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Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation

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Abstract

The measured net ecosystem exchange (NEE) of CO_2 between the ecosystem and the atmosphere reflects the balance between gross CO_2 assimilation [gross primary production (GPP)] and ecosystem respiration (R_{eco}). For understanding the mechanistic responses of ecosystem processes to environmental change it is important to separate these two flux components. Two approaches are conventionally used: (1) respiration measurements made at night are extrapolated to the daytime or (2) light–response curves are fit to daytime NEE measurements and respiration is estimated from the intercept of the ordinate, which avoids the use of potentially problematic nighttime data. We demonstrate that this approach is subject to biases if the effect of vapor pressure deficit (VPD) modifying the light response is not included. We introduce an algorithm for NEE partitioning that uses a hyperbolic light response curve fit to daytime NEE, modified to account for the temperature sensitivity of respiration and the VPD limitation of photosynthesis. Including the VPD dependency strongly improved the model's ability to reproduce the asymmetric diurnal cycle during periods with high VPD, and enhances the reliability of R_{eco} estimates given that the reduction of GPP by VPD may be otherwise incorrectly attributed to higher R_{eco}. Results from this improved algorithm are compared against estimates based on the conventional nighttime approach. The comparison demonstrates that the uncertainty arising from systematic errors dominates the overall uncertainty of annual sums (median absolute deviation of GPP: 47 g C m^{-2} yr^{-1}), while errors arising from the random error (median absolute deviation: ~ 2 g C m^{-2} yr^{-1}) are negligible. Despite site-specific differences between the methods, overall patterns remain robust, adding confidence to statistical studies based on the FLUXNET database. In particular, we show that the strong correlation between GPP and R_{eco} is not spurious but holds true when quasi-independent, i.e. daytime and nighttime based estimates are compared.

Keywords: eddy covariance, flux partitioning, FLUXNET, GPP, hyperbolic light response curve, R_{eco}, uncertainty

Introduction

The eddy covariance technique measures the net ecosystem exchange (NEE) of CO_2, the balance between carbon released and taken up by ecosystem respiration (R_{eco}) and gross primary production (GPP). The separation of NEE into its components, which represent underlying processes, helps obtain mechanistic, process-level understanding of the terrestrial carbon cycle. Global, multi-site flux synthesis studies require that NEE be partitioned in a standardized manner, to minimize site-specific biases due to differences in processing (Foken & Wichura, 1996; Aubinet *et al.*, 2000; Baldocchi, 2003, 2008; Rebmann *et al*., 2005; Reichstein *et al*., 2005; Papale *et al*., 2006; Göckede *et al*., 2008).

Various flux partitioning methods are available and have been previously compared using measured or modelled data from single or multiple sites (Yi *et al*., 2004; Reichstein *et al*., 2005; Hagen *et al*., 2006; Stoy *et al*., 2006; Desai *et al*., 2008). Methods that rely on nighttime data for partitioning may be biased due to the frequent nighttime suppression of turbulence and dominance of advective fluxes not measured by conventional EC systems (Goulden *et al*., 1996; Aubinet *et al*., 2000; Feigenwinter *et al*., 2004; Aubinet, 2008). The second common approach, extrapolating respiration from light-response curves conditioned on daytime data, usually does not account for the fact that NEE varies both as a function of temperature (mostly affecting R_{eco}) and vapor pressure deficit (affecting GPP via stomatal regulation), among other factors. Confounding effects introduced by this shortcoming may have contributed to the large observed between-method variability in extracted diurnal cycles of R_{eco} (Desai *et al*., 2008). The diurnal cycle of NEE observations during dry periods with high VPD often has an asymmetric shape that is partly caused by higher respiration in the afternoon but also due to stomatal limitation of GPP as VPD tends to peak well after maximum diurnal radiation. As a consequence, measured carbon uptake at the same level of insulation may be substantially lower in the afternoon compared with morning hours. This phenomenon has effects on carbon gain and water-use efficiency of the ecosystem as well as partitioning of sensible and latent heat fluxes between the land surface and the atmosphere (Williams *et al*., 1996; Baldocchi, 1997; Reichstein *et al*., 2003b).

