

Estimating net ecosystem exchange in a patterned ecosystem: Example from blanket bog

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Abstract

Net ecosystem exchange (NEE) was measured in a patterned peatland with eddy covariance (EC) and chamber methods during a 12-month period. The peatland surface was composed of microforms characterized by a difference in water level and vegetation composition. The distribution of microforms varied spatially within the peatland. To achieve correspondent half-hourly EC and chamber NEE estimates, we modelled microform level chamber fluxes, estimated them at each instance of weather recordings and integrated them over the year. We then scaled the fluxes up to the EC footprint. On a half-hourly time scale the correlation coefficient (R) of the NEE between the methods was 0.80 and the slope of regression 0.91. Measurements made in summer and during daylight were more highly correlated than measurements made in winter and during darkness. When integrated on a monthly time scale the methods agreed better, with R of 0.98 and slope of regression 1.00. The annual NEE for the EC and chamber methods were 206 and 242 $\text{g}(\text{CO}_2) \text{m}^{-2}$, respectively. The study confirmed that the surface pattern of the EC footprint in the blanket bog was sufficiently homogeneous, that the changing wind direction did not influence the half-hourly NEE. However, the chamber estimates found that the annual NEE of the driest area within the footprint was 130% larger than that in the wettest area, indicating that large spatial variation can be found in NEE.

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1. Introduction

Blanket bogs are ombrotrophic peatlands receiving water and nutrients from precipitation and atmospheric deposition. They are usually located in flat to moderately sloping terrain. The surface pattern of these bogs is typically a mosaic of undulating microforms namely, hummocks, lawns and hollows (Lindsay, 1995). Micro-

forms differ from each other in terms of water table level, plant composition (Doyle, 1990) and peat pH (Doyle, 1982) and their distribution within a bog varies spatially (Lindsay, 1995). In blanket bogs this structural and functional differentiation is reflected in the spatial variation in carbon (C) accumulation rate (Tallis and Livett, 1994) and methane (CH₄) emissions (MacDonald et al., 1998). Studies in raised bogs (Alm et al., 1999b; Waddington and Roulet, 2000) have found similar spatial variation in carbon dioxide (CO₂) dynamics.

Net ecosystem exchange (NEE) is the difference between CO₂ uptake through photosynthesis and loss

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via respiration. The two main methods used to measure NEE are chamber (Alm et al., 1997; Bubier et al., 1998) and eddy covariance (EC) (Aurela et al., 1998; Lafleur et al., 2003). Both have advantages and disadvantages when used to assess the NEE of an area over specific time periods. The chamber method enables measurement of a homogenous miniature ecosystem (~ metre scale). Measurements at this scale allow observation of small-scale variation within the ecosystem, e.g. variation between microforms (Griffis et al., 2000). Furthermore, the chamber method enables the development of environmental response functions (Tuittila et al., 2004). It permits investigation of the functioning of the ecosystem at process level and also allows measurements in conditions when the flux rates are small, i.e. winter time (Alm et al., 1999a). However, difficulties are encountered when integrating the measurements over longer time periods and in scaling them up to ecosystem level (~1 km scale). The EC method allows non-intrusive, direct and continuous ecosystem scale measurement of NEE (Baldocchi, 2003) of fairly homogenous areas over a range of time scales varying from days to years (Baldocchi et al., 2001). In the EC method the source area of the measured CO₂ exchange, called the footprint, moves with the wind direction. The upwind spatial distribution of the corresponding surface emission (or deposition) flux was called footprint by Schuepp et al. (1990). The footprint is the relative weight given to each elemental emission or uptake flux (Horst and Weil, 1992). In order to estimate the footprint, Schuepp et al. (1990) developed a simple analytical model, which was then further developed by Horst and Weil (1992, 1994). Yet, discussions about the feasibility and reliability of analytical and Lagrangian stochastic models are ongoing (Schmid, 2002). Hsieh et al. (2000) combined similarity theory and a Lagrangian stochastic dispersion model into an easy-to-use analytical model that describes the relationship between footprint, atmospheric stability, observation height and surface roughness. Given that in a patterned peatland, CO₂ fluxes differ between microforms (Alm et al., 1999b, 1997) and that the microform distribution within a bog varies (Lindsay, 1995), different instantaneous footprints might show dissimilar CO₂ fluxes. If this were the case, the consequent EC measurements would not constitute a single time series, but a different time series for each different footprint. As a consequence the EC method would not operate in a homogeneous ecosystem as is generally assumed.

We measured the NEE with EC and chamber methods in an Atlantic blanket bog, which has a

characteristically patterned surface structure, over a 1-year time period.

The objectives of this study were

- (1) To investigate the variation in NEE between microforms.
- (2) To compare the EC and chamber estimates of NEE over short (half-hour, day) and long (month, year) time periods.
- (3) To investigate the effect of different environmental conditions on the reliability of the two methods.
- (4) To investigate how the patterned microform structure and shifting footprint affects the performance of the EC method.

2. Materials and methods

2.1. Site description

The study was conducted at an Atlantic blanket bog situated at 150 m asl. in Glencar, County Kerry, Ireland (51°55'N, 9°55'W). The average temperatures of the warmest month (July) and the coldest month (February) were 14.8 and 6.6 °C, respectively, over the past 30 years at the Valentia weather station (30 km west of the site) (<http://www.meteireann.ie/climate/valentia.asp>). The annual precipitation in the study site was 2510 and 2356 mm in years 2003 and 2004, respectively.

The surface of the study site is a mosaic of microforms, which were divided into four classes: hummocks (HU), high lawns (HL), low lawns (LL) and hollows (HO). They differ from each other in terms of relative altitude, water level (Fig. 1) and vegetation composition. Hummocks were covered by bryophytes (*Sphagnum* spp., *Racomitrium lanuginosum*) and had *Calluna vulgaris*, *Erica tetralix* and *Molinia caerulea* as dominant vascular plant species. Lawn level vegetation ranged from a dense cover of *M. caerulea* and *Schoenus nigricans* in drier areas, to wet areas dominated by *Rhynchospora alba*. Moss cover was sparse in lawns. Hollows supported bryophytes (*Sphagnum cuspidatum*, *S. auriculatum*) and a scattered vegetation of *R. alba*, *Eriophorum angustifolium* and *S. nigricans*. Two classes were used for lawns, as the vegetation of LL was both shorter and less dense in comparison to HL vegetation. The diameter of hummocks varied from 50 to 100 cm and they were relatively round in form. The shape and size of hollows varied greatly, with length being 50–300 cm. Lawns were flat areas between the previously noted microforms.

