



# Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling

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## Abstract

Aim of the present paper is to quantify the ecosystem respiration of a mountain meadow in the Austrian Alps during the vegetation period 2002 by constraining nighttime eddy covariance measurements with ecosystem respiration derived from (i) daytime eddy covariance, (ii) ecosystem chamber and (iii) scaled up leaf and soil chamber measurements. The study showed that the discrimination of valid nighttime eddy covariance measurements based on friction velocity ( $u^*$ ), the so-called  $u^*$ -correction, is very sensitive to the imposed quality control criteria. Excluding half-hourly nighttime data, which deviate more than 30% from the stationarity and integral turbulence tests caused the magnitude of the  $u^*$ -correction to be significantly reduced. Based solely on nighttime eddy covariance data, we are currently unable to decide whether the observed high  $\text{CO}_2$  fluxes during intermittent turbulence represent artefacts and should be screened out, or whether these reflect a genuine transport of  $\text{CO}_2$  not accounted for by the storage term and must be retained. Evidence against the inclusion of these data is derived from soil respiration rates measured in situ and calculated inversely from the other approaches, which were significantly lower as compared to soil respiration calculated from inversion of the half-hourly nighttime data inclusive of the observations which failed to meet the specified quality control criteria. Seasonal (8 March–8 November 2002) nighttime carbon balances simulated based on the parameters derived from the remaining approaches agreed with each other to within 35%, which is of the order of the uncertainty of each individual approach.

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## 1. Introduction

The steady rise in atmospheric carbon dioxide ( $\text{CO}_2$ ) concentrations since the industrial revolution

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### Nomenclature

$a, b, c$	parameters of Eq. (A.2a) and (A.2b)
$E_x$	activation energy of plant ( $x = p$ ) and soil ( $x = s$ ) respiration ( $\text{J mol}^{-1}$ )
$f$	normalised frequency
$F_{\text{NEE}}$	net ecosystem $\text{CO}_2$ exchange ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$F_{\text{GPP,sat}}$	gross primary production at high irradiance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$f_x$	normalised peak frequency of cospectral reference model
$L$	plant area index ( $\text{m}^{-2} \text{m}^{-2}$ )
$N$	normalisation constant of cospectral reference model
$Q_{\text{PPFD}}$	photosynthetically active radiation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R$	universal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ )
$R_{\text{eco}}$	ecosystem respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R_{\text{eco}}^*$	ecosystem respiration normalised to $10^\circ\text{C}$ and unit leaf area ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R_x$	plant ( $x = p$ ) and soil ( $x = s$ ) respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R_{x,\text{Tref}}$	plant ( $x = p$ ) and soil ( $x = s$ ) respiration at reference temperature ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$T_{\text{ref}}$	reference temperature (283.16 K)
$T_x$	plant ( $x = p$ ), air ( $x = a$ ) and soil ( $x = s$ ) temperature ( $^\circ\text{C}$ )
$u^*$	friction velocity ( $\text{m s}^{-1}$ )
$w'c'$	covariance of vertical velocity and $\text{CO}_2$ mixing ratio ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
<i>Greek letters</i>	
$\alpha$	apparent quantum yield ( $\mu\text{mol CO}_2 \mu\text{mol photon s}^{-1}$ )
$\beta$	slope parameter of cospectral reference model
$\Delta_{\text{ITT}}$	deviation from integral turbulence test (%)
$\Delta_{\text{ST}}$	deviation from stationarity test (%)
$\zeta$	Monin–Obukhov stability parameter
$\mu$	broadness parameter of cospectral reference model
$\sigma_w$	vertical velocity standard deviation ( $\text{m s}^{-1}$ )
$\phi_w$	stability function for vertical velocity

(30% increase over the last 150 years) and the anticipated adverse consequences on the global climate system, have triggered a strong scientific and public interest in the global carbon cycle (Steffen et al., 1998; Lloyd, 1999). A key variable in this context is the net ecosystem  $\text{CO}_2$  exchange (NEE), which is the (small) difference between daytime photosynthetic  $\text{CO}_2$  uptake and respiratory losses of  $\text{CO}_2$  during nighttime. If photosynthetic uptake prevails over respiratory losses, NEE, according to meteorological notation, is negative and the ecosystem is said to be a net sink for  $\text{CO}_2$ . Conversely, NEE is positive and the ecosystem is said to be a net source of  $\text{CO}_2$  if losses exceed uptake of  $\text{CO}_2$ .

Measurements of NEE usually require the quantification of the net flux of  $\text{CO}_2$  across the boundaries of a notional or real control volume erected above the ecosystem using micrometeorological or ecophysiological (chamber) methods, respectively. Among the micrometeorological methods, the eddy covariance technique is the currently most widely used (Aubinet et al., 2000; Baldocchi et al., 2001), and in principle, allows derivation of daily to decadal estimates of NEE by integrating quasi-continuous short-term (usually 0.25–2 h) measurements of NEE (e.g. Barford et al., 2001). Employing a single set of instruments the eddy covariance method relies upon the assumption of horizontal homogeneity of fluxes, when NEE reduces to the sum of the vertical net exchange and the storage flux, the latter accounting for the net storage of  $\text{CO}_2$  in the control volume (Finnigan et al., 2003; Massman and Lee, 2002). This assumption is often violated under calm and stable nighttime conditions, when  $\text{CO}_2$  is suspected to leave the control volume other than in the vertical (advection, drainage flows) and thus undetected by the eddy covariance sensors, leading to an underestimation of nighttime respiration and consequently to an overestimation of NEE (Aubinet et al., 2003; Staebler and Fitzjarrald, 2004). The widely adopted engineering-type approach to deal with what is often referred to as the ‘nighttime-problem’, is to discard NEE measurements during calm conditions and replace the missing values with NEE modelled as a function of temperature parameterised with measurements during windy conditions, when the eddy covariance system is supposed to capture the ‘true’ biological flux (Massman and Lee, 2002). Discrimination between calm and windy

conditions is usually based on friction velocity,  $u^*$ , thus also the name  $u^*$ -correction. The  $u^*$ -correction has not escaped criticism for the fact that the underlying empirical relationship suffers from statistical autocorrelation and regression statistics are usually poor (Falge et al., 2001; Baldocchi, 2003). In addition, several studies (e.g. Anthoni et al., 2004; Saleska et al., 2003) have shown that the  $u^*$ -correction represents one of the largest factors of uncertainty for long-term NEE estimates (but see, Barford et al., 2001; Xu and Baldocchi, 2004). Recently, a few groups (Aubinet et al., 2003; Feigenwinter et al., 2004; Staebler and Fitzjarrald, 2004) have attempted to measure nighttime horizontal advection in forest ecosystems, but both the experimental methodology and theory still require considerable refinement before being routinely applicable (Aubinet et al., 2003; Finnigan and Raupach, 2003).

Alternatively, ecosystem respiration may be derived from daytime eddy covariance data by extrapolating the relationship between daytime NEE and solar radiation to zero irradiance. The few comparisons between ecosystem respiration derived both from night- and daytime eddy covariance data that exist in literature (Suyker and Verma, 2001; Falge et al., 2002; Gilmanov et al., 2003; Griffis et al., 2003; Kowalski et al., 2003; Xu and Baldocchi, 2004) indicate that ecosystem respiration extrapolated from daytime data is usually lower (up to 20%) and less responsive to temperature changes. This mismatch is generally believed to be due to the inhibition of leaf respiration in light (Brooks and Farquhar, 1985) and higher daytime temperatures, respectively.

Another alternative means for estimating ecosystem respiration are chamber methods, which may be categorised into (i) chambers which enclose the entire ecosystem and directly yield NEE (e.g. Norman et al., 1992; Dugas et al., 1997; Angell et al., 2001; Dore et al., 2003; Zamolodchikov et al., 2003), and (ii) chambers which enclose only some ecosystem component (leaves, boles, soil, etc.) and thus require some additional up-scaling logic to derive NEE (e.g. Goulden et al., 1996; Lavigne et al., 1997; Law et al., 1999, 2001; Granier et al., 2000; Bolstad et al., 2004). Both approaches work best during nighttime conditions—whole ecosystem chambers because modifications of the soil/plant environment (air temperature and humidity effects) are minimised in the absence of

solar radiation (Dore et al., 2003), and ecosystem component chambers because the up-scaling procedure does not need to account for the bi-modal distribution of sunlight within the plant canopy. Previous comparisons between nocturnal eddy covariance and chamber measurements have produced mixed results. Some studies report fairly good correspondence (Granier et al., 2000); others find eddy covariance to miss up to 50% of the respiration measured by chambers (Law et al., 1999; Bolstad et al., 2004).

Aim of the present paper is to quantify the ecosystem respiration of a mountain meadow in the Austrian Alps in order to, in a future step, derive defensible estimates of its CO<sub>2</sub> source/sink strength. To this end, a multiple-constraints approach is followed, comparing ecosystem respiration estimated from:

- (i) nighttime eddy covariance measurements;
- (ii) extrapolating the relationship between daytime eddy covariance measurements and solar radiation to zero irradiance;
- (iii) measurements by means of whole ecosystem chambers;
- (iv) scaling up leaf and soil respiration measurements to the ecosystem level.