In this study, we address the following questions: (1) whether it is necessary to include VPD effects on photosynthesis when partitioning measured NEE using a light–response curve approach, (2) whether estimated annual sums of carbon fluxes based on daytime data show systematic differences compared with those based on nighttime data, and (3) whether this affects the strength of the often-noted relation between annual GPP and R_{eco} (Janssens *et al*., 2001; Reichstein *et al*., 2007; Wang *et al*., 2008). Here, we perform these analyses for the first time using a quasi-global biosphere-atmosphere carbon dioxide flux data set.

Materials and methods

Data

We used data from the FLUXNET 'La Thuile' database (http://www.fluxdata.org), where half hourly data had been provided by site managers and further processed in a standardized methodology described in Papale *et al*. (2006) and Reichstein *et al*. (2005). While an unprecedented level of standardization has been achieved in this database, one should still note that the derivation of half hourly fluxes from the high frequency raw data still varies from site to site (Moore, 1986; Foken & Wichura, 1996; Aubinet *et al*., 2000; Lee *et al*., 2004). We used the database version of December 2007 containing 976 site-years of half hourly eddy covariance data. The data are storage corrected, spike filtered, u*-filtered, and subsequently gap-filled. For the optimization of the model parameters only measured (i.e. nongapfilled) half hourly data were used. The sites chosen for the first part of the study (Table 1) were selected to cover a wide range of climates and vegetation types and to meet the requirement of a high fraction of original nongapfilled flux observations. The second part of the study, the global comparison of nighttime based and daytime based estimates, included all FLUXNET sites that satisfied the following criteria: (1) data availability for the whole year is higher than 80%, (2) data availability was sufficient to allow the estimation of the light-response curve parameter time series with no gaps larger than 750 h during the whole year, (3) the statistical uncertainty, due to the uncertainty of the estimated parameters [see 'Statistical uncertainty of the model output (GPP)'] of the annual GPP estimate was below $20\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. The third criterion was added to exclude extrapolation to conditions far from the data used for fitting, but only five site-years were affected additionally by this last criterion. After applying these criteria 417 site-years out of 976 from 145 sites were included in the comparison (site details are given in Appendix B). Five hundred and eleven sites were affected by criterion (2), 273 sites by criterion (1), 265 by both criteria (1 and 2).

Models

In this study we compare three different algorithms to partition NEE into GPP and R_{eco}; we are implicitly assuming that geochemical (i.e. nonbiological) processes can be ignored in this partitioning (Hofmeister, 1997; Kowalski *et al*., 2008). In all cases, models were fit to a short time window (4–15 days) to account for seasonal parameter variability, reflecting changes in the state of the ecosystem that are not represented in the models. The algorithm of the daytime data based estimates is described in detail in Appendix A.

Nighttime data-based estimate. This estimate is according to Reichstein *et al*. (2005), which is currently used to partition data in the FLUXNET database compilation and available as online tool at http://gaia.agraria.unitus.it/database/eddyproc. Briefly, GPP is assumed

Table 1 Eddy covariance sites selected for the first part of this study, EBF: evergreen broadleaf forest, GRA: Grassland, CRO: Crops, DBF: Deciduous broadleaf forest, ENF: Evergreen needle leaf forest, WSA: Wet Savanna

Site code	Name	Country	Latitude	Longitude	Vegetation type	Year	VPD range
FR-Pue	Puechabon	France	43.74	3.6	EBF	2001	4.1–25.9
US-IB2	IL – Fermi National Accelerator Laboratory- Batavia	USA	41.84	−88.24	GRA	2005	3.4–30
US-Bo1	IL – Bondville	USA	40.01	−88.29	CRO	2000	0.4–20.9
DE-Hai	Hainich	Germany	51.08	10.45	DBF	2003	3.1–17.6
CA-Sj1	Sask. – 1994 Harv. Jack Pine	Canada	53.91	−104.66	ENF	2005	1.6–22.7
CA-Oas	Sask. – SSA Old Aspen	Canada	53.63	−106.2	DBF	2003	2.4–21.3
BW-Ma1	Maun – Mopane Woodland	Botswana	−19.92	23.56	WSA	2000	3.7–35.2
BR-Ma2	Manaus – ZF2 K34	Brazil	−2.61	−60.21	EBF	2005	3.2–22.2

VPD range is the mean diurnal VPD range of the data used in Fig. 1.