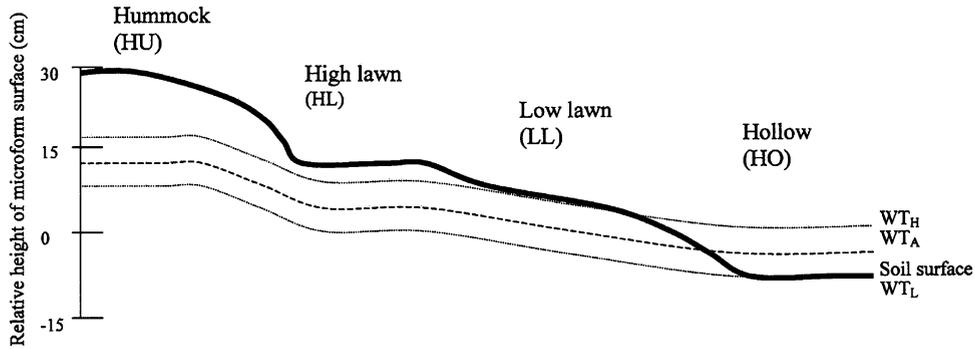


Fig. 1. Schematic representation of microforms and associated water level (WT) parameters: highest WT (WT_H), average WT (WT_A) and lowest WT (WT_L).

2.2. Microform distribution within the EC footprint

In order to compare the chamber and EC methods it is necessary to use the same spatial scale for both. We achieved this by scaling the chamber measurements up to the EC footprint area. To facilitate this, the microform distribution around the EC tower was surveyed along 16 radial transects extending from the tower at 22.5° intervals (Fig. 2). At each transect starting 10 m away from the tower, the proportion of each microform was assessed at 5 m intervals along a 2 m line, perpendicular to the transect. The transect length was 300 m, except in directions NE, E and ENE, where the extent of pristine bog ecosystem was met between 235 and 270 m from the EC tower. An X^2 test was carried out to distinguish which of the transects differed significantly from the average and from the

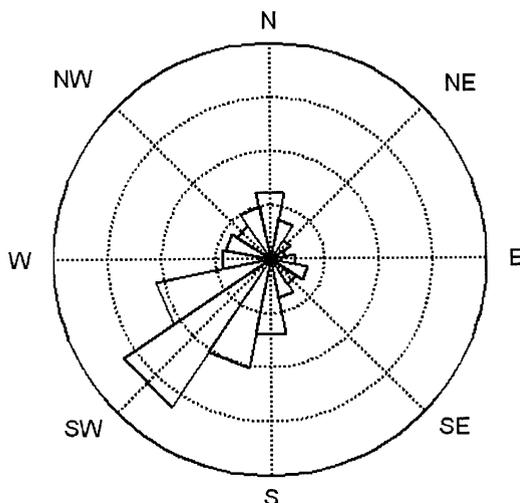


Fig. 2. Wind rose around the eddy covariance (EC) tower, illustrating the distribution of the wind directions over the study period. The prevailing wind direction is from the South West. Microform distribution was surveyed along 16 radial transects starting at the EC tower.

prevailing wind direction (SW) in terms of microform composition.

2.3. Eddy covariance (EC) measurements

The EC system consisted of a three dimensional sonic anemometer (Model 81000, R.M. Young Company, Traverse City, Michigan, USA) and an open-path CO_2/H_2O gas analyser (LI-7500, LI-COR Biosciences, Lincoln, NE, USA) mounted on a tower 3 m above the peatland surface. Data were recorded on a CR23X data logger (Campbell Scientific Ltd., Loughborough, UK) at a frequency of 10 Hz and fluxes were Reynolds-averaged every 30 min (Reynolds, 1895). The EC system was set up in a moderately flat section of the bog.

2.3.1. Environmental measurements

Micrometeorological equipment included a net radiometer (CNR 1, Kipp & Zonen, Delft, The Netherlands) and a photosynthetic photon flux density (PPFD) sensor (PAR Lite, Kipp & Zonen, Delft, The Netherlands). Air temperature (T_{AIR}) and relative humidity were measured at 2 m height with a temperature and relative humidity sensor (HMP45C, Vaisala, Vantaa, Finland), while soil temperature was recorded at 20 cm depth (T_{20}) (107, Campbell Scientific Ltd., Loughborough, UK) below HL vegetation. Precipitation was measured with two tipping bucket rain gauges (ARG100, Environmental Measurements Ltd., Sunderland, UK and Obsermet OMC-200, Observator BV, Ridderkerk, The Netherlands). The averaging time for EC and meteorological data was 30 min and data were transferred from the tower to the office at weekly intervals via telemetry.

2.3.2. EC data handling

Raw EC flux data were double rotated, so that mean horizontal wind speed was rotated into the mean wind

direction and vertical wind velocity was set to zero. The vertical rotation was based on the averaged 30 min angle between the horizontal and vertical axes. The CO₂ fluxes were then corrected for variations in air density due to fluctuation in water vapour and heat fluxes (Webb et al., 1980). The dataset was divided into day and night files using short-wave incoming radiation of 10 W m⁻² as the threshold between day and night. 46% of all the data were daytime data.

Filters were used to remove bad flux values. Records collected during rainy half hours, and up to 1 h after rain events, were rejected because of the poor performance of the open path gas analyser in wet weather. In low wind speed conditions the computation of the vertical angle used for the vertical rotation can give unrealistic outputs; therefore, fluxes that were rotated for angles < -2° or > 10° were rejected. In order to assess the existence of adequate turbulence required by the EC system for good performance, the nighttime fluxes are usually examined in different friction velocity (u^*) conditions and a lower u^* threshold established (Gu et al., 2005). In our study, no clear correlation was found between dry night CO₂ fluxes and u^* . Consequently, the night u^* filter was not applied. Nighttime uptake values were, however, rejected. Flux records were divided into bimonthly data sets for both day and night and filtered for unrealistic low or high values.