## 2. Material and methods

### 2.1. Site description

Investigations were carried out at a meadow in the vicinity of the village Neustift (47°07'N, 11°19'E) in the Stubai Valley (Austria). The study site is situated at an elevation of 970 m a.s.l. in the middle of the flat valley bottom. The fetch is homogenous up to 300 m to the East and 900 m to the West of the instrument tower, the dominant day and nighttime wind directions, respectively. The average annual temperature is 6.3 °C, average annual precipitation amounts to 850 mm. The snow-free (vegetation) period usually extends from mid March to mid November, in the study year 2002 from 8 March to 28 November. The meadow is cut between two and three times a year, during 2002 on 6 June, 2 August and 30 September.

The vegetation has been classified as a Pastinaco–Arrhenatheretum and consists mainly of a few dominant graminoid (*Dactylis glomerata*, *Festuca pratensis*, *Phleum pratensis*, *Trisetum flavescens*) and forb (*Ranunculus acris*, *Taraxacum officinale*, *Trifolium repens*, *Trifolium pratense*, *Carum carvi*) species. The soil has been classified as a Fluvisol (FAO classification) and is approximately 1 m deep. Below a thin (0.001 m) organic layer, an A horizon, with an organic volume fraction of approximately 14%, extends down to 0.02 m, followed by the B horizon, which is best described as a (sandy) loam. Roots reach down to 0.5 m, but 80% of them are concentrated in the upper 0.13 m of the soil.

## 2.2. Eddy covariance

Net ecosystem CO<sub>2</sub> exchange was measured using the eddy covariance method (Baldocchi et al., 1988; Baldocchi, 2003) using the same instrumentation as and following the procedures of the EUROFLUX project (Aubinet et al., 2000). Briefly, the three wind components and the speed of sound were measured by a three-dimensional sonic anemometer (R3A, Gill Instruments, Lymington, UK). CO<sub>2</sub> mole fractions were measured by a closed-path infra-red gas analyser (Li-6262, Li-Cor, Lincoln, NE, USA). Air was pumped from the intake, a distance of 0.1 m from the centre of the sensor volume of the sonic anemometer mounted at 3 m above ground, through a 4 m Teflon tube of 0.004 m inner diameter through a filter (Acro 50, Gelman, Ann Arbor, MI, USA) to the infra-red gas analyser at a flow rate 91 min<sup>-1</sup> (N035ANE, KNF Neuberger, Freiburg, Germany). The infra-red gas analyser was operated in the absolute mode, flushing the reference cell with dry N<sub>2</sub> from a gas cylinder at 100 ml min<sup>-1</sup>. Raw voltage signals of the CO<sub>2</sub> mole fraction were output at 5 Hz to the analogue input of the sonic, where they were synchronised with the sonic signals, which were measured at 20 Hz. All raw data were saved to the hard disc of a personal computer for post-processing using the *Edisol* software (University of Edinburgh).

Half-hourly mean eddy fluxes were calculated as the covariance between the vertical wind speed and the CO<sub>2</sub> mixing ratio using the post-processing software *Edire* (University of Edinburgh). Means and turbulent departures therefrom were calculated by Reynolds

(block) averaging. The tube-induced time delay of the CO<sub>2</sub> signal was determined by optimising the correlation coefficient with the vertical wind velocity (McMillen, 1988). A three-axis co-ordinate rotation was performed aligning the co-ordinate system's vector basis with the mean wind streamlines (Kaimal and Finnigan, 1994). Finally, frequency response corrections were applied to raw eddy fluxes accounting for low-pass (sensor separation, dynamic frequency sensor response, scalar and vector path averaging, frequency response mismatch and the attenuation of concentration fluctuations down the sampling tube) and high-pass filtering following Moore (1986) and Aubinet et al. (2000). Experimentally derived frequency response correction factors, according to Aubinet et al. (2000, 2001), were used to calibrate and assess the validity of the theoretical low-pass filtering correction method, as detailed in the Appendix. NEE was calculated as the sum of the corrected vertical eddy term and the storage flux, the latter being estimated from the time-rate-of-change of the CO<sub>2</sub>-mixing ratio at the reference height, which in a previous comparison with a profiling system was found to be sufficiently accurate. Negative flux densities represent transport towards the surface, positive values the reverse.

Quality control of half-hourly NEE data was exercised in a two-step procedure. First, hard flags were assigned to data with (i) the CO<sub>2</sub> signal outside the specified range, (ii) the infra-red gas analyser internal pressure standard deviation to mean ratio exceeding specified limits (due to calibration or pump malfunction) and (iii) the third rotation angle exceeding ± 10° (McMillen, 1988). In a second step, data were assigned soft flags, if the deviation from the integral turbulence or stationarity test exceeded 30% (Foken and Wichura, 1996). The integral turbulence test is based on the Monin–Obukhov (MO) hypothesis according to which various atmospheric parameters and statistics, when normalised by appropriate powers of the scaling velocity,  $u^*$ , become universal functions of the MO stability parameter,  $\zeta$ . Here, we employ the stability function for vertical velocity ( $\phi_w$ ) by Kaimal and Finnigan (1994):

$$\phi_w = \frac{\sigma_w}{u^*} = \begin{cases} 1.25 \left( 1 + 3|\zeta|^{1/3} \right) & -2 \leq \zeta < 0 \\ 1.25(1 + 0.2\zeta) & 0 \leq \zeta < 1 \end{cases}, \quad (1)$$

where  $\sigma_w$  is the vertical velocity standard deviation. The deviation from MO theory (%) is then expressed as the percentage difference between the measured ratio of  $\sigma_w$  to  $u^*$  and the theoretical MO value as:

$$\Delta_{\text{ITT}} = \frac{|\sigma_w/u^* - \phi_w|}{\phi_w} 100. \quad (2)$$

Deviation from stationarity (%) was assessed by comparing the 30 min average covariance of vertical velocity and CO<sub>2</sub> mixing ration ( $w'c'$ ) with the average covariance of six consecutive 5 min blocks of data, i.e.

$$\Delta_{\text{ST}} = \frac{|\overline{w'c'_5} - \overline{w'c'_{30}}|}{\overline{w'c'_{30}}} 100. \quad (3)$$

Hard-flagged data were excluded from the subsequent analysis, while soft-flagged data were used conditionally (see below).

### 2.3. Auxiliary data

Incoming photosynthetically active radiation (PPFD) was measured by means of a heated quantum sensor (BF2H, Delta-T, Burwell, UK). Air temperature at 3 m above ground and soil temperature at 0.05 m depth were measured by means of a combined temperature/humidity sensor in a ventilated radiation shield (RFT-2, UMS, München, Germany) and home-made thermocouples, respectively. These data were recorded by a data logger (DL2e, Delta-T, Burwell, UK) each minute and saved as half-hourly averages.

### 2.4. Ecosystem chambers

Ecosystem respiration was measured by means of home-made, closed-dynamic ecosystem chambers described in detail by Drösler et al. (in preparation). Briefly, ecosystem respiration was calculated from the time-rate-of-change of the chamber head space CO<sub>2</sub> concentration measured with an infra-red gas analyser (LCA-2, ADC, Hoddesdon, UK). Chambers, made out of transparent plexiglass (0.4–0.7 m high, 95% light transmission), were manually placed onto square PVC collars (three replicates each with 0.6 m<sup>2</sup> ground area, put into place in spring 2002) during each measurement cycle, which lasted 3 min. A rubber seal around the ground collar ensured gas tightness to the chamber. Chamber air was stirred by two mini-fans, a vent prevented pressure differences to the atmosphere

during enclosure. Measurements reported in this paper were made in darkness, either during nighttime or during daytime by completely darkening the canopy and the chamber with a reflective cloth. No systematic differences could be detected between ecosystem respiration determined both ways, thus the corresponding data were pooled.

### 2.5. Soil/plant ecological/physiological measurements

Canopy structure was assessed in a destructive fashion by stratified clipping (Monsi and Saeki, 1953) of square plots of 0.25 m<sup>2</sup> on 17 March, 13 May, 3 June, 25 July, 2 October and 28 November. Thickness of the harvested layers ranged between 0.05 and 0.1 m, depending on plant area density. The harvested plant material was separated according to combined functional and taxonomical criteria. Leaves were separated into those species that had the largest fractional contribution to the total plant area index (PAI; m<sup>2</sup> plant area/m<sup>2</sup> ground area), i.e. *R. acris*, *T. officinale*, *T. repens*, *T. pratense*, *C. carvi*. The remaining leaves, as well as all stems, were pooled to two functional groups, namely remaining forbs and graminoids. The remaining plant components, i.e. reproductive organs, attached dead plant matter and cryptogams, were pooled over all species. Silhouette plant areas were determined by the means of an area meter (LI-3100, Li-Cor, Lincoln, NE, USA). Continuous time series of PAI were derived by linear interpolation between the harvesting dates.

Leaf dark respiration measurements were carried during the vegetation periods 2000–2002 on the forb species mentioned above and the graminoid *D. glomerata*, as described by Wohlfahrt et al. (1998). Briefly, leaf dark respiration rates were measured on healthy, fully developed leaves by means of CO<sub>2</sub>/H<sub>2</sub>O porometer (CIRAS-1, PP-Systems, Hitchin, UK) by increasing leaf temperature from 10 to 40 °C in one-degree steps. During and at least 30 min prior to measurements, individuals from which the studied leaves originated were kept in darkness by shading with a large sheet of aluminium foil.

Bulk soil respiration was measured continuously using an steady-state system described in detail by Cernusca and Decker (1989) and an infra-red gas

analyser (CIRAS-Sc, PP-Systems, Hitchin, UK). Soil temperature inside the collar, at 0.05 m depth, was measured by means of a home-made thermocouple.