to be zero during nighttime periods (defined here as global radiation (R_g) $<20\,W\,m^{-2}$) and measured NEE is composed entirely of R_{eco}, to which a model is fit and extrapolated to daytime periods. An Arrhenius-type model after Lloyd & Taylor (1994) is used to describe the temperature dependence of R_{eco}:

$$R_{eco} = rb \exp\left(E_0\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{air} - T_0}\right)\right), \qquad (1)$$

where rb ($\mu mol\,C\,m^{-2}\,s^{-1}$) is the base respiration at the reference temperature [T_{ref} ($^\circ C$), set to $15\,^\circ C$], E_0 ($^\circ C$) is the temperature sensitivity, T_{air} is the air temperature, and parameter T_0 ($^\circ C$) is kept constant at $-46.02\,^\circ C$ as in Lloyd & Taylor (1994). For E_0 a constant value is used for the whole year while rb was estimated every 5 days using a 15 days window (as in Reichstein *et al.*, 2005). Using daytime temperature, respiration is extrapolated to the daytime and the difference between modeled R_{eco} and measured NEE yields estimated GPP. We refer to this estimate as 'NB' (nighttime data-based).

Daytime data-based estimate including temperature sensitivity of respiration. For the daytime data based estimate NEE was modelled using the common rectangular hyperbolic light–response curve (Falge *et al.*, 2001):

$$NEE = \frac{\alpha\beta R_g}{\alpha R_g + \beta} + \gamma, \qquad (2)$$

where NEE is net ecosystem exchange, α ($\mu mol\,C\,J^{-1}$) is the canopy light utilization efficiency and represents the initial slope of the light–response curve, β ($\mu mol\,C\,m^{-2}\,s^{-1}$) is the maximum CO_2 uptake rate of the canopy at light saturation, γ ($\mu mol\,C\,m^{-2}\,s^{-1}$) is the ecosystem respiration and R_g is the global radiation ($W\,m^{-2}$). Although the nonrectangular light response model was shown to improve results, here we preferred the parsimonious rectangular curve. Gilmanov *et al.* (2003b) found that for the respiration parameter the differences between the two models, rectangular and nonrectangular, are small ($<10\%$). We modified the hyperbolic light–response curve to account for the temperature dependency of respiration after Gilmanov *et al.* (2003a) by replacing the constant respiration γ with a respiration model, in this case the Lloyd & Taylor model (Lloyd & Taylor, 1994) as given in Eqn (1)

$$NEE = \frac{\alpha\beta R_g}{\alpha R_g + \beta} + rb \exp\left(E_0\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{air} - T_0}\right)\right). \qquad (3)$$

T_{ref} and T_0 were fixed as in the nighttime data-based approach. The other parameters (E_0, rb, α, β) of the model were estimated in two different ways: (1) E_0 was estimated using nighttime data ($R_g<4\,W\,m^{-2}$), then E_0 was fixed and rb, α, β were derived from daytime data ('DB noVPD', daytime data-based, E_0 estimated with nighttime data). (2) all parameters (E_0, rb, α, β) were estimated using daytime data ('DB noVPD all', daytime data based with all parameters estimated using daytime data). The upper bound of the parameter E_0 as given in Table A1 was not used, as otherwise often the E_0 parameter was rejected during periods with high VPD.

For estimates of daily or annual NEE, respiration was extrapolated into the nighttime using T_{air} measured during the night and the values obtained for E_0 and rb. The threshold for the definition of nighttime data ($R_g<4\,W\,m^{-2}$) is lower here than in the nighttime data based approach, as excluding all data with $R_g<20\,W\,m^{-2}$ leads to long gaps for high latitude sites.

Daytime data-based estimate including temperature sensitivity of respiration and VPD limitation of GPP. The second modification of the hyperbolic light response curve accounts for the VPD limitation of GPP. Here, the fixed parameter β in Eqn (3) was replaced with an exponential decreasing function (Körner, 1995) for β at high water VPD:

$$\beta = \begin{cases} \beta_0 \exp(-k(\mathrm{VPD} - \mathrm{VPD}_0)), & \mathrm{VPD} > \mathrm{VPD}_0, \\ \beta = \beta_0, & \mathrm{VPD} < \mathrm{VPD}_0. \end{cases} \quad (4)$$

