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Estimating nocturnal ecosystem respiration from the vertical turbulent flux and change in storage of CO_2

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ABSTRACT

Micrometeorological measurements of nighttime ecosystem respiration can be systematically biased when stable atmospheric conditions lead to drainage flows associated with decoupling of air flow above and within plant canopies. The associated horizontal and vertical advective fluxes cannot be measured using instrumentation on the single towers typically used at micrometeorological sites. A common approach to minimize bias is to use a threshold in friction velocity, u_*, to exclude periods when advection is assumed to be important, but this is problematic in situations when in-canopy flows are decoupled from the flow above. Using data from 25 flux stations in a wide variety of forest ecosystems globally, we examine the generality of a novel approach to estimating nocturnal respiration developed by van Gorsel et al. (van Gorsel, E., Leuning, R., Cleugh, H.A., Keith, H., Suni, T., 2007. Nocturnal carbon efflux: reconciliation of eddy covariance and chamber measurements using an alternative to the u_*-threshold filtering technique. Tellus 59B, 397–403, Tellus, 59B, 307-403). The approach is based on the assumption that advection is small relative to the vertical turbulent flux (F_C) and change in storage (F_S) of CO_2 in the few hours after sundown. The sum of F_C and F_S reach a maximum during this period which is used to

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derive a temperature response function for ecosystem respiration. Measured hourly soil temperatures are then used with this function to estimate respiration R_{Rmax}. The new approach yielded excellent agreement with (1) independent measurements using respiration chambers, (2) with estimates using ecosystem light-response curves of $F_c + F_s$ extrapolated to zero light, R_{LRC}, and (3) with a detailed process-based forest ecosystem model, R_{cast}. At most sites respiration rates estimated using the u_*-filter, R_{ust}, were smaller than R_{Rmax} and R_{LRC}. Agreement of our approach with independent measurements indicates that R_{Rmax} provides an excellent estimate of nighttime ecosystem respiration.

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1. Introduction

Forest ecosystems play a vital role in buffering the accumulation of carbon dioxide in the atmosphere by storing large amounts of carbon and by removing 3 billion tons of carbon every year through net growth (Canadell and Raupach, 2008). Given the threat of global climate change, scientists have been devoting ever more attention to quantifying the carbon exchange between the terrestrial biosphere and the atmosphere, to determine the detailed dynamics and to predict possible future trajectories of carbon dioxide (CO_2) absorbed by vegetation (Schimel et al., 2008). The micrometeorological method has become increasingly popular to measure the surface-atmosphere exchange of carbon dioxide (Baldocchi et al., 2001) and the number of CO_2-flux measurement sites, has increased strongly during the last decade. This increase has had two effects. It allows ecological comparisons across widely varying climates and biomes and expectations are that this network will provide a high quality constraint on carbon budget modelling at various scales. But it has also meant that many towers have been erected in landscapes that pose severe problems for interpreting the data (Finnigan, 2008).

Under ideal conditions, when the surrounding terrain is flat and homogeneous, daily net ecosystem exchange (NEE) of CO_2 can be measured with an eddy covariance system, supplemented by measurements of the change in storage term. Few tower flux sites are located in sufficiently simple surroundings to allow NEE to be assessed with point or one-dimensional measurements. Stable atmospheric conditions are often associated with decoupling of air flows above and within the plant canopy leading to the development of advection by drainage flows (Belcher et al., 2008; Finnigan, 2007, 2008; Froelich and Schmid, 2006; Mahrt et al., 2001). At most sites not considering advection leads to a systematic bias in calculated nighttime respiration rates. As net daytime and nighttime fluxes are often of similar magnitude but opposite in sign, the resulting systematic bias can lead to large errors in ecosystem carbon budgets (Moncrieff et al., 1996).

Measuring the full CO_2 mass balance is one strategy to avoid bias in quantifying land surface exchange of CO_2. Such campaigns are very labour intensive and require elaborate three-dimensional experimental setups. Hence only a few groups have attempted this approach (Aubinet et al., 2005; Aubinet, 2008; Feigenwinter et al., 2004, 2008; Falk, 2005; Heinesch et al., 2008; Kutsch et al., 2008; Leuning et al., 2008; Marcolla et al., 2005; Paw U et al., 2004; Staebler and Fitzjarrald, 2004, 2005; Sun et al., 2007; Tóta et al., 2008; Yi et al., 2008). These experiments have led to highly valuable insights into the dynamics of advection but the magnitude of the advective fluxes is associated with large uncertainties. This is due to the difficulties of measuring small gradients in the mean wind and horizontal CO_2 concentration fields (Leuning et al., 2008; Yi et al., 2008), the accurate assessment of the mean vertical wind component (Leuning et al., 2008; Heinesch et al., 2007) and possibly the spatial resolution of the measurements. Aubinet (pers.comm.) concludes that it is unlikely that advection measurements will help to solve the problem of bias occurring in measured nighttime respiration and propose to focus research on better identification of data measured during conditions when advection is significant and to replace these data with modelled values.

A first step in this direction has been proposed by Goulden et al. (1996) who observed a systematic underestimation of flux during calm nocturnal periods. They used the friction velocity (u_*) as a proxy to detect periods with low turbulent mixing, an approach that is widely used in the micrometeorological community. The underlying assumption in determining a u_*-threshold is that NEE is biologically determined and independent of turbulence. The threshold is the magnitude of u_* above which NEE normalized to a given soil temperature is constant. The main drawback of this method is that it uses turbulence measurements above the canopy to determine the degree of coupling between air flows within and above the canopy. Belcher et al. (2008) have demonstrated that different transport mechanisms of heat and momentum at leaf level result in faster changes in the wind profile through the canopy than of the temperature profile. When the atmosphere above the canopy is stably stratified this difference in wind and temperature gradients results in supercritical Richardson numbers below the canopy top and a collapse of within-canopy turbulence. Turbulence can still be maintained above the canopy and hence using u_* as a single filtering criterion is not sufficient to identifying periods when advection is negligible and NEE is measured correctly by the eddy flux alone.

Alternative filtering approaches are thus needed (van Gorsel et al., 2007; Loescher et al., 2006). van Gorsel et al. (2007, 2008) have shown that at their site in Tumbarumba (SE Australia, Leuning et al., 2005) a peak in the sum of the vertical turbulent flux (F_C) and change in storage (F_S) of CO_2 (defined as R_{max}) occurs for a few hours in the early evening when advection is small relative to the other terms governing the mass balance. Advection dominates only later, following the development of large horizontal and vertical gradients of CO_2 (Leuning et al., 2008). Use of R_{max} to derive a temperature response function (TRF) for respiration led to excellent agreement with respiration rates derived from independent chamber measurements of soil, leaf and wood scaled up to the whole canopy (Keith et al., 2009). This method was applied successfully at other sites too (Saigusa et al., 2008) and the underlying dynamics were also observed in modelling studies (e.g. Sun et al., 2007). Its general applicability however still remains to be assessed. To this aim we compare respiration derived from R_{max} values (hereafter referred to as R_{Rmax}) with up to four different estimates of respiration that are described in Section 2. In Section 3 results from the comparison are shown for 25 sites globally covering a wide range of climate and topography. After briefly re-establishing the methodology, we test its applicability in very complex terrain by comparing results against independent chamber measurements. We test the postulate that there is a time window in the early evening where advection is small by comparing micrometeorological data with chamber measurements. We use data of all sites that have independent estimates of respiration to compare R_{Rmax} against, and show how we can make use of standard flux tower data to increase our confidence in nighttime estimates. Finally we quantify the effect of using different methods to estimate cumulative nighttime respiration.

