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A high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in peatland vascular plant communities

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Abstract We studied vegetation dynamics at peatlands, differing in their climate, land use management history and vegetation community in Ireland and Finland over a two-year period. Our aim was to develop a species-specific method to be used to (1) describe the seasonal dynamics of green (photosynthetic) area (GA) of the vegetation and (2) incorporate these changes into CO_2 exchange models. The extent of temporal and spatial variation between and within communities indicated the need for a two-step calculation approach for each community. Firstly, at biweekly to monthly intervals, GA of all species within a range of vascular plant communities was estimated by non-destructive field measurements. Gaussian or log-normal models were fitted to describe the seasonal dynamics of each species. Secondly, an estimate of community vascular green area (VGA) was obtained by summing the modelled daily GA of all species within the community. The highest values of VGA (2.1–6.0 m^2 m^{-2}) occurred within the reed communities at the rewetted cutaway peatland in Ireland and the lowest at the ombrotrophic lawn communities in Finland (0.5–1.0 m^2 m^{-2}). The relationship between light saturated gross photosynthesis (P_G) and VGA was either linear or hyperbolic depending on the degree of self-shading that occurred within each community. The addition of the VGA term into P_G models improved the explaining power of the model by 57.6, 24.5 and 23% within the *Typha latifolia*, *Phalaris arundinacea* and *Eriophorum angustifolium/Carex rostrata* communities, respectively. VGA proved useful in recording the seasonal development of a wide range of peatland vascular plant communities over geographically and climatically different regions.

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Introduction

The role of vascular plant communities in controlling and regulating carbon dioxide (CO_2) fluxes within peatland ecosystems is significant (Shannon et al. 1996; Thomas et al. 1996; Joabsson et al. 1999). During photosynthesis, plants fix CO_2 within their photosynthetically active (green) parts, some of which is either released back to the atmosphere through respiration or used to provide the basis for new plant tissue. A proportion of the carbon (C) fixed as CO_2, is deposited below ground through litter input and root exudation, where a part is released through heterotrophic respiration.

In peatlands, the rate of CO_2 fluxes vary with the seasonal development of the plants (Alm et al. 1997; Bubier et al. 1998; Kim et al. 1998; Tuittila et al. 1999). The photosynthetic capacity of individual plant species varies as a result of physiological and morphological factors, such as differences in the photosynthetic pathway (Kemp and Williams 1980), and in the size, shape and orientation of the leaves (Falster and Westoby 2003). These factors, in turn, influence canopy architecture, the level of light interception and the degree of carbon assimilation. In multi-layered plant canopies there is attenuation in the amount of light that reaches the leaves or plant individuals at ground level (Valladares and Pearcy 1999). The effect of this increased self-shading within the canopy is likely to reduce the potential photosynthetic rate (Pearcy and Valladares 1999).

The vegetative cover of peatlands consists of individual plant species that compete with each other for resources such as nutrients and light. This competition results in a range of plant adaptations and growth strategies such as the production of evergreen leaves (Small 1972), increased leaf life span (Robertson and Woolhouse 1984a), rapid growth rates (Odland 2002), the production of leaves early in the season (Anten and Hirose 1999) and shade tolerance (Burrows 1990). Thus, a species-specific means of accounting for the dynamic change in leaf area in an individual plant species that occurs both temporally and spatially is needed (Williams and Rastetter 1999). Leaf area dynamics are influenced by variation in factors such as

climate, moisture and nutrient supply (Ewert 2004) and since CO_2 uptake and respiration processes are highly sensitive to weather patterns and the physiological status of the plants during the growing season (Alm et al. 1997, 1999a; Larmola et al. 2003), any models of gas exchange dynamics must include a measure to describe seasonality.

Degree-days and threshold temperatures (Alm et al. 1997; Trumbore et al. 1999; Tuittila et al. 1999; Kettunen 2000) have been used to incorporate seasonality into C exchange modelling. However, the utilisation of a common temperature threshold approach does have disadvantages especially in a diverse environment with a mosaic of plant communities with varying phenological patterns and differential responses to changes in temperature (Weltzin et al. 2000, 2003).

Leaf area index defined as the functional (green) leaf area of the canopy per ground area (Asner et al. 2003) is recognised as an important parameter in process based models (Cowling and Field 2003; Ewert 2004) and has been utilised for decades in agricultural modelling (Wiegand et al. 1979; Cogle et al. 1997; Kashyap and Panda 2003) and in remote sensing (Curran and Williamson 1988; Spanner et al. 1994; Butson and Fernandes 2004), accounting for differences in patterns of canopy development among plant species and the associated effects on assimilation and biomass growth. Gower et al. (1999) reported a number of approaches to estimate leaf area. These include direct methods, such as harvesting of plant material (Kim et al. 1998; Williams and Rastetter 1999; Moore et al. 2002) and the use of allometric equations (Haase et al. 1999; Bubier et al. 2003b). Indirect methods commonly involve the use of an optical instrument such as a LiCor LAI-2000 (Rudorff et al. 1996; Zhang et al. 2002). While harvesting measurements are considered to be the more accurate (Gower et al. 1999) they are not suitable for CO_2 exchange studies, where it is necessary to keep the vegetation intact in order to follow the seasonal dynamics of photosynthesis and respiration within a community. Furthermore, Gower et al. (1999) suggested that optical instruments tend to underestimate LAI when the foliage in the canopy is non-randomly distributed (i.e., clumped) and overestimate LAI when there

are significant amounts of brown plant tissue present (Rudorff et al. 1996). Griffis and Rouse (2001) reported the sensitivity of gross photosynthesis (P_G), ecosystem respiration (R_{TOT}) and net ecosystem exchange (NEE) models to small errors in LAI and highlighted the need for improved estimates of LAI. In this paper we describe a method to calculate a high-resolution vascular green area index (VGA) based on species-specific allometric equations. Such an index will provide a more accurate determination of seasonality for a wide range of vascular plant communities. Furthermore, it will also provide a means to investigate the relationship between plant canopy architecture and CO_2 fluxes that will further enhance our understanding of plant dynamics and also improve the functioning of net CO_2 exchange models in peatlands.