Please note that the VPD in the atmosphere is used here, while physiologically more relevant would be the leaf-to-air VPD which is higher or lower than atmospheric VPD when leaf temperatures are higher or lower then air temperature, respectively. For the empirical purpose of this study we deem the use of atmospheric VPD sufficient, given the fact that leaf-to-air VPD (or leaf temperatures) is usually not observed at FLUXNET sites. The k parameter was estimated for each 4-day data window to quantify the response of the maximum carbon uptake to VPD. Since we found that the parameter k was not well constrained after including the VPD_0 in the optimization, the VPD_0 threshold was set to 10 hPa in accordance with earlier findings at the leaf level (Körner, 1995), at this point ignoring potential vegetation specific differences. We will refer to this method as 'DB VPD' (daytime data based including VPD). E_0 was estimated using nighttime data as in the 'DB noVPD'-method and α, β_0, k and rb were estimated using daytime data (Appendix A).

Parameter estimation

We assume a serially uncorrelated Gaussian distributed random error and a heteroscedastic flux magnitude-varying standard deviation (SD) of the random error as found by Lasslop *et al.* (2008). Hence, parameter estimation made use of this information by applying a weighted least squares cost function (cf. Hollinger & Richardson, 2005). We estimated the error SD of the data (data uncertainty), σ_{meas}, for each data point following Lasslop *et al.* (2008) and used these estimates to weigh the data in the cost function in Eqn (5). The optimal parameters are found by minimizing the weighted least squares cost function J:

$$J(p) = \sum_{i=1}^{n} \frac{(y_{\mathrm{meas},i} - y_{\mathrm{mod},i}(p))^2}{\sigma^2_{\mathrm{meas},i}}, \quad (5)$$

where y_{meas} is the observed value and y_{mod} is the parameter (p) dependent modeled value. The model parameters were estimated using the Levenberg–Marquardt algorithm of the PV-wave advantage software package (Visual Numerics, 2005).

Statistical uncertainty of the model output (GPP)

The uncertainty estimate of the model output is based on the classical frequentist approach as described in Omlin & Reichert (1999). The covariance matrix of the model parameters is used to calculate the uncertainty of the model output by linear error propagation:

$$\mathrm{Cov}(y_{\mathrm{mod}}) = \left(\frac{\partial y_{\mathrm{mod}}}{\partial p}\right) \mathrm{Cov}(p_{\mathrm{opt}}) \left(\frac{\partial y_{\mathrm{mod}}}{\partial p}\right)^{\mathrm{T}}. \quad (6)$$

When interpolating between the model output of two parameter sets (see description of the algorithm, Appendix A) the error variance was interpolated as follows:

$$\mathrm{Var}(y) = w_1^2 \mathrm{Var}(y_1) + w_2^2 \mathrm{Var}(y_2), \quad (7)$$

where w_1 and w_2 are the weights representing the temporal distance of y to the middle of the time window of the neighboring parameter sets.

When aggregating the variance to annual sums, we included the covariance between n half hourly values (Rüger, 1996), $y_1, \ldots, y_n$ of the model output:

$$\mathrm{Var}(\Sigma y_i) = \sum \mathrm{Var}(y_i) + \sum_{i \neq j} \mathrm{Cov}(y_i, y_j). \quad (8)$$

Here i and j go from 1 to the number of values being aggregated.

The statistically expected differences, err, in annual sums of GPP caused by the random error, assuming a normal distribution of the random error, are computed as

$$\mathrm{err} = \sqrt{\mathrm{Var}(\mathrm{GPP}_{\mathrm{annual}})}\, randn, \quad (9)$$

where $\mathrm{Var}(\mathrm{GPP}_{\mathrm{annual}})$ is the variance of the annual sum of GPP and randn is a normally distributed random number with zero mean and unit SD. We draw 100 samples from the distribution for each site.

Results and discussion

VPD limitation of the light response curve

Particularly on warm, dry days, the diurnal cycle of NEE is often asymmetric: carbon uptake at comparable insulation is substantially lower in the afternoon compared with morning hours. This behavior could be caused by higher respiration due to higher temperatures or by a limitation of GPP due to stomatal closure at high VPDs (Körner, 1995).

