Plant biomass and production and CO_2 exchange in an ombrotrophic bog

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Summary

1 Above-ground biomass was measured at bog hummock, bog hollow and poor-fen sites in Mer Bleue, a large, raised ombrotrophic bog near Ottawa, Ont., Canada. The average above-ground biomass was 587 g m^{-2} in the bog, composed mainly of shrubs and *Sphagnum* capitula. In the poor fen, the average biomass was 317 g m^{-2}, comprising mainly sedges and herbs and *Sphagnum* capitula. Vascular plant above-ground biomass was greater where the water table was lower, with a similar but weaker relationship for *Sphagnum* capitula and vascular leaf biomass.

2 Below-ground biomass averaged 2400 g m^{-2} at the bog hummock site, of which 300 g m^{-2} was fine roots (< 2 mm diameter), compared with 1400 g m^{-2} in hollows (fine roots 450 g m^{-2}) and 1200 g m^{-2} at the poor-fen site.

3 Net Ecosystem Exchange (NEE) of CO_2 was measured in chambers and used to derive ecosystem respiration and photosynthesis. Under high light flux (PAR of 1500 µmol m^{-2} s^{-1}), NEE ranged across sites from 0.08 to 0.22 mg m^{-2} s^{-1} (a positive value indicates ecosystem uptake) in the spring and summer, but fell to –0.01 to –0.13 mg m^{-2} s^{-1} (i.e. a release of CO_2) during a late-summer dry period.

4 There was a general agreement between a combination of literature estimates of photosynthetic capacity for shrubs and mosses and measured biomass and summer-time CO_2 uptake determined by the eddy covariance technique within a bog footprint (0.40 and 0.35–0.40 mg m^{-2} s^{-1}, respectively).

5 Gross photosynthesis was estimated to be about 530 g m^{-2} year^{-1}, total respiration 460 g m^{-2} year^{-1}, and export of DOC, DIC and CH_4 10 g m^{-2} year^{-1}, leaving an annual C sequestration rate of 60 g m^{-2} year^{-1}. Root production and decomposition are important parts of the C budget of the bog. Root C production was estimated to be 161–176 g m^{-2} year^{-1}, resulting in fractional turnover rates of 0.2 and 1 year^{-1} for total and fine roots, respectively.

Key-words: carbon cycling, hydrology, net ecosystem exchange, net primary production, roots

Journal of Ecology (2002) **90**, 25–36

Introduction

Peatlands cover extensive areas of boreal and temperate regions and are characterized by slow rates of CO_2 uptake from, and release to, the atmosphere. Based on several chamber and tower measurements of CO_2 flux, bright-sunshine CO_2 fixation rates in peatlands range from 0.15 to 0.35 mg m^{-2} s^{-1} and summer CO_2 respiration

rates range from 0.1 to 0.2 mg m^{-2} s^{-1} (Frolking *et al.* 1998). Both values are small compared to forest and grassland ecosystems but persistent C sequestration at 20–30 g m^{-2} year^{-1} (Gorham 1991; Clymo *et al.* 1998), resulted in a store of between 250 and 450 Gt of C accumulating in northern peatlands over the past 10 000 years. This represents about one-third of the C stored in soils globally in regions which are anticipated to undergo significant changes in climate associated with increasing atmospheric concentrations of greenhouse

gases (Moore *et al.* 1998). Consequently, there has been considerable interest in determining the rates of C exchange between peatlands and the atmosphere and the ecological and climatic controls on this exchange, with the aim of being able to predict the effect of climatic change.

At the Mer Bleue ombrotrophic bog, eddy covariance measurements of CO_2 flux (Lafleur *et al.* 2001) have shown an annual net CO_2-C exchange with the atmosphere of *c.* 80 g CO_2-C m^{-2} $year^{-1}$. Export of C as dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and methane emission were estimated to total approximately 10 g m^{-2} $year^{-1}$ (Fraser 1999), yielding an annual uptake of about 70 g m^{-2} $year^{-1}$. This is about three times the long-term C sequestration rate over the past 6000 years (P. Richard *pers. comm.*). The rates of, and controls on, CO_2 emission through peat decomposition and export of DOC and DIC at Mer Bleue have been reported by Scanlon & Moore (2000) and Fraser *et al.* (2001), respectively. Vegetation patterns of boreal–temperate peatlands are well known and the primary controls on these patterns, such as water table position and peat water chemistry, have been established (e.g. Glaser *et al.* 1990). Earlier studies (e.g. Smith & Forrest 1978; collated in Campbell *et al.* 2000) have described the distribution of biomass within peatlands, primarily above-ground, but there have been few measurements of below-ground biomass. Little attempt has been made to relate biomass values to rates of net primary production (NPP) and photosynthetic capacity, or to rates of ecosystem CO_2 exchange and C sequestration in order to develop C exchange models for peatlands.

We describe further results from this peatland in the cool temperate region of eastern Canada. We examine above- and below-ground plant biomass at bog hummock, bog hollow and poor-fen sites, and we estimate rates of plant production. We relate these measurements to the observed net ecosystem exchange of CO_2 (NEE) derived from chamber and micrometeorological measurements and develop an overall C budget of the Mer Bleue peatland.

Materials and methods

The Mer Bleue peatland is a raised, low-shrub, ombrotrophic bog covering 25 km^2, 10 km east of Ottawa, Ontario, Canada. The central portion of the peatland, which started to form about 8400 years ago (P. Richard, *pers. comm.*), is 5–6 m thick, thinning towards the margins. The peatland pore-water is acid, rich in DOC but poor in nutrients. On the bog hummocks, the vegetation is a mixture of evergreen shrubs (dominantly *Chamaedaphne calyculata*, *Kalmia angustifolia*, and *Ledum groenlandicum*), occasional deciduous shrubs (such as *Vaccinium myrtilloides*), underlain by *Sphagnum* mosses (dominantly *Sphagnum capillifolium* and *Sphagnum fuscum*). *K. angustifolia*, *Maianthemum trifolium* (*Smilacina trifolia*), *Eriophorum vaginatum*

and *Sphagnum magellanicum* and *Sphagnum angustifolium* are dominant species in bog hollows and *Carex oligosperma*, *Sphagnum magellanicum* and *S. papillosum*, with some *K. angustifolia*, in areas of poor fen. The nomenclature follows Anderson (1990) for *Sphagnum* and Fernald (1950) for vascular species.