## 2.6. Model

In the present paper, ecosystem respiration is conceptualised to consist of a below-ground component, i.e. bulk soil respiration,  $R_s$ , and an above-ground component attributed to the respiration by various plant components,  $R_p$ , i.e.

$$R_{\text{eco}} = R_s + R_p$$

$$= R_{s,\text{Tref}} \exp \left[ \frac{E_s}{RT_{\text{ref}}} \left( 1 - \frac{T_{\text{ref}}}{T_s} \right) \right]$$

$$+ \sum_{i=1}^n L^i R_{p,\text{Tref}}^i \exp \left[ \frac{E_p^i}{RT_{\text{ref}}} \left( 1 - \frac{T_{\text{ref}}}{T_p^i} \right) \right]. \quad (4)$$

Above-ground respiration is the sum of the phytoelement-level respiration rates of all components ( $i = 1$  to  $n$ ) times the corresponding PAI ( $L$ ), as indicated by the summation on the RHS of Eq. (4). Respiration rates are assumed to increase exponentially with temperature according to an Arrhenius relationship,  $R_{x,\text{Tref}}$  and  $E_x$  corresponding to the respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at a reference temperature ( $T_{\text{ref}}$ ) and an activation energy ( $\text{J mol}^{-1}$ ) of the soil ( $x = s$ ) and the plant components ( $x = p$ ), respectively ( $R$  is the universal gas constant,  $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ). Soil respiration is assumed to be driven by soil temperature,  $T_s$  (K), at 0.05 m depth, since (i) this is the depth where most of the roots are concentrated and (ii) because this temperature resulted in higher correlation coefficients with measured soil respiration as compared to temperatures measured at 0.02 and 0.10 m depth. In the case of plant respiration, air temperature ( $T_a$ ) is used as surrogate for phytoelement temperature,  $T_p$  (K). Measured bulk soil respiration showed no apparent correlation to soil water content at 0.05 m depth, allowing to neglect any such effects. A comparison between the Arrhenius function used in the present paper and the soil respiration model put forward by Lloyd and Taylor (1994), which allows the activation energy to decrease with increasing temperature by introducing a third parameter, yielded similar quantitative and qualitative statistics and was, therefore, not adopted.

In the following analysis, the model of ecosystem respiration will be used both in a forward or bottom-up and an inverse or top-down fashion. In the forward mode, Eq. (4) is used to scale up phytoelement-level and soil respiration rates to the ecosystem level using measured time courses of PAI, soil and air temperature as input. In the backward mode, Eq. (4), constrained by measured time courses of PAI, soil and air temperature, is used to decompose ecosystem respiration measured by eddy covariance or ecosystem chambers into a below- and an above-ground component. In the latter case, the index  $i$  in Eq. (4) is constrained to one, the resulting parameters referring to an above-ground average. Non-linear regression analysis and a Monte Carlo Bootstrap method (SPSS 11.5.1, SPSS Inc., Chicago, IL, USA) were applied to inversely estimate parameters and their uncertainty, respectively.

An uncertainty analysis, accounting for random and systematic errors (Moncrieff et al., 1996), was conducted in order to obtain confidence intervals for the simulated carbon balances. Random errors account for the statistical uncertainty of model parameters and model drivers (Eq. (4)). The former represent the 95% confidence interval derived from the Bootstrap method, the latter have been determined by independently varying PAI, air and soil temperatures. A fractional error of 20% was assumed for PAI, as this reflects both the spatial variability of this meadow (Wohlfahrt, unpublished results), as well as the accuracy of destructive PAI measurements determined in a comparison with indirect methods for several grassland canopies (Wohlfahrt et al., 2001). A 20% fractional error was assigned also to air and soil temperature measurements, representing a conservative ad hoc estimate. Systematic errors pertaining to eddy covariance data were evaluated by independently changing various steps of the standard method of data processing (Anthoni et al., 2004), i.e. coordinate rotation (2D, planar fit), averaging period (60 and 120 min), detrending algorithm (linear, running mean with 400 s time constant), and by assuming a 20% error in the frequency response correction factors. Lacking a detailed error analysis of ecosystem and ecosystem component chamber measurements we conservatively assigned a 20% systematic error to these data. All errors have been calculated by summing the squares of the component errors and then taking the square root (Moncrieff et al., 1996).

### 3. Results

#### 3.1. Ecosystem respiration derived from nighttime eddy covariance data

In order to test for a potential underestimation of ecosystem respiration by the eddy covariance method during calm and stable nighttime conditions, we followed current practise and plotted nighttime NEE (PPFD = 0) as a function of  $u^*$ . Due to the confounding effect of temperature, respiration was normalised to a reference temperature of 10 °C. To this end, all valid half-hourly fluxes which showed less than 30% deviation from the integral turbulence and stationarity test (Eqs. (2) and (3)), i.e. exclusive any soft-flagged data, were sorted by  $u^*$  into 10 classes, each with equal number (99) of observations. For each class, Eq. (4), constrained by measured time courses of PAI, soil and air temperature (Fig. 1), was then used to inversely estimate soil and average plant respiration at 10 °C. For convenience, soil and average plant respiration at 10 °C were combined to a single

parameter,  $R_{\text{eco}}^*$ , ecosystem respiration normalised to 10 °C and unit leaf area. As evident from Fig. 2 (open circles),  $R_{\text{eco}}^*$  increased with increasing friction velocity from 2.5 to around 4.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at a friction velocity of 0.1  $\text{m s}^{-1}$  and remained at that level at higher friction velocities. In order to assess the influence of the imposed quality control criteria, the same procedure as above was repeated including all soft-flagged data (375 observations per class).  $R_{\text{eco}}^*$  calculated this way (closed circles in Fig. 2) increased with  $u^*$  up to friction velocities of 0.15  $\text{m s}^{-1}$ , when it levelled off at values of around 7.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . In contrast, no differences existed between the two approaches with regard to the storage flux (squares in Fig. 2). The differences in  $R_{\text{eco}}^*$  were due to the fact that  $R_{\text{eco}}^*$  increased with increasing violation of the two quality control tests, once 20–30% deviation is exceeded, as shown in Fig. 3. Since calm and stable nighttime conditions are often characterised by unsteady and intermittent turbulence, the same procedure as above was repeated with ensemble average nighttime fluxes, calculated as the arithmetic

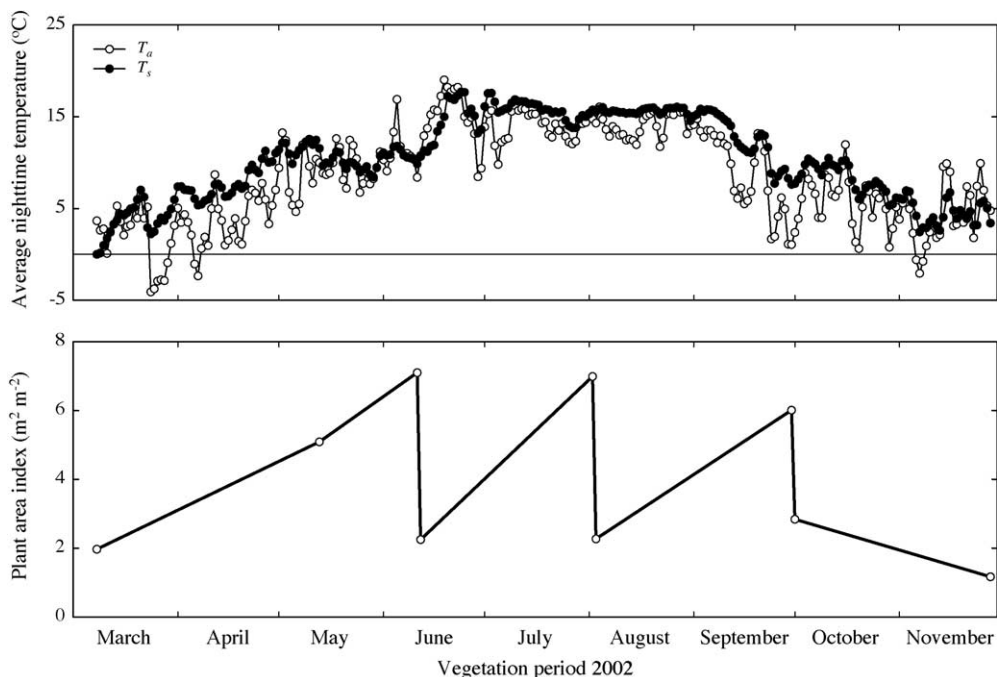


Fig. 1. Seasonal (8 March–28 November 2002) course of average nighttime air ( $T_a$ , at 3 m above ground, open symbols) and soil ( $T_s$ , 0.05 m soil depth, closed symbols) temperature in the upper panel, and the plant area index (PAI) in the lower panel, respectively.