The decrease of NEE magnitude with high VPD is evident to varying degrees at each of the eight sites selected for more detailed analysis (see Table 1, Fig. 1). When the VPD effect is not accounted for in a light–response curve, the consequences are systematic model

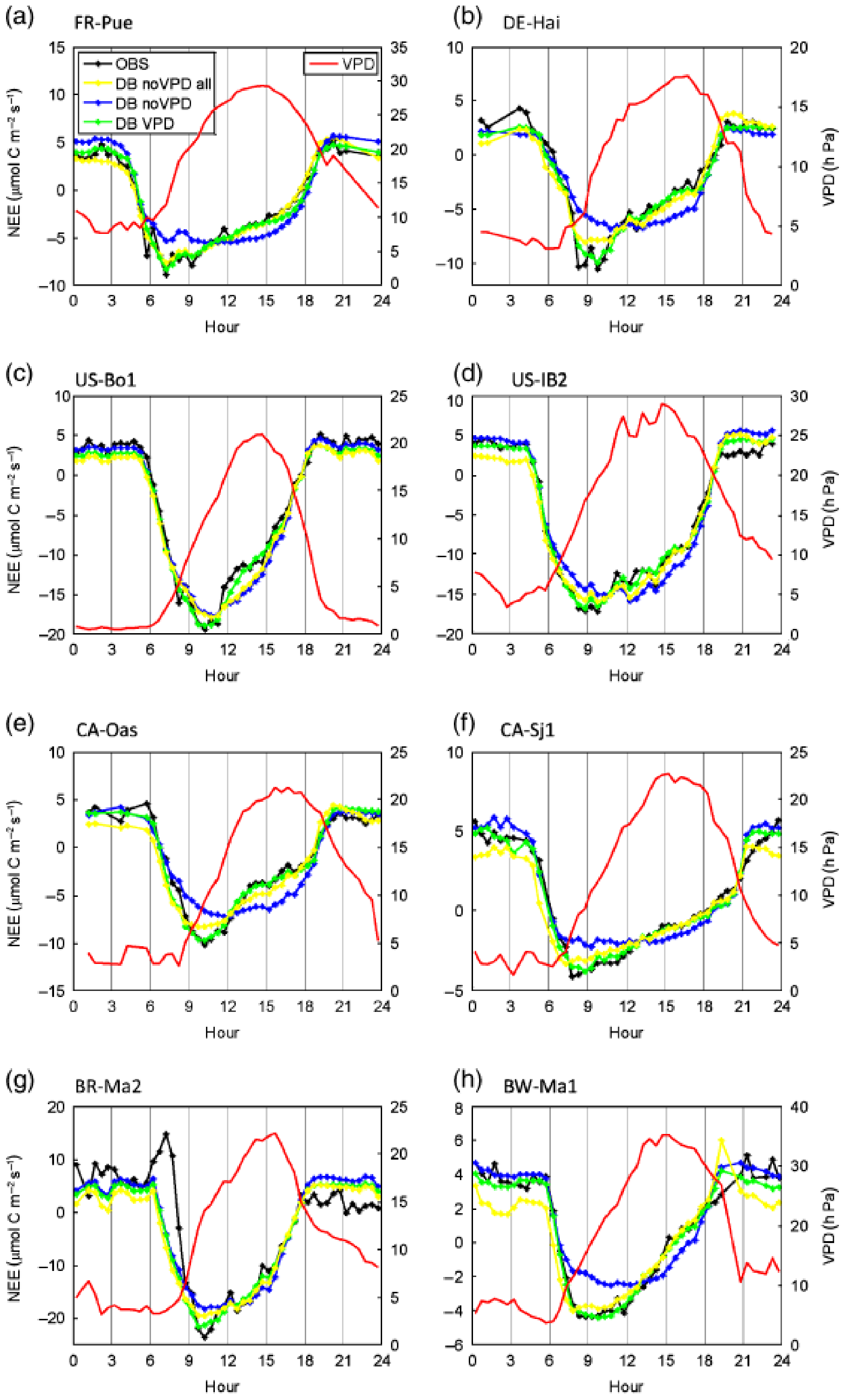

Fig. 1 Mean diurnal cycle of NEE observations and the three approaches of the light response curve and VPD for periods with 10 days with high daily maximum VPD (> 15 hPa) for sites in different climatic regions and different vegetation types, see Table 1 for site details.

errors whose magnitude depends on the response of GPP to VPD (Fig. 2). Using the DB noVPD approach, the diurnal cycle of the modeled NEE has the symmetric properties of the diurnal cycle of the global radiation, and the model under-predicts the flux magnitude in the morning and over-predicts during the afternoon (see