Above-ground biomass was measured by clipping 19 0.5×0.5 m quadrats in mid-August and sorting the material by species and into leaves and shoots. An estimate of the photosynthetically active portion of the *Sphagnum* biomass was made by clipping at the base of the capitulum. As noted by Clymo (1970), there is no clear division of live and dead plant material in *Sphagnum*, so this is an arbitrary but consistent approach. Plant tissues were oven-dried at 80 °C. Leaf Area Index (LAI) was calculated from the leaf mass and density for individual species. Water table position, relative to the *Sphagnum* surface, was monitored in a 3-cm diameter well inserted into each quadrat. Here, we use the September 17, 1999 (Julian day 260) water table measurements, which are very close to the 1999 growing season average (Julian days 100–300) recorded continuously within the bog (Lafleur *et al.* 2001). Fraser (1999) showed that there was a very strong temporal correlation among water tables in the peatland.

Below-ground biomass was determined by the excavation of 0.25×0.25 m pits at eight quadrats (three hummock, two hollow and three fen) in early September to a depth of 110 cm in 10 cm increments. The live below-ground biomass was sorted from the peat and ascribed to coarse and fine fractions (> and < 2 mm diameter, respectively), and to a shrub or a sedge/herb origin, and weighed after oven-drying at 80 °C.

Above-ground net primary productivity (NPP) was estimated for the shrubs from published relationships between above-ground biomass and NPP. *Sphagnum* NPP was measured by the cranked wire method (Clymo 1970) at bog hummock and hollow and fen sites during the 1998 and 1999 growing seasons.

Relationships between net ecosystem exchange of CO_2 (NEE) and photosynthetically active radiation (PAR) were established using clear, climate-controlled chambers, in which all plants, including shrubs, were enclosed. The chamber walls ($0.6 \times 0.6 \times 0.45$ m height) were constructed of clear lexan, plexiglass and Teflon film with a removable top to allow equilibration of plant communities to ambient conditions before and after sampling. A circulation fan and a heat exchanger controlled temperature and humidity to within 1 °C and 10% of ambient conditions, respectively. Aluminium collars were inserted into the peat (three each in the bog hummocks and hollows; four in the poor fen) and the chamber inserted into a groove that was filled with water before each sampling run to ensure an air-tight seal. Shrouds with different mesh sizes were used to reduce the light entering the chamber to 1/2 and 1/4 full light when measuring NEE and an opaque shroud was used when measuring ecosystem respiration (autotrophic and heterotrophic). Four 2.5 min sampling

Table 1 Above-ground biomass and Leaf Area Index at the bog and fen sections of Mer Bleue, based on the mean of 15 bog and four fen quadrats. Numbers in parentheses represent the standard deviation among the quadrats

| Site | Species | Above-ground biomass (g m^{-2}) | | Leaf Area Index |
		Leaf	Shoot	
Bog	*Chamaedaphne calyculata*	52 (68)	72 (78)	0.44
	Kalmia angustifolia	52 (58)	41 (46)	0.32
	Ledum groenlandicum	28 (42)	22 (32)	0.18
	Vaccinium myrtilloides	13 (25)	16 (30)	0.14
	Maianthemum trifolium	2 (3)		0.04
	Sedges (*Eriophorum* spp.)	8 (17)		0.13
	Other vascular plants*	37 (46)		0.05
	Sphagnum capitula	144 (39)		n.a.
	Total	487 (93)		1.30
Poor-fen	Sedges (*Carex oligosperma* and *Eriophorum* spp.)	118 (51)		1.95
	Kalmia angustifolia	29 (40)	10 (13)	0.18
	Sphagnum capitula	160 (22)		n.a.
	Total	317 (36)		2.13

*e.g. *Vaccinium oxycoccus, Andromeda glaucophylla, Kalmia polifolia.*

runs at different light fluxes were conducted at each collar location three times on May 28–30, July 7–8 and August 31–September 2, 1999. See Bubier *et al.* (1998) for more detail on NEE methods.

NEE is the instantaneous difference between gross photosynthesis (GP) and respiration (R). The relationship between NEE and photosynthetically active radiation (PAR) was described by a rectangular hyperbola using a curve-fitting technique (Thornley & Johnson 1990):

$$NEE = \frac{-\alpha \times PAR \times GP_{max} + R}{(\alpha \times PAR) + GP_{max}} \qquad \text{eqn 1}$$

where α is the initial slope of the rectangular hyperbola (also called the apparent quantum yield), GP_{max} is the asymptotic gross photosynthesis above light saturation, and R is the *y* (GP) axis intercept, or dark respiration. We adopted a sign convention of CO_2 uptake by which the ecosystem is positive and CO_2 emission from respiration is negative. Data analyses were performed with the statistical software JMP-IN (SAS Institute 1996).

Results

ABOVE- AND BELOW-GROUND BIOMASS

The above-ground biomass by major species or groupings of species for the bog and fen sections of Mer Bleue is given in Table 1. In the bog, the average above-ground biomass was mainly composed of *Sphagnum* capitula (30%) and the four dominant shrubs (61%) with little contribution from sedges and herbs. There was modest spatial variability in both the total biomass and the *Sphagnum* capitula biomass (coefficients of variation of 19 and 27%, respectively). Spatial variability was higher for individual vascular species: coefficients of variation for the four shrubs ranged from 98 to

190%, being lowest for *C. calyculata* and *K. angustifolia* and highest for *V. myrtilloides*. Although total biomass was smaller at the fen, sedge biomass was much larger and *Sphagnum* slightly smaller than at the bog, with a minor input from the other vascular plants (mainly *K. angustifolia*, Table 1).

The leaf mass of vascular plants is probably more relevant for CO_2 exchange than their overall biomass. At the bog, leaf biomass averaged 192 g m^{-2}, with an overall LAI of 1.3 (Table 1). Average leaf : shoot ratios of the four shrubs ranged from 0.72 and 0.81 for *C. calyculata* and *V. myrtilloides* to 1.27 for both *L. groenlandicum* and *K. angustifolia*. At the fen section, average vascular leaf biomass (147 g m^{-2}) was close to the total vascular biomass, because of the dominance of the sedge component, yielding an overall LAI of 2.1.

