Abundance and composition of plant biomass as potential controls for mire net ecosystem CO$_2$ exchange

Anna M. Laine, Jill Bubier, Terhi Riutta, Mats B. Nilsson, Tim R. Moore, Harri Vasander, and Eeva-Stiina Tuittila

Abstract: We compared the amount and composition of different aboveground biomass (BM) fractions of four mires with their net ecosystem CO$_2$ exchange (NEE) measured by eddy covariance. We found clear differences in response of green biomass (GBM) of plant functional types (PFTs) to water table (WT), which resulted in larger spatial variation in GBM within a mire than variation between mires. GBM varied between mires from 126 ± 7 to 336 ± 16 g·m$^{-2}$ (mean ± SE), while within mire variation at largest was from 157 ± 17 to 488 ± 20 g·m$^{-2}$ (mean ± SE). GBM of dominant PFTs appeared to be better in explaining the peak growing season NEE than the total BM or GBM of a mire. The differences in photosynthetic capacity between PFTs had a major role, and thus a smaller GBM with different species composition could result in higher NEE than larger GBM. Vascular plant GBM, especially that of sedges, appeared to have a high impact on NEE. Eleven PFTs, defined here, appeared to capture well the internal variation within mires, and the differences in GBM between communities were explained by the water table response of PFTs. Our results suggest the use of photosynthesizing BM, separated into PFTs, in modelling ecosystem carbon exchange instead of using just total BM.

Key words: bog, fen, microtopography, net ecosystem exchange, peatland, plant functional type, water table.

Introduction

Mires have a dual effect on atmospheric greenhouse gas concentrations. They assimilate atmospheric carbon dioxide (CO$_2$) in photosynthesis and release CO$_2$ and methane (CH$_4$) in respiration. Mires have stored a significant amount of carbon into peat over the last millennia (Gorham 1991; Turunen...
et al. 2002) and during the Holocene they have had a net cooling effect on the atmosphere radiation balance, as the effect of long-term carbon accumulation overrules the transient warming caused by the CH4 emissions (Frolking et al. 2006). Carbon gas exchange has been studied in several mire ecosystems during the past decades (e.g., Alm et al. 1997; Lund et al. 2010; compilation by Saarnio et al. 2007), and since the 1990s the increased use of eddy covariance (EC) method has enabled long-term landscape level measurements of CO2 and to a lesser extent CH4 exchange (Baldocchi 2003). Today, long-term data on mire–atmosphere CO2 exchange exist from a very limited number of sites, the most extensive ones being Kaamasensuo, northern Finland, since 1997 (Aurela et al. 1998, 2004), and Mer Bleue, southern Canada, since 1998 (Lafleur et al. 2001; Roulet et al. 2007; Teklemariam et al. 2010). To estimate the regional and global carbon gas exchange between mires and the atmosphere, the long-term measurement data is used for parameterization of models and photosynthesizing biomass (BM) is a prerequisite for CO2 assimilation (Frolking et al. 2002; Schubert et al. 2010).

Within mires, plant communities and corresponding BM may vary to a large extent (Kosyk et al. 2008; Reinkainen et al. 1984; Vasander 1982, 1987). The dominant controls on species composition and BM are water table (WT) position and nutrient status. Nutrient-poor bogs that are isolated from groundwater influence are characterized by dwarf shrubs and Sphagnum mosses, while sedges and herbs are more abundant in fens that receive groundwater from the catchment.

Most mires in the northern hemisphere have a distinct surface pattern of microforms. While the variation in vegetation between mires is largely caused by nutrient status, the plant communities in microforms vary due to the WT (Bragazza and Gerdol 2002). Spatial diversity varies between mires; some fens have a rather uniform surface, while most bogs and the northerly fens have a conspicuous pattern of high ridges/hummocks and open water pools/flarks (Ruuhijärvi 1983). The optimal WT conditions vary between different plant species, with shrubs generally occurring in drier habitats than most sedge species (Lumiala 1944). Vascular plants tend to have a wider tolerance for the WT than Sphagnum species (Lumiala 1944; Vääränta et al. 2007). Different Sphagnum species replace each other along the hummock–hollow gradient and therefore, as a genus, are able to inhabit the wide range of WT conditions met in the mires (Andrus et al. 1983; Laine et al. 2009; Rydin and McDonald 1985). Owing to differences in WT and plant communities, all components of carbon balance vary substantially between microforms and plant communities, and the C balance of microforms within a mire may vary from net uptake to net loss (Alm et al. 1999; Laine et al. 2007; Waddington and Roulet 2000; Sullivan et al. 2008).