2. Methods

2.1. Site description

The data set covers 25 tower flux sites that cover a wide range of vegetation, climate and topographic characteristics (Table 1). Ten sites have deciduous broadleaf forest, nine have evergreen needle leaf forests, four have evergreen broadleaf forests and two have mixed forests. The majority of the sites are situated in temperate climates (21) but there are also one boreal, one sub-tropical and two tropical sites. Further variation is introduced as the sites span a large range of elevations. Four sites are less than 100 m a.s.l., four between 100 and 250 m a.s.l., thirteen between 250 and 750 m a.s.l., three between 750 and 1500 m and one site above 1500 m a.s.l.. We used the height difference observed within a 2500 m sided square, centred on the flux tower, as a measure for the topographic complexity of the surrounds. Height differences are <100 m for 13 sites (flat terrain), between 100 and 250 m for 10 sites, one in the range 250–500 m and one where the height difference exceeds 500 m.

Data sets include eddy covariance measurements of ecosystem carbon and energy exchange (e.g. Aubinet et al., 2000) and measurements of the change in storage term of CO_2. Key meteorological variables were made available as well. At some sites there were additional chamber measurements of soil, wood and leaf respiration, which were upscaled to the site. Chamber measurements of respiration are especially valuable for this study as they can be used as independent estimates of nighttime respiration.

2.2. Estimates of nighttime respiration

Micrometeorological data were analysed in three different ways to develop temperature response functions for nighttime ecosystem respiration. The first was to apply the so-called u_*-filter (Goulden et al., 1996; Gu et al., 2005) to select NEE measurements during periods of high turbulent mixing when advection is expected to be insignificant. The second is the approach of van Gorsel et al. (2007, 2008) that uses the maximum NEE in the few hours after sunset computed from the eddy flux and the change in storage term of the mass balance. The third estimates ecosystem respiration by extrapolating the daytime light response curve for NEE to near-zero incoming solar radiation. We compare results to estimates from models of different complexity that are constrained by chamber measurements and also compare results of four sites to a complex process-based multi-layer model. The parameters of this model are independent of flux and chamber measurements.

2.3. Respiration derived from micrometeorological data

In micrometeorology we express NEE (E_{NE}) as

$$E_{ne} = \underbrace{\overline{c_d w' \chi_c'}}_{\mathbf{I}(F_C)} + \underbrace{\int_0^{h_r} \overline{c_d} \frac{\overline{\partial \chi_c}}{\partial t} dz}_{\mathbf{II}(F_S)} + \frac{1}{L^2} \int_0^L \int_0^L \int_0^{h_r} \times \underbrace{\left[\overline{uc_d} \frac{\partial \overline{\chi_c}}{\partial x} + \overline{vc_d} \frac{\partial \overline{\chi_c}}{\partial y} + \overline{wc_d} \frac{\partial \overline{\chi_c}}{\partial z} \right] dzdydx}_{\mathbf{III}(F_A)} \quad (1)$$

where x, y, z define the Cartesian coordinates of a notional control volume with sides of length L and height h and t is time. The scalar quantity under consideration is carbon dioxide. χ_c is the mixing ratio of the molar density of CO_2 (c_c) in dry air (c_d) (Leuning, 2004). u, v, w are the longitudinal, lateral and vertical components of wind velocity, respectively. Overbars denote time averages and primes stand for departures from the mean. We have assumed that the canopy is sufficiently homogeneous to neglect the horizontal turbulent flux divergence terms in deriving Eq. (1). Terms I and II in Eq. (1) are the vertical turbulent flux (F_c) and change in storage of CO_2 (F_s), respectively. Note that term F_s, the rate of change in storage term, is written as a one-dimensional integral, emphasising that it is usually calculated from a single profile, where ideally it should be derived from instantaneous profiles of space averaged concentrations (Finnigan, 2006). Term III denotes the horizontal and vertical advection terms (F_a).

Advection occurs mainly in presence of flows associated with topography (drainage flows) or with land use changes (breezes) (Aubinet, 2008). During daytime when the atmosphere is unstably stratified and well mixed, advection is small at sites situated in reasonably flat and homogeneous terrain and NEE reduces by a good approximation to the sum of terms I and II of Eq. (1) (later referred to as $F_{c,s}$). After sunset, drainage flows in even moderately complex topography can lead to significant horizontal and vertical advection and a consequent underestimation of nocturnal respiration derived from eddy covariance measurements on a single tower. Belcher et al. (2008) showed that due to the different adjustment lengths of momentum and heat in the canopy, turbulence in the canopy collapses after sunset even though fully developed turbulence can continue in the layer above. This dynamic decoupling means that respired CO_2 accumulates in the sub canopy and F_s then dominates the mass balance. The collapse of turbulence further leads to an accelerated cooling of the air layer within the canopy (Finnigan, 2008). If the canopy is situated on a slope then the within-canopy cooling leads to an additional pressure force, with air close to the surface being cooler than air at the same altitude away from the slope. When this hydrostatic pressure overcomes the sum of hydrodynamic pressure and canopy drag, drainage flows will start (Finnigan, 2007) and F_A is likely to be no longer negligible.

2.3.1. Respiration from well mixed conditions R_{ust}

During well mixed atmospheric conditions F_A in eq. (1) is often negligible and NEE is well approximated by $F_{C,S}$. As NEE is biologically determined it is expected to be independent of atmospheric turbulence and to remain constant above a threshold value of friction velocity, u_* (Goulden et al., 1996). Due to the diurnal variation in windspeed and temperature there is the potential for correlation between NEE and u_* that must be removed before a threshold can be determined. The method we applied to determine the u_*-threshold (Gu et al. (2005)) uses an iterative approach to simultaneously determine a TRF, to normalize NEE and to detect a threshold with an automated statistical method, a Moving Point Test (MPT). MPT uses a stepwise comparison of the mean value of a normalised reference sample of NEE to moving sub-samples to detect the range over which NEE is independent of u_*. To derive R_{ust} we used a temperature response function (TRF) that represents NEE (E_{NE}) solely as a function of soil temperature (T_{soil}) (van't Hoff, 1898)

$$E_{NE} = \varepsilon_1 \exp(\varepsilon_2 T_{soil}) \quad (2)$$

where ε_1 and ε_2 are the regression coefficients. The same TRF equation was then applied to all data. 30-day moving windows were used to relate E_{NE} to T_{soil}, where T_{soil} was taken from the top layer (down to −0.2 m depth), due to the dampened amplitude of T_{soil} with depth. If more than one measurement from the top-soil layer was available we used an average of these. Use of relatively small moving windows allows for seasonal variations in the TRF arising due to e.g. change in soil water or organic matter content.