Despite the apparent uniformity of the bog in terms of overall biomass, there is much spatial variability in the biomass of individual species, particularly the shrubs and sedges. Total above-ground biomass (vascular and mosses) was strongly related ($r^2 = 0.71$, $n = 19$, $P < 0.001$) to water table position among the quadrats (an average of 589 g m^{-2} with a water table at -50 to -60 cm vs. 308 g m^{-2} at -20 to -30 cm, Fig. 1). There was also a strong negative relationship ($r^2 = 0.75$, $n = 19$, $P < 0.001$) between vascular above-ground biomass and water table position among the quadrats, with a range from 461 to 133 g m^{-2}. The relationship was weaker ($r^2 = 0.52$, $n = 19$, $P < 0.001$, range 127–283 g m^{-2}), however, with only the vascular green biomass (shrub and sedge/herb leaves). Where the water table was low, a larger proportion of the above-ground shrub biomass was contained in stems and branches.

Green biomass also revealed a relationship with water table position, but the pattern depended on species or species group. The *Sphagnum* capitula biomass, although species vary across the fen and bog, is
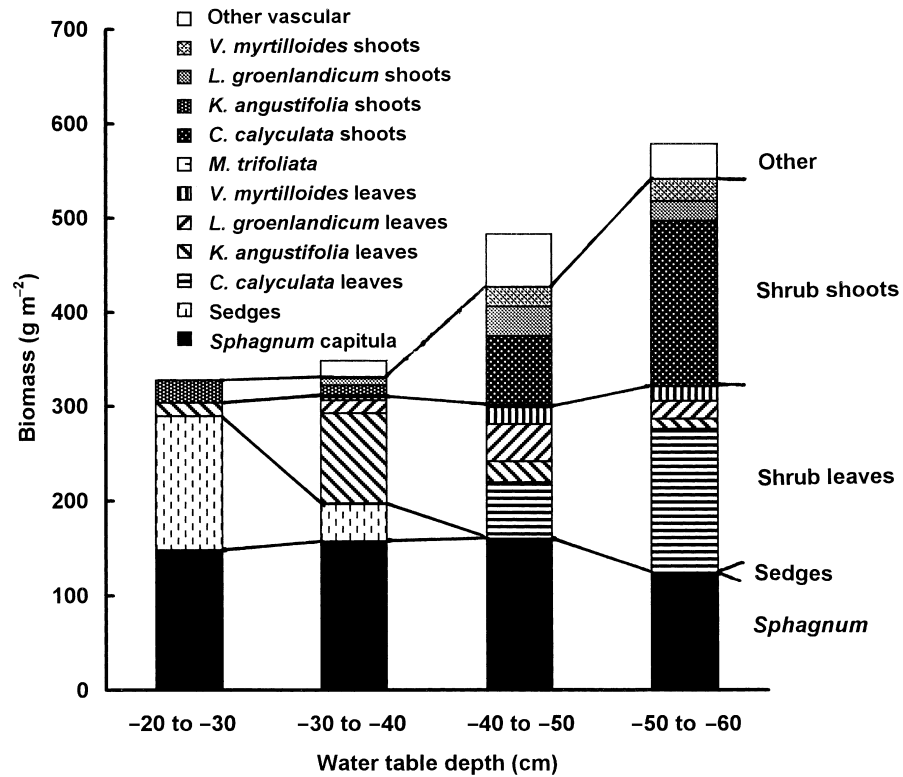
Fig. 1 Relationship between water table position and above-ground total and green biomass of plant species at the bog and poor-fen sections of the Mer Bleue peatland, by water table depth category.

Table 2 Relationships between above-ground NPP and above-ground biomass for herb/sedge, shrub and tree groups within northern peatlands, derived from Backéus (1990), Grigal *et al.* (1985), Reader & Stewart (1972), Szumigalski & Bayley (1997), Thormann & Bayley (1997), and Vasander (1982, 1992). Units, NPP g m^{-2} year^{-1}; biomass g m^{-2}

Group	Regression	n	r^2
Herb/sedge	$\log_{10}$ NPP = 1.000 $\log_{10}$biomass – 0.001	28	0.999
Shrub	$\log_{10}$ NPP = 0.985 $\log_{10}$biomass – 0.409	52	0.963
Tree	$\log_{10}$ NPP = 0.846 $\log_{10}$biomass – 0.600	5	0.327

remarkably constant over the water table range, with the exception of a decrease at the sites with the lowest water table, less than –50 cm (Fig. 1). Among the shrubs, *L. groenlandicum* and *V. myrtilloides* showed little consistent difference (their distribution appears to be patchy) whereas leaf biomass of *C. calyculata* and *K. angustifolia* peaked at –50 to –60 cm and –30 to –40 cm, respectively. The sedge biomass (*Carex* spp. and *Eriophorum* spp.) showed a pronounced increase where the water table was higher than –35 cm (Fig. 1).

Below-ground biomass at the bog hummock averaged a total of 2400 kg m^{-2} to a depth of 1.1 m (Fig. 2a). Shrub coarse roots formed 86% of the total, but these were mainly shoots that developed root functions after being enveloped by the rising moss. Shrub fine roots (< 2 mm diameter) amounted to only 300 g m^{-2} and the herbs and sedges contributed 48 g m^{-2}. The shrub root biomass peaked at a depth of 20–40 cm, but did not extend beneath the average growing season water table depth of about –50 cm. The sedge and herb roots peaked

close to this depth and extended down to 1 m, albeit in small amounts (< 10 g m^{-2}). The bog hollow root biomass averaged 1500 kg m^{-2}, again mainly coarse material representing old shrub shoots (70% of the total), whereas shrub fine roots amounted to 231 g m^{-2} (Fig. 2b). The peak shrub root biomass in the hollows occurred at 10–30 cm and was again not found beneath the average growing-season water table depth of –30 cm. The herb/sedge roots amounted to 215 g m^{-2}, peaking close to the water table and extending down to 1 m.

At the fen site the root biomass totalled 1200 g m^{-2}, dominated by sedges (87% of the total) and there was a significant amount of sedge shoots (36 g m^{-2}) growing through the *Sphagnum* mat near the surface (Fig. 2c). The sedge root biomass peaked at a depth of 30–50 cm, just beneath the average growing-season position of the water table (–25 cm), and significant amounts of sedge roots were noted at depths down to 1 m (10–20 g m^{-2}).