Because plant species composition varies largely between mires, BM at the species level may be too detailed for models when examining feedbacks between vegetation, WT, nutrients, and ecosystem carbon dynamics. Plant functional types (PFTs) that combine species with similar responses to environmental factors are more useful for predicting vegetation responses to the environment (Chapin et al. 1996). Typical mire PFTs such as shrubs, sedges, forbs, and mosses, show different seasonal growth dynamics (Leppälä et al. 2008), photosynthetic capacities and respiration rates (Bubier et al. 2003; Leppälä et al. 2008; Riutta et al. 2007b), quality of litter (Moore et al. 2007; Szumigalski and Bayley 1996), and roles in CH4 dynamics (Joabsson et al. 1999; Shannon et al. 1996). In addition, their responses to changing environmental conditions may vary (Walker et al. 2006; Weltzin et al. 2001). Owing to their close linkage to mire ecosystem function, PFTs offer a useful tool for describing vegetation abundance and structure as a part of ecosystem models. Recently Frolking et al. (2010) presented a peatland development model (Holocene peat(land) model, HPM) where 12 PFTs are responsible for peat growth over the Holocene time scale. HPM is a first modelling attempt to quantitatively link carbon accumulation process to vegetation composition and dynamics. A close link between vegetation composition and CH4 emission exists, related to the close relationship between net distribution and WT and to the abundance of aerenchymatous species (Bubier 1995; Dias et al. 2010; Granberg et al. 1997; Koelbener et al. 2010; Nilsson et al. 2001). However, such a relationship between net ecosystem CO2 exchange (NEE) and PFTs BM has not been established.

In this paper, we compare the amount and composition of BM of four mires, at which NEE has been measured by EC. We hypothesize that (i) there is larger spatial variation in the BM within a mire than variation between mires that results from a strong relationship between vegetation and WT, and (ii) NEE is related to the BM of the dominant PFTs.

## Material and methods

### Study sites

The study was carried out in four northern mires located in Finland, Sweden, and Canada. The sites are part of the Carbo Europe and Canadian Carbon Program networks, which coordinate and facilitate regional and global analysis of observations from micrometeorological tower sites. Climatic information for the sites is given in Table 1.

Kaamasensuo (Aurela et al. 1998, 2001, 2002, 2004) is a mesotrophic flark fen located in Kaamanen, Finland, in the northern boreal zone (Ahti et al. 1968; Kalela 1961) with a subarctic climate. Typical of northern fens, also called aapa mires, the surface forms a distinctive pattern of strings and flarks. On the flarks, sedges such as Carex and Trichophorum species and brown mosses mostly belonging to Drepanoclados species sensu lato dominate, while the plant communities on the strings are composed of dwarf shrubs such as Ledum palustre L. and Calluna vulgaris (L.) Hull, and feather mosses such as Pleurozium schreberi (Br.) Mitt. For more details on the site see Maanavilja et al. (2010).

Siikaneva (Aurela et al. 2007) is an oligotrophic fen located in Ruovesi, Finland, close to the border of the southern and middle boreal zones (Ahti et al. 1968; Kalela 1961). The Siikaneva mire consists of relatively homogenous lawn vegetation dominated by sedges (Carex spp., Eriophorum spp.), Scheuchzeria palaustris L., and Sphagnum mosses. Hollows are covered by Sphagnum species adapted to the wettest conditions and somewhat higher hummocks by dwarf shrub vegetation occur among the lawn level vegetation. For more details on the site see Riutta et al. (2007a).