2.3.2. Respiration derived from daytime light response curve R_{LRC}

A simple empirical model was used to describe the response of net canopy photosynthesis to light (Lee et al., 1999; Jassal et al., 2007). We obtained daytime estimates (R_{LRCd}) from daytime

Table 1
List of abbreviations, site information and measurements provided. In Biomes e stands for evergreen, d for deciduous, m for mixed subscript n stands for needle, b for broadleaf. In Climate bo stands for boreal, te for temperate, s-tr for subtropical and tr for tropical. Elevation indicates the height above sea level of the site where vl stands for <100 m, l for 100–500 m, m for 500–1000, h for 1000–1500 and vh for >1500 m a.s.l. The height difference is the range between minimum and maximum height a.s.l in a square centred around the site, where the sidelength of the square is 2500 m. This is one measure of the topographic complexity with l standing for low complexity (difference <100 m), m for medium (100–250 m), h for high (250–500 m) and vh for very high complexity (>500 m). Ticks indicate that measurements or modelled values were available, or in the case of R_{Rmax} that the algorithm produced a plausible value. X stands for measurements or modelled values that were not available, or in the case of R_{Rmax} that it was not possible to construct a temperature response function (TRF). – stands for 'not available'. Routines were only run for sites that provided all variables necessary to derive a TRF (soil temperature) and a light response curve (incoming photosynthetic active radiation or incoming shortwave radiation).

Abbreviation	Site	Coordinates	Data provider	Biome	Climate	Elevation (m)	Height difference (m)	Variables for TRF and lrc	R_{tot}	R_{soil}	R_{cast}	R_{Rmax}	Objective u_*–threshold (ms^{-1})
CA	Canada, BC DF 49	49°52′N 125°20′W	Chen et al. (2009) Humphreys et al. (2006) Morgenstern et al. (2004)	e_n	te	m	m	√	×	√	×	√	0.38
DO	USA, FL Donaldson	29°45′N 82°09′W	Leclerc et al. (2003)	e_n	s-tr	vl	l	×	×	×	×	–	–
FR	France, Fontainebleau	48°28′N 02°46′E	Chemidlin-Prevost-Bouré et al. (2009)	d_b	te	vl	l	√	×	√	√	√	0.21
GR	UK, Griffin	56°37′N 03°47′W	Clement et al. (2003)	e_n	te	m	m	×	×	×	×	–	0.23
GU	French Guyana Guyaflux	05°16′N 52°55′W	Bonal et al. (2008)	e_b	tr	vl	l	√	×	×	×	×	×
HA	Germany Hainich	51°04′N 10°27′E	Kutsch et al. (2008)	d_b	te	m	l	√	√	√	√	√	0.45
HV	USA, MA Harvard EMS	42°32′N 72°10′W	Urbanski et al. (2007)	d_b	te	m	m	√	×	×	×	√	0.34
HY	Finland Hyytiälä	61°51′N 24°17′E	Suni et al. (2003)	e_n	bo	l	l	√	√	√	√	√	0.39
LA	Switzerland Laegeren	47°28′N 08°21′E	Eugster et al. (2007)	$m_{b,d}$	te	m	h	√	×	×	×	×	×
LO	Netherlands Loobos	52°10′N 05°44′E	Dolman et al. (2002)	e_n	te	vl	l	√	×	√	√	√	0.09
MI	USA, MO Ozark	38°44′N 92°12′W	Yang et al. (2007)	d_b	te	l	l	√	×	√	×	√	0.32
MM	USA, IN MMSF	39°19′N 86°25′W	Schmid et al. (2000)	d_b	te	m	l	√	×	×	×	×	0.42
OH	USA, OH Oak Openings	41°33′N 83°50′W	Noormets et al. (2008)	d_b	te	l	l	√	×	×	×	×	0.38
OR	USA, OR old Ponderosa Pine site	44°27′N 121°33′W	Law et al. (1999) Anthoni et al. (2002)	e_n	te	h	m	√	√	√	×	√	×
RE	Italy, Renon	46°35′N 11°26′E	Montagnani et al. (2009)	e_n	te	vh	vh	√	×	√	×	√	0.39
SY	USA, WI Sylvania Wilderness	46°14′N 89°20′W	Desai et al. (2005)	d_b	te	m	l	√	×	×	×	√	0.30
TA	Brazil, Tapajos National Forest	02°51′S 54°57′W	Saleska et al. (2003) Hutyra et al. (2007)	e_b	tr	l	l	X	×	×	×	–	×
TH	Germany Tharandt Anchor Station	50°57′N 13°34′E	Grünwald and Bernhofer (2007)	$m_{b,n}$	te	m	m	√	×	×	√	√	0.31
TU	Australia, NSW Tumbarumba	35°39′S 148°09′E	Leuning et al. (2005)	e_b	te	h	m	√	√	√	×	√	×
VI	Belgium, Vielsalm	50°18′N 05°59′E	Aubinet et al. (2001)	d_b	te	m	m	√	×	×	×	√	0.74
WA	Australia, VIC Wallaby Creek	37°25′S 145°11′E	Wood et al. (2008)	e_b	te	m	l	√	×	×	×	√	0.37
WE	Germany Wetzstein	50°27′N 11°27′E	Anthoni et al. (2004)	e_n	te	h	m	√	×	√	×	√	0.76
WI	USA, WI Willow Creek	45°48′N 90°04′W	Cook et al. (2004)	d_b	te	m	l	√	×	×	×	√	0.21
WS	USA, WI Mature Hardwood	46°38′N 91°05′W	Noormets et al. (2007)	d_b	te	m	m	×	×	×	×	–	×
WR	USA, WA Wind River Crane	45°49′N 121°57′W	Wharton et al. (2009)	e_n	te	m	m	√	×	×	×	√	×

measurements of $F_{C,S}$, using a Michaelis-Menten type light response curve:

$$E_{NE} = R_{LRCd} - \frac{\alpha Q_t A_{max}}{\alpha Q_t + A_{max}} \quad (3)$$

where α is the apparent quantum yield, A_{max} is the canopy scale photosynthetic capacity and Q_t the total incident photosynthetic active radiation (PAR) above the canopy. Where Q_t measurements were not available we used incoming shortwave radiation as a substitute. We applied a 10 day moving window to obtain R_{LRCd} values from the regression of daytime measurements of $F_{C,S}$ against PAR. These estimates of R_{LRCd} were then used to build an exponential relationship with T_{soil} (Eq. (2)). The values used for T_{soil} were averages over periods corresponding to the Q_t values used for the regression (Eq. (3)). This TRF was then used to derive nighttime values of R_{LRC} from nighttime T_{soil} measurements.