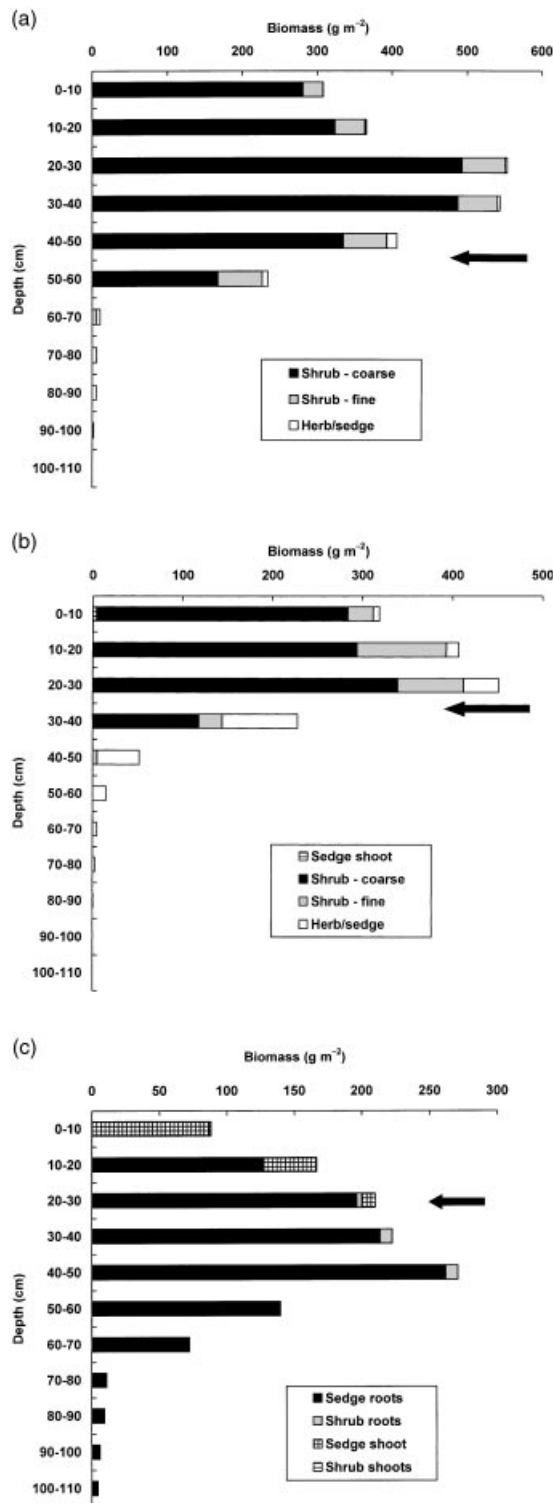Above- and below-ground biomass at the hummock, hollow and fen sites were related, with an average ratio

Fig. 2 Average below-ground biomass for (a) bog hummock, (b) hollow and (c) poor-fen sites in the peatland. Arrows indicate the position of the summer water table.

of above- to below-ground of 0.16 : 1 (Fig. 3). At the hummock and hollow sites, however, most of the below-ground biomass was coarse and probably played little function in the physiology of the shrubs, whereas nearly all the below-ground biomass at the fen sites was fine and probably active in sedge physiology.

The ratio between the above-ground and fine below-ground biomasses averaged 1.0 : 1 at the hummock and hollow sites, whereas it averaged 0.16 : 1 at the fen site. The fine root biomass at the hummock and hollow sites was about twice the vascular leaf biomass and at the fen it was eight times larger.

NET PRIMARY PRODUCTIVITY (NPP)

A review of the literature revealed strong correlations between above-ground biomass and NPP for plants in boreal/temperate bogs and fens (Table 2). These correlations were applied to the herb/sedge and shrub biomass data collected for the bog and fen sites at Mer Bleue. Shrub NPP at the bog was predicted to be 160 g m^{-2}: this may be an underestimate, because the shrub leaves, with the exception of *V. myrtilloides*, are shed after two years, resulting in a leaf NPP of *c.* 100 g m^{-2}. The small herb and sedge biomass here would contribute 10 g m^{-2} to NPP. At the poor-fen site, shrub NPP is 20 g m^{-2}, much less than for the dominant sedges (120 g m^{-2}) but total vascular above-ground NPP at both poor-fen and bog sites was predicted to be 140–170 g m^{-2}. The lower vascular biomass in the hollows compared to the hummocks at the bog site, is likely to be reflected in lower NPP values.

Sphagnum growth was measured over 2 years, and converted into NPP using the bulk density of the 2-cm section beneath the capitulum. *Sphagnum* growth was generally greatest in the spring and fall, when the water table was closest to the surface (Fig. 4). Average *Sphagnum* NPP was 140, 210 and 225 g m^{-2} year^{-1} at the hummock, hollow and fen sites, respectively. When combined with the above-ground NPP for the vascular plants, this resulted in estimated above-ground NPP of 290, 330 and 360 g m^{-2} for the bog hummock and hollow and fen sites, respectively.

NET ECOSYSTEM EXCHANGE OF CO₂ (NEE)

In late May, the rate of gross photosynthesis at PAR of 1500 µmol m^{-2} s^{-1} was similar at the bog hummock, bog hollow and poor-fen sites, ranging from 0.25 to 0.27 mg m^{-2} s^{-1} (Fig. 5 and Table 3). At this time, respiration was greatest in the bog hummock and hollow sites, resulting in a NEE of 0.08, 0.12 and 0.18 mg m^{-2} s^{-1} for the bog hummock, bog hollow and poor-fen sites. July photosynthetic rates were also similar among sites, ranging from 0.29–0.33 mg m^{-2} s^{-1}, as were respiration rates (–0.15 to –0.18 mg m^{-2} s^{-1}), resulting in a similar NEE (0.13–0.16 mg m^{-2} s^{-1}) at a PAR value of 1500 µmol m^{-2} s^{-1}. Following a dry period with lowered water tables during late August, all sites showed a net loss of CO₂ at a PAR of 1500 µmol m^{-2} s^{-1}: NEE ranged from –0.05 to –0.13 mg m^{-2} s^{-1}. This arose partly from smaller rates of photosynthesis in August (0.20–0.24 mg m^{-2} s^{-1}) compared to July or May, but mainly from larger respiration rates (–0.25 to –0.36 mg m^{-2} s^{-1}).