Materials and methods

Study sites

The study sites were located at a rewetted cutaway peatland at Turraun, Co. Offaly, Ireland (53°14′–53°19′ N; 7°42′–7°48′ W) and Lakkasuo mire, Finland (61°47′ N; 24°18′ E). The two sites differ in their climate, land use management history and vegetation community composition and provide a suitable means of testing the applicability of our method.

Climate

Turraun is located within the temperate climatic zone. The climate is strongly influenced by its maritime location and proximity to the North Atlantic Gulf stream (Keane and Sheridan 2004) and is characterised by prevailing south-westerly winds, a mean annual rainfall of 804 mm and a mean temperature range from 7.5°C in January to 19.2°C in July (Met Éireann—Birr Station, 1961–1990). Lakkasuo is located within the boreal climatic zone. Annual rainfall is 710 mm, of which about a third falls as snow. Average temperatures for January and July are—8.9 and 15.3°C (Finnish Meteorological Institute, Juupajoki weather station 1961–1990).

Land use management

Lakkasuo mire is an eccentric raised bog, situated in central Finland. Its development has been influenced to a certain extent by disturbances such as fires and human activities, which have occurred throughout its 7,000 year history. In contrast, Turraun has been subject to considerable disturbance. Milled peat harvesting ceased in the 1970s and the vegetation was allowed to regenerate naturally. The residual peat deposit ranges from 0 m to 1.8 m depth and is mainly composed of *Phragmites australis* peat with some woody fen deposits. In 1991, the area was rewetted by the blocking of drainage ditches and the creation of a peat and marl bund.

Vegetation

Turraun is composed of a mosaic of vegetation communities representing a hydroseral gradient i.e., the sequence of vegetation communities, which occur during the transition from shallow open water at the edge of the lake to drier terrestrial ecosystems. These include aquatic reedswamp (*Typha latifolia* L., *Phalaris arundinacea* L.), terrestrial (*Eriophorum angustifolium* Honck., *Carex rostrata* Stokes.) and pioneer colonising communities (*Juncus effusus* L., *Holcus lanatus* L.).

Similarly, in Lakkasuo, a clear hydroseral gradient from the centre to the lagg area with changing ecohydrological conditions can be distinguished in the mire. The study was carried out at three sites, representing mesotrophic, oligotrophic and ombrotrophic vegetation types. The vegetation at the mesotrophic site comprises lawn and minerotrophic hollow level communities. The field layer in both cases is characterised by sedges (*Carex rostrata*, *C. lasiocarpa* Ehrh.) and some herbaceous species, such as *Potentilla palustris* (L.) Scop. and *Menyanthes trifoliata* L. In the drier lawn surfaces, the moss layer is dominated by Sphagna (*Sphagnum fallax* (Klinggr.) Klinggr., *S. flexuosum* Dozy & Molk, *S. magellanicum* Brid.), whereas the wetter hollow surfaces have higher covers of *Utricularia intermedia* Hayne, *Sphagnum subsecundum* Nees and *Warnstorfia exannulata* (Schimp.) Loeske. The oligotrophic

site consists of a fairly homogenous lawn level vegetation, dominated by *Carex lasiocarpa* with some *Betula nana* L. in the field layer, and *Sphagnum papillosum* Lindb., *S. fallax* and *S. flexuosum* in the moss layer. The ombrotrophic site at the centre area of the bog is a mosaic of ecohydrological gradients shown as changing plant communities from wet hollows to intermediate lawns and finally to drier hummock communities. *Eriophorum vaginatum* L., together with *Andromeda polifolia* L. and *Rubus chamaemorus* L. are the most abundant field layer species; *Sphagnum cuspidatum* Ehrh. Ex Hoffm., dominates in the moss layer of the hollows, *S. balticum* (Russ.) C. Jens in the lawns and *S. fuscum* in the hummocks.

Field measurements

In order to determine the area of photosynthetically active (green) plant material over a defined ground area within each of the study areas, 3–4 sample plots (60 × 60 cm) were placed within a range of vascular plant communities. Within each sample plot, five sub-sample plots (8 × 8 cm) were established. At biweekly to monthly intervals, the total number of leaves and stems of individual vascular plant species within the sub-sample plots were counted and extrapolated to provide an estimate of the average number of leaves (L_n) and stems (S_n) of each species per m². In sample plots with a relatively low ratio of plants:ground area (e.g., *Typha latifolia*, *Phalaris arundinacea* and *Juncus effusus* dominated plots) the total number of leaves and stems in the sample plot were counted and extrapolated accordingly.

As regular handling of the plants in the sample plot might have resulted in damage to the plants and disruption of gas exchange, three plants of each species recorded within the sub-sample plots were identified outside the main sample plot and tagged with plastic strips. At biweekly to monthly intervals, these dynamic sample plants were measured for the following; leaf length, width at the base, centre or radius (depending on the morphology of the plant species), stem height and diameter. Only green material was measured.

Calculation of the green area

The green area (GA) of each species was calculated as the product of leaf size and number of leaves. The area of the leaves and stems of the sample plants was estimated by applying species-specific formulae (Table 1) based on the geometric shape of the leaf (e.g., ellipse, circle, rectangle). For species with leaf shapes that did not conform to strict geometric shapes (e.g., *Typha latifolia*, *Phalaris arundinacea*) it was necessary to introduce a correction figure in order to more accurately reflect the shape of the leaf (Misra and Misra 1981). The green surface area of the plant stem (if present) was calculated by using the formula for the surface area of a cylinder as follows:

$$\text{Green stem area} = (2 * \pi * r) * h \tag{1}$$

where r is the radius and h is the height of the plant stem. The green area of plants with both a horizontal growth form and irregular leaf margins (e.g., *Ranunculus repens* L.) were estimated from their percentage cover within the sample plot. The average leaf (L_A) and stem areas (S_A) of the sample plants were calculated to provide a representative leaf and stem size for each species. The green area GA of each species i (m² m⁻²) was calculated as follows:

$$\text{GA}_i = (L_A * L_n) + (S_A * S_n) \tag{2}$$

where L_A is the average leaf area of the three tagged dynamic sample plants (m²), L_n is the average number of leaves per m², S_A is the average stem area of the dynamic sample plants (m²) and S_n is the average number of stems per m².