The gaps in CO₂ fluxes were filled with gap filling equations defined using the Curve Fitting Function of MATLAB 6.5 (The MathWorks, Inc., USA). Separate non-linear regression equations were used for daytime and nighttime gap filling. Daytime gaps were filled using rational functions of polynomials in one variable of different powers between good NEE values and PPFD or air temperature for bimonthly or monthly periods. The functions used for October 2003 and September 2004 were defined with a bimonthly data analysis together with September 2003 and October 2004, respectively. For nighttime a single Q_{10} relationship between good NEE values and soil temperature at 20 cm depth was used for the 12-month study period computed from the full data set collected in the biennium 2003–2004 (Sottocornola and Kiely, 2005).

In keeping with the chamber measurements we used the ecological sign convention in which fluxes from the biosphere to the atmosphere are negative.

2.4. Chamber measurements

Six stainless steel collars (0.6 m × 0.6 m × 0.15 m) were inserted into the peat in HU, HL and LL, respectively in June 2003. In March 2004 three more

sample plots were established in microform HO. Each collar had a water channel at the top to allow water sealing during gas sampling. Boardwalks were constructed around the sample plots to minimize disturbance. The sample plots, with microforms similar to those within the EC footprint, were located 300–350 m northwest of the EC tower.

CO₂ exchange measurements were made at weekly to biweekly intervals using a closed transparent plastic chamber (0.6 m × 0.6 m × 0.33 m). The square chamber was vented and included a cooling system (Alm et al., 1997). The CO₂ concentration (ppm) inside the chamber was monitored with a portable infrared gas analyser (EGM-4, PP Systems, Hitchin, Hertfordshire, UK). Instantaneous net CO₂ exchange (P_N , this term is used to distinguish it from the ecosystem scale NEE) was first measured under a stable ambient illumination at 15 s intervals over a 60–240 s period. This was then repeated with the chamber covered with an opaque canvas cover, in order to obtain P_N in the dark, which is used here as an estimate of the instantaneous ecosystem respiration rate (R_E). For a description of the method see Alm et al. (1997) and Tuittila et al. (1999). Measurements were carried out between 9:00 a.m. and 7:00 p.m.

In order to relate the gas fluxes to prevailing environmental conditions, PPFD and air temperature inside the chamber (T_{AIR}) were recorded simultaneously with P_N measurements. At the same time, soil temperature at 20 cm depth (T_{20}) and water level (WT), relative to the sample plot surface, were measured. The PPFD was measured with a quantum sensor in $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR-1, PP-Systems, Hitchin, Hertfordshire, UK).

Vascular green area (VGA), which describes the area of green vascular plant material, was measured according to Wilson et al. (in press) in order to simulate the phenological changes of the vegetation communities during the study period and to incorporate these changes into the CO₂ flux models. VGA was measured by counting the leaves of each vascular plant species within the sample plot and multiplying the number by the leaf area, which was measured concurrently. Measurements were made at biweekly to monthly intervals throughout the study period. Non-linear regression analysis was used in interpolating data between measurements to describe the seasonal changes in phenology.

2.5. Response functions for chamber CO₂ fluxes (P_G , R_E)

Instantaneous CO₂ flux rates P_N and R_E were calculated from the linear rate of change in CO₂ concentration inside the chamber headspace.

Table 1

Estimated parameter values (with standard error in parenthesis) and coefficient of determination (R^2) for gross photosynthesis (P_G) models for microforms: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO)

	HU	HL	LL	HO
P_{MAX}	0.66 (0.04)	0.64 (0.04)	0.82 (0.06)	
k	322.7 (27.03)	346.6 (29.70)	306.3 (45.56)	612.8 (239.51)
a_1	1.49 (0.11)	1.25 (0.12)	0.28 (0.05)	
a_2	19.11 (0.24)	19.58 (0.26)	21.06 (0.83)	
a_3	7.35 (0.33)	6.96 (0.34)	8.44 (1.25)	
b				0.29 (0.05)
b_1				-0.02 (0.01)
b_2				0.003 (0.00)
R^2	0.81	0.81	0.70	0.51

Instead of directly modelling the P_N flux, we computed the separate components of gross photosynthesis (P_G) and ecosystem respiration (R_E). This was made in order to describe the direct environmental controls on fluxes and decrease the overlap of effects. P_G was calculated as a sum of P_N and R_E . We developed regression models for each microform (Tables 1 and 2) following the ecological interpretation of Tuittila et al. (2004). We used a multiplicative model format for P_G and based the model construction on the Michaelis–Menten relationship between PPFD and photosynthesis (Stryer, 1988). VGA was used to describe the seasonal changes in P_G . For microforms HU, HL and LL, P_G was also dependent on the temperature of the active soil layer (T_A), which was calculated as the average of T_{AIR} and T_{20} measured simultaneously with chamber measurements. For HO, P_G was dependent on water level (WT). The model for HU, HL and LL had the following form:

$$P_G = P_{MAX} \left(\frac{Q_P}{k + Q_P} \right) (a_1 + V) \times \exp \left(-0.5 \left(\frac{T_A - a_2}{a_3} \right)^2 \right) \quad (1)$$

Table 2

Estimated parameter values (with standard error in parenthesis) and coefficient of determination (R^2) for ecosystem respiration (R_E) models for microforms: hummock (HU), high lawn (HL), low lawn (LL) and hollow (HO)

	HU	HL	LL	HO
a	0.02 (0.02)	0.04 (0.01)	0.01 (0.00)	0.02 (0.01)
b	0.08 (0.05)	0.09 (0.13)	0.12 (0.03)	0.09 (0.02)
b_1	0.01 (0.00)	0.02 (0.00)	0.01 (0.01)	0.00 (0.00)
b_2	0.08 (0.01)	0.04 (0.01)	0.14 (0.01)	
b_3	-0.00 (0.00)	-0.00 (0.00)	-0.0 (0.00)	-0.01 (0.00)
R^2	0.76	0.80	0.78	0.51

The model for HO had the following form:

$$P_G = \left(\frac{Q_P}{k + Q_P} \right) (b + b_1 W) \left(\frac{V}{b_2 + V} \right) \quad (2)$$

where Q_P is the photosynthetic photon flux density, V the vascular green area, T_A the temperature of the active soil layer and W is water level. P_{MAX} is the maximum light saturated photosynthesis rate, k the half saturation constant and a_1 , a_2 , a_3 , b , b_1 , b_2 are parameters.