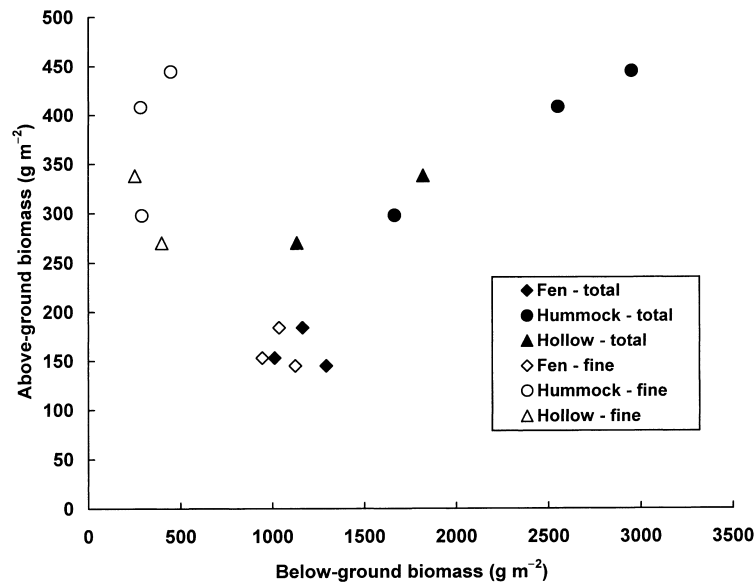These results suggest that, despite differences in

Fig. 3 Relationship between vascular above- and below-ground biomass at the bog hummock and hollow and poor-fen sites.
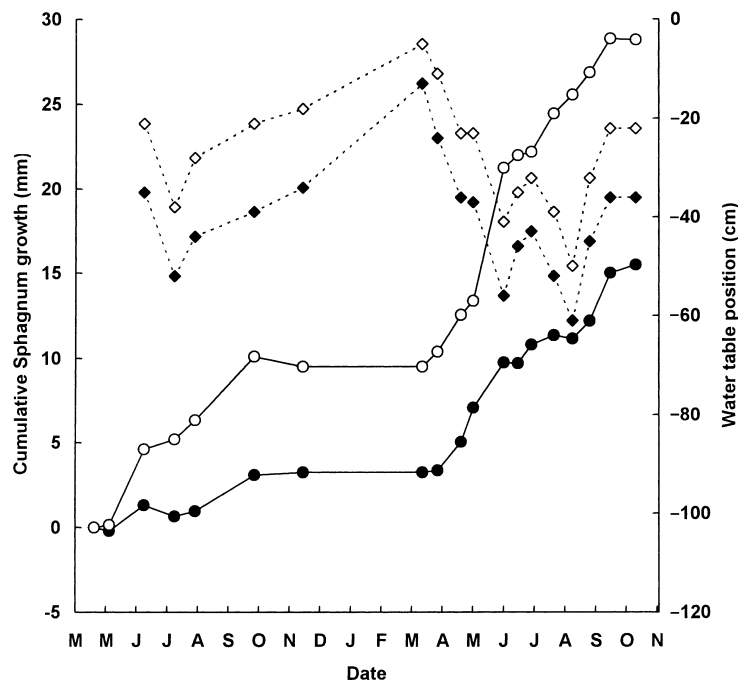

Fig. 4 Cumulative *Sphagnum* growth at Mer Bleue bog hummock and hollow sites and water table position, over two years.

plant species composition and biomass, rates of photosynthesis under bright sunshine are similar at the hummock, hollow and poor-fen sites during the three sampling periods. Photosynthetic capacities of the moss and vascular plant components may complement each other. Differences in growing-season NEE were controlled primarily by differences in respiration among the sites. Respiration was controlled primarily by soil temperature and water table depth, which rise and fall, respectively, from spring through the summer and resulted in a loss of C from the system in late summer 1999 under warm, dry conditions, as has been noted in Finland by Alm *et al.* (1999).

Discussion

BIOMASS AND PRODUCTION

Species composition and richness for Mer Bleue Bog is modal (24 vascular plant species) for raised bogs in eastern North America (Glaser & Janssens 1986; Glaser 1992). The bog is located in the transitional semiforested floristic region of Ontario and Quebec, where bogs have an average of between 20 and 26 vascular plant species. This species richness is greater than the continental bogs of western Ontario and Manitoba (< 20 species), but less than the maritime region of Nova
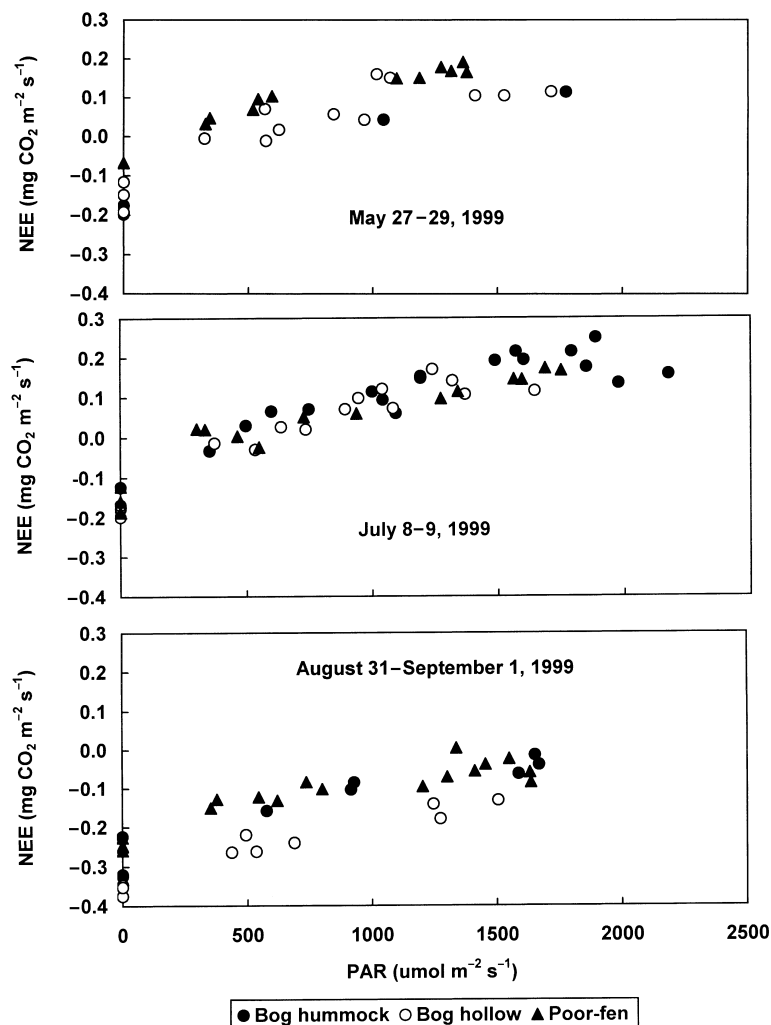
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*Plant biomass,
production and CO₂
exchange in a bog*

Fig. 5 Net ecosystem exchange (NEE) of CO_2 at the bog hummock and hollow and poor-fen sites, in late May, early July and late August, 1999.