Sampling procedure for method validation

In order to determine whether the leaf area estimated by our method was comparable to the actual leaf area it was necessary to validate the estimated values. At bimonthly intervals throughout the growing season in 2002, leaves from *Typha latifolia*, *Phalaris arundinacea* and *Eriophorum angustifolium* were randomly harvested from

Table 1 Species-specific formulae for the calculation of leaf area. TR = triangle $(0.5*W*L)$, RA = rectangle $(W*L)$, CC = cut cone $(\pi*r*L)$, EL = ellipse $(\pi*r_1*r_2)$, CL = circle $(\pi*r^2)$, HC = half cone $(r*L*\pi/2)$ where W = width, L = length of leaf and r = radius. Formula for CC is modified to exclude the basal area of the cone. Model parameters are taken from selected sample plots at each site. A range of values is shown when the species appears in more than one study site. Model parameter GA_{max} denotes maximal GA reached during the season, x_{max} is the Julian day when maximal GA is reached and b denotes the shape of the model. Goodness of fit (r^2) values for the species-specific models are shown

Species	Leaf shape	Correction coefficient	Model parameters			
			GA_{max} $(m^2\ m^{-2})$	x_{max} (Julian day)	b	r^2
Agrostis stolonifera[a]	TR		0.15	167	65.4	0.46
Andromeda polifolia[b]	EL		0.05–0.11	196–227	0.18–0.31	0.71–0.92
Betula nana[b]	CL		0.16–0.19	192–199	0.26–0.29	0.69–0.77
Carex lasiocarpa[b]	HC		0.44–2.03	198–210	0.16–0.18	0.74–0.88
Carex rostrata[a]	RA	0.85	0.31–0.78	217–237	37.3–49.7	0.74–0.90
Drosera rotundifolia[b]	CL		0.002	219	17.1	0.99
Eriophorum angustifolium[a]	RA	0.53	2.33	226	45.5	0.91
Eriophorum vaginatum[b]	HC		0.26–0.89	206–212	0.17–0.21	0.70–0.96
Holcus lanatus[a]	TR		0.14–0.26	263–282	49.6–49.8	0.63–0.98
Hydrocotyle vulgaris[a]	%		0.34	237	16.3	0.75
Juncus effusus[b]	CC		0.98–1.50	179–180	0.33–0.55	0.72–0.80
Juncus stygius[b]	RA		0.04	176	0.23	0.84
Phalaris arundinacea[a]	RA	0.85	2.20–4.96	183–194	43.3–54.4	0.92–0.98
Pinus sylvestris[a]	RA		0.001	183	9.7	0.99
Scheuchzeria palustris[b]	HC		0.06–0.08	222–223	0.10–0.18	0.94–0.97
Trichophorum cespitosum[a]	HC		0.03	146	15.8	0.99
Typha latifolia[a]	RA	0.93	5.61–5.84	188–2014	0.7–49.5	0.91–0.93
Vaccinium oxycoccos[b]	EL		0.03–0.11	190–231	0.29–0.36	0.49–0.75
Viola palustris[a]	CL		0.03	203	26.3	0.93

[a] Gaussian model (Eq. 3)

[b] Log-normal model (Eq. 4)

around the sample plots and taken immediately to the laboratory where the length and width of each leaf was measured and recorded. The leaves were then passed through a LI-3000 Portable Area Meter in combination with a LI-3050A Transparent Belt Conveyor (LICOR, Lincoln, Nebraska) to determine the actual surface area (m^2) of each individual leaf (Bianco et al. 2003).

Modelling the annual development of vascular green area

For most species, seasonal development of green area (GA_i) was unimodal and normally distributed (Gaussian) with clearly defined maxima:

$$\text{Daily } GA_i = GA_{max}\ e^{\left(-0.5\left(\frac{julian-x_{max}}{b}\right)^2\right)} \tag{3}$$

where julian is Julian day, model parameter GA_{max} denotes the maximal GA of species i

during the season, x_{max} denotes the Julian day when maximal GA occurs and b denotes the shape of the curve. For some species, the rate of increase in green area in the spring was greater than the rate of decrease in the autumn resulting in a skewed growth curve. For these species, a log-normal curve was applied as follows:

$$\text{Daily } GA_i = GA_{max}\ e^{\left(-0.5\left(\frac{\ln\left(\frac{julian}{x_{max}}\right)}{b}\right)^2\right)}. \tag{4}$$

In order to capture the seasonal dynamics of *Juncus effusus* as accurately as possible, it was necessary to make the assumption that the end of the growing season for a temperate evergreen species, such as *Juncus*, is likely to occur early in the spring of the following year. The model fit was improved by applying it from March in the first year of the study and it was allowed to run until the same date in the second year (Fig. 1).
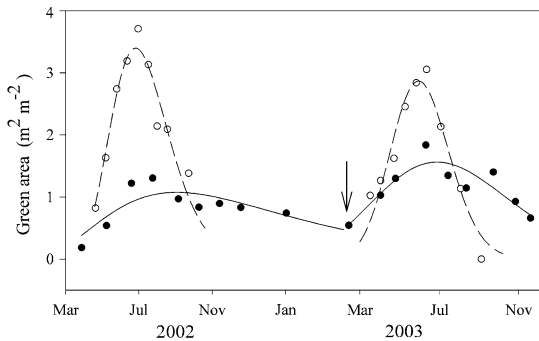
Fig. 1 Seasonal development of green area (GA) in *Juncus effusus* (solid line) in Turraun and *Carex lasiocarpa* (broken line) in the mesotrophic site in Lakkasuo in 2002 and 2003 within a sample plot. Vertical arrow indicates the point where the model for the second growing season in *Juncus* was started