Several studies suggest that for equal temperature leaf respiration in light is reduced relative to that in darkness (Brooks and Farquhar, 1985; Villar et al., 1994; Hurry et al., 2005 and references therein). This leads to a possible underestimation of nighttime respiration when using functional relationships with daytime data. The reduction of respiration on canopy scale depends on the amount of radiation that is available to the leaves. Therefore forests with low LAI, steep leaf angles and a high fraction of diffuse radiation will show the strongest reduction in respiration in the light compared to dark respiration (Wohlfahrt et al., 2005). Particularly for deciduous forest the underestimation of total ecosystem respiration will be strongest during the summer months. Unfortunately this is the time when observations are best captured by the Michaelis-Menten model (Jassal et al., 2007; Lee et al., 1999).

While reduced leaf respiration in light may lead to an underestimation of nighttime respiration it has been shown that diel patterns of respiration, associated with root activity and metabolism, and driven by root exudates might lead to stronger respiration during the day with a peak in the evening (Liu et al., 2006; Savage and Davidson, 2003) and hence lead to an overestimation of nighttime respiration.

2.3.3. Respiration derived from early evening maximum R_{Rmax}

Indications of the presence of drainage flows can be found in the time series of CO_2 concentrations. Given a continuous input of carbon dioxide from soil-, wood- and leaf respiration into a volume we expect CO_2 concentrations to increase with time if there is no flux through the upper lid and no advective transport. Time series usually show a strong increase in CO_2 concentrations once the atmosphere becomes stably stratified (i.e. F_S is large), but after this initially strong increase the temporal build-up of concentrations is slower and concentrations can even remain relatively constant (F_S is small or tends to zero). If this steady-state situation is not associated with fluxes through the top of the volume we can assume that advection is draining CO_2 away (term III dominates the mass balance).

A maximum (defined as R_{max}) is often observed in $F_{C,S}$ in the early evening (Fig. 1a, see also Aubinet et al., 2005) and suggests that after the occurrence of this maximum, F_A becomes significant. Based on this observation van Gorsel et al. (2007, 2008) developed an alternative to the u_*-filtering technique that uses R_{max} values to develop a TRF for NEE (Eq (2)). We determine the time of R_{max} for each 30-day window by calculating the mean daily course of $F_{C,S}$. Subsequently a 3 h period is chosen which starts 1 h prior to the time of R_{max} (see Appendix A for a discussion on how sensitive results are to the selected time period). Within these 3 h the following conditions need to be fulfilled to consider the data point to be of high quality:

- To ensure that above canopy atmospheric conditions are not strongly stable and favourable to intermittent turbulence and hence lead to unreliable estimates of R_{max}, we exclude days where stability within this time period exceeds $(z–d)/L > 0.5$. z stands for the measuring height, d for the zero-plane displacement height (approximated with 2/3 the canopy height) and L for the Monin-Obukhov length.
- To avoid outliers in R_{max}, we only use respiration estimates within a plausible range $r = [0.5\bar{R}_{LRC}, 2\bar{R}_{LRC}]$, where $\bar{R}_{LRC}$ is the average obtained from the light response curve approach. (See Appendix A for a discussion on how sensitive results are to the selected range r).
- To avoid nights with high intermittency, data were only used when the ratio of the mean NEE to its standard deviation ($\bar{E}_{NE}/\sigma_{E_{NE}}$) exceeds unity. We used $\bar{R}_{LRC}$ as our best estimate for $\bar{E}_{NE}$, while $\sigma_{E_{NE}}$ is the standard deviation of $F_{C,S}$ within the time window.
- Finally, data obtained during rainy periods were excluded because these are usually of poor quality and because respiration is likely to be unrepresentative during rain periods. This is due to enhanced respiration due to wetting of previously dry soil or suppression of respiration by reduced diffusion in waterlogged soils (Lee et al., 2004 and Savage and Davidson, 2003).

2.4. Respiration derived from chambers R_{cham}

Upscaled chamber measurements of respiration from soil (R_s), leaves (R_l) and wood (R_w) provide an estimate of ecosystem respiration (R_{cham}) which is independent of micrometeorological data:

$$R_{cham} = R_s + R_l + R_w \quad (4)$$

R_s is usually assessed by taking weighted averages of soil chamber measurements placed to represent different soil types

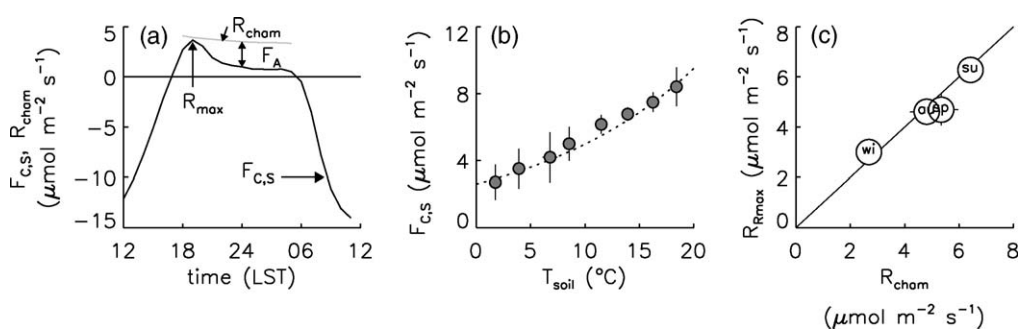

Fig. 1. (a) Mean daily course of the sum of eddy flux and change in storage term $F_{C,S}$ and total ecosystem respiration derived from chamber measurements (R_{cham}) (b) temperature response function of nighttime NEE derived from hourly values of R_{max}. Dots represent 2.5 °C bin averages. (c) Respiration derived from micrometeorological measurements (R_{Rmax}) against R_{cham}. Data were measured at Tumbarumba in the time period (a,b) 2001–2005, and (c) summer (su): 12–16/11/2001, autumn (au): 11-15/02/2002, winter (wi): 06–10/05/2002, spring (sp): 19–23/08/2002. In (b) and (c) error bars indicate 95% confidence levels.

and vegetation strata. Models used for soil respiration are usually response functions of temperature and soil water content (e.g. Irvine and Law, 2002; Keith and Wong, 2006; Falk et al., 2005; Pumpanen et al., 2001). R_l is measured per leaf surface area and scaled to site using Leaf Area Index (LAI). Rw (stem, branch and root fraction) can be measured per sap wood volume and scaled to site using tree inventory data. An alternate approach to upscale chamber measurements is taken by Kutsch et al. (2008) who use a set of models to estimate ecosystem carbon fluxes. A model for soil, stem and foliage respiration and photosynthesis were developed for a bottom-up modelling approach of carbon balances. These were calibrated with data from chamber measurements and driven with meteorological data from the site. In this study we used only chamber measurements from sites that provided us with fully upscaled data sets (Law et al., 1999 and Anthoni et al., 2002 [Oregon], Mammarella et al., 2007 [Hyytiälä], Keith et al., 2009 [Tumbarumba], Kutsch et al., 2008 [Hainich]).