For R_E we used an additive model format. R_E had a positive exponential relationship to T_A and the response to WT and VGA was linear in all microforms, except in HO, where VGA did not have explanatory power. The models for P_G and R_E were parameterised individually for each microform (Tables 1 and 2). The R_E model for HU, HL and LL had the following form:

$$R_E = a \exp(bT_A) + (b_1 W) + (b_2 V) + (b_3 WT_A) \quad (3)$$

The R_E model for HO had the following form:

$$R_E = a \exp(bT_A) + (b_1 W) + (b_3 WT_A) \quad (4)$$

where T_A is the temperature of the active soil layer, V the vascular green area, W the water level and a , b , b_1 , b_2 , b_3 are parameters. The R_E model for HU underestimated and gave negative flux rates in low temperatures ($<3.9^\circ\text{C}$). Given that such temperatures occurred rarely (50 h annum⁻¹), the effect was ignored.

Using the models (1)–(4) and environmental data, P_G and R_E were calculated at half hourly intervals for each microform over the hydrological year 1 October 2003–30 September 2004. The PPFD and T_A data used in the reconstructions were obtained from half hourly meteorological data at the EC tower. Daily WT for each sample plot was interpolated from WT measurements made during chamber measurement campaigns. Microform WT was calculated by averaging the WT of sample plots representing each microform. Average daily VGA was estimated for each microform using the VGA models. There were no WT or VGA measurements of HO during the period from 1st October 2003 to 5th April 2004. Therefore, the daily WT was estimated from LL values using the difference in the relative altitude between microforms LL and HO. To estimate the average daily VGA of the HO for this period, the VGA models based on data from 2004 were used. P_N was calculated half-hourly for each microform using the following equation:

$$P_N = P_G - R_E. \quad (5)$$

2.6. Scaling chamber fluxes up to ecosystem level

In order to compare the chamber and EC methods it was necessary to scale the chamber P_N estimates up to ecosystem level to obtain the chamber net ecosystem exchange (NEE) estimate. Hereafter the acronym CHA is used for scaled up chamber fluxes. Three scaling up approaches were performed.

The first approach considered the changes in the footprint at half-hourly intervals. The footprint length changes depending on the fluctuating atmospheric conditions and momentum flux. Consequently, the span of the transect to be considered in the scaling up process also changes. Hsieh et al. (2000) described the half hourly EC footprint as a positive skew distribution curve. Using this curve we described the area, which contributed the maximum to the flux. We considered this area to be located between the points where 1% and 67% of the contributing area to the footprint occurred. The positive skew distribution curve is asymmetric with a steep slope before the peak and a long tail after the peak. By setting the end of the considered source area at 67%, we eliminate the long tail and reduce the impact of areas with a low flux contribution to the considered footprint span. For each half hour measurement, the microform distribution of the defined transect span was averaged along the existing wind direction. However, when the 67% end point occurred at a distance further than the length of the transect in that wind direction, or when the computation of the footprint boundary failed (3047 out of 17,568 instances), the average microform distribution of the full transect was used. The half hourly P_N of the different microforms (HU, HL, LL, HO)

HO) were then weighted by the proportion of the microform within the estimated transect span. Finally the area weighted P_N for each microform were summed up to an ecosystem NEE, hereafter referred to as wind direction scaled NEE (CHA_{WD} NEE). Monthly and annual NEE during the study period were calculated from the half-hourly CHA_{WD} estimates.

The second scaling up approach did not consider the changing footprint but was simply based on the average microform distribution around the EC tower, covering a more or less circular area of ~ 300 m radius; hereafter this NEE is referred to as CHA_{AV} NEE.

Finally, chamber fluxes were scaled up according to the average microform distribution of each of the 16 transects (Fig. 3) and integrated over the study period to produce a separate annual NEE estimate for each transect. This was made in order to distinguish the spatial variation of NEE within the EC footprint.

2.7. Variability of microform level P_N fluxes

In order to test whether the microforms supported different P_N fluxes, a simple model describing the relationship between P_N and PPFD (Q_P) was parameterised for each of the 21 chamber measurement sample plots. The model took the form:

$$P_N = P_{MAX} \frac{Q_P}{(k + Q_P)} - R \quad (6)$$

where parameter P_{MAX} is the maximum photosynthesis, k the half saturation constant and R is the constant. To obtain the corresponding flux rate for each sample plot we calculated $P_{N(1000)}$ using a PPFD of

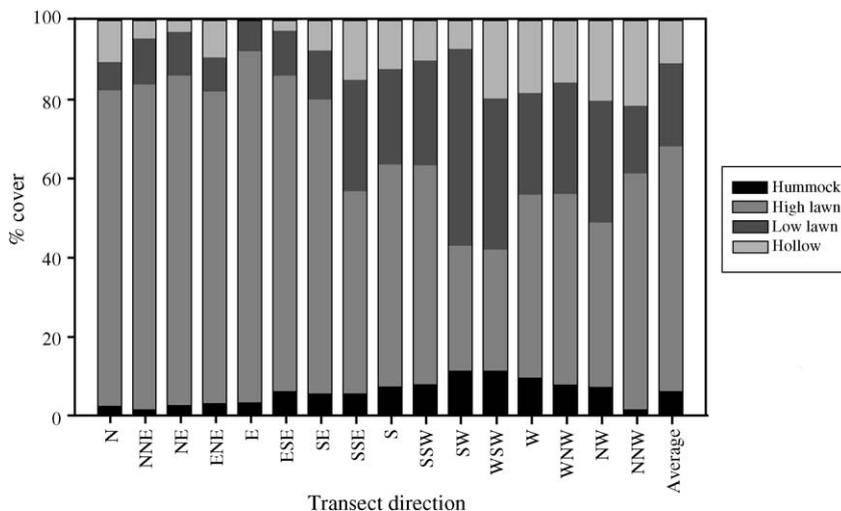


Fig. 3. Percentage cover of microforms along the 16 transects around the eddy covariance (EC) tower. The dominant microform in the prevailing wind direction (SW) is low lawn (LL); while on average high lawn (HL) dominates.