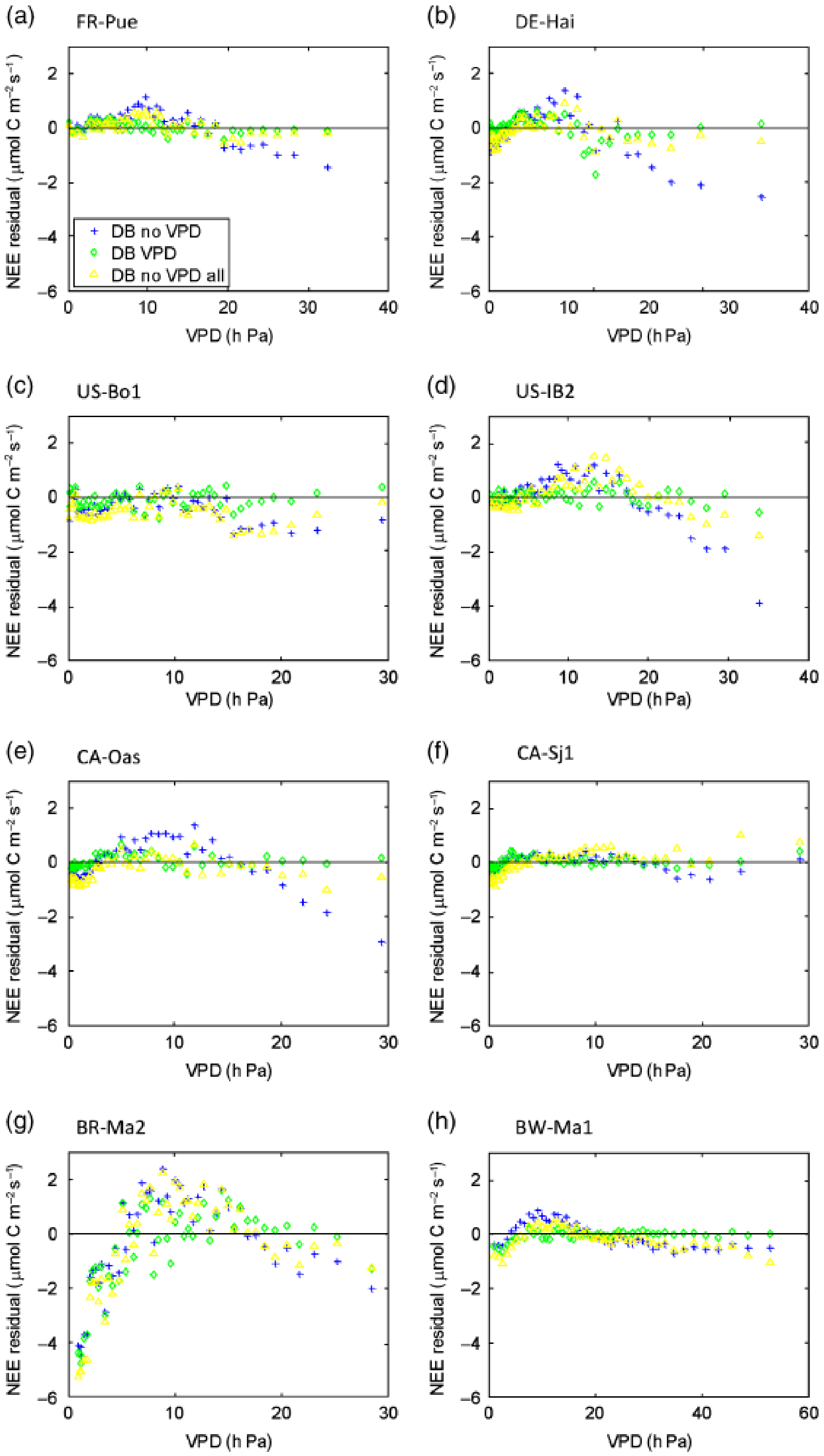

Fig. 2 Half hourly NEE residuals assembled into 50 VPD bins, high quality daytime observations of the whole year are used. Positive residuals mean the modeled fluxes are higher (more positive, signifying less ecosystem CO_2 uptake) than the observations.