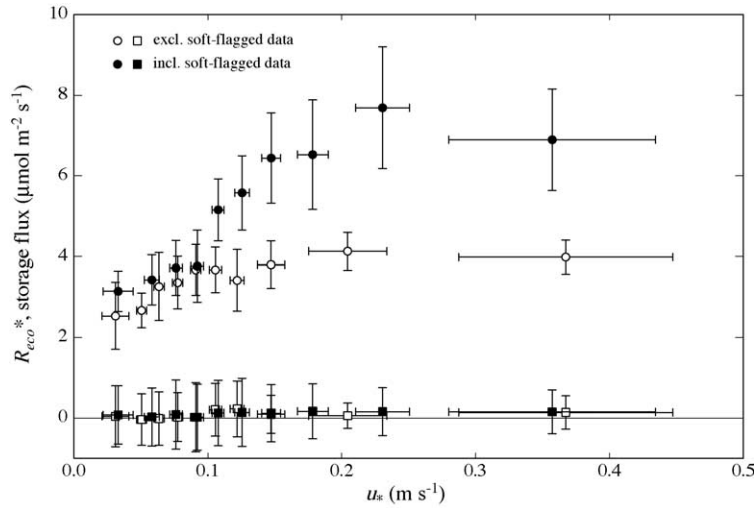


Fig. 2. Half-hourly values of nighttime ecosystem respiration (normalised to 10 °C and unit leaf area;  $R_{eco}^*$ ; circles) and the storage flux (squares) vs. friction velocity ( $u^*$ ). Open symbols exclude, closed symbols include observations exhibiting more than 30% deviation from the integral turbulence and stationarity test (so-called soft-flagged data; Foken and Wichura, 1996). Data were sorted by friction velocity into 10 classes, each with equal number of observations (99 and 375 excluding and including soft-flagged data, respectively). Error bars refer to  $\pm 1$  S.D.

mean of at minimum 10 half-hourly observations per night (discarding only hard-flagged data). As shown in Fig. 4, ensemble average nighttime  $R_{eco}^*$  showed only a weak correlation with  $u^*$  (below  $0.1 \text{ m s}^{-1}$ ) and fell within the error bars of the quality controlled half-hourly nighttime respiration rates.

Based on these findings, three scenarios were considered for deriving ecosystem respiration parameters from nighttime eddy covariance measurements. On a half-hourly basis, we used both the data set with and without the soft-flagged data, discarding measurements made at friction velocities below  $0.15$

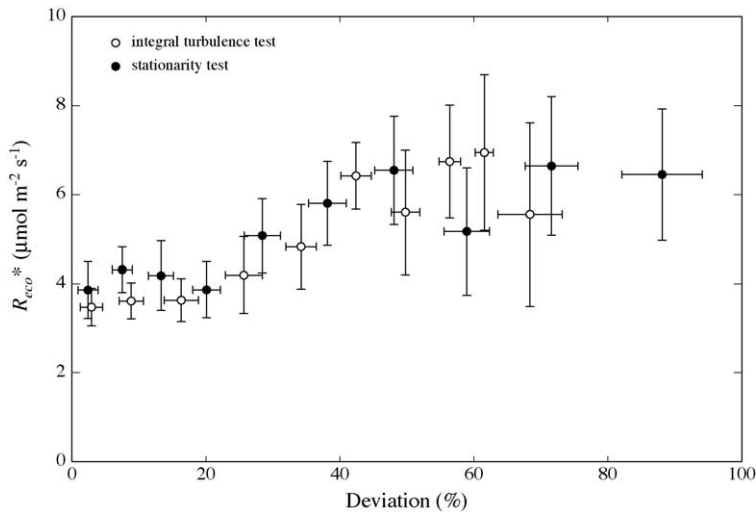


Fig. 3. Half-hourly values of nighttime ecosystem respiration (normalised to 10 °C and unit leaf area;  $R_{eco}^*$ ) vs. deviation from integral turbulence (open symbols) and stationarity (closed symbols) test (Foken and Wichura, 1996). Data were sorted into 10 classes, each with equal number (375) of observations. Error bars refer to  $\pm 1$  S.D.



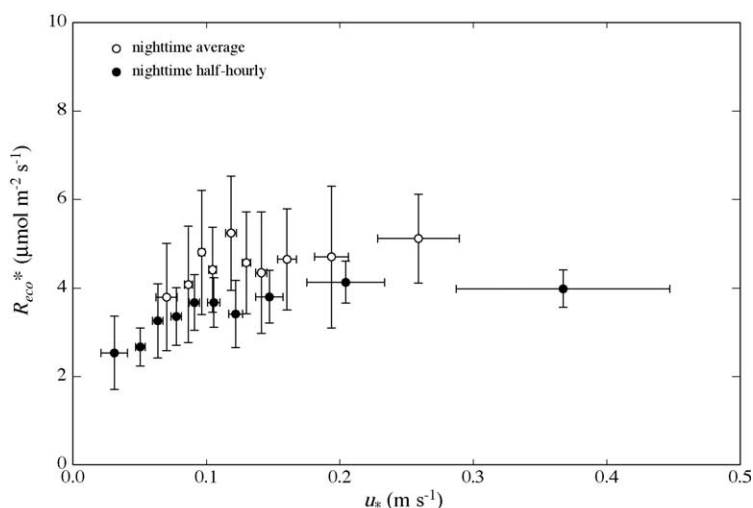


Fig. 4. Average (open symbols) and half-hourly (closed symbols) values of nighttime ecosystem respiration (normalised to 10 °C and unit leaf area;  $R_{\text{eco}}^*$ ) vs. friction velocity ( $u^*$ ). Data were sorted by friction velocity into 10 classes, each with equal number of observations (25 and 99 for average and half-hourly fluxes, respectively). Error bars refer to  $\pm 1$  S.D.

and  $0.1 \text{ m s}^{-1}$ , respectively. An  $u^*$  cut-off of  $0.1 \text{ m s}^{-1}$  was also applied to the nighttime average fluxes. The resulting parameters and linear regression statistics are shown in Table 1.  $R_{\text{eco}}^*$  was least for the half-hourly quality controlled ( $3.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), followed by

the nighttime average data set ( $4.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and significantly higher for the parameterisation of the half-hourly data set which included the soft-flagged data ( $7.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). The latter value resulted mainly from a significantly higher soil contribution

Table 1

Parameters, number of observations ( $n$ ), root mean squared error (RMSE,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) and linear regression statistics from inversion of Eq. (4) for half-hourly nighttime (first and second column), ensemble average nighttime (third column) and daytime eddy covariance (fourth column), and chamber measurements (fifth column)

	Nighttime			Extrapolated from light response	Ecosystem chamber
	Half-hourly excluding soft-flags ( $u^* \geq 0.10$ )	Half-hourly including soft-flags ( $u^* \geq 0.15$ )	Average including soft-flags ( $u^* \geq 0.10$ )		
$R_{\text{eco}}^*$	3.81 <sup>a</sup>	7.11	4.71 <sup>a</sup>	4.59	5.19
$R_{\text{s,Tref}}$	3.23 <sup>a</sup>	6.40	3.93 <sup>a</sup>	3.82 <sup>a</sup>	4.27 <sup>a</sup>
$E_{\text{s}}$	78844	68269	71228	64813	65579
$R_{\text{p,Tref}}$	0.58	0.71	0.78	0.77	0.92
$E_{\text{p}}$	69571	47019	42320	29594	16115
$n$	487	1285	178	39	71
RMSE	2.47	9.21	2.64	2.00	1.36
Slope	0.61	0.16	0.57	0.66	0.85
y-Intercept	2.15	6.63	2.72	2.17	1.26
$r$	0.77	0.40	0.75	0.86	0.93

Parameters are  $R_{\text{eco}}^*$ : ecosystem respiration normalised to 10 °C and unit leaf area ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ );  $R_{\text{s,Tref}}$ ,  $R_{\text{p,Tref}}$ : soil and plant respiration at reference temperature of 10 °C ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ );  $E_{\text{s}}$ ,  $E_{\text{p}}$ : soil and plant activation energy ( $\text{J mol}^{-1}$ ). Linear regression statistics are slope; y-intercept ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ );  $r$ : correlation coefficient.

<sup>a</sup> Significantly ( $p < 0.05$ ) different from nighttime half-hourly data set inclusive soft-flagged data (i.e. second column).

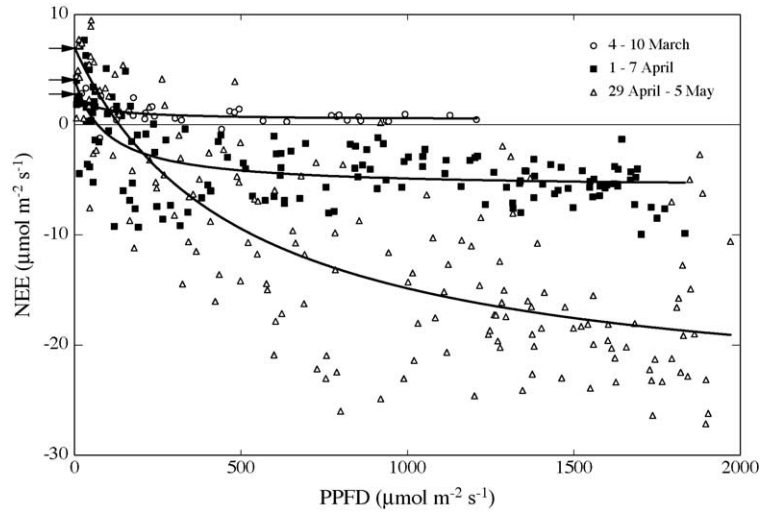


Fig. 5. Daytime net ecosystem CO<sub>2</sub> exchange (NEE) vs. photosynthetically active radiation (PPFD) for 3-week long periods between March–May 2002 (PAIs are 2.0, 2.9 and 4.4 m<sup>2</sup> m<sup>-2</sup>, respectively). Lines represent best fits of Eq. (5) to data. Arrows indicate the y-intercept of Eq. (5), which is interpreted as an estimate of ecosystem respiration.