1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. One-way analysis of variance (ANOVA) was used to test if $P_{N(1000)}$ differed between the microforms. Following this the Tukey test was used as a post hoc test, to find out which microforms differed significantly from each other, in terms of $P_{N(1000)}$.

2.8. Comparison between the chamber and EC methods

Linear regressions were performed between the chamber and EC estimates of NEE in order to quantify the similarity of the methods under different conditions. Firstly, all half-hour measurements during the study period were used to compare the EC measurements with the two scaling up methods CHA_{WD} and CHA_{AV} . Secondly, the EC NEE estimates were compared with the CHA_{WD} NEE during winter (November–February) and summer (June–September) in order to investigate if the performance of the methods varied between seasons. Finally, the data set was divided into separate groups according to the tower data quality and environmental conditions (radiation, temperature and wind properties), which could affect the performance of the EC and chamber method (Table 3). Linear regression was performed for each of these groups.

Table 3

The year's data set was divided into groups according to environmental variables and eddy covariance (EC) data quality in order to investigate the performance of the methods in different conditions

Group	<i>n</i>	<i>R</i>	Slope
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)			
<20	9222	0.51	0.68
20–1000	7413	0.68	0.82
>1000	930	0.55	0.58
Temperature ($^{\circ}\text{C}$)			
<5	1808	0.58	1.18
5–10	6373	0.64	1.06
10–15	7071	0.83	0.97
>15	2312	0.76	0.74
Wind property			
<i>ū</i>			
<1	1812	0.84	0.88
>1	15590	0.79	0.91
<i>u</i> *			
<0.1	1697	0.84	0.89
>0.1	15724	0.79	0.91
EC data quality			
Good	8750	0.75	0.87
Gap filled	8816	0.92	0.96

Correlation coefficient (*R*), *n* and the slope of the regression between the wind direction scaled up chamber (CHA_{WD}) and EC method are provided for each group.

SPSS 12.0.1 for windows statistical package (SPSS, Inc.) was used in statistical analysis and chamber flux modelling.

3. Results

3.1. Microform distribution of the EC footprint

The average microform distribution around the EC tower was 6%, 62%, 21% and 11% for HU, HL, LL and HO, respectively (Fig. 3), while between transects their cover varied within 1–11% (HU), 31–90% (HL), 7–50% (LL) and 0–22% (HO). Microforms are relatively small (~ 100 cm diameter) formations and their spatial variation is large. Each of the microform types can be found within an area of e.g. 2 m diameter. Drier microforms (HU and HL) dominated most transects showing the highest occurrence (93%) in transect E (Fig. 3). Only three transects were dominated by wetter microforms (LL and HO), with WSW being the wettest direction (58% cover of LL and HO). HU was the least common of all microforms (Fig. 3). Statistical differences were found when the microform frequency of the 16 transects was compared against the footprint average microform frequency of the study area (X^2 -test, p -value < 0.05) only transects ESE, SE, S and SSW were not different from the average. The comparison with the main wind direction (SW) showed even stronger differences, while only transect SSE did not have significantly different microform composition (p -value > 0.05) compared to that observed in the prevailing wind direction.

3.2. Eddy covariance NEE

The average daytime flux was 0.18 $\text{g}(\text{CO}_2) \text{m}^{-2} \text{h}^{-1}$ and when PPFD > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the average flux was 0.27 $\text{g}(\text{CO}_2) \text{m}^{-2} \text{h}^{-1}$. The average nighttime flux was $-0.11 \text{g}(\text{CO}_2) \text{m}^{-2} \text{h}^{-1}$. From the daytime and nighttime flux data, 31% and 66%, respectively, were considered bad and needed to be gap filled. Between the seasons the proportion of bad data was 70% in wintertime (November–February) and 35% in summertime (June–September). The coefficient of determination (R^2) of the daytime gap filling functions ranged between 0.17 (November–December 2003) and 0.52 (July–August 2004). The nighttime Q_{10} gap filling function had R^2 of 0.16. The combined estimate of systematic and random error for the EC measurements was approximately 35% and 30% for 2003 and 2004, respectively (Sottocornola and Kiely, 2005).

3.3. Chamber CO₂ exchange

The observed maximum and average P_N fluxes, in conditions with PPFD > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were as follows: HU, 1.7 and 0.69; HL, 1.16 and 0.61; and LL, 0.83 and 0.23; and HO, 0.33 and 0.11 $\text{g}(\text{CO}_2) \text{m}^{-2} \text{h}^{-1}$. The maximum and average R_E fluxes were as follows: HU, -0.74 and -0.30; HL, -0.67 and -0.27; and LL, -0.75 and -0.17; and HO, -0.22 and -0.05 $\text{g}(\text{CO}_2) \text{m}^{-2} \text{h}^{-1}$. P_N and R_E showed similar seasonal variation in all microforms with highest uptake and release in mid-summer and lowest fluxes during winter months (Fig. 4).

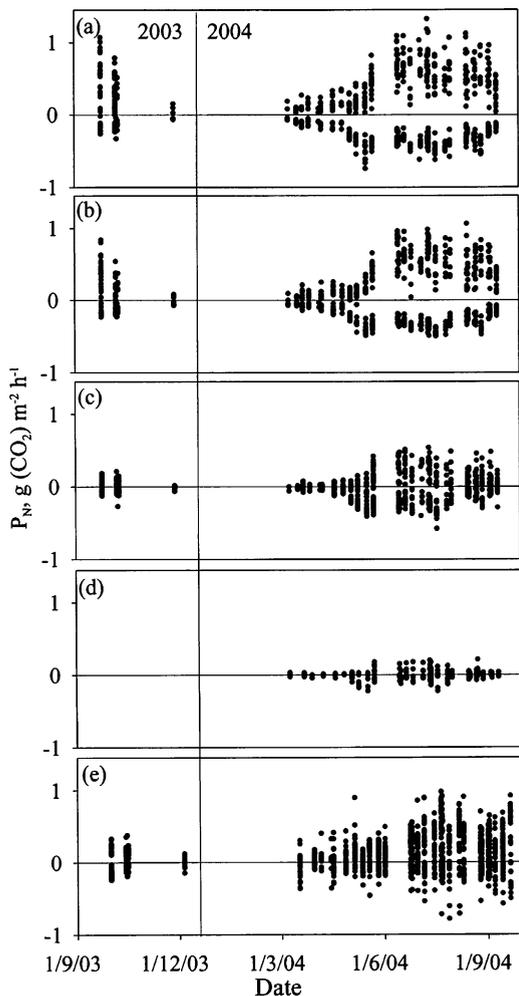


Fig. 4. Net photosynthesis (P_N) of individual microforms (a) hummock (HU), (b) high lawn (HL), (c) low lawn (LL) and (d) hollow (HO) measured with the chamber method. Different values during the same day within each microform represent P_N measured from different sample plots under different environmental conditions. (e) Net ecosystem exchange (NEE) measured by the eddy covariance tower during the same dates when chamber measurement campaigns were carried out.