Chamber measurements need to be interpreted with care (e.g. Kutzbach et al., 2007 and references therein). Problems arise as chambers always interfere with the object they measure and another major source of error is the upscaling of the measurements. Soil respiration is the most important component of total respiration (Law et al., 2001; Keith et al., 2009) and to address the former problem, Pumpanen et al. (2004) have investigated different soil chamber techniques in a calibration tank. As a general trend they observed that non-steady-state non-through-flow chambers [as used in TU, HA, OR] tend to underestimate the efflux by 4–14% while through-flow chambers [HY] overestimated the fluxes on average by 2–4%. Standard errors of upscaled soil respiration measurements have been assessed by Law et al. (2001) to be in the order of 13-18% [OR] and Mammarella et al. (2007) report a value of 7%. Keith et al. (2009) report the standard error of total ecosystem respiration R_{cham} to be in the order of 10% [TU].

While chamber measurements need to be interpreted with care they certainly provide a valuable mutual constraint for eddy covariance data.

2.5. Respiration derived from forest ecosystem models (R_{cast})

As long as parameter values are not derived from flux or chamber data, ecosystem respiration from forest ecosystem models provides another independent estimate of total respiration. At four sites (Hainich, HA, Hyytiälä HY, Fontainebleau, FR, Tharandt, TH), we used the CASTANEA model (Dufrêne et al., 2005; Davi et al., 2006; Delpierre et al., 2009) to simulate the elementary components of ecosystem respiration. CASTANEA is a process-based model, aiming at simulating fluxes of carbon and water and the growth of monospecific, even-aged forest ecosystems. Ecosystem respiration is defined as the sum of the independently modelled autotrophic and heterotrophic respiration. Autotrophic respiration is simulated on a half hourly basis, as the sum of maintenance and growth respiration of leaves, aerial wood, coarse and fine roots. Heterotrophic respiration is simulated on a daily basis through a soil organic carbon model (Epron et al., 2001). Carbon contents of the heterotrophic pools were initiated to satisfy steady state at the end of the simulation period (i.e. the integral amount of carbon entering carbon pools matches the integral amount of carbon losses by respiration over the simulation period). The CASTANEA model includes both species-specific and site-specific parameters. The former are compiled from the literature (see Dufrêne et al., 2005 for a thorough review), while the latter are measured on site and refer to canopy properties (e.g. leaf mass per area, nitrogen content), stand structure (e.g. leaf area index), and soil properties (e.g. soil texture, depth).

3. Results

In the early evening respiration estimates from micrometeorological data agree very well with estimates from chamber measurements at Tumbarumba, confirming that $F_{C,S}$ provide a good estimate of NEE during this time window (Fig. 1a). Throughout the remaining night however $F_{C,S}$ strongly underestimates total ecosystem respiration when compared to the chamber measurements. The underestimation is the result of cold air drainage and associated advection when F_A dominates the mass balance (van Gorsel et al., 2007). van Gorsel et al. (2008) used the maximum $F_{C,S}$ in the early evening (R_{max}), when the advection term is still small, to build a temperature response function for nighttime ecosystem respiration (Fig. 1b). Fitting the unbinned high quality R_{max} data to soil temperature provided the parameters needed to estimate R_{Rmax} (Eq (2)). Compared to using u_* as filtering criteria, the explained variance increased from $r^2 = 0.22$ for $u_* = 0.25\ ms^{-1}$ (Leuning et al., 2005) to $r^2 = 0.48$. Confidence in the validity of this approach is given by the high level of agreement between respiration rates calculated using the TRF derived from R_{max} and independent chamber measurements, taken during intensive measurement campaigns in four seasons (Fig. 1c).

Steepness and complexity of terrain might both be limiting factors for deriving reliable estimates of R_{Rmax}. To test the former we use data from RE (Renon), which is the site with the highest elevation and steepest topography used in this study (Table 1). Nighttime advection is known to be an issue there with positive vertical and horizontal advection contributing to the mass balance (i.e. the wind components are directed along the concentration gradient; Feigenwinter et al., 2008). Neglecting these terms will therefore lead to significant underestimation of respiration.

We used soil chamber measurements to investigate the overall decline of respiration through the night (Fig. 2a) which is similar to the decline observed for R_{Rmax}. Confirming previous findings R_s and R_{Rmax} decline much slower than $F_{C,S}$, which decreases rapidly after peaking in the early evening. As measurements of R_l and R_w were not available at RE, literature values of the ratio of soil to total ecosystem respiration were used to test whether R_{Rmax} estimates are within a plausible range. Urban et al. (2007) studied a forest similar in climate and species composition to RE but younger stand age and reported that total ecosystem respiration exceeded soil respiration by factors varying between 1.37 ± 0.23 and 1.51 ± 0.14. Fig. 2b shows that the multiplying R_s with these factors leads to good agreement with R_{Rmax}, despite the fact, that chamber measurements are more dynamic on an hourly basis. As not many sites globally are situated in such steep terrain we can conclude that steepness does not limit the use of R_{Rmax}.

The same does not apply for complexity. Site LA (Laegeren) is situated in steep and complex topography. It is located on a small shoulder 2/3 up a W-E oriented ridge that extends for several

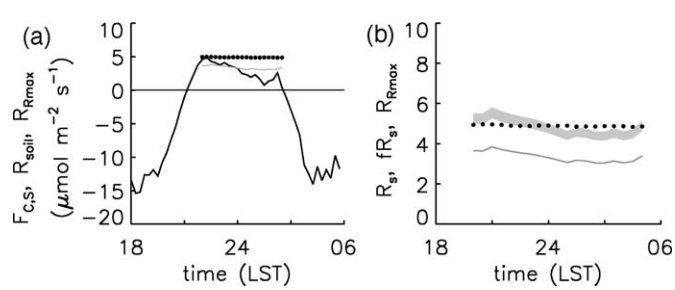

Fig. 2. (a) Mean daily course of $F_{C,S}$ (thick black line), soil respiration (grey line) and total ecosystem respiration estimated from R_{Rmax} (black dots) (b) the grey area indicates total ecosystem respiration inferred from soil chamber measurements and linear expanison factors (f) from Urban et al. (2007), grey line and black dotted line as in (a). Data were measured at Renon in the time period 01–25/07/2005.

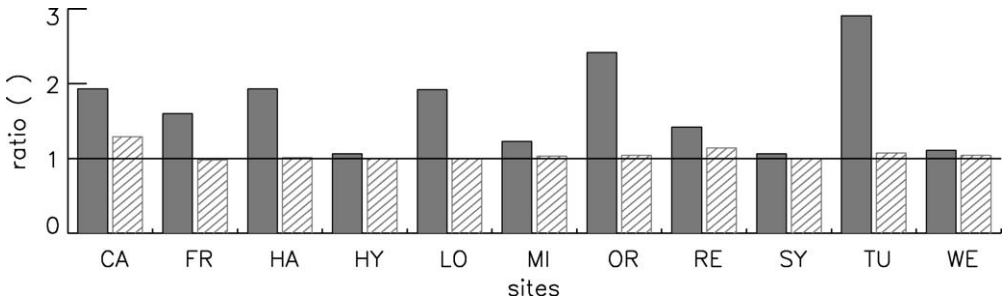

Fig. 3. The ratio of respiration measured at the time maximum respiration (R_{max}) is observed to that measured at midnight. The dark grey bars stand for the ratios obtained using $F_{C,S}$ and the hatched bars for the ratios obtained using soil chamber measurements. For site names refer to Table 1.

kilometres. It was not possible to determine a u_* threshold using the method by Gu et al. (2005) nor to derive estimates of R_{LRC} and R_{Rmax} (Table 1). In such topography we do not expect to generally observe simple slope and drainage wind systems. Channeled flows occur (Göckede et al., 2008) and a more detailed approach is needed that takes larger scale flow patterns into account.