(6.4 μmol m<sup>-2</sup> s<sup>-1</sup> versus 3.2–3.9 μmol m<sup>-2</sup> s<sup>-1</sup>) and was characterised by comparatively poor regression statistics (40% versus 75–77% of variance explained; 9.2 μmol m<sup>-2</sup> s<sup>-1</sup> versus 2.5–2.6 μmol m<sup>-2</sup> s<sup>-1</sup> RMSE). Average leaf respiration rates and soil/plant activation energies varied by 25 and 15–40%, respectively, and were statistically not significantly different.

### 3.2. Ecosystem respiration derived from daytime eddy covariance data

Another set of ecosystem respiration estimates was obtained by extrapolating plots of daytime NEE against PPFD, so-called light response curves, to zero irradiance. To this end, data were sorted into week-long blocks and fitted to the following Michaelis–Menten-type function:

$$F_{\text{NEE}} = \frac{\alpha Q_{\text{PPFD}} F_{\text{GPP,sat}}}{F_{\text{GPP,sat}} - \alpha Q_{\text{PPFD}}} - R_{\text{eco}} \quad (5)$$

Where  $F_{\text{NEE}}$  represents NEE (μmol m<sup>-2</sup> s<sup>-1</sup>),  $\alpha$  the apparent quantum yield (μmol CO<sub>2</sub> μmol photons<sup>-1</sup>),  $Q_{\text{PPFD}}$  the PPFD (μmol m<sup>-2</sup> s<sup>-1</sup>),  $F_{\text{GPP,sat}}$  the asymptotic value of the gross primary production at high irradiance (μmol m<sup>-2</sup> s<sup>-1</sup>) and  $R_{\text{eco}}$  is the ecosystem

respiration (μmol m<sup>-2</sup> s<sup>-1</sup>). To discriminate daytime data, a threshold PPFD of 5 μmol m<sup>-2</sup> s<sup>-1</sup> was used, thus, there was no overlap between daytime and nighttime data. An example of this procedure is shown in Fig. 5 for 3 weekly periods between March and May 2002.

Ecosystem respiration estimated this way, plotted as a function of weekly average air temperature in Fig. 6, was then used to inversely estimate the parameters of Eq. (4) as described above. As shown in Table 1,  $R_{\text{eco}}^*$  derived from the light response curves amounts to 4.6 μmol m<sup>-2</sup> s<sup>-1</sup> (3.8 and 0.8 μmol m<sup>-2</sup> s<sup>-1</sup> soil and plant contribution, respectively).

### 3.3. Ecosystem respiration measured by means of ecosystem chambers

Ecosystem respiration derived from ecosystem chamber measurements increased exponentially with air temperature, albeit with a fairly large scatter due to differences in canopy development (Fig. 7). This scatter was largely reduced (63% versus 93% of variance explained, Table 1) after optimising the parameters of Eq. (4) against these data.  $R_{\text{eco}}^*$  derived this way is 5.2 μmol m<sup>-2</sup> s<sup>-1</sup> (4.3 and 0.9 μmol m<sup>-2</sup> s<sup>-1</sup> soil and plant contribution, respectively; Table 1).

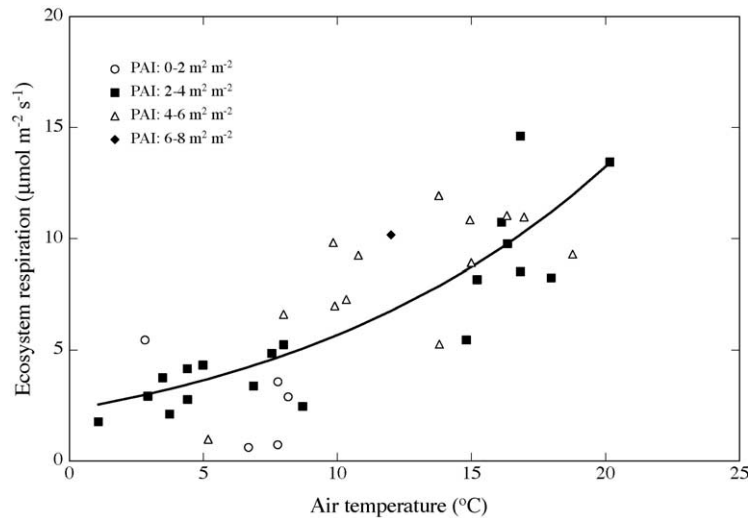


Fig. 6. Ecosystem respiration, derived from extrapolating weekly plots of daytime NEE against PPFD to zero irradiance (cf. Fig. 5) vs. weekly average air temperature, separately for four PAI classes. The line shows the best fit to all data using the function:  $y = a \exp(bx)$  ( $r = 0.81$ ).

### 3.4. Ecosystem component respiration measurements

Leaf respiration of the investigated key species, normalised to 10 °C, varied about three-fold ranging between 0.5 and 1.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , as shown in Table 2. Temperature sensitivities of leaf respiration ranged between 24 and 35  $\text{kJ mol}^{-1}$ , except for *T. repens*, which was characterised by a comparatively higher activation

energy (Fig. 8, Table 2). Soil respiration, at a reference temperature of 10 °C, amounted to 3.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , thus, being significantly lower as compared to soil respiration derived from the inversion of the half-hourly nighttime eddy covariance inclusive the soft-flagged data (Table 1), and increased in a similar fashion with temperature (at 0.05 m soil depth) as compared to leaf respiration (Fig. 9, Table 2).

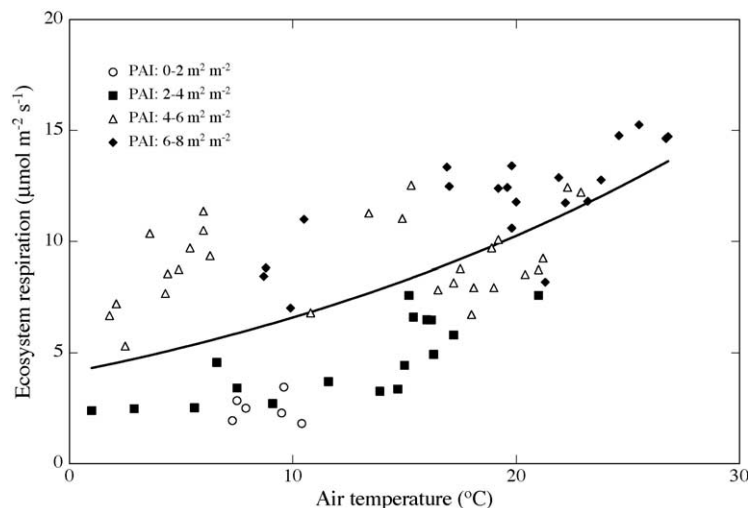


Fig. 7. Ecosystem respiration, derived from ecosystem chamber measurements, vs. instantaneous air temperature, separately for four PAI classes (measurement period: May–November 2002). The line shows the best fit to all data using the function:  $y = a \exp(bx)$  ( $r = 0.63$ ).

Table 2

Parameters, number of observations ( $n$ ), root mean squared error (RMSE,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and linear regression statistics for parameterisation of models of leaf ( $x = p$ ) and soil ( $x = s$ ) respiration from chamber measurements

	$R_{x,\text{Tref}}$	$E_x$	$n$	RMSE	Slope	y-intercept	$r$
<i>Carum carvi</i>	1.00	26402	90	0.57	0.60	-0.80	0.78
<i>Dactylis glomerata</i> <sup>a</sup>	1.46	24570	83	0.39	0.76	-0.55	0.86
<i>Ranunculus acris</i>	0.91	31497	126	0.40	0.81	-0.40	0.91
<i>Taraxacum officinale</i>	0.46	35138	158	0.26	0.79	-0.25	0.88
<i>Trifolium pratense</i>	1.28	31623	78	0.55	0.79	-0.58	0.89
<i>Trifolium repens</i>	0.56	45367	85	0.51	0.83	-0.31	0.90
Herbs <sup>b</sup>	0.79	33442	—	—	—	—	—
Soil	3.34 <sup>d</sup>	33535	34 <sup>c</sup>	0.31	0.91	0.44	0.97

Parameters are  $R_{x,\text{Tref}}$ : respiration at reference temperature of 10 °C ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ );  $E_x$ : activation energy ( $\text{J mol}^{-1}$ ). Linear regression statistics are slope; y-intercept ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ );  $r$ : correlation coefficient.

<sup>a</sup> Applied to all Graminoids species.

<sup>b</sup> Geometric mean of all investigated herb species, applied to cryptogams and all herbs not listed above.

<sup>c</sup> Number of bins (cf. Fig. 9).

<sup>d</sup> Significantly ( $p < 0.05$ ) different from soil respiration of nighttime half-hourly data set inclusive soft-flagged data (i.e. second column of Table 1).

### 3.5. Seasonal nighttime ecosystem respiration

The consequences of the different sets of respiration parameters for calculating seasonal carbon budgets are explored in Table 3, which shows seasonal (8 March–28 November 2002) simulations of nighttime ecosystem respiration and their uncertainty. Simulations are based on Eq. (4), the parameters of Tables 1 and 2, and the driving forces shown in Fig. 1. Note that these carbon balances are 100%

simulated, i.e. do not include the valid original measurements, as would be done for gap-filling (cf. Falge et al., 2001).