A significant difference was found between the P_N of microforms, when PPFD was set to value 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (ANOVA ($F(3, 17) = 32.1, p < 0.001$)). According to the Tukey test the microforms could be divided into dry (HU and HL) and wet (LL and HO) groups, whose P_N differed significantly from each other ($p < 0.001$).

The regression models of microform P_G and R_E , which were used to integrate the chamber fluxes over the study period, explained 51–81% of the variation in P_G (Table 1) and 51–80% in R_E (Table 2). The poorer performance of the models for HO can be explained by the smaller number of data points and the lower flux rates. The narrow range of observed CO₂ fluxes, compared to the other microforms, made the development of robust ecological response functions difficult. The standard error estimates of the P_G models varied from 0.16 $\text{g m}^{-2} \text{h}^{-1}$ for hummocks to 0.11 $\text{g m}^{-2} \text{h}^{-1}$ for hollows. The standard error estimates of the R_{TOT} models varied from 0.07 $\text{g m}^{-2} \text{h}^{-1}$ for hummocks to 0.04 $\text{g m}^{-2} \text{h}^{-1}$ for hollows.

3.4. Comparison of short-term EC and chamber NEE

The detailed wind direction scaled (CHA_{WD}) NEE estimates were used to compare the instantaneous performance of the chamber and EC methods. Daily NEE determined by the two methods followed a similar seasonal pattern (Fig. 5). NEE was highest during the growing season (summer) and lowest during the winter period. Throughout the year the daily EC measurements were more variable than the modelled chamber estimates, but no systematic difference could be observed between the methods (Fig. 5). The correlation coefficient (R) between the half-hourly NEE estimates obtained by the two methods was 0.80 and the slope of regression 0.91

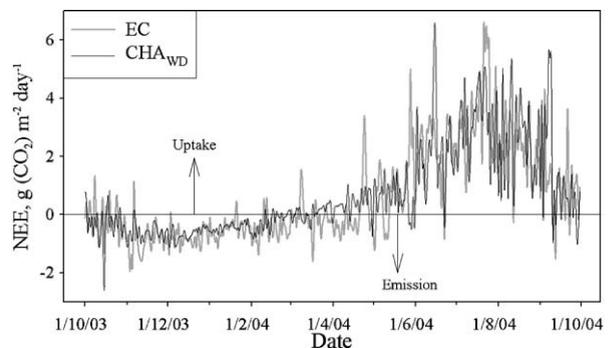


Fig. 5. Daily sum of net ecosystem exchange (NEE) derived from wind direction scaled up chamber measurements (CHA_{WD} NEE) (black line) and from eddy covariance measurements EC NEE (grey line).

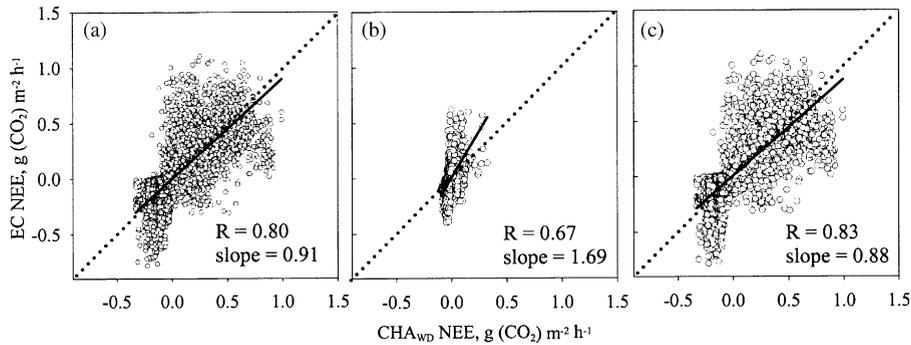


Fig. 6. Regression of half hourly net ecosystem exchange (NEE) fluxes between eddy covariance (EC) and chamber (CHA_{WD}) estimates (a) over the 12-months time period, (b) in winter (November 2003–February 2004) and (c) in summer (June 2004–September 2004). The dotted line represents a 1:1 relationship.

(Fig. 6a). The methods agreed better in summer than in winter. Correlation coefficients were 0.67 in winter (Fig. 6b) and 0.83 in summer (Fig. 6c). In winter the slope of regression (1.69) indicated departure from a 1:1 relationship (Fig. 6b).

The effect of environmental variables and EC data quality on the performance of the methods was investigated by comparing data groups collected in different conditions (Table 3). The two methods agreed best in normal daylight (PPFD 20–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), while the correlation between NEE measurements made in darkness (PPFD < 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or under high irradiation PPFD > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was poorer (Table 3). Similarly, the two methods showed highest agreement in intermediate temperatures (T_{AIR} 10–15 °C), while agreement decreased towards the extreme ends of the temperature range. The wind properties, friction velocity (u^*) and horizontal wind speed (\bar{u}) did not affect the agreement of the two methods, since the correlation coefficient and slope were similar in all groups (Table 3). The gap-filled (i.e. modelled) EC NEE correlated better with chamber estimates (modelled) than the measured EC NEE (Table 3).

3.5. Comparison of long-term EC and chamber NEE

The agreement between the results from the two methods increased when the time period was extended. The regression between the 12 monthly EC and Chamber (CHA_{WD}) NEE estimates had high correlation ($R = 0.98$) and the slope of the regression (1.00) was equal to one to one line (Fig. 7). The annual (October 2003–September 2004) NEE estimated by the EC and chamber (CHA_{WD}) methods were 206 and 242 $\text{g}(\text{CO}_2) \text{m}^{-2}$, respectively.