Table 3 Chamber-derived respiration, NEE and gross rate of CO_2 fixation at bog hummock, bog hollow and poor-fen sites at Mer Bleue on May 28, July 8 and September 1, 1999. Respiration was measured under dark conditions and NEE and gross photosynthesis estimated for a PAR of 1500 $\mu mol\ m^{-2}\ s^{-1}$, based on fitting eqn 1 to the data. Standard errors of the estimate are indicated in parentheses

Date	Site	Respiration $(mg\ m^{-2}\ s^{-1})$	NEE $(mg\ m^{-2}\ s^{-1})$	Gross photosynthesis $(mg\ m^{-2}\ s^{-1})$
May 28	Bog hummock	−0.19 (0.01)	0.08	0.27 (0.13)
	Bog hollow	−0.15 (0.01)	0.12	0.27 (0.07)
	Poor-fen	−0.07 (0.00)	0.18	0.25 (0.03)
July 8	Bog hummock	−0.15 (0.01)	0.16	0.31 (0.07)
	Bog hollow	−0.18 (0.01)	0.15	0.33 (0.08)
	Poor-fen	−0.16 (0.01)	0.13	0.29 (0.05)
September 1	Bog hummock	−0.29 (0.02)	−0.05	0.24 (0.25)
	Bog hollow	−0.36 (0.00)	−0.13	0.23 (0.11)
	Poor-fen	−0.25 (0.01)	−0.05	0.20 (0.03)

Scotia and Newfoundland (32–50 species). Species richness is associated with mean annual precipitation and temperature, and annual freezing degree-days.

Above-ground biomass and NPP at Mer Bleue also appear to be within the normal range for treeless

peatlands. Table 4 summarizes published data for boreal and cool temperate bogs and fens from North America and Europe, and much of the variability within and among these peatland ecosystems can be related to the tree cover (Dyck & Shay 1999), leading to estimates

Table 4 Above-ground biomass and NPP of bogs and poor-fens, derived from Backéus (1990), Bartsch & Moore (1985), Bartsch & Schwinzter (1994), Campbell *et al.* (2000), Dyck & Shay (1999), Grigal *et al.* (1985), Reader & Stewart (1972), Szumigalski & Bayley (1997), Thormann & Bayley (1997), Vitt (1990), Wallén (1986) and Wallén & Malmer (1992). Values for bogs and poor-fens are means and range, with standard deviation in parentheses and number (*n*) in italics

Component	Bog	Mer Bleue bog	Poor-fen	Mer Bleue poor-fen
Total above-ground biomass (g m^{-2})	2177, 109–7740 (2259), *20*	356	1039, 18–3727 (949), *36*	158
Shrub above-ground biomass (g m^{-2})	478, 80–1020 (294), *16*	347	359, 21–1615, (436), *19*	40
Herb above-ground biomass (g m^{-2})	40, 0.1–130 (40), *14*	9	193, 52–640 (162), *14*	118
Above-ground NPP (g m^{-2} year^{-1})	438, 158–755 (224), *6*	340	273, 122–505 (104), *14*	365
Shrub above-ground NPP (g m^{-2} year^{-1})	180, 43–338 (113), *8*	160	50, 7–157 (56), *8*	20
Herb above-ground NPP (g m^{-2} year^{-1})	16, 3–34 (11), *6*	10	244, 52–965 (297), *13*	120
Moss NPP (g m^{-2} year^{-1})	188, 17–380 (127), *8*	170	122, 27–287 (73), *14*	225

spanning at least one order of magnitude. Both bog and poor-fen data for Mer Bleue are at the low end of the range reported in the literature. In bogs, vascular and moss NPP tend to be of a similar magnitude, as is the case at Mer Bleue. Within fens, shrub biomass is extremely variable, with Mer Bleue at the low end. The moss capitulum biomass (average 160 g m^{-2}) was less than that (278 g m^{-2}) reported by Dyck & Shay (1999) in a similar peatland in central Canada, based on sampling to the depth of green colour. This value remains at the lower end of the range of published results, when mean annual temperature is taken into account (Moore 1989).

It has long been recognized that species are distributed in peatlands in response to environmental gradients, particularly water table depth and peat pore-water chemistry (e.g. Glaser *et al.* 1990). At Mer Bleue, pore-water chemistry shows little spatial or temporal variability (Fraser 1999) and plant distribution and biomass are primarily related to water table position. Although the total above-ground vascular biomass decreases as the summer water table position rises, shrub leaf biomass is less variable. For each of the major shrubs biomass and leaf : shoot ratio are strongly related to summer water table depth, producing a mosaic of species within the microtopography of the peatland. At sites in an English blanket bog, Smith & Forrest (1978) also noted an increase in plant production with a fall in water table position. Interestingly, despite differences in species, there appeared to be little variation in *Sphagnum* capitula biomass across the sites at Mer Bleue, similar to results reported by Clymo (1970) for a wide range of sites in England.

Jackson *et al.* (1996) and Canadell *et al.* (1996) collated data on root biomass and depth for major biomes, but excluded peatlands and wetlands. The few available measurements indicate that most of the total plant biomass occurs beneath the peat surface, in a quest for nutrient and water resources. In Scandinavia, Backéus (1990), Finér *et al.* (1993), Saarinen (1996) and Wallén (1986) have estimated below-ground peatland biomasses of over 2 kg m^{-2}, with fine root biomass between 0.5 and 2 kg m^{-2}, and rooting depths of 2 m in some systems. The Mer Bleue peatland has a high below-

ground biomass of 1.2–2.4 kg m^{-2}, with fine roots (< 2 mm diameter) of between 0.4 and 1.0 kg m^{-2}. As in Scandinavia, shrub roots rarely penetrate beneath the depth of the summer water table, whereas the roots of herbs and sedges may reach a peak density at greater depth. The bog results are also similar to those reported in tundra: 1.2 kg m^{-2} biomass, mostly in the upper 30 cm, a maximum rooting depth of 0.5 m, and an above- to below-ground biomass ratio of 0.15 : 1 (Canadell *et al.* 1996; Jackson *et al.* 1996). Although it is difficult to measure root production rates (e.g. Wallén 1993; Saarinen 1996), roots probably play an important role in nutrient and C cycling in peatlands.