The vascular green area (VGA) within each sample plot was calculated in order to determine the total green plant material at a community level by summing the GA values of the individual species (GA_i) for each Julian day:

$$\text{Daily VGA} = \sum_{i=1}^{n} GA_i. \tag{5}$$

CO_2 gas exchange measurements

Each sample plot consisted of a stainless steel collar (60×60 cm) that was inserted to a depth of 30 cm into the peat prior to the start of the study. Each collar was topped by a 4 cm wide and 3 cm deep channel that was filled with water to provide an airtight seal during gas measurements. Wooden walkways were constructed around each of the collars to minimise damage to the soil surface and plant cover.

CO_2 gas exchange was measured using the static chamber method at Turraun at weekly to biweekly intervals from March 2002 to December 2003. The static chamber system employed in this study consisted of a transparent polycarbonate chamber ($60 \times 60 \times 33$ cm) equipped with a battery-operated fan, which ensured that the air within the chamber headspace was mixed. Transparent extension chambers (20–150 cm) were used to facilitate measurements within the taller plant communities. The chamber was fitted with a thermostat connected to a cooling apparatus that ensured that the temperature within the chamber was maintained to within 1°C of ambient temperature. CO_2 concentration (ppmv) in the chamber headspace was measured with a portable CO_2 analyser (EGM-2 and 4) (PP Systems UK) and Photosynthetically Active Radiation (PAR) (μmol m^{-2} s^{-1}) was measured by a quantum sensor (PAR-1. PP Systems) located at the top of the chamber.

Instantaneous net CO_2 exchange (NEE) was measured under stable light (PAR) conditions. CO_2 concentration (ppmv) in the chamber headspace was recorded at 15-s intervals over a period of 60–180 s. At the same time, air temperature and PAR values within the chamber were recorded.

After each measurement, the chamber was vented for a short time by removing it from the collar. This was carried out in order to ensure equilibration of the gas concentration. The chamber was then replaced in the collar and covered with an opaque material in order to estimate ecosystem respiration (R_{TOT}). CO_2 concentration (ppmv) in the chamber headspace was again recorded at 15-s intervals over a period of 60–180 s. CO_2 flux rates (mg CO_2 m^{-2} h^{-1}) were calculated from the linear change in CO_2 concentration in the chamber headspace over time with respect to the chamber volume and temperature. Gross photosynthesis (P_G) was estimated as the sum of NEE and R_{TOT}.

Incorporation of VGA into CO_2 exchange modelling

The primary objective of the VGA method is to improve CO_2 exchange models by incorporating the seasonal changes in the green leaf area available for photosynthesis. The rate of photosynthesis (P_G) depends on photosynthetically active radiation (PAR). This saturating relationship between P_G and PAR (Mooney and Ehleringer 1997) is often described using the Michaelis–Menten function (Alm et al. 1997; Komulainen et al. 1999; Tuittila et al. 1999; Kettunen 2000):

$$P_G = P_{\max(PAR)} * PAR/(PAR + k_{PAR}) \tag{6}$$

where $P_{\max(PAR)}$ denotes the maximal PAR dependent photosynthesis and k_{PAR} is the PAR value at which P_G reaches half its maximum.

In addition to PAR, the area available for photosynthesis regulates how efficiently a plant community can utilise the available PAR. In a sparse community or community with a highly organised leaf structure, there is a linear increase in PAR dependent P_G ($P_{\max(PAR)}$) with increasing VGA (Eq. 7). However, in communities with self-shading, the PAR use efficiency begins to decrease after a certain VGA threshold. In those cases, a saturating response describes this relationship better (Eq. 8). We applied a multiplicative form of model to describe the simultaneous effect of PAR and VGA on P_G in a manner similar to Tuittila et al. (2004).

For communities such as *Typha*, where self-shading was observed to be minimal (Fig. 5), we applied a form:

$$P_G = P_{\max(PAR,VGA)} * PAR/(PAR + k_{PAR}) * VGA \tag{7}$$

and for communities such as *Phalaris* and *Eriophorum/Carex* where self-shading was observed (Fig. 5) a hyperbolic term (Eq. 8) was added:

$$P_G = P_{\max(PAR,VGA)} * PAR/(PAR + k_{PAR}) * (VGA/(VGA + k_{VGA})) \tag{8}$$

where $P_{\max (PAR, VGA)}$ denotes the maximal PAR and VGA dependent photosynthesis and k_{VGA} is the VGA value at which P_G reaches half its maximum. P_G parameter values were estimated (Table 2) using the non-linear Levenberg–Marquardt technique (SPSS for Windows software package. Version 11.0 SPSS Inc. Chicago. USA), which aims to minimise the sum of squares error function by an iterative approach, whereby the initial parameters specified by the modeller are adjusted until the most likely parameter values are reached when no further reduction in the sum of squares takes place.