Figs. 1 and 2a show that $F_{C,S}$ reaches a maximum in the early evening. There is good agreement between R_{Rmax} and the scaled up chamber measurements of ecosystem respiration at that time. According to the chamber measurements respiration rates drop slowly with decreasing air and soil temperature overnight. In contrast, $F_{C,S}$ decreases rapidly after the peak and hence underestimates respiration because F_A increasingly dominates the mass balance. To test if the increase of F_A through the night is a general feature, we compared the ratios of respiration measured at the time R_{max} is observed, to that measured at midnight using $F_{C,S}$ and R_{soil}. Fig. 3 shows that for the 11 sites that provided soil chamber measurements the ratios of soil respiration remain between 0.98 and 1.29 while ratios vary between 1.06 and 2.91 when micrometeorological measurements are used. Given the strong correlation between R_{eco} and R_{soil} there is no biological reason why the ratios should differ so strongly between the two methods, suggesting that advection is often increasingly important at night and that after the early evening, NEE can not be assessed by eddy flux and change in storage of CO_2 alone.

To test whether R_{Rmax} generally provides a good estimate of nighttime respiration, we compared R_{Rmax} with up to four different estimates of respiration for sites where additional chamber measurements of soil, leaf and wood respiration or modelling results were available. Fig. 4a shows that $R_{Rmax} \geq R_{LRC}$ but that results from the two methods are within the 95%-confidence intervals of each other. The good agreement indicates that the underestimate of respiration, due to a reduction of leaf respiration in light relative to respiration in the dark, and the overestimate of respiration, due to the diurnal cycle of root activity and metabolism, are small or balance each other.

All R_{ust} estimates are smaller than R_{Rmax} and do not fall within the 95%-confidence intervals (Fig. 4b). R_{ust} is also smaller than R_{LRC}. To exclude the possibility that this is due to an overestimate of R_{LRC} due to enhanced respiration later in the day, we tested whether respiration estimates based on morning data varied significantly from estimates based on evening data (with incoming shortwave radiation ranging from 10–500 Wm^{-2}). A t-test revealed no significant difference for any of the sites included in the analysis (FR: $p < 0.16$, HA: $p < 0.57$, TH: $p < 0.59$, HY: $p < 089$) and we can thus conclude that R_{ust} underestimates respiration.

That R_{Rmax} provides a good estimate of nighttime respiration is further supported by model estimates: R_{cast}, agrees very well with R_{Rmax} at all sites (Fig. 4c) with estimates that are within the corresponding 95%-confidence intervals. Agreement within the 95% confidence levels is also found for R_{cham} and R_{Rmax} (Fig. 4d) which is of particular importance, as chambers provide the only measured independent estimates of respiration.

The correlation between calculated monthly respiration rates R_{Rmax} and all other methods is generally high for all sites (Table 2), which is partly due to the use of a common TRF with different parameter values (Eq. (2)). Minimum correlation coefficients are reached between R_{ust} and R_{Rmax}. The bias, calculated as $2(R - R_{Rmax})/(R + R_{Rmax})$ (Hanna et al., 1993), where R is used as placeholder for any of the respiration estimates, is small but consistently negative between R_{Rmax} and R_{LRC}. An underestimation of respiration derived from daytime measurements however cannot be confirmed by a t-test ($p < 0.13$). The bias between R_{Rmax} and R_{ust} is generally biggest compared to the other respiration estimates and a t-test confirms that R_{ust} is significantly smaller than R_{Rmax} ($p < 0.04$). t-tests of R_{Rmax} and independent estimates of R_{cast} and R_{cham} indicate that there is no significant difference in their means ($p < 0.99$ and $p < 0.56$, respectively).

Respiration parameterisations that are readily available from micrometeorological measurements (namely R_{LRC}, R_{Rmax} and R_{ust}) can be compared at all sites. There is a good linear agreement

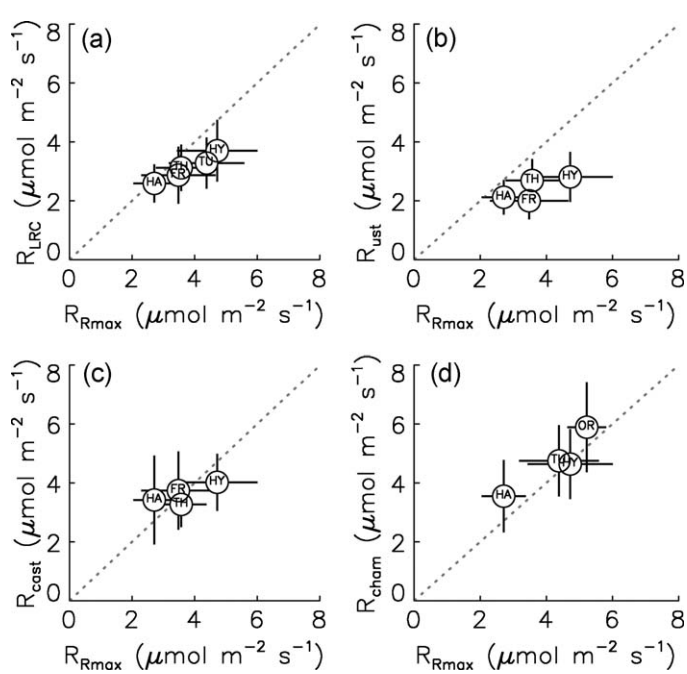

Fig. 4. Respiration derived from (a) the light response curve (R_{LRC}) (b) well mixed conditions (R_{ust}) (c) model output (R_{cast}) and (d) chambers R_{cham} versus (d) R_{Rmax} for sites where either soil, leaf and wood chamber measurements and/or model estimates were provided. For site names refer to Table 1. Time periods used to calculate averages are given in Table 2 and are identical for all methods. 95% confidence intervals are indicated with black lines, and the dotted lines represent the 1:1 line.

Table 2
Pearson correlation coefficients and bias between monthly R_{LRC}, R_{ust}, R_{cast}, R_{cham} and R_{Rmax}. The bias is calculated as, $2(R - R_{Rmax})/(R + R_{Rmax})$, where R is used as placeholder for any of the respiration estimates. Site name abbreviations are given in Table 1.