Degerö Stormyr (Nilsson et al. 2008; Sagerfors et al. 2008) is an oligotrophic fen located in northern Sweden in the mid-
The climate of the site is defined as cold, temperate, and humid. The part of the mire complex used for the NEE measurements is dominated by lawn and hollow plant communities. The vascular plant community is dominated by *Eriophorum vaginatum* L., *Trichophorum cespitosum* (L.) Hartm., *Vaccinium oxycoccos* L., *Andromeda polifolia* L., and *Rubus chaemomorus* L., with both *Carex limosa* L. and *S. palustris* occurring more sparsely. The bottom layer of the hollows (approximate average WT level during the growing season, 0–10 cm below the mire surface) is dominated by *Sphagnum majus* (Russ.) C. Jens. and of the lawns (approximate average WT level during the growing season, 10–25 cm below the mire surface) is dominated by *Sphagnum balticum* (Russ.) C. Jens. and of the lawns (approximate average WT level during the growing season, 10–25 cm below the mire surface) is dominated by *Sphagnum lindbergii* Schimp. ex Lindb. For more details on the site see Näslund et al. (2008) and Eppinga et al. (2010).

Mer Bleue (Lafleur et al. 2001; Roulet et al. 2007) is an ombrotrophic bog located near Ottawa, Canada, in the southeastern boreal zone. The mire area can be divided into clearly ombrotrophic and poor fen areas. The EC tower is located in the bog area that has a relatively homogenous hummocky surface dominated by a dense ericaceous dwarf shrub cover (*Chamaedaphne calyculata* (L.) Moench., *Ledum groenlandicum* Oeder, *Kalmia angustifolia* L., and *Vaccinium myrtilloides* Michx.) accompanied by sparse clusters of *E. vaginatum*. The bottom layer is a dense moss carpet formed by *Sphagnum capillifolium* (Ehrh.) Hedw. and *Sphagnum magellanicum* Brid., interspersed with *Polystichum strictum* Menzies ex Bridel. For more details on the site see Bubier et al. (2006).

**Vegetation sampling**

The aboveground BM of vascular plants was collected from circular 15 cm radius plots, except in Mer Bleue, where the plots were 50 cm × 50 cm square. Bryophytes and lichens were inventoried from a one-quarter section of the total plot. In Degerö Stormyr, all the vegetation was inventoried from a one-quarter section of the circular 15 cm plot. Only the capitula were collected for *Sphagnum* mosses for consistency in comparing BM data across sites. For other mosses the uppermost 2 cm was harvested. The number of sample plots was 36, 59, 93, and 32 in Kaamasensuo, Siikaneva, Mer Bleue, and Degerö Stormyr, respectively.

At Kaamasensuo the sampling was done in August 2006 and sample plots were divided into two vegetation types, flarks (*n* = 18) and strings (*n* = 18). At Siikaneva the sampling was also conducted in August 2006 and sample plots were stratified to inventory seven different plant communities: *E. vaginatum* dominated lawns (EV, *n* = 10); *Carex rostrata* Stokes dominated lawns (CR, *n* = 8); and *Carex lasiocarpa* Ehrh. dominated lawns (CL, *n* = 9), hollows (HO, *n* = 9), low hummocks (HU, *n* = 9), minerotrophic hummocks (MI, *n* = 9), and ombrotrophic hummocks (OM, *n* = 5). At Mer Bleue the samples were collected in early September 2003 from the EC tower footprint (*n* = 31) and from two additional locations, i.e., Poor Fen (*n* = 32) and Blue Dome, which is a slightly wetter bog area (*n* = 28) (Bubier et al. 2006). All samples at Degerö Stormyr were located at lawn level vegetation from the EC tower footprint and the sampling was carried out in August 2008.