Results

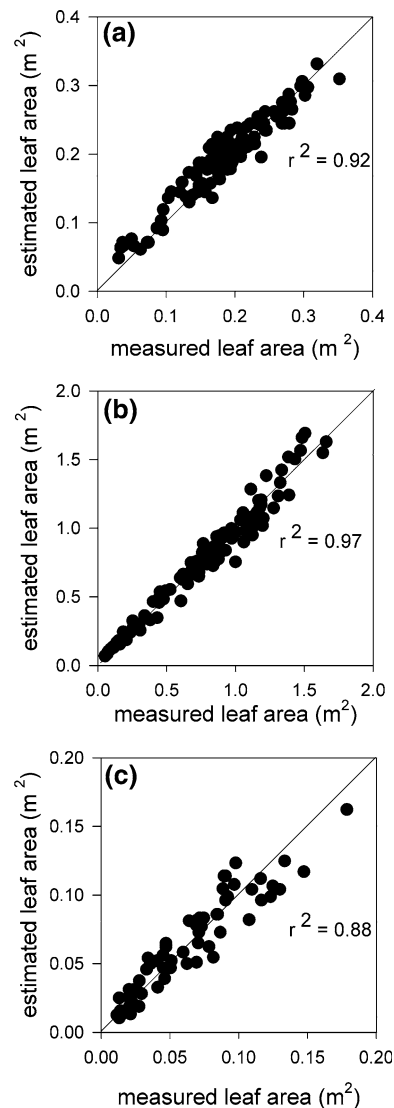### Validation of the method for estimating leaf area

A strong relationship was observed between leaf area values measured in the laboratory and those estimated based on field measurements for the three plant species (Fig. 2). Goodness of fit (r^2) values ranged from 0.88 to 0.97 with the closest fit occurring with the reed species, *Typha latifolia* and *Phalaris arundinacea*. The relationship between the measured and estimated leaf area values for *Eriophorum angustifolium* was not as strong. The method performed well at low values (0.01–0.09 m^2) but thereafter tended to slightly underestimate the leaf area. No notable heteroscedasity was observed for any of the species.

Estimating the annual development of vascular green area

The Vascular Green Area (VGA) index varied between the plant communities. Although the GA of all species studied had unimodal seasonal development with clearly defined maxima, the spring phenology varied between communities. Under the maritime, temperate conditions at Turraun, GA values increased early in March in the reed communities (Fig. 3a, b) and in early April in the *Eriophorum/Carex* community (Fig. 3c). In contrast, initiation of growth at the boreal Lakkasuo was more uniform across all sites with GA values increasing in May following snowmelt (Fig. 3d–f). At all the sites studied, GA

Table 2 Estimated parameter values for gross photosynthesis (P_G) models for three sample plots at Turraun, Co. Offaly. Standard errors are shown in parentheses

Plant community	$P_{\max(PAR, VGA)}$ (mg CO$_2$ m^{-2} h^{-1})	$k_{(PAR)}$ (μmol m^{-2} s^{-1})	$k_{(VGA)}$ (m^2 m^{-2})
Phalaris (P2)	4302 (480.2)	383 (82.2)	1.06 (0.21)
Typha (T1)	906 (173.8)	337 (176.9)	–
Eriophorum/Carex (EC1)	3308 (296.2)	406 (80.8)	0.17 (0.04)

Fig. 2 The relationship between measured and estimated leaf area (m^2) for (**a**) *Phalaris arundinacea* ($n = 112$), (**b**) *Typha latifolia* ($n = 112$) and (**c**) *Eriophorum angustifolium* ($n = 62$). Leaves were harvested at Turraun, Co. Offaly during 2002

Eriophorum/Carex community. At all sites, GA values subsequently decreased in the autumn with the onset of senescence.

In all sample plots, one species was clearly dominant and the development of community VGA was controlled primarily by the contribution of the GA of this species within each plot (Fig. 3). Spatial variation in alpha diversity between study sites was also observed with the highest species numbers occurring in the mesotrophic sample plots and the lowest in the reed community sample plots at Turraun and the ombrotrophic lawn sample plots at Lakkasuo.

Spatial variation of VGA was observed both between and within communities at both study sites (Fig. 4). The highest VGA values occurred in the *Typha/Phalaris* communities (Fig. 4a) and ranged from 2.1 m^2 m^{-2} to 6.0 m^2 m^{-2}. Considerable variation occurred within the *Eriophorum/Carex* communities and maximum VGA values ranged from 0.2 m^2 m^{-2} to 3.2 m^2 m^{-2}. At Lakkasuo, the variation in the rate of the VGA development and in the timing of the peak season was small both between and within the plant communities. VGA followed the ecohydrological gradient with the mesotrophic site exhibiting the highest values (1.6–3.3 m^2 m^{-2}), the oligotrophic site exhibiting intermediate values (0.6–1.9 m^2 m^{-2}) and the ombrotrophic site exhibiting the lowest values (0.5–1.0 m^2 m^{-2}). The variation in maximum VGA was greatest in the mesotrophic site, owing to the greater number of species. The oligotrophic fen and ombrotrophic lawns were spatially more homogeneous. At Turraun, VGA values in all communities, with the exception of the *Juncus/Holcus* communities, remained at zero throughout the winter period. At Lakkasuo, no VGA values were recorded during the winter period as a result of snow cover on the vegetation.

Canopy architecture and gross photosynthesis

A strong relationship was observed between VGA and the gross photosynthetic potential (P_G) of the plant communities (Fig. 5). A linear relationship was observed between light saturated P_G (potential P_G measured in full daylight (PAR > 600 µmol m^{-2} s^{-1}) and VGA in the *Typha* communities. In contrast, the

values reached a maximum in mid-summer. Goodness of fit values (r^2) for the species GA models ranged from 0.46 to 0.99 (Table 1). There was also a range in the model parameter values; GA_{max}, tolerance of the curve b and x_{max} for all species that were measured at more than one location. Temporal variability in the date of maximal GA production was observed with x_{max} in early July within the reed community, late July at all sites at Lakkasuo and in early August in the