The smallest seasonal nighttime carbon budget was simulated with the parameterisation based on the quality controlled half-hourly nighttime eddy covariance data, whereas the highest seasonal nighttime carbon loss resulted from the half-hourly nighttime eddy covariance data inclusive the soft-flagged data (555 and 952 g C m<sup>-2</sup>, respectively). Yet, overall

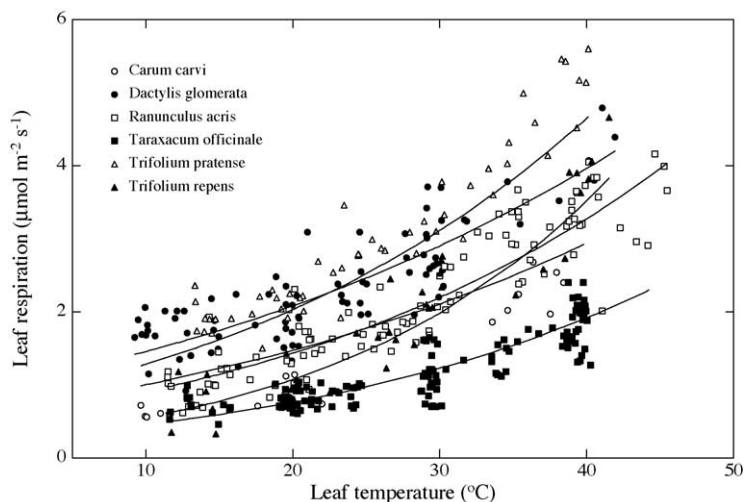


Fig. 8. Leaf dark respiration vs. instantaneous leaf temperature of *Carum carvi*, *Dactylis glomerata*, *Ranunculus acris*, *Taraxacum officinale*, *Trifolium pratense* and *Trifolium repens* (measurement period: April–October in years 2000–2002). Lines show the best fit to the data of each species using an Arrhenius function as in Eq. (4).

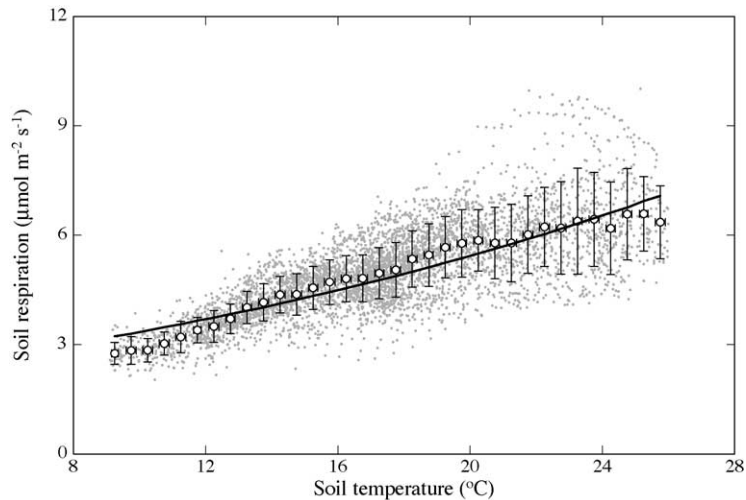


Fig. 9. Bulk soil respiration vs. soil temperature at 0.05 m depth. Small closed symbols refer to half-hourly and large open symbols to bin-averaged ( $0.5^\circ$  bins) soil temperatures and respiration rates. The line shows the best fit to the bin-averaged data using the first part on the RHS of Eq. (4). Error bars refer to  $\pm 1$  S.D. of bin-averaged data.

uncertainties of 30–34% prevented this  $400 \text{ g C m}^{-2}$  difference from being statistically significant (Table 3). The parameterisation based on the scaled up ecosystem component chamber measurements, the extrapolation of daytime eddy covariance measurements to zero irradiance, and the ensemble average nighttime eddy covariance measurements yielded seasonal nighttime respiration estimates of  $647\text{--}676 \text{ g C m}^{-2}$ , the parameterisation based on ecosystem chamber measurements  $744 \text{ g C m}^{-2}$  (Table 3). Again, these differences were statistically not significant due to uncertainties of 23–38%.

Given relatively similar activation energies (Table 1), the seasonal course of simulated ecosystem respiration rates for the various top-down approaches differed mainly with regard to amplitude (grey area in Fig. 10). Simulations based on scaled up ecosystem component measurements fell within that same range before mid June and then again after mid September (Fig. 10), but were consistently lower in the intermediate period characterised by high soil and air temperatures (Fig. 1), due to comparatively low activation energies of soil, and to a lesser degree, leaf respiration measurements (Table 2).

Table 3

Seasonal (8 March–28 November 2002) simulations and uncertainty analysis of nighttime ecosystem respiration using Eq. (4), parameters from Tables 1 and 2, and input data from Fig. 1

	Nighttime			Extrapolated from light response	Ecosystem chamber	Scaled up chambers
	Half-hourly excluding soft- flags ( $u^* \geq 0.10$ )	Half-hourly including soft- flags ( $u^* \geq 0.15$ )	Average including soft- flags ( $u^* \geq 0.10$ )			
NEE ( $\text{g C m}^{-2}$ )	$555 \pm 166$	$952 \pm 333$	$676 \pm 243$	$651 \pm 247$	$744 \pm 260$	$647 \pm 149$
Random error (%)	29	30	31	37	29	11
Systematic error (%)	8	18	18	8	20	20
Overall error (%)	30	35	36	38	35	23

All errors have been calculated by summing the squares of the component errors and then taking the square root (Moncrieff et al., 1996).

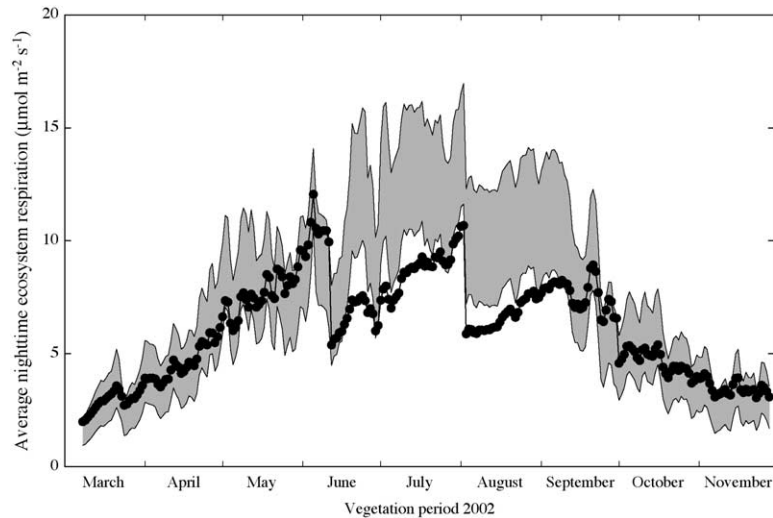


Fig. 10. Comparison between simulated average nighttime ecosystem respiration based on ecosystem component chamber measurements (symbols; parameters from Table 2) and the range covered by top-down measurements (shaded area; parameters from Table 1).

#### 4. Discussion

The analysis of the nighttime eddy covariance measurements presented in this paper showed the saturation-type increase of ecosystem respiration with increasing  $u^*$  (Fig. 2) observed at the majority of flux measurement sites around the world (Baldocchi, 2003). However, it also could be shown that the suspected underestimation of nighttime ecosystem respiration during calm conditions (low  $u^*$ ) was greatly reduced once data were subject to stringent quality control criteria (Fig. 2). This difference resulted from (i) an increase of nighttime NEE with increasing violation of the stationarity and integral turbulence quality tests, once 20–30% deviation was exceeded (Fig. 3), and (ii) a bias of periods which failed to meet the specified quality control criteria towards higher friction velocities (Fig. 2). The latter was, at least partly, due to intermittent, non-stationary turbulence being characterised by large  $\sigma_w$  values, which in turn yield high friction velocities. Essentially, this means that a considerable part of the half-hourly runs deemed to represent the ‘true’ biological respiratory source strength based on the specified  $u^*$  threshold, did in fact not satisfy the requirement of stationarity and/or were characterised by large deviations from the MO similarity theory.

While the sporadic nature of turbulence caused spurious nighttime ‘uptake’ of  $\text{CO}_2$  during some runs as well (cf. Baldocchi et al., 2000; Cava et al., 2004), the net effect was to increase the release of  $\text{CO}_2$  during intense, intermittent updrafts of air. A potential explanation for the observed bias towards high  $\text{CO}_2$  fluxes during non-stationary conditions is, that  $\text{CO}_2$  not accounted for by the storage term was released during these intermittent turbulent events. Support for this hypothesis derives from (i) the observation that the storage term was unaffected by the exclusion of soft-flagged data (Fig. 2) and (ii) the ensemble average nighttime respiration, which was largely independent of  $u^*$  (Fig. 4), consistent with the findings by Xu and Baldocchi (2004) for a Mediterranean annual grassland. Such observations may be explained by spatial heterogeneity of storage in the notional control volume below the measurement height (cf. Finnigan et al., 2003), for example Xu and Baldocchi (2004) argued that under stable conditions respired  $\text{CO}_2$  might accumulate in micro-topographic troughs. Another explanation may be the venting of  $\text{CO}_2$  stored in the soil air space during short turbulent episodes, a process referred to as pressure pumping (Massman and Lee, 2002; Takle et al., 2003, 2004). Recently, Flechard et al. (2004) were able to show that accounting for the time-rate-of-change of  $\text{CO}_2$  in the air-filled pore space of a soil under a permanent

grassland accounted for much of the observed underestimation of nighttime CO<sub>2</sub> fluxes during calm conditions. Indirect evidence in support of a potential contribution of pressure pumping during intermittent turbulent events comes from the inversion analysis of the data set inclusive of the soft-flagged data, which suggested a significantly higher soil contribution (Table 1). If the storage term is indeed underestimated and if high CO<sub>2</sub> fluxes during non-stationary periods reflect the venting of this unaccounted CO<sub>2</sub> to the atmosphere, then non-stationary runs must be kept in, as filtering them out will systematically bias fluxes towards lower values.