CO_2 EXCHANGE

The biomass information can be used to estimate CO_2 uptake by the peatland ecosystem. Most bog species reach maximum net photosynthesis at light fluxes of 900 µmol m^{-2} s^{-1}, except for *C. calyculata*. The deciduous species (e.g. *V. myrtilloides*, *Larix laricina* and *Betula populifolia*) have a higher net photosynthetic rate than the evergreen species (e.g. *C. calyculata*, *L. groenlandicum* and *K. angustifolia*), primarily related to greater N content (Small 1972a). At high PAR levels (1500 µmol m^{-2} s^{-1}), a green leaf bog biomass of about 200 g m^{-2} and an average shrub net CO_2 photosynthetic rate of 7 mg g h^{-1}, the net vascular CO_2 photosynthetic rate during mid-summer would be 0.39 mg m^{-2} s^{-1}. The vascular shrubs at Mer Bleue are probably not affected by water stress (Small 1972b), but the photosynthetic capacity of *Sphagnum* is strongly dependent on water content of the capitula (e.g. Titus & Wagner 1984; Silvola 1990). During summer at Mer Bleue, the surface moss mat dries, and gravimetric water contents of 500–700% were recorded in the capitula of the hummock and hollow sites, respectively, during a dry period in late August, 1999. At a water content of 500%, hummock *Sphagnum fuscum* or *Sphagnum nemorum* net photosynthetic rates are 0.02–0.04 mg CO_2 m^{-2} s^{-1} (Titus & Wagner 1984; Silvola 1990). Combining shrub and moss net photosynthetic rates produces an overall photosynthesis rate estimate of 0.41–0.43 mg CO_2 m^{-2} s^{-1} for the
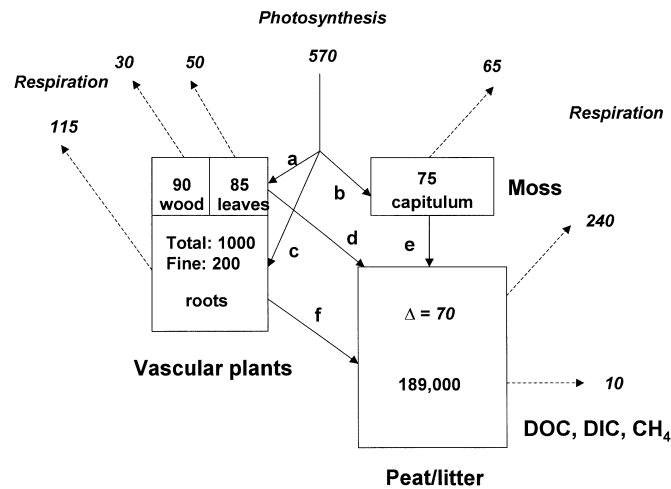
Fig. 6 A tentative C budget for the bog section of the Mer Bleue peatland. Stocks are in g C m^{-2} and fluxes are in g C m^{-2} year^{-1}.

hummocks. In the hollows, the shrub leaf biomass is smaller (160 g m^{-2}), but this is compensated by a *Sphagnum* mat with a larger water content. Combination of vascular (0.31 mg CO$_2$ m^{-2} s^{-1}) and moss (0.07 mg CO$_2$ m^{-2} s^{-1}, *Sphagnum fallax* – Titus & Wagner (1984)) net photosynthetic capacities results in an overall estimate of 0.38 mg CO$_2$ m^{-2} s^{-1} in the hollows.

These estimated photosynthetic rates can be compared with the peatland CO$_2$ uptake rates observed by the eddy-covariance measurements (Lafleur *et al.* 2001) and chamber measurements. During July and August, 1998, NEE rates determined by eddy-covariance were 0.24 mg CO$_2$ m^{-2} s^{-1} at a PAR value of 1500 μmol m^{-2} s^{-1}. Subtracting the respiration values, derived from night-time flux, these translate into photosynthetic rates of 0.35–0.40 mg CO$_2$ m^{-2} s^{-1} and GP$_{max}$ values of 0.39–0.46 mg CO$_2$ m^{-2} s^{-1}. This range is similar to that obtained above for hummock and hollow sites (0.42 and 0.38 mg CO$_2$ m^{-2} s^{-1}, respectively) using the biomass data and net photosynthetic rates from Small (1972a) and Titus & Wagner (1984). The photosynthetic rates from the chamber measurements at hummock and hollow sites in July, 1999 range from 0.31 to 0.33 mg CO$_2$ m^{-2} s^{-1}, somewhat less than observed by eddy-covariance techniques and predicted from biomass.

STORAGE AND FLUXES OF C IN THE MER BLEUE BOG

We have developed a tentative annual C budget for the Mer Bleue bog (Fig. 6) based on measured biomass values and a combination of measured and predicted C fluxes. The overall C budget is constrained by a complete year of CO$_2$ flux measurements by the eddy covariance technique (Lafleur *et al.* 2001) and annual estimates of CH$_4$, DOC and DIC export (Fraser *et al.* 2001). Total gross photosynthesis from June 1998 to May 1999 was 529 g C m^{-2} year^{-1} and

ecosystem respiration as CO$_2$ was 461 g C m^{-2} year^{-1} (Lafleur *et al.* 2001). CH$_4$ flux to the atmosphere and DOC and DIC export in runoff resulted in a loss of 10 g C m^{-2} year^{-1} (Fraser *et al.* 2001). The net sequestration of C in the peatland was estimated at 60 g m^{-2} year^{-1}. We assume that the vegetation was in approximate equilibrium (NPP equalled litter fall), so that the accumulation occurred in the peat.