3.6. Heterogeneity of the footprint

We postulate that if the footprint had a homogeneous distribution of microforms, the microform distribution, which changes with the wind direction, would not affect the performance of chamber or EC methods. If this were the case the half-hourly chamber NEE estimates scaled up by the average microform distribution of the footprint (CHA_{AV}) should be correlated with the EC NEE measurements in a way similar to the CHA_{WD} NEE estimates. The linear regression between EC and CHA_{AV} NEE estimates had R of 0.82 and slope of 0.86. This correlation was nearly identical with the correlation between EC and CHA_{WD} NEE estimates ($R = 0.80$ and slope = 0.91) (Fig. 6a).

We found a large variation in annual cumulative NEE when we scaled the chamber estimates individually up

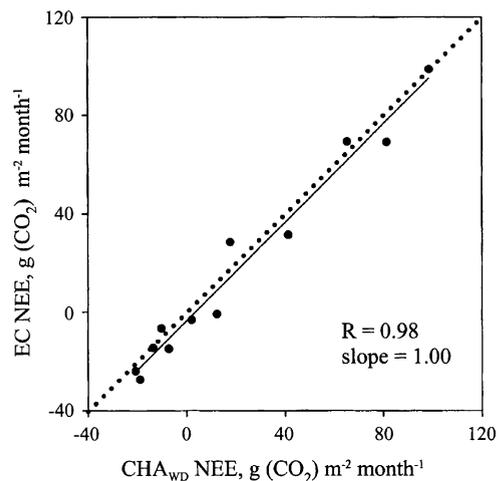


Fig. 7. Regression of monthly net ecosystem exchange (NEE) estimated by wind direction scaled up chamber (CHA_{WD}) and eddy covariance (EC) methods. The dotted line represents a 1:1 relationship.

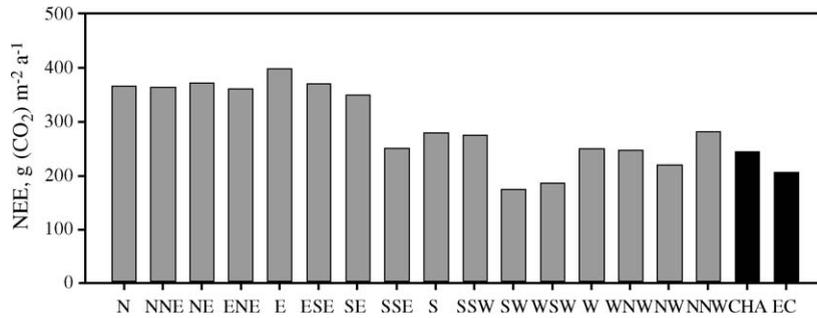


Fig. 8. Annual net ecosystem exchange (NEE) in different transects around eddy covariance (EC) tower, modelled chamber flux is weighted by the microform distribution of each transect (grey bars). Black bars represent annual NEE of whole EC footprint with WCHA being the wind direction scaled up chamber estimate and EC the eddy covariance estimate.

for each of the 16 radial transects around the EC tower (Fig. 8). The annual NEE of the driest transect (E) was 130% larger than NEE of the transect in the prevailing wind direction (SW).

4. Discussion

4.1. Spatial and temporal variation in CO₂ exchange

As has been reported for raised bogs (Alm et al., 1999b; Bubier et al., 1998) and fens (Alm et al., 1997; Heikkinen et al., 2002), microforms in blanket bogs supported different CO₂ dynamics (P_N and R_E fluxes) (Fig. 4). Statistically the microforms could be divided into wet (LL and HO) and dry (HU and HL) groups, which support similar net CO₂ fluxes. Similar to the findings of Waddington and Roulet (2000) we found that the drier microforms were more effective CO₂ sinks even if their respiration was higher than that of wet microforms. The flux differences between the microforms are primarily due to differences in water level, since it controls both gross photosynthesis and respiration (Alm et al., 1997; Bubier et al., 1999; Tuittila et al., 2004; Waddington and Roulet, 2000).

Both chamber and EC methods found similar seasonality in NEE, although the chamber method estimated the onset of daily net CO₂ uptake to occur earlier in spring than the EC method (Fig. 5). NEE was highest at the middle of the summer and lowest during mid-winter (Fig. 5). The seasonal dynamics are controlled by the changes in photosynthesising leaf area of vascular plants (Tuittila et al., 1999), the intensity of photosynthetic photon flux density (Bubier et al., 1998) and soil temperature, which is one of the key factors determining the respiration rate (Bridgham and Richardson, 1992; Lloyd and Taylor, 1994).

4.2. Comparison of chamber and EC methods

The net flux rates (both release and uptake) measured by the EC method were within the range of the observed chamber fluxes from dry and wet microforms (Fig. 4). Therefore, it can be said that on average the measurements of both methods are in agreement with each other, which supports the results of Frohking et al. (1998) and Heikkinen et al. (2002) and is in contrast to Griffis et al. (2000) who found that the chamber method overestimated respiration or underestimated photosynthesis.

More detailed analysis showed, however, that over short time periods (half hour, day) the methods were less in agreement. We made the modelled half hourly chamber NEE estimates correspond with half hourly EC NEE by weighting them according to the microform distribution of the current wind direction (CHA_{WD}). In this way the microform composition of the flux source area should be similar for both methods at all times. Similarly to a study by Lavigne et al. (1997) we found that EC measurements were noisy, which caused relatively low correlation ($R=0.80$) between the instantaneous measurements made by the two methods (Fig. 6a). However, the slope of regression ($\beta=0.91$) shows EC measurements to be 9% smaller than chamber estimates. The correlation in our study is higher and the difference between the methods smaller than that reported by Lavigne et al. (1997) who compared nighttime respiration measurements in coniferous forest sites. However, if we consider only measurements made in darkness (PPFD < 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$, generally the nighttime conditions), the correlation was similar to that observed by Lavigne et al. (1997) (Table 3). Since the EC system encounters problems especially during nighttime (Baldocchi, 2003; Goulden et al., 1996), this type of difference between

correlations made for daytime and nighttime measurements is expected.