Vascular plant BM was first separated by species. Woody species were further separated into leaf and stem BM. Samples were oven dried (at 60 °C) and weighed. In most analyses we use green biomass (GBM) that combines the leaf BM of woody vascular plants, all aboveground BM of herbaceous vascular plants, and the upper part of mosses. To define BM variation using more general terms than species, the plant species were divided into 11 PFTs (Frolking et al. 2010), namely minerotrophic sedges, ombrotrophic sedges, minerotrophic forbs, ombrotrophic forbs, deciduous shrubs, evergreen shrubs, hollow sphagna, lawn sphagna, hummock sphagna, brown mosses, and feather mosses (including lichens). Plant species were classified into PFTs based on the literature according to their ecological niche optima along fertility and WT gradients. In the logic of PFTs classification, minerotrophic plant types are those that need minerotrophic conditions to form a substantial BM. Ombrotrophic plant types, on the other hand, are capable of growing also in minerotrophic conditions, but in more nutrient-rich conditions such as in mesotrophic fens they are outcompeted by minerotrophic species. In nutrient-poor minerotrophic conditions, namely in oligotrophic fens, the competitive superiority of minerotrophic species is weak and ombrotrophic plant types can form large parts of the communities. The division of moss PFTs is based on their ecological niche optimization; species have their highest abundance in those conditions where the environment is optimal or close to optimal and where they are able to successfully compete with other species. Outside of the optimum, species abundance decreases as conditions become suboptimal and at the end of their tolerance range they disappear (Austin 2005). In addition to nutrient requirements, *Sphagnum* species have an optimum along the microtopographic gradient (Väliranta et al. 2007). Hollow sphagna have the narrowest tolerance and can generally grow only in wet conditions, while the tolerance of lawn sphagna is the largest and they can be found along the whole gradient. Hummock sphagna are usually outcompeted from wet hollows. Brown mosses and feather mosses are divided by the

**Table 1. Study site descriptions.**

<table>
<thead>
<tr>
<th>Location</th>
<th>Kaamasensuo</th>
<th>Siikaneva</th>
<th>Mer Bleue</th>
<th>Degerö Stormyr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>69°08′N, 27°17′E</td>
<td>61°49′N, 24°11′E</td>
<td>45°41′N, 75°48′W</td>
<td>64°11′N, 19°33′E</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td>441</td>
<td>713</td>
<td>943</td>
<td>567</td>
</tr>
<tr>
<td>Average temperature in July (°C)</td>
<td>13.1</td>
<td>15.5</td>
<td>20.9</td>
<td>14.8</td>
</tr>
<tr>
<td>Average temperature in January (°C)</td>
<td>−13.9</td>
<td>−7.4</td>
<td>−10.8</td>
<td>−11.2</td>
</tr>
<tr>
<td>Average annual temperature (°C)</td>
<td>−1.1</td>
<td>3.0</td>
<td>6.0</td>
<td>1.2</td>
</tr>
</tbody>
</table>

Table 2: Classification of species occurring in the study sites into plant functional types (PFTs).

<table>
<thead>
<tr>
<th>PFTs</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evergreen shrub</td>
<td>Andromeda glauca, Empetrum nigrum, Kalmia angustifolia, Ledum palustre,</td>
</tr>
<tr>
<td></td>
<td>Pinus sylvestris, Vaccinium oxycoccus, Vaccinium vitis-idaea</td>
</tr>
<tr>
<td>Deciduous shrub</td>
<td>Vaccinium myrtillus, Vaccinium uliginosum</td>
</tr>
<tr>
<td>Ombro forb</td>
<td>Rubus chamaemorus, Scheuchzeria palustris</td>
</tr>
<tr>
<td>Minero forb</td>
<td>Drosera longifolia, Maianthemum trifolium</td>
</tr>
<tr>
<td>Ombro sedge</td>
<td>Carex pauciflora, Eriophorum vaginatum, Melampyrum sp., Riccardia sp.</td>
</tr>
<tr>
<td>Brown moss</td>
<td>Campylium stellatum, Limprichtia intermedia</td>
</tr>
<tr>
<td>Hummock sphagna</td>
<td>Spirophila angustifolia, Spirophila baltica, Spirophila subsecundum</td>
</tr>
<tr>
<td>Lawn sphagna</td>
<td>Sphagnum angustifolia, Sphagnum balticum, Sphagnum fallax</td>
</tr>
<tr>
<td>Hollow sphagna</td>
<td>Sphagnum magellanicum, Sphagnum papillosum, Sphagnum russowii</td>
</tr>
</tbody>
</table>