We disaggregated the C budget into sub-budgets for the peat, the moss capitula and vascular leaves, shoots and roots, for each of which we had measured biomass values (Fig. 6). Using literature values for base metabolic rates per unit of biomass (photosynthesis and respiration), and general assumptions about active season length and temperature effects, we estimated the annual CO$_2$ fluxes for each component of the system (Table 5). Total photosynthesis, about 550 g C m^{-2} year^{-1}, is in agreement with the eddy-covariance estimate of 529 g C m^{-2} year^{-1}. Autotrophic respiration totals about 250 g C m^{-2} year^{-1}, so that NPP is about 300 g C m^{-2} year^{-1} (photosynthesis minus respiration), with moss NPP of about 35 g C m^{-2} year^{-1} and vascular NPP of about 245 g C m^{-2} year^{-1}. The eddy-covariance method estimated total ecosystem CO$_2$ respiration as 461 g C m^{-2} year^{-1} (Lafleur *et al.* 2001), so heterotrophic respiration (decomposition) would account for 211 g C m^{-2} year^{-1}. A generalized peatland decomposition model (Frolking *et al.* 2001) estimates that about 290 g C m^{-2} year^{-1} is lost from the peat as heterotrophic respiration (CO$_2$ plus CH$_4$), DOC and DIC, for an 8000-year-old bog with 3.2 m of peat and an annual NPP of 300 g C m^{-2} year^{-1}. Moss litter production will equal moss NPP (54 g C m^{-2} year^{-1}). The majority of the vascular plant biomass at the bog consists of shrubs (Table 1), and the majority of the shrubs are evergreen, with a 2-year leaf retention time (Small 1972a); we estimate that vascular leaf litter fall is half the leaf biomass, or about 45 g C m^{-2} year^{-1}. In addition, the shrub shoots contribute to the input of organic matter, as the mosses grow up the stems; this

Table 5 Derivation of the annual atmosphere-surface exchange of CO_2-C for the Mer Bleue bog

Component	C mass (g m^{-2})	Base rate (mg g C^{-1} h^{-1})	Day length (h)	Year length (days)	Temperature factor	Annual C budget (g m^{-2} year^{-1})
Leaf psn	85	3.8	10	150	1.00	487
Leaf res	85	0.57	24	150	0.75	131
Shoots	90	0.0032	24	200	0.75	1
Fine roots	200	0.20	24	200	0.49	94
Moss psn	75	0.87	10	150	1.00	98
Moss res	75	0.22	24	150	0.75	44

psn, photosynthesis; res, respiration.
Base rates: leaf psn, Small (1972a) value of 7 mg CO_2 g^{-1} h^{-1} and assumption of 50% C in biomass; leaf res, 0.15 times psn (Aber & Federer 1992); shoots, Ryan *et al.* (1995) value of 15 μmol CO_2 m^{-3} s^{-1}; roots, Ryan (1991) value of 0.01 mol C mol N^{-1} h^{-1} and an assumption of C : N ratio of 50 : 1; moss psn, Titus & Wagner (1984) value of 1.6 mg CO_2 g^{-1} h^{-1}; moss res, Titus & Wagner (1984) value of 0.4 mg CO_2 g^{-1} h^{-1}.
Day length, typical day during active season (May–Oct.).
Year length, length of active season.
Temperature factor for above-ground tissues: daytime = 1, night-time = 0.5; value is 1.0 for photosynthesis and 0.75 for respiration of roots, base rate for 20 °C, Q_{10} of 1.75, assumption of half season at 10 °C and half at 5 °C.

may amount to 30–45 g C m^{-2} year^{-1}. The remaining litter fall (between 161 and 176 g C m^{-2} year^{-1}) must come from vascular plant roots. The C budget for the peat itself is roughly 300 g C m^{-2} year^{-1} input as litter fall and 250 g C m^{-2} year^{-1} loss as CO_2 respiration and CH_4, DOC and DIC, for a net accumulation of about 50 g C m^{-2} year^{-1}.

This budgeting exercise can only be considered a rough approximation, and relies upon the observational estimate of total respiration to complete the budget. Using the generalized decomposition model value for decomposition would reduce net accumulation in the peat to 10 g C m^{-2} year^{-1}. Crude as it is, however, the budgeting exercise makes three important points. First, we have developed the components of a C budget which, when added together, are generally consistent with the total ecosystem budget. This has not been done previously for peatlands. Second, the budget emphasizes the overall importance of roots, which dominate the vegetation biomass and litter fall budgets, and contribute a significant portion of total vascular plant respiration. If root turnover occurs primarily in the fine root pool, this budget implies the fractional fine root turnover rates of about 1 year^{-1} and fractional total root turnover rates of about 0.2 year^{-1}. Estimates of root production in other peatlands have ranged from 25 to 200 g C m^{-2} year^{-1} (Backéus 1990; Finér *et al.* 1993; Wallén 1993; Saarinen 1996). In boreal and cool temperate forests, root NPP ranges from 20 to 250 g C m^{-2} year^{-1}. Measurement of root production in most ecosystems is difficult and in peatlands is compounded by the wet conditions and the difficulty in separating roots from the surrounding organic matrix (e.g. Wallén 1993). Nevertheless, under current and changing conditions, below-ground activities are likely to be very important to C cycling and to respond to climatic change (Van Noordwijk *et al.* 1998). About half the total ecosystem respiration comes from the decomposition of the peat.

Several important aspects of the exchange of CO_2 between the atmosphere and the peatland surface are demonstrated by this study. Firstly, the previously reported importance of spatial and temporal variability of the supply of moisture is confirmed. The position of the water table dictated the distribution of several peatland species and was related to above and below-ground biomass and productivity. Secondly, below-ground biomass and productivity are critical to the determination of the overall store and flux of carbon in this bog ecosystem. Ignoring the below-ground component, which is the usual practice because of the difficulties of measurement, excludes well over 50% of the biomass and a large portion of the annual production. Additional studies that include both above- and below-ground biomass are needed to help build functions that can be used to estimate below-ground biomass from measurements of above-ground biomass and simple environmental variables. Thirdly, by determining the stocks and fluxes of the components of the active carbon cycling, this study has clearly demonstrated that no one component dominates and that the complete analysis is required to characterize the system. Fourthly, biomass estimates in this bog ecosystem in combination with literature functions for NEE based on PAR measurements can produce similar estimates of NEE to those measured by micrometeorological techniques and can be employed on many wetlands in an area. In contrast, the micrometeorological approach to CO_2 exchange yields a much more accurate estimate of NEE, but is restricted, because of logistics and expense, to a single site. The success of the biomass approach, however, required a good estimate of the change in storage of carbon in the peat, which was derived from the eddy-covariance approach. Without this independent estimate measure of change in storage, all errors in estimating the individual pieces and incorporated into the sink term will quickly exceed the magnitude of the sink/source term of C.

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