Strong evidence against the inclusion of half-hourly soft-flagged nighttime data derives from soil respiration, both measured in situ, as well as calculated inversely from the other top-down approaches. These measurements yielded significantly lower soil respiration rates (3.2–4.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  versus 6.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 10 °C), and at the same time, were consistent with each other within their range of uncertainty (Tables 1 and 2). Furthermore, soil respiration rates (normalised to 10 °C) reported for other grasslands are even lower: 2.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a lowland grassland site in Switzerland (Volk and Niklaus, 2002); 2.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a lightly grazed meadow on the Tibetan plateau (Cao et al., 2004); 1.4–1.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for a tallgrass prairie in the USA (Bremer et al., 1998; Wan and Luo, 2003). In contrast, there was good correspondence between measured (0.5–1.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and inversely estimated (0.6–0.9  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) leaf respiration rates (Tables 1 and 2), and these also fell into the range of 0.2–1.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  reported by Bahn et al. (1999) for 34 mountain grassland species (all normalised to 10 °C).

At present, despite the fact that our inability to identify the mechanism responsible for the observed increase in CO<sub>2</sub> fluxes during non-stationary conditions prevents us from deciding whether these should be screened out or not, we conclude that inclusion of half-hourly soft-flagged data, causes soil, and in consequence ecosystem, respiration of the investigated meadow to be overestimated.

The parameters derived from the remaining approaches, when applied to simulate the nighttime ecosystem respiration of the 2002 vegetation period (8 March–28 November), yielded seasonal nighttime

carbon budgets which agree with each other within 35%, which is on the order of the uncertainty of each individual approach (Table 3). Uncertainties between 18 and 62% for annual carbon balances simulated on the basis of scaled up component chamber measurements have been reported also by Ryan et al. (1997) and Law et al. (1999). While uncertainties of this magnitude are sufficient to turn a carbon balance from a sink to a source, these are largely statistical in nature and will thus diminish as more data become available (Moncrieff et al., 1996).

Seasonal nighttime ecosystem respiration simulated based on the parameters obtained from extrapolating daytime eddy covariance measurements was 4% lower and 22% higher as compared to the one derived from ensemble average and half-hourly quality controlled nighttime data, respectively (Table 3). Similar comparisons in literature found ecosystem respiration derived from daytime data to fall short of nighttime measurements by up to 20% (Suyker and Verma, 2001; Falge et al., 2002; Gilmanov et al., 2003; Griffis et al., 2003; Kowalski et al., 2003; Xu and Baldocchi, 2004). This underestimation is often attributed to the inhibition of canopy respiration during daytime (Griffis et al., 2003), leaf respiration in light being reduced by up to 85% relative to darkness (Azcón-Bieto and Osmond, 1983; Brooks and Farquhar, 1985; Villar et al., 1995). Model simulations (Wohlfahrt et al., in preparation), however, show that this phenomenon is not likely to cause an underestimation of ecosystem respiration estimated as the y-intercept of light response curves, for two reasons. First, even in the unlikely case that the inhibition at leaf level involved a step-change from full activation to full inhibition at a certain light level, the resulting canopy-level inhibition with increasing radiation would be, at least for sufficiently dense canopies, a gradual one, due to the attenuation of radiation within the canopy. Second, for ecosystems with low amounts of leaf area, the canopy-level transition to full inhibition might indeed be relatively sharp, albeit in these cases, soil respiration will usually by far exceed the canopy contribution and thus dampen the resulting effect on ecosystem respiration. Therefore, provided the threshold PPFD used to discriminate between day and night is close to zero (5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in this study), the extrapolation to zero irradiance will be done on NEE values where

inhibition of leaf respiration is almost absent or plays quantitatively a minor role.

Differences in footprint are another potential source of mismatch between respiration parameters derived from nighttime and daytime data, since at our site air generally flows out of the valley during nighttime and into the valley during daytime. This mountain valley wind system (Oke, 1987) makes it very difficult to assess any bias in respiration parameters due to the different source areas, as only a very limited number of observations is available for the same meteorological conditions from both wind directions.

Seasonal nighttime ecosystem respiration simulated based on the parameters obtained from leaf and soil chamber measurements was almost identical to the carbon budget obtained from the daytime eddy covariance measurements (Table 3). In literature, cross comparisons between nighttime eddy covariance measurements and scaled up chamber measurements produced mixed results. Excellent correspondence was reported by Granier et al. (2000) for a young beech forest; Law et al. (2001) found eddy covariance measurements to overestimate scaled up ecosystem respiration of a young ponderosa pine forest under windy conditions by 26%. In most other comparisons, nighttime eddy covariance was reported to underestimate scaled up component chamber measurements. Lavigne et al. (1997) found the eddy covariance method to underestimate scaled up component chamber measurements at six coniferous boreal sites on average by 27%, similar to the 35 and 32% underestimation determined by Goulden et al. (1996) and Kominami et al. (2003) for a deciduous hardwood and a mixed evergreen deciduous forest, respectively; Law et al. (1999) and Bolstad et al. (2004) reported an underestimation of 50% for a tall ponderosa pine stand and northern deciduous forests, respectively.

The largest deviation from nighttime eddy covariance measurements was observed for the seasonal nighttime ecosystem respiration simulated based on the parameters obtained from inverting ecosystem chamber measurements, exceeding the nighttime carbon budget derived from ensemble average and half-hourly quality controlled nighttime data by 10 and 35%, respectively (Table 3). Errors in ecosystem chamber measurements are mainly due to

modifications of the chamber environment during the measurement cycle, in particular chamber air temperature and humidity, pressure and mixing of chamber air (Dore et al., 2003; Drösler et al., in preparation). Changes in chamber air temperature and humidity are generally minor in the absence of solar radiation (Dore et al., 2003) and were furthermore minimised by short enclosure times (Drösler et al., in preparation). Overpressure inside the chamber usually leads to a suppression of soil respiration (Lund et al., 1999) and was avoided by using a vent which allowed equilibration with atmospheric pressure. Mixing of chamber air is necessary in order to obtain representative gas samples, and in particular, with large chambers, to prevent an artificial build-up of CO<sub>2</sub> in the lower layers of the canopy, which depresses diffusion of CO<sub>2</sub> out of the soil. Vigorous mixing of chamber air, on the other hand, may artificially increase the soil CO<sub>2</sub> diffusion gradient and exaggerate soil respiration (Le Dantec et al., 1999). One possible explanation for the larger soil respiration rates derived from the ecosystem chamber measurements (Table 2) might be, that chamber air mixing, as compared to the actual calm nighttime conditions, was too vigorous. Another source of mismatch are differences in footprint, which is several magnitudes larger (and variable) for eddy covariance as opposed to ecosystem chamber measurements, the latter having a small (0.6 m<sup>2</sup>, three replicates) and well defined footprint (Steduto et al., 2002).

Using 3 weeks of micrometeorological flux measurements over crop and pasture ecosystems to inversely derive parameters for the CSIRO Biospheric Model, Wang et al. (2001) concluded that resolving the contribution of plant and soil respiration to the net CO<sub>2</sub> flux was impossible due to a strong correlation between leaf and soil respiration parameters. Our results suggest that below- and above-ground respiration parameters may be derived from measurements of ecosystem respiration, provided available data cover a wide range of fractional contributions of plants and the soil to ecosystem respiration. Further work is required in order to reveal the causes for the differences in the activation energies derived from top-down and bottom-up approaches (Tables 1 and 2), which results in a bias of seasonal simulations during periods of high



temperatures (Fig. 10). Temperature acclimation of specific respiration rates (e.g. Janssens and Pilegaard, 2003), and a bias of the data basis towards certain temperature conditions could account for the observed differences.

## 5. Conclusion and summary

The present study showed that the discrimination of valid nighttime eddy covariance measurements based on friction velocity, the so-called  $u^*$ -correction, is very sensitive to the imposed quality control criteria. Excluding half-hourly nighttime data which deviate more than 30% from the stationarity and integral turbulence tests, caused ecosystem respiration of the investigated meadow under turbulent conditions, and thus, the magnitude of the  $u^*$ -correction, to be significantly reduced. Based solely on nighttime eddy covariance data, we are currently unable to decide whether the observed high CO<sub>2</sub> fluxes under intermittent conditions represent artefacts and should be screened out, or whether these reflect a genuine transport of CO<sub>2</sub> not accounted for by the storage term and must be retained. Evidence against the inclusion of these data derives from soil respiration rates measured in situ and calculated inversely from the other approaches, which were significantly lower as compared to soil respiration calculated from inversion of the half-hourly nighttime data inclusive the soft-flagged observations. Seasonal (8 March–28 November 2002) nighttime carbon balances calculated based on the parameters derived from the remaining approaches agreed with each other to within 35%, which is on the order of the uncertainty of each individual approach. While uncertainties of this magnitude are sufficient to turn a carbon balance from a sink to a source, it should not be dismissed that, until an improved understanding of nighttime exchange processes is obtained, employing multiple-constraints approaches remains the only option for deriving defensible CO<sub>2</sub> source/sink strength estimates. An appreciable proportion of the overall uncertainties in this study were due to random errors and will thus diminish as more data become available, providing justification for (continuing) long-term studies of biosphere–atmosphere exchange. Finally, this study also showed the

potential of the inverse approach for disentangling above- and below-ground contributions to ecosystem respiration.