The methods showed less agreement in wintertime compared to summertime (Fig. 6b and c). Aurela et al. (2002) explained a similar large scatter in half-hourly flux rates in winter by the relatively low flux rates, which cause a low signal-to-noise ratio, compared to summer. The less favourable weather conditions in winter were reflected in the higher percentage of bad data that needed gap filling, compared to summertime. Since a large quantity of EC data required gap filling in winter, the procedure and functions used influenced the EC result. As the gap filled data correlated strongly ($R = 0.92$ and slope 0.96) with the chamber estimates (Table 3) we can expect the EC gap filling procedure to obey the same rules as chamber estimates with respect to the environmental controls. However, the daytime gap filling functions for summer months were more reliable, since they had a higher R^2 value than the functions for winter months. This can explain part of the difference between summer and wintertime correlations.

Distinguishing environmental conditions when the methods agreed best was difficult, since the conditions were strongly correlated with each other. However, correlation between EC and CHA_{WD} NEE was high during daytime and in warm temperatures (Table 3). Such conditions commonly occur together in summertime when the photosynthesising leaf area is large. These are optimal conditions for photosynthesis and as a result the CO_2 fluxes are high. Therefore, it can be generalised that the detection of NEE is more accurate in summer days than in winter nights. Fewer data points can explain the low correlation in the highest PPFD and temperature groups (Table 3). Wind properties (u^* , \bar{u}) did not have an effect on the correlation between the EC and chamber methods (Table 3). This observation is in line with the lack of a clear relationship between nighttime EC NEE and u^* , which prevented the use of a night u^* filter.

In contrast to the short-term comparison we found a strong correlation between the methods when estimating NEE on a monthly and annual basis. When fluxes were integrated over longer time periods, the random variation in EC data was reduced and correspondence between the methods increased. The monthly (Fig. 7) and annual estimates of NEE were closely consistent between the two methods. This suggests that the difference between the methods was more due to random variation than systematic error. Consequently, the longer sampling period gave more reliable estimates both in time and space as found by Amiro (1998).

4.3. Heterogeneity in the landscape and in the footprint

In grassland the spatial heterogeneity of the source area has been found to cause large wind direction related variation in N_2O EC fluxes (Laville et al., 1999). Our aim was to investigate if the studied EC footprint was homogeneous enough to fulfil the assumption that the EC method operates in a homogeneous ecosystem and all measurements compose a single time series. The landscape of an Atlantic blanket bog is derived from the underlying terrain and the peat depth within the bog varies considerably (Belyea and Lancaster, 2002; Tallis, 1998). The landscape is often formed by convex and concave regions, which are water-shedding and water-collecting, respectively (Tallis, 1994). The distribution of microforms inside these areas differ: a hummock-hollow pattern is more distinctive in the wet depressions, while the more homogenous lawn vegetation dominates the drier areas (Lindsay, 1995; Tallis, 1998). The high occurrence of lawn vegetation, especially HL, was characteristic for the whole study area but we found that even over a small area around the EC tower there were significant differences in microform distribution between angular directions (Fig. 3). Importantly, the microform composition of the prevailing SW wind direction differed significantly from other directions, except from SSE. Due to the variable surface pattern the study site is ideal for testing the performance of the EC system in a patterned ecosystem.

The comparison of correlations between EC NEE and chamber NEE weighted with either wind direction determined microform distribution (CHA_{WD}) or average microform distribution (CHA_{AV}) gave similar results and therefore showed no difference between the scaling up methods. This suggests that more detailed knowledge of the footprint surface structure did not increase the agreement between the methods and therefore the footprint can be considered homogeneous. However, the annual NEE, based on chamber measurements and scaled up according to microform distribution of each transect, differed between the transects (Fig. 8) and followed the division of wet and dry microforms (Fig. 3). Transects with high cover of high lawns (HL) were the largest CO_2 sinks; for example the NEE of the driest transect E was 130% larger than that of SW, which was the wettest transect, having the highest cover of low lawns. This variation between the transects shows that since the landscape of blanket bogs is often a combination of wetter and drier areas, the location of the EC tower might be a significant factor when determining areal CO_2 budgets. If the aim is to

obtain an estimate for the whole bog area it is important to place the tower in a location, which is representative of the whole landscape. Knowledge of the footprint helps to identify and include the desired parts of the landscape and also to define the number of sample points (EC towers) required to cover the desired landscape unit for reliable flux estimates (Amiro, 1998).

It has been stated that scaling chamber measurements up to landscape level is problematic, since each sample plot represents such a small part of the landscape (Aurela et al., 1998) and that differences can occur if the chamber sample plots are not located within the EC footprint (Heikkinen et al., 2002b). In our study the chamber sample plots were not within the EC footprint, but approximately 300 m away from the EC tower; however the sample plots were chosen to represent the microforms in the footprint. The study shows that with a reasonable knowledge of the spatial variation in the flux sources (e.g. microform distribution in peatland) within the studied ecosystem it is possible to achieve similar monthly and annual C budgets with chamber and EC methods.

5. Concluding remarks

Measurements of NEE are needed to quantify the contribution of land use and land use changes to global warming and climate change. Measurements at both large (landscape level) and small scale (homogeneous miniature ecosystems) are necessary in order to understand NEE and its relationship to environmental and climatic variables. Closed chambers and eddy covariance are the most widely used methods to estimate NEE. We demonstrated that, despite, disagreement over the short term (half-hour, day), both methods give similar estimates of monthly and annual NEE. This is an important result, as it strengthens trust in the accuracy of both methods. When planning a study of NEE the choice of method should be based upon the purpose of the study. If the aim is to achieve long-term C budgets over a landscape unit, the EC method is a more direct and straightforward method for the purpose. However, it may be more beneficial to use a closed path gas analyser rather than an open path, due to the wet environment. On the other hand, if the aim is to study direct responses of the ecosystem to environmental variables or changes in these variables, the chamber method is appropriate. The surface pattern of the studied bog was composed of microforms, which supported dissimilar net CO₂ fluxes. The distribution of microforms varied within the studied area and this resulted in spatial variation in NEE. Dry and wet regions

showed significantly different annual NEE. Therefore it is necessary to carefully consider the location of the EC tower if the landscape of patterned peatland is not homogeneous. Similarly, if chamber fluxes are scaled up to landscape level, the microform distribution of the area should be well known and the sample plots should well represent the chosen microform classes.

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