Note: Plant species were classified into PFTs based on their ecological niche along fertility and water level gradients. Vascular plant types are divided by the convergent effect of fertility and moisture to rich–wet and poor–dry PFTs, respectively. For the classification of vascular plant species into PFTs we used Malmer (1962), Eurola et al. (1995), and Gignac et al. (2004), and for the mosses we used Lumiala (1944), Andrus et al. (1983), Glaser et al. (1990), and Laine et al. (2009) and references therein. Species included in each PFTs are given in Table 2.

To estimate the average BM for the footprint of EC tower we used area-weighted BM for different plant communities in Kaamasensuo and Siikaneva. In Kaamasensuo, on average, flarks covered 70% and strings covered 30% of the mire area (Maanavilja et al. 2010); the area proportions for Siikaneva are given in Riutta et al. (2007a). In Mer Bleue and Degerö Stormyr, the sampling next to EC tower represented variation in the footprint and we therefore used the arithmetic average of the sample plots to estimate the average BM for the footprint.

In Siikaneva and Kaamasensuo WT was monitored during the growing season from permanent sample plots representing the plant communities from which BM was collected. An average WT was calculated for each plant community based on these measurements. In Mer Bleue and Degerö Stormyr WT was measured adjacent to each sample plot over the growing season when BM was collected. We express WT as relative to mire surface, i.e., negative when it is below the soil surface.

Data analysis

To quantitatively compare the plant compositional variation in the tower footprints of each mire we applied multivariate methods. We performed detrended correspondence analysis (DCA) using Hill's scaling and detrending by segments (ter Braak and Smilauer 2002) separately for each mire. The resulting length of the first axis is a measure of the largest compositional variation in the data sets (ter Braak and Prentice 1988). For Mer Bleue bog we used only data collected from the tower site representing the EC tower footprint.

To study the general pattern in mire vegetation, we related BM of PFTs to WT using DCA and generalized additive models (GAM) available in CanoDraw 4.12 (ter Braak and Smilauer 2002b). Here we also used the additional BM data from Mer Bleue bog, namely from Poor Fen and Blue Dome sites. We first performed a DCA analysis with detrending by second-order polynomials based on the BM of PFTs including sample plots from all four studied mires. WT was included in the analysis as a supplementary environmental variable. In GAM, response variables are related to the predictor using semiparametric smoothing functions that do not have fixed shapes. We set the number of degrees of freedom to four to allow response curves to be highly flexible (Guisan et al. 2002). We used log-link function with Poisson distribution for model residuals (Lepš and Smilauer 2003).

Results

Composition of GBM in EC footprint

The amount of variation in plant species GBM differed greatly between the EC tower footprints of the four mires as indicated by the lengths of the first gradient (the longest distance between the sample plot scores in the first axis) in
DCA (Fig. 1). The compositional variation was largest in the footprint of the northern fen Kaamasensuo, where the string and flark sample plots had only one species (*E. vaginatum*) in common (Fig. 1A). In the Siikaneva footprint, the sample plots formed a gradient from wet hollows through lawns that are dominated by different sedge species (*E. vaginatum* in EV lawns, *C. lasiocarpa* in CL lawns, and *C. rostrata* in CR lawns) to hummocks (Fig. 1B). In the footprint of Mer Bleue bog, the variation was small and all sample plots belonged to a similar hummock community (Fig. 1C). In the footprint of Degerö Stormyr, the gradient was short as well and all sample plots represented similar lawn level vegetation (Fig. 1D).

**Abundance of BM**

Total area weighted average aboveground BM within the EC tower footprint was $303 \pm 31$, $253 \pm 25$, $543 \pm 27$, and $141 \pm 45\, \text{g} \cdot \text{m}^{-2}$ ($\pm$SE) in Kaamasensuo, Siikaneva, Mer Bleue, and Degerö Stormyr, respectively. For the list of species present in the figure see Table 2.