## Acknowledgements

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## Appendix A. Low-pass frequency-response corrections

Experimental low-pass transfer functions were derived according to Aubinet et al. (2000, 2001) by forming the normalised ratio between the cospectra of sensible heat and CO<sub>2</sub>. Low-pass frequency response correction factors were then derived by applying these experimental transfer function, in the form of a one parameter sigma function (Eq. (A.2a) and (A.2b) of Aubinet et al., 2001), to a cospectral reference model derived from 24 months of sensible heat cospectra at this site. Monthly averaged cospectra of sensible heat, separated into eight stability classes, were fitted to the following equation (Bill Massman, personal communication):

$$C_{wt}(f) = N \frac{\frac{f}{f_x}}{\left[ 1 + \beta \left( \frac{f}{f_x} \right)^{2\mu} \right]^{\frac{1}{2\mu} \left( \frac{\beta + 1}{\beta} \right)}}, \quad (\text{A.1})$$

where  $N$  is a normalisation constant,  $f$  the normalised frequency,  $f_x$  the normalised frequency, where the cospectrum reaches its maximum value (i.e. the peak frequency),  $\mu$  a parameter describing the broadness of the cospectrum, and  $\beta$  is fixed at 0.75 for a  $-7/3$  power law decay at higher frequencies. The  $f_x$

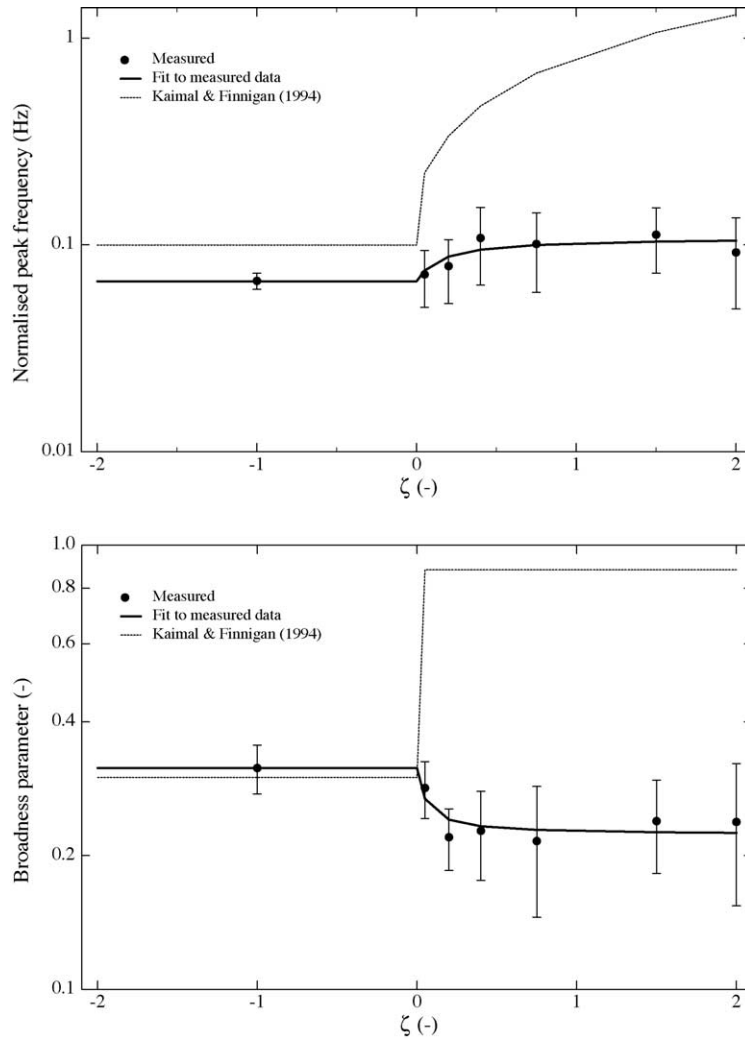


Fig. 11. Parameterisation (solid line) of the stability dependencies of the peak frequency (upper panel) and the broadness parameter (lower panel) of Eq. (A.2a) and (A.2b). Symbols refer to measured values ( $\pm 1$  S.D.). The stability dependencies of the peak frequency and the broadness parameter calculated for the model by Kaimal and Finnigan (1994) are shown for reference.

and  $\mu$  were parameterised as functions of stability,  $\zeta$ , using:

$$Y(\zeta) = a \quad \zeta \leq 0 \tag{A.2a}$$

$$Y(\zeta) = a + \frac{b\zeta}{c + \zeta} \quad \zeta > 0, \tag{A.2b}$$

where  $Y(\zeta)$  may stand for both  $f_x$  ( $a = 0.067$ ,  $b = 0.042$ ,  $c = 0.196$ ; upper panel Fig. 11) and  $\mu$  ( $a = 0.315$ ,  $b = -0.092$ ,  $c = 0.049$ ; lower panel Fig. 11). Cospectra of sensible heat calculated this way resembled the widely used cospectral model by Kaimal and

Finnigan (1994) during unstable and near-neutral conditions, but did not exhibit the pronounced shift of cospectral energy to higher frequencies and featured a broader peak with increasing stability (Fig. 11).

Experimental correction factors, as a function of wind speed, are shown as open symbols in Fig. 12 for unstable (upper panel) and stable (lower panel) conditions, respectively. Theoretical transfer functions and correction factors, closed symbols in Fig. 12, were calculated according to Moore (1986)

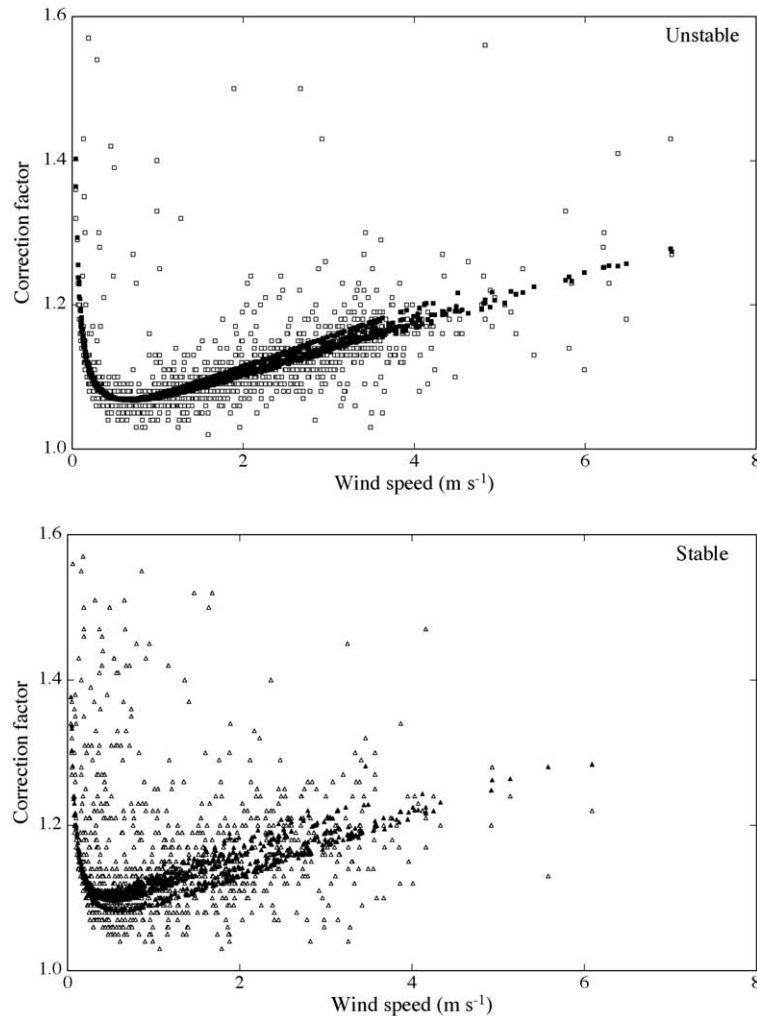


Fig. 12. Experimental (open symbols) and theoretical (closed symbols) low-pass frequency response correction factors for  $\text{CO}_2$  as a function of wind speed. Upper panel refers to unstable, lower panel to stable stratification.

and Aubinet et al. (2000). The following parameters were used: path length sonic anemometer, 0.15 m, path length infra-red gas analyser, 0.152 m; sensor separation, 0.1 m; tube flow,  $91 \text{ min}^{-1}$ ; tube inner diameter, 0.004 m; tube length, 4 m and sonic anemometer time response, 0.05 s. The effective  $\text{CO}_2$  time response of the infra-red gas analyser, 0.38 s, was determined by calibration against the experimental correction factors, thereby incorporating all effects not accounted for by the theoretical transfer functions (e.g. presence of filters in sample air stream).

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