Site		FR	HA	HY	OR	TH	TU	WE
Time period		04/2005–12/2006	01/2005–01/2006	05/2004–09/2004	07/2004–09/2004	01/2004–12/2005	01/2003–12/2005	01/2005–12/2006
Pearson correlation coefficient	R_{LRC}, R_{Rmax}	0.98	0.85	0.85	0.94	0.99	0.96	0.97
	R_{ust}, R_{Rmax}	0.76	0.75	0.92	–	0.92	–	0.83
	R_{cast}, R_{Rmax}	0.86	0.94	0.99	–	0.98	–	–
	R_{cham}, R_{Rmax}	–	0.93	0.95	0.87	–	0.96	–
Bias	R_{LRC}, R_{Rmax}	−0.20	−0.05	−0.24	−0.07	−0.14	−0.30	−0.02
	R_{ust}, R_{Rmax}	−0.36	−0.25	−0.50	–	−0.28	–	0.07
	R_{cast}, R_{Rmax}	0.07	0.27	−0.16	–	0.09	–	–
	R_{cham}, R_{Rmax}	–	0.23	−0.02	0.12	–	0.09	–

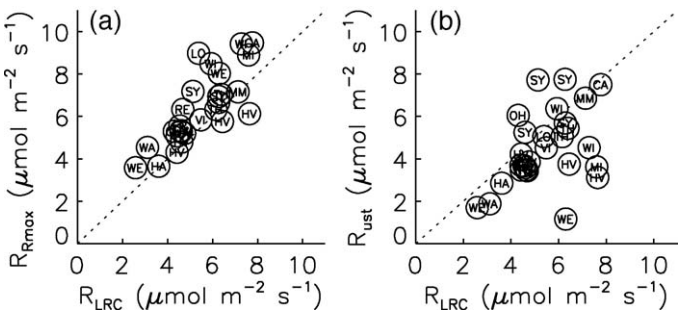

Fig. 5. Monthly averages of (a) R_{Rmax} versus R_{LRC} and (b) R_{Rmax} versus R_{ust}. For site names refer to Table 1. Data used was measured in July (Nothern Hemisphere) and in January (Southern Hemisphere). To display the same data in panels (a) and (b), only site years were used, where values for all respiration estimates could be derived. The black dotted line is the 1:1 line.

between monthly-average R_{Rmax} and R_{LRC} ($r = 0.78$) (Fig. 5a) and a t-test indicates that R_{LRC} is generally smaller than R_{Rmax} ($p < 0.02$). Smaller R_{LRC} than R_{Rmax} is found at all but one site and two out of 24 site-months (HV, Harvard). During summer the effect of reduced leaf respiration in light relative to that in darkness is expected to be largest and can explain the observed underestimation of total respiration by R_{LRC}. The linear agreement between R_{ust} and R_{LRC} is poor ($r = 0.07$) and R_{ust} estimates are on average lower than R_{LRC} ($p < 0.01$). Pooling the data sets into morning and evening data to calculate R_{LRC} does not result in significantly different estimates over all sites ($p < 0.69$) and hence R_{ust} is likely to underestimate true ecosystem respiration

Fig. 6 demonstrates the effect of using four different approaches to calculate the cumulative annual nighttime respiration over 2 site years. TH (Tharandt) is used as an example because for this site more than one site year, an independent estimate (R_{cast}) and all micrometeorological estimates (R_{ust}, R_{LRC} and R_{Rmax}) are available. Estimates range from 515 g C m^{-2} to 670 g C m^{-2} in 2004 and from 502 g C m^{-2} to 679 g C m^{-2} in 2005. Both years have cumulative $R_{Rmax} \approx 1.1\ R_{cast}$, $R_{LRC} \approx R_{cast}$, $R_{ust} \approx 0.85\ R_{cast}$. The micrometeorological estimates bracket the independent estimate within ± 15%.

Fig. 7 shows average respiration rates calculated using R_{LRC}, R_{Rmax} and R_{ust} for those sites where all three estimates were available for 3 or more months. At many sites data were available for a full 12 months but fewer months were analysed at the other sites due to lack of data or because it was not possible to construct light-response curves, particularly for the winter. Comparison of the nighttime respiration rates confirms that R_{Rmax} values tend to be higher than R_{LRC}. For 7 out of 14 sites R_{Rmax} and R_{LRC} are within 10% of each other. At 10 sites they agree to within the standard error. Largest differences are observed at LO (19%). R_{ust} estimates are often lowest. R_{ust} and R_{LRC} agree to within 20% and at 8 sites they agree to within the standard error. Differences between R_{ust} and R_{Rmax} are somewhat bigger (agreement to within 25%) and only at 4 sites the estimates agree to within the standard error (Fig. 7).

For some sites listed in Table 1, such as Tumbarumba (TU in 2001–5), Ponderosa Pine, Oregon (OR 06-10, 2004) and Wind River Crane, Washington (WR in 2006) it was necessary to have an alternative to the u_*-filtering method of Gu et al. used in this study, as no u_*-threshold was found. Wind River Crane, Washington (WR) data for other years show a clearly defined u_* threshold (1998–2004—see Paw U et al., 2004; Falk, 2005 and Falk et al., 2008). For two sites none of the micrometeorological approaches to calculate R_{LRC}, R_{Rmax} or R_{ust}, led to a satisfactory estimates of ecosystem respiration. One site, French Guyana (GU), is situated in the tropics and the temperature range was too small to build a TRF. While the filtering approaches might still be valid, a different model is required to estimate nighttime respiration, or one could simply use mean respiration rates because temperatures do not vary much. The other site, LA (Laegeren), is situated in steep and complex topography where we do not expect to observe simple slope and

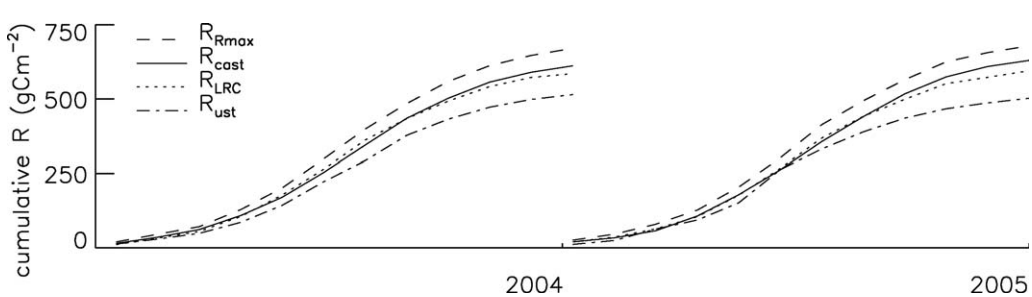

Fig. 6. Four different estimates of cumulative nighttime respiration (R_{Rmax}, R_{cast}, R_{LRC}, R_{ust}) for 2 years worth of data for TH (Tharandt) leading to 670, 611, 585 and 515 g C m-2 in 2004 and 679, 630, 595 and 502 g C m-2 in 2005, respectively.

