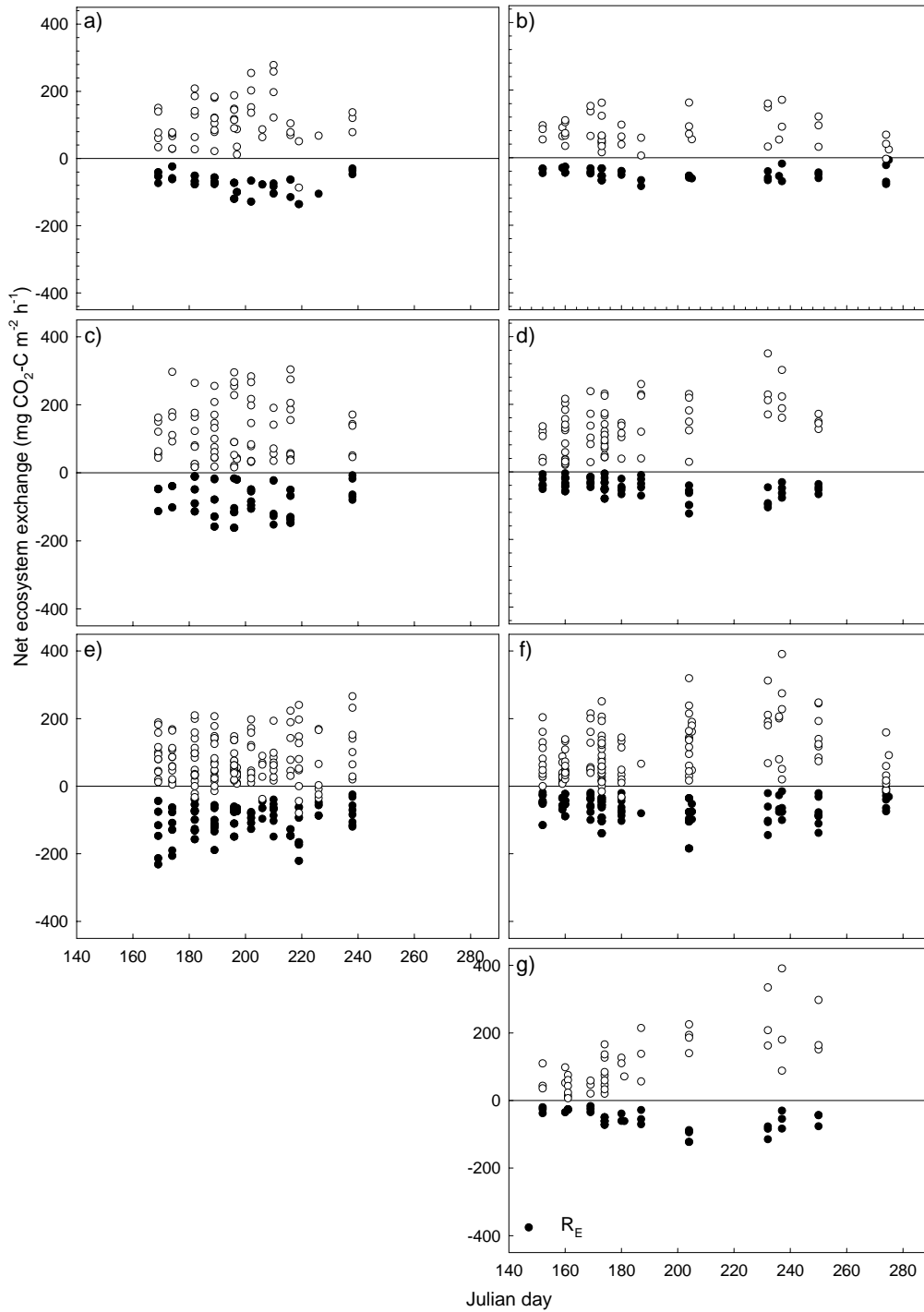
Figure 3. The measured net ecosystem exchanges (NEE) of the different stands during the growing

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.*