Fig. 3 Contribution of species composition to the annual development of Vascular Green Area (VGA) in Turraun, Co. Offaly (**a**, **b**, **c**) and in Lakkasuo (**d**, **e**, **f**) in 2003. For clarity purposes, only one sample plot (in parentheses) per vegetation community is shown. Each species-specific GA model is represented by a broken line that has been fitted to the monthly calculated GA value of each species (symbols) within the sample plot. VGA (solid line) is calculated by summing the daily estimates of the species-specific GA models
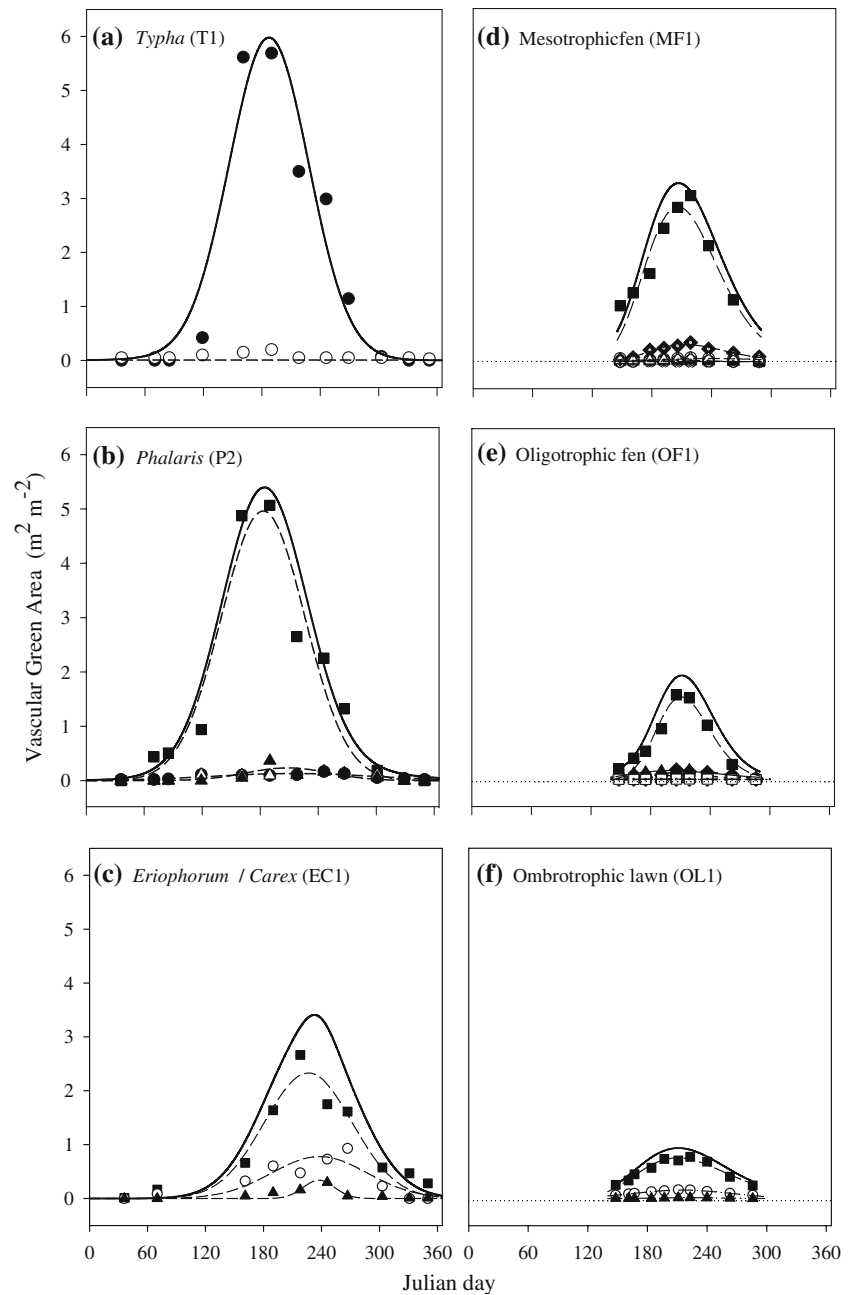
relationship between P_G and VGA in *Phalaris* communities takes the form of a rectangular hyperbolic model approaching an asymptotic maximum. Initially, P_G rates increased rapidly with a concomitant increase in VGA values but showed a saturating response to VGA at values greater than 2. The addition of VGA improved the explaining power of P_G exchange models within *Typha*, *Phalaris* and *Eriophorum*/*Carex* communities at Turraun by 57.6, 24.5 and 23%, respectively (Table 3). The combination of PAR and VGA explained between 82% and 93% of the variation in P_G in these communities.