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**Fig. 1.** Ordination of sample plots and plant species green biomass for (A) Kaamasensuo and (B) Siikaneva (MI, minerotrophic hummocks; OM, ombrotrophic hummocks; HU, low hummocks; EV, *Eriophorum vaginatum* dominated lawns; CL, *Carex lasiocarpa* dominated lawns; CR, *Carex rostrata* dominated lawns; and HO, hollows). (C) Mer Bleue (including sample plots around EC tower) and (D) Degerö Stormyr. Ordination was done by detrended correspondence analysis that was detrended by segments; therefore the length of the first axis describes the maximal amount of compositional variation. The longest distance between the sample plot scores in the first axis that is a measure of the largest compositional variation in the data sets was 7.2, 5.8, 1.7, and 1.4 for Kaamasensuo, Siikaneva, Mer Bleue, and Degerö Stormyr, respectively. For the list of species present in the figure see Table 2.
flarks and strings differed strongly with GBM of 160 ± 20 and 415 ± 44 g·m$^{-2}$ (±SE), respectively (Fig. 3). In flarks, the BM was composed of brown mosses and minerotrophic sedges, while in hummocks feather mosses and evergreen shrubs dominated. In Siikaneva, the C. rostrata lawns had the highest (488 ± 20 g·m$^{-2}$) and hollows had the lowest (157 ± 14 g·m$^{-2}$) GBM (Fig. 3). Sphagnum mosses composed the largest share of the GBM in all plant communities. In Mer Bleue bog, each of the three sites was relatively homogeneous, and the amount and composition of GBM varied only little between the sites being 336 ± 16, 238 ± 12, and 348 ± 17 g·m$^{-2}$ in the Tower, Blue Dome, and Poor Fen sites, respectively. Shrubs dominated the vascular vegetation in all Mer Bleue sites. In the Poor Fen, the sedges were most abundant in lawns, with the WT around −10 cm (Fig. 5A). Feather mosses dominated the bottom layer in the driest sites, while hummock sphagna had a BM peak at the WT of −30 cm; both groups were missing from sites with the WT higher than −10 cm below surface. Lawn sphagna occurred throughout the gradient, but had its highest BM at the WT around −10 cm. Hollow sphagna occurred in sites with WT near the surface, while the brown mosses were restricted to flarks of Kaamasensuo (Fig. 5B).

**Discussion**

**Abundance of BM**

The total aboveground BM of all four studied mires (from 0.1 to 0.5 kg·m$^{-2}$) was within the range measured from other treeless mires (Kosykh et al. 2008; Reinikainen et al. 1984; Vasander 1982, 1987). In comparison with other ecosystems, the total aboveground BM of treeless mires is clearly smaller.
than in temperate and boreal forests (21 and 6 kg·m\(^{-2}\), respectively) and about the same as in temperate grasslands (~0.25 kg·m\(^{-2}\)) and in arctic tundra, ~0.25 kg·m\(^{-2}\) (Chapin et al. 2002). The GBM of vascular plants and mosses was quite similar in Kaamasensuo and Siikaneva, which are very different types of mires. Kaamasensuo is a northern aapa mire with a remarkably distinct surface pattern of high ridges and open water flarks and Siikaneva is a fen with continuous Sphagnum cover. Mer Bleue that had 1.5× larger GBM than Kaamasensuo and Siikaneva is a rather dry bog with abundant shrub cover. Although Degerö Stormyr is visually similar to Siikaneva, the GBM was much lower, and especially the moss GBM was only one third of that in Siikaneva.