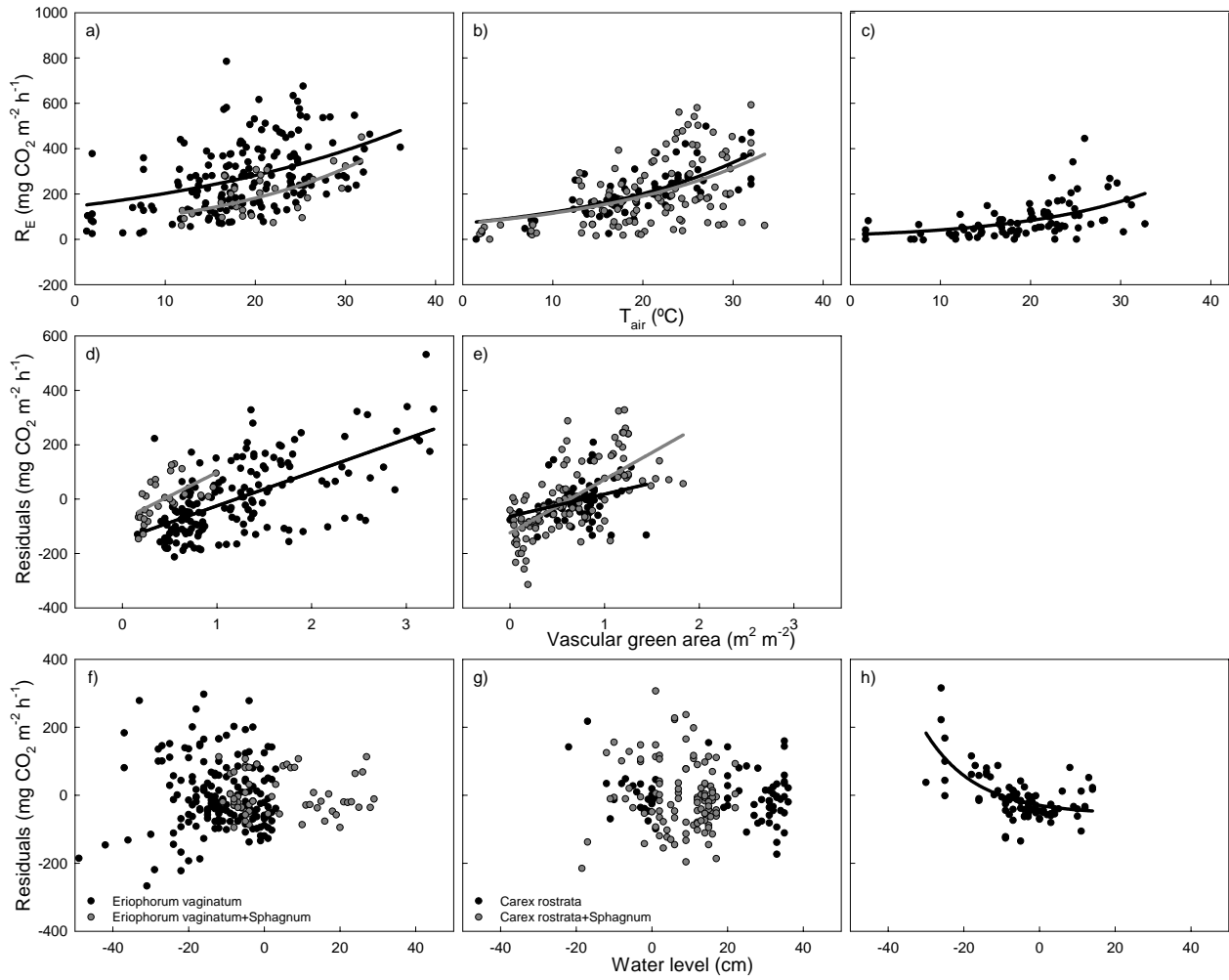
vaginatum+*Sphagna.*

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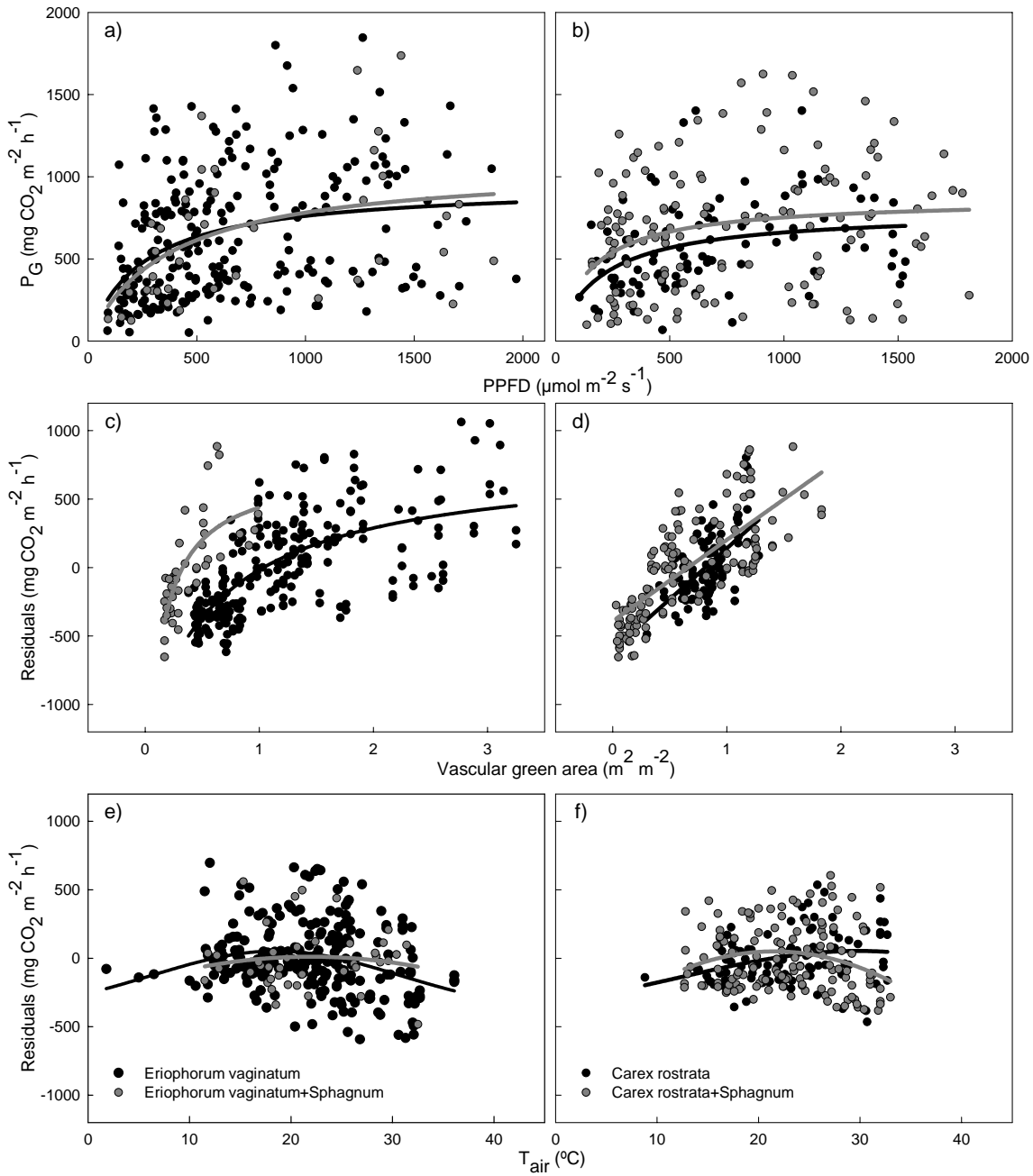
Figure 4. The measured gross photosynthesis (P_G) values against different environmental variables.

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.

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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.
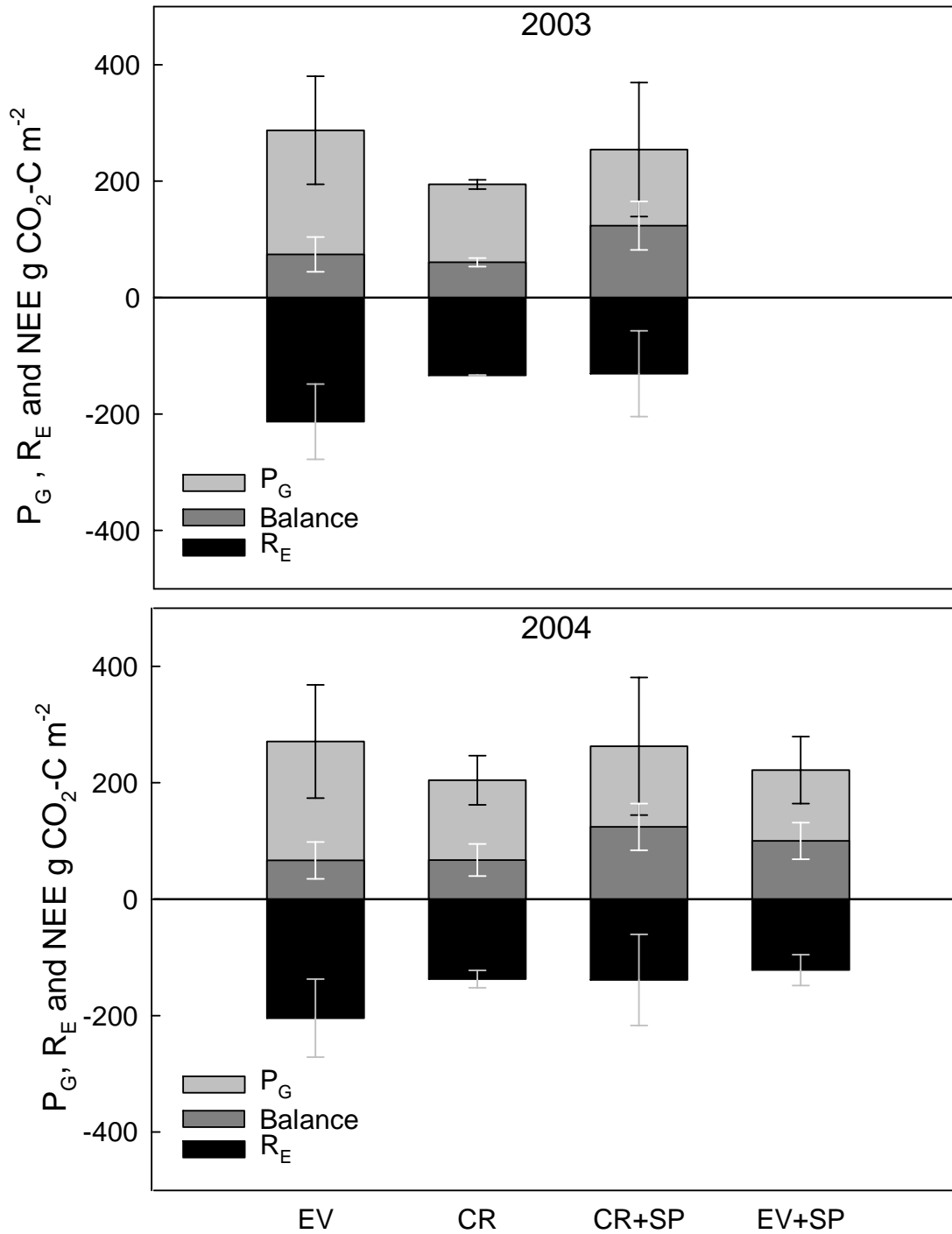
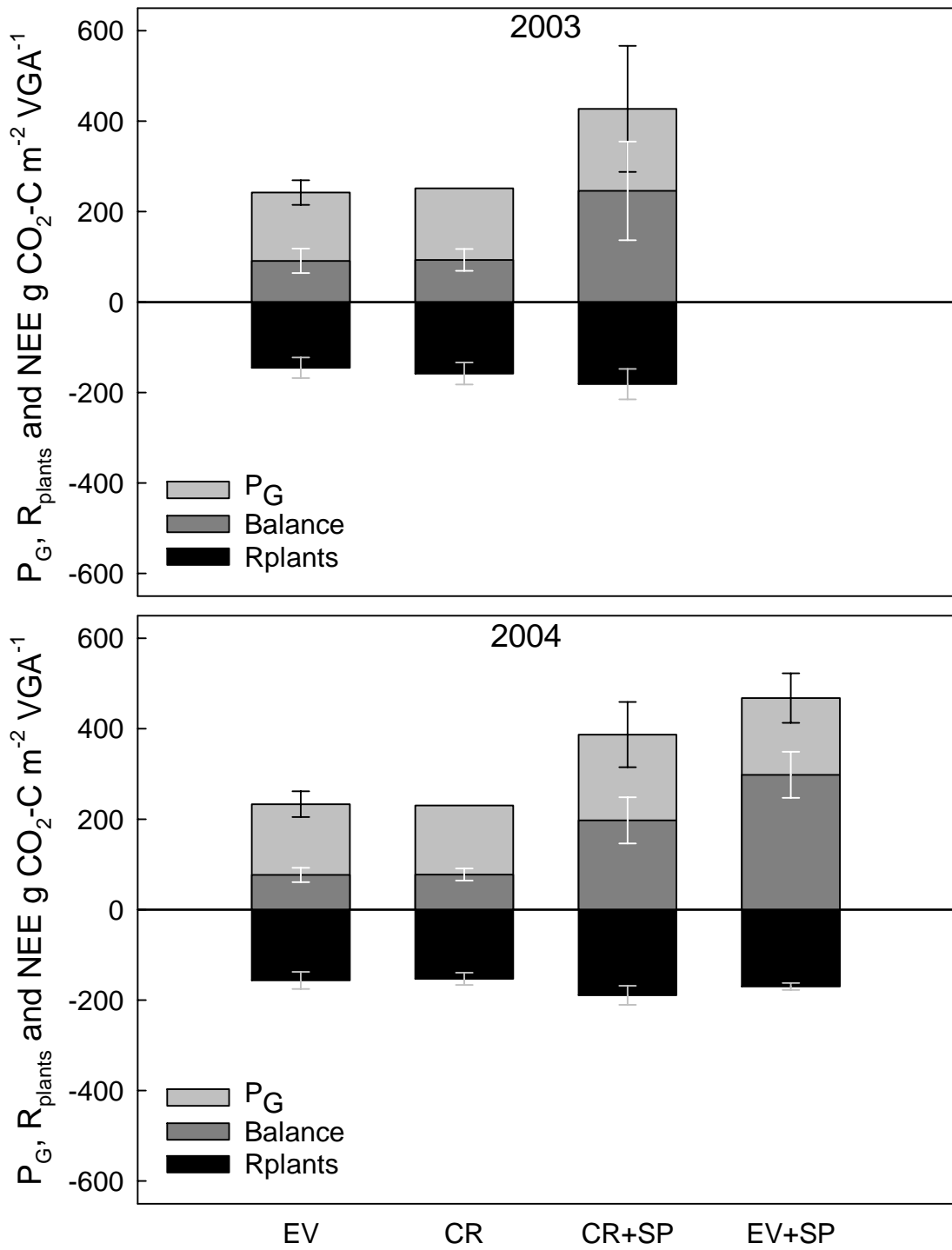Figure 6. P_G, R_E and CO_2 balance of the growing seasons for different groups in growing seasons 2003 and 2004. The mixed stands of *Eriophorum vaginatum* and *Sphagnum* were only measured in the growing season 2004.

Figure 7. The P_G, R_{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.