Fig. 4 Spatial variation of VGA in Turraun, Co. Offaly (**a**, **b**, **c**) and in Lakkasuo (**d**, **e**, **f**) in 2003. Each line represents the VGA of sample plots within each plant community. VGA is calculated by summing the daily estimates of the species-specific GA models within each sample plot
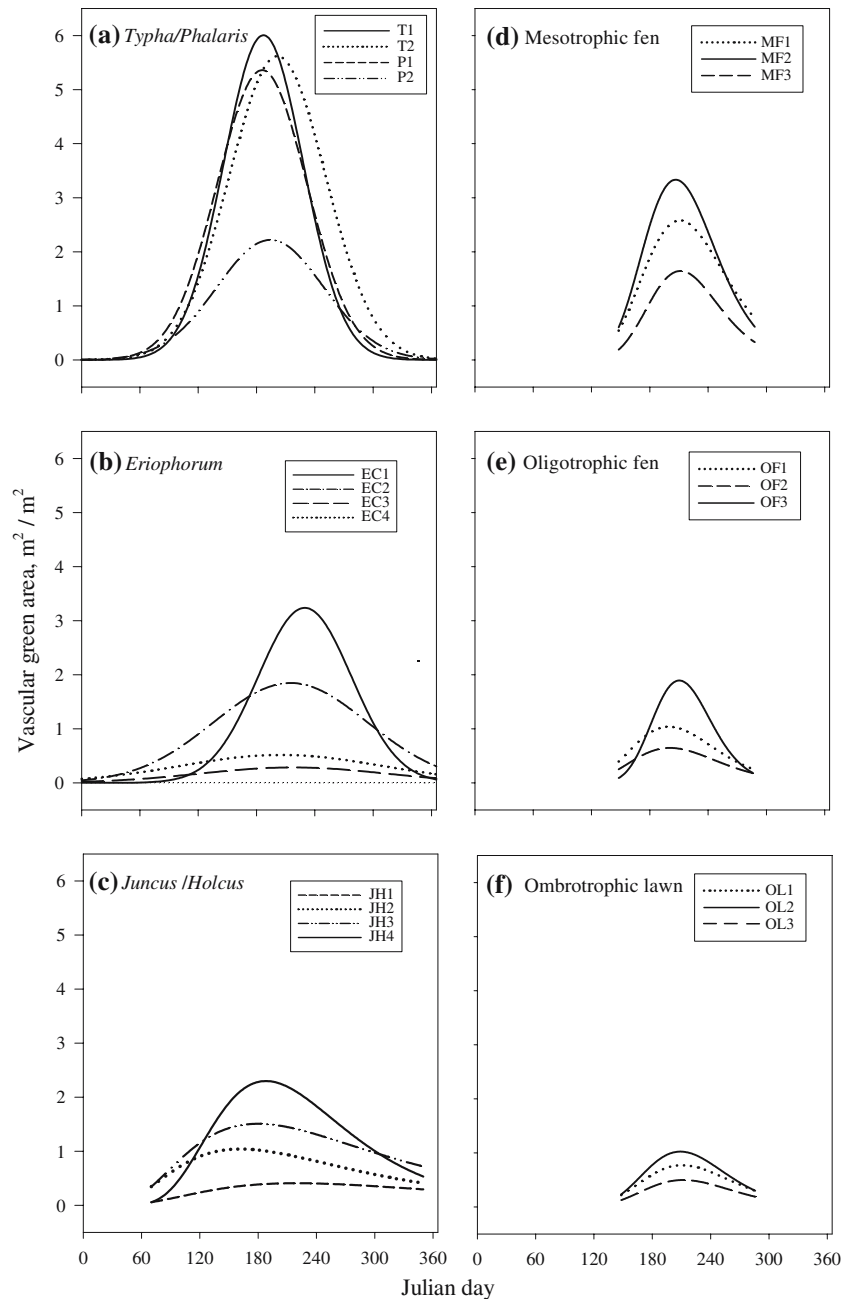

Discussion

The species-specific green area approach provides an opportunity to examine the seasonal dynamics of a wide range of peatland vascular plant communities over geographically and climatically different regions and incorporate the seasonal variation of leaf area into CO_2 models.

Species-specific GA

Differences in phenological patterns between plant species make the application of a single type of model prone to errors. Instead, the use of a species-specific approach permits the utilisation of individual models, which can more accurately estimate the leaf area dynamics of each species

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Fig. 5 Observed relationship between the Vascular Green Area (VGA) and gross photosynthesis (P_G) in full daylight (PAR > 600 μmol m^{-2} s^{-1}) in (**a**) *Typha* (sample plot T1), (**b**) *Phalaris* (sample plot P2) and (**c**) *Eriophorum/ Carex* (sample plot EC1) in 2003
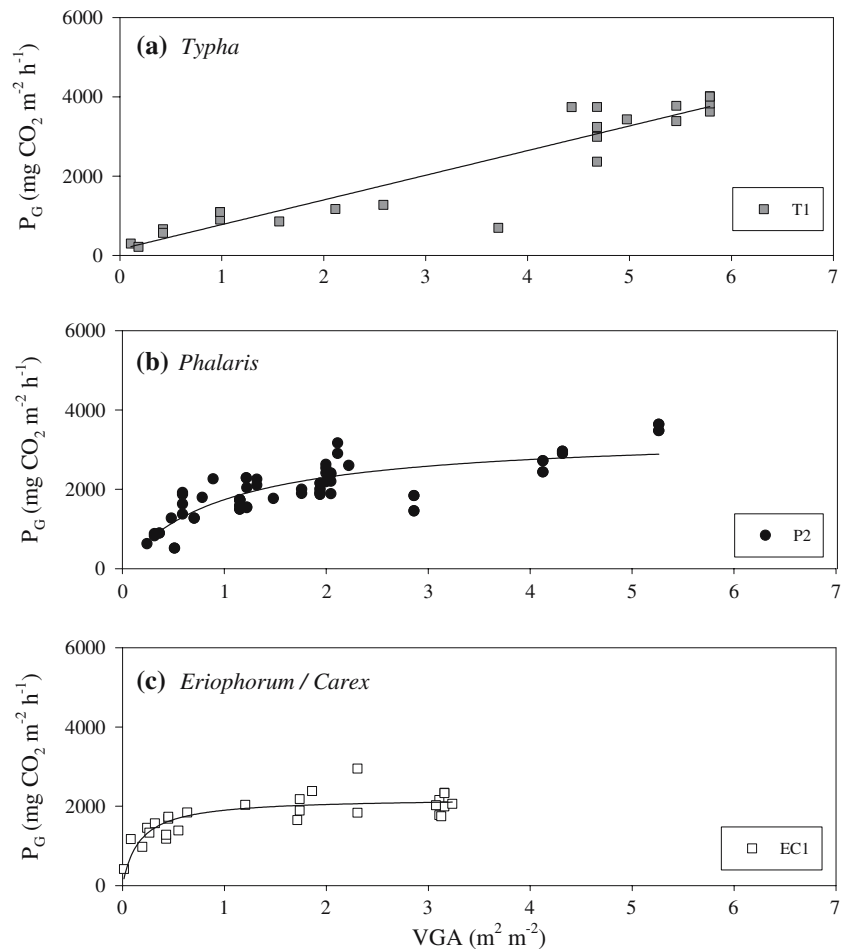
Table 3 Comparison of the performance of gross photosynthesis (P_G) models for three sample plots at Turraun, Co. Offaly

Plant community	df	r^2	F ratio
Phalaris (P2)			
PAR	2,63	0.624	326.3
PAR + VGA	3,62	0.869	653.8
Typha (T1)			
PAR	2,53	0.350	88.6
PAR + VGA	2,53	0.926	78.0
Eriophorum/Carex (EC1)			
PAR	2,63	0.587	292.5
PAR + VGA	3,62	0.817	459.8