**Composition of BM**

As expected, the GBM of PFTs responded differently to WT. Shrubs had their peak abundance in dry sites. However, evergreen shrubs, which had by far the highest proportion of vascular BM, occurred throughout the WT gradient, although to a smaller extent in the wetter sites. The group includes species V. oxycoccos and A. polifolia that are known to have a wide WT tolerance (Lumiala 1944). Also sedge BM had a wide tolerance for the WT. Ombrotrophic sedges, mainly E. vaginatum, occurred in all sites apart from Kaamasensuo, but their BM peaked at lawns with the WT around ~10 cm. Minerotrophic sedges include several Carex spp. with contrasting response to the WT. Firstly, they were common in relatively dry poor fen communities (Mer Bleue and Siikaneva), and secondly, their GBM was high in the inundated flarks of Kaamasensuo. Sedges are deep-rooting species with aerenchymous cell tissue, which enables them to habit a wide range of sites. Forbs constituted little of the BM; of the ombrotrophic forbs R. chamaemorus inhabited the dry sites, while Maianthemum trifolium (L.) Sloboda, Menyanthes trifoliata L., and S. palustris occurred in wetter lawns and Hollows. Earlier findings show that mosses have narrower tolerance to the WT than vascular plants (Väliranta et al. 2007). Our results seem to support this idea to some extent, and the wider ranges are due to pooling species into groups. Feather mosses occur in the driest hummocks and strings. Hummock sphagna (S. capillifolium in Mer Bleue and Sphagnum fuscum (Schimp.) Klinggr. in Siikaneva) occurred in relatively dry hummocks, having GBM optima at ~30 cm. Lawn sphagna had clearly the highest proportion of all moss GBM and occurred throughout the sites; the optima at ~12 cm was still quite distinct. Hollow sphagna (S. majus) was restricted to the hollows in Siikaneva, while the brown mosses occupied the minerotrophic flarks of Kaamasensuo. One needs to bear in mind that WTs used here represent only the period of the sampling time, while the vegetation
response may relate to the WT during the life history of plants. The long-term WT may vary from those used here.

**BM as potential control for mire NEE**

In all studied sites, multiyear biosphere–atmosphere CO₂ exchange has been measured by the EC method. The average annual NEE is 22 ± 20 g C·m⁻²·a⁻¹ in Kaamasensuo (Aurela et al. 2004), 56 ± 18 g C·m⁻²·a⁻¹ in Siikaneva (Aurela et al. 2007), 40.2 ± 40.5 g C·m⁻²·a⁻¹ in Mer Bleue (Roulet et al. 2007), and 55 ± 7 g C·m⁻²·a⁻¹ in Degerö Stormyr (Sagerfors et al. 2008). NEE represents the difference in photosynthesis and ecosystem respiration and the length of the growing season is important in determining to what extent the photosynthetically active BM can contribute to the annual NEE (Lund et al. 2010). Therefore, we compared the different BM compartments with the average July NEE, which represents the maximal capacity of the vegetation. Vascular plant GBM was more closely connected to NEE than total BM or GBM. July NEE was clearly higher in mires with high vascular plant GBM, namely in Kaamasensuo and Mer Bleue. Further, the different photosynthetic capacity of PFTs appeared to matter and thus the smaller BM with different species composition may result in similar or higher CO₂ flux rates. Sphagnum mosses are known to be less efficient photosynthesizers under all light levels than vascular plants and of vascular plants both ombrotrophic and minerotrophic sedges have higher capacity to photosynthesize than shrubs, when comparing the efficiency per green area unit (Leppälä et al. 2008; Riutta et al. 2007b). In our study, the composition of BM varied between and within the mires more than the total BM. Siikaneva and Degerö Stormyr have nearly identical July NEE, despite the difference in total BM. Siikaneva and Degerö Stormyr have nearly identical July NEE, despite the difference in total BM. Furthermore, the vascular...
plant composition is rather similar in these two mires. The significance of the vascular PFTs composition is most obvious when comparing Kaamasensuo and Mer Bleue. The total BM was clearly lower in Kaamasensuo than in Mer Bleue. However, the higher proportion of sedge BM resulted in equally high NEE in Kaamasensuo than in Mer Bleue. In Mer Bleue, BM was formed mostly of shrubs. In our study, the composition of BM varied between and within the mires more than the total BM. Siikaneva and Degerö Stormyr have nearly identical July NEE, despite the difference in total BM. The difference in BM at these two mires is formed by the Sphagnum mosses, and therefore, vascular plants appeared to drive the growing season maximum NEE.