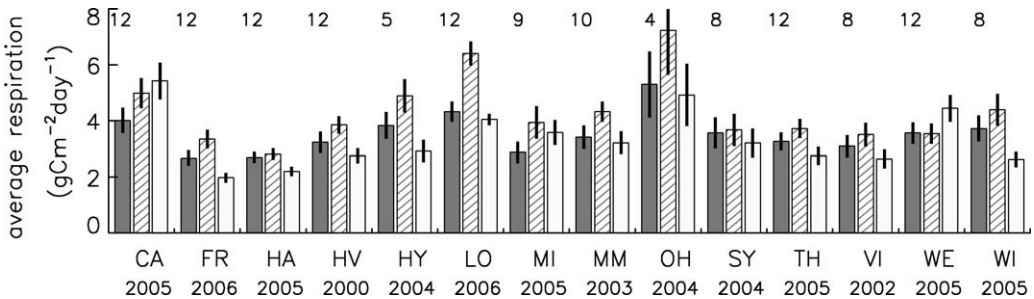

Fig. 7. Estimates of average nighttime respiration (R_{LRC}, R_{Rmax}, R_{ust}) commonly available from micrometeorological measurements. The grey bars stand for R_{LRC}, hatched bars for R_{Rmax} and white bars for R_{ust}. Numbers above grey bars indicate the number of months that were averaged. Only sites where all estimates were available for >3 months were used for this figure. The black line indicates 95% confidence intervals. Site names are given in Table 1.

drainage wind systems and a more detailed approach is needed that takes site specific flow patterns into account (Etzold, pers. comm.). Steep topography however is not a limiting factor, as different methods agreed well at Renon (RE) where height differences within the footprint exceed those of LA.

4. Conclusions

Compared to chamber measurements, the sum of the eddy flux of CO_2 plus change in storage terms in the mass balance equation underestimates ecosystem respiration for most of the night. This is because measurements on a single tower cannot account for vertical and horizontal advection of CO_2 due to drainage flows.

We used data from 25 sites covering a broad range of forest ecosystems and topographical conditions to test the general applicability of a novel approach (van Gorsel et al., 2007, 2008) to derive nighttime respiration rates R_{Rmax} from commonly available micrometeorological measurements (turbulent flux and change in storage term). The approach is based on the understanding of the processes leading to the onset of drainage currents for computing nighttime respiration. It uses data from the time period between sunset and the time when the canopy air layer has cooled to the extent that drainage currents are initiated, to derive a temperature response function for ecosystem respiration. Measured (half-) hourly soil temperatures are then used with this function to estimate respiration throughout the year.

Comparison with chamber measurements lends support to the notion that advection occurs at many sites including ones located in relatively gentle topography. We found very good agreement between R_{Rmax} and respiration derived from chamber measurements, which is of particular importance, as chambers provide the only measured independent estimates of respiration. The agreement between the methods also showed that terrain steepness is not a limiting factor for the use of R_{Rmax}. Terrain complexity however can be limiting when flow patterns deviate from simple slope and drainage wind systems. Detailed process-based forest ecosystem modelling provides another independent estimate of ecosystem respiration as long as parameter values are not derived from flux or chamber measurements. CASTANEA uses species-specific parameters compiled from literature and site-specific parameters such as soil characteristics and stand structure. Comparison of results derived from CASTANEA with R_{Rmax} led to equally good agreement.

Estimates using ecosystem light-response curves extrapolated to zero light, R_{LRC}, were very well correlated with R_{Rmax} and during summer months were generally smaller than R_{Rmax}. This is likely due to reduced leaf respiration in light relative to that in darkness. At most sites respiration rates estimated using the u_*-filter, R_{ust}, were smaller than both R_{LRC} and R_{Rmax} and at some sites R_{ust} underestimates true ecosystem respiration.

The high agreement of our approach with independent measurements R_{cham} and independent model output R_{cast} indicates that R_{Rmax} leads to excellent estimates of nighttime ecosystem respiration and can be used as further constraint in deriving ecosystem respiration.

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Appendix A

The time when the early evening maximum in $F_{C,S}$ ($t_{m,m}$) is expected to occur is detected from the mean daily course of $F_{C,S}$ for each 30-day period (see e.g. Fig. 1). Changing meteorological conditions may lead to some day-to-day variation in the timing of the daily maximum in $F_{C,S}$ ($t_{m,d}$) and thus a 3 h window, starting 1 h prior to $t_{m,m}$, was used to search for the daily maximum in $F_{C,S}$. To investigate how strongly the estimates of annual average respiration depend on the choice of this window width we calculated R_{Rmax} using a window size to 2 h, starting 1 h prior to $t_{m,m}$ and a window size of 4 h, starting 2 h prior to $t_{m,m}$. Fig. A1 shows that the estimates are within the 95% confidence of each other.

To exclude outliers from data used to construct a temperature response function, only respiration estimates within a plausible range $r = [0.5\bar{R}_{LRC}, 2\bar{R}_{LRC}]$ are used ($\bar{R}_{LRC}$ is the 30 day average respiration obtained from the light response curve approach). To test whether

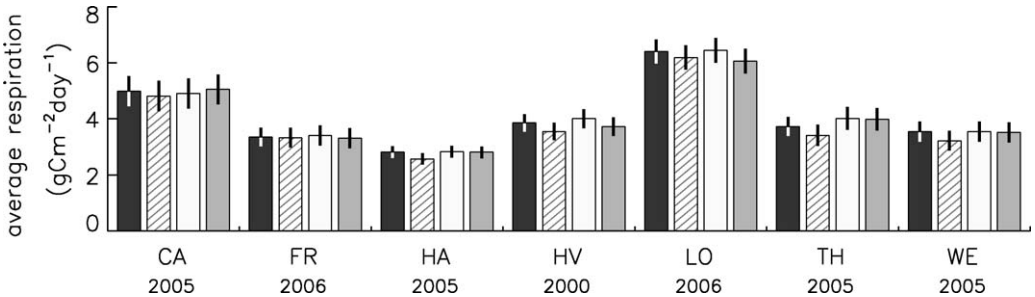

Fig. A1. Estimates of R_{Rmax} (black bars) obtained using a time window of 3 h (starting 1 h prior the time when the maximum in $F_{C,S}$ ($t_{m,m}$) is expected to occur) to detect the daily maximum in $F_{C,S,B}$Only values that lie in the range $r = [0.5\bar{R}_{LRC}, 2\bar{R}_{LRC}]$ are used to construct temperature response functions. Hatched and white bars indicate respiration estimates derived by applying a smaller (2 h, starting 1 h prior to $t_{m,m}$) and larger (4 h, starting 2 h prior to $t_{m,m}$) time window, respectively. Another estimate of R_{Rmax} (grey bars) was derived by using a 3 h time window and use values that lie in a range $r = [0.25\bar{R}_{LRC}, 4\bar{R}_{LRC}]$. Lines indicate 95% confidence intervals.

estimates of annual average respiration are sensitive on the range chosen we changed r to $r = [0.25\bar{R}_{LRC}, 4\bar{R}_{LRC}]$ and recalculated the annual average respiration. Fig. A1 shows that both estimates agree to within the 95% confidence intervals.

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