The first model is based on the Michaelis–Menten function with PAR as the only explaining variable (Eq. 6). The second model includes the addition of vascular green area (VGA) as an explaining variable (Eqs. 7 or 8). Degrees of freedom (df), goodness of fit (r^2) and F ratio values are shown. P values < 0.0001 for all models

under the prevailing climatic and edaphic conditions. As leaf area dynamics are strongly controlled by factors such as irradiation, moisture, nutrient status and temperature, which in turn are subject to considerable inter-annual variation, the VGA dynamics (Fig. 4) and parameter values (Table 1) reported here apply only to those conditions under which they were measured. As such,

the models must be re-parameterised for each year/season. This flexibility can be observed within our study where the growth patterns of both the temperate and boreal vascular plants differed considerably. For most species under the temperate, maritime climatic conditions of Turraun, the three parameter Gaussian model (Eq. 3) provided the best fit for the seasonal development of these plants (Table 1). The symmetrical form indicated the relative lack of climatic pressure and corresponds to the seasonal pattern in the length of daylight. In comparison to the boreal, the growing season in the temperate zone is greatly extended and the seasonal dynamics of an evergreen species such as *Juncus* do not necessarily conform to a strict calendar time scale. The fitting of a model for a 12-month period beginning and ending in spring rather than a January–December partition enabled the dynamics of this evergreen species to be captured more accurately (Fig. 1). In contrast, the growing season of *Carex lasiocarpa* in the boreal zone is constrained by snowfall and low temperature resulting in a short but intense growing season (Aurela et al. 2004). Growth in the spring is initiated following the melting of the snow and GA rapidly increased to a maximum in mid-summer when photoperiod was at its greatest. The subsequent decline in GA that occurs at a slower rate produces a skewed growth curve and the fitting of a log-normal model (Eq. 4) is more likely to produce better estimates. Furthermore, the strategies employed by the plants growing in different habitats are likely to play a large role in determining the parameters for different species. Reeds such as *Typha* and *Phalaris* tend to have fast growth rates at the beginning of the season (Wetzel and Van der Valk 1998), an adaptative mechanism in the competition for light in habitats with high availability of nutrients. In contrast, *Eriophorum/Carex* communities characteristic of nutrient poor habitats show much slower rates of increase but a more extended growing season. The continuous emergence and senescence of shoots throughout the year in *Juncus/Holcus*, also reported by Wetzel and Howe (1999), is similarly a strategy to lengthen growing season in habitats with low resource availability. The production of overwintering leaves by evergreen species can provide a

competitive advantage in the spring (Thormann and Bayley 1997) and possibly compensate for relatively low growth rates during the main growing season (Robertson and Woolhouse 1984b; Greulich and Bornette 2003).

Seasonal development of communities and VGA

The seasonal development of VGA within our study sites is in agreement with studies elsewhere (Kim et al. 1998; Nieveen et al. 1998; Käki et al. 2001). Most plant communities show an increase in green area and photosynthetic activity during the spring as a result of an increase in temperature and radiation levels towards the peak in mid-summer (Mooney and Ehleringer 1997). The main advantage of our method is that it provides not only a means of capturing the phenological variation that occurs between vascular peatland communities but that it allows us to assess the variation which occurs *within* communities. The results demonstrate that an individual vascular plant species can show considerable variation in the timing of the seasonal peak, which may result from the biotic interactions within communities. The large phenological variation over relatively narrow spatial distances that was observed in Turraun, may reflect the dynamic successional stage of the studied restored cut-away peatland (Rowlands 2001).

Canopy architecture and VGA

The relationship between canopy architecture and photosynthesis has been well documented (Turitzin and Drake 1981; Valladares and Pearcy 1999). In our study, the linear relationship observed between light saturated P_G and VGA in the *Typha* plants suggests minimised effects of self-shading, primarily through the production of leaves with almost vertical orientation. This is in accordance with the observation by Dykyjová (1973) that the canopy structure and leaf orientation of *Typha* allows increased penetration of light, maximising the photosynthetic potential of the whole plant stand. Similarly, Bradbury and Grace (1983) suggested almost uniform distribution of light within stands with vertically orientated leaves. In contrast, for

plants like *Phalaris* there is a maximum VGA value beyond which any further increase does not necessarily result in an increased CO_2 uptake (Bonan 2002) due to the self-shading of horizontally orientated leaves.

Incorporation of VGA into carbon gas modelling

The inclusion of the VGA term to the P_G models significantly improved the performance of these models (Table 3). However, as the models were not tested against independent data (i.e., the same data were used for model testing) they would benefit from being employed in other peatland C studies to assess their performance and ability to estimate P_G. The necessity of accounting for the phenology and green area dynamics of the vegetation and their influence on CO_2 exchange rates has been recognised by other studies (Alm et al. 1997; Trumbore et al. 1999; Griffis et al. 2000; Roehm and Roulet 2003). The variation in phenology is likely to have a strong influence on C gas cycling both between and within these communities. Spatial and temporal variations in C gas fluxes have been widely reported in peatlands (Shurpali et al. 1995; Lafleur et al. 2003; Bubier et al. 2003a). Results from this study would suggest that part of the variation is likely to occur as a result of the cumulative differences in growth patterns occurring at the species and reflected at the community level. To obtain improved estimates of C gas exchange it is therefore necessary to focus on the changes that occur at the species level. Although our modelling approach combines community P_G measurements with species-specific development of leaf area, our results indicate that as a dominant species is the principal component of VGA (Fig. 3) and is likely to be the main control on CO_2 uptake and respiration rates such an approach is reasonable. Future research will be required to assess the importance of the growth dynamics of the dominant species to variation in CO_2 exchange rates within a particular peatland community and the contribution of the other species within the community. Although we have focused on peatland ecosystems in this paper, the adoption of the method within other ecosystems should not present difficulties although the species number and the density of community may differ.

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