The dominant impact of sedge GBM over the NEE is evident also when the internal GBM variation within mires is observed. The amount of internal variation in plant species GBM was highest in Kaamasensuo and lowest in Degerö Stormyr. The plant communities in Kaamasensuo, strings

**Fig. 6.** Average cumulative July net ecosystem CO₂ exchange (NEE) (g C·m⁻²·month⁻¹ ±SE) of each site related to (A) total aboveground biomass (BM), (B) green biomass (GBM), (C) GBM of vascular plants, (D) GBM of mosses, (E) GBM of evergreen shrubs, and (F) GBM of minerotrophic sedges. NEE represents the difference in photosynthesis and ecosystem respiration. The July NEE is an average (±SE) of 6, 2, 7, and 12 years from sites Kaamasensuo, Siikaneva, Degerö Stormyr, and Mer Bleue, respectively. Reference for NEE data for Kaamasensuo (Aurela et al. (2004)); Siikaneva (Aurela et al. (2007)); Mer Bleue (Roulet et al. (2007) and Humphreys, personal communication); and Degerö (Sagerfors et al. (2008), Nilsson et al. (2008), and Nilsson, unpublished data).
and flarks, strongly differed from each other in terms of WT, species composition, and BM PFTs. Consequently, their NEE vary considerably. In Kaamasensuo the closed chamber measurements showed that flark communities with fen vegetation had higher NEE during the growing season (average and cumulative NEE) than the string tops with bog vegetation (Maanavilja et al. 2010). Second largest variation in GBM composition was observed in Siikaneva, where the hol lows and ombrotrophic hummocks differed from the dominating lawns. In Siikaneva the NEE was highest in C. lasiocarpa lawns and lowest in hol lows, according to chamber measurements (Riutta et al. 2007a). Degerö Stormyr vegetation showed little variation, being most similar to E. vaginatum lawns of Siikaneva. Eriophorum vaginatum lawns are the dominant plant community in Siikaneva covering 34% of the mire, which may explain the equally high NEE in the two mires. Our findings seem to contrast with those of Shaver et al. (2007) that showed leaf area index (LAI) to be the only plant parameter needed to successfully predict NEE in tundra vegetation. As Shaver et al. (2007) conclude, this indicates that in spite of species composition any kind of vegetation over the tundra landscape produces the same functions with same leaf area unit. This high convergence, not found in our study in different peatlands, may relate to smaller spatial variation in tundra than in peatlands. While the study plots in the tundra study had variable plant communities, the main components (namely deciduous and evergreen shrubs, sedges, and forbs) were present in all of them with relatively high cover. That was not the case in the peatlands of this study where the differences in the plant community compositions were quite high. The other, more interesting, explanation for the quite different results may be due to the different plant units studied. In our study, we relate NEE to BM, while Shaver et al. (2007) were linking NEE to LAI. It has already been shown that among different dwarf shrub species there can be remarkable variation in photosynthetic capacity per BM. Kulmala et al. (2008) found that Vaccinium myrtillus, with its thin deciduous leaves, can have two or three times higher momentary photosynthesis per leaf mass than Vaccinium vitis-idaea or Calluna vulgaris that have evergreen leaves. However, per LAI the photosynthetic capacities did not differ much because of the heavier leaves of V. vitis-idaea. A mechanism behind the functional divergence in vegetation might be the differentiation between plants in how they allocate BM to build leaf area.

**Conclusions**

The results supported our first hypothesis that the spatial variation in BM within a mire can be larger than the differences in BM between mires. In the mires Kaamasensuo and Siikaneva, where the internal variation within plant communities was distinctive, the differences in the GBM between mires were smaller than between the plant communities. The similarity of NEE and GBM of vascular PFTs in the dominant plant community types in Degerö Stormyr and Siikaneva gave support to the second hypothesis that NEE is related to BM of the dominant PFTs. Eleven PFTs appeared to capture the internal variation; the differences in BM between communities, which were defined using species level approach, were explained by the WT response of PFTs. Our results suggest the use of photosynthesizing BM, separated into PFTs, in modelling ecosystem carbon exchange instead of using just total photosynthesizing plant BM.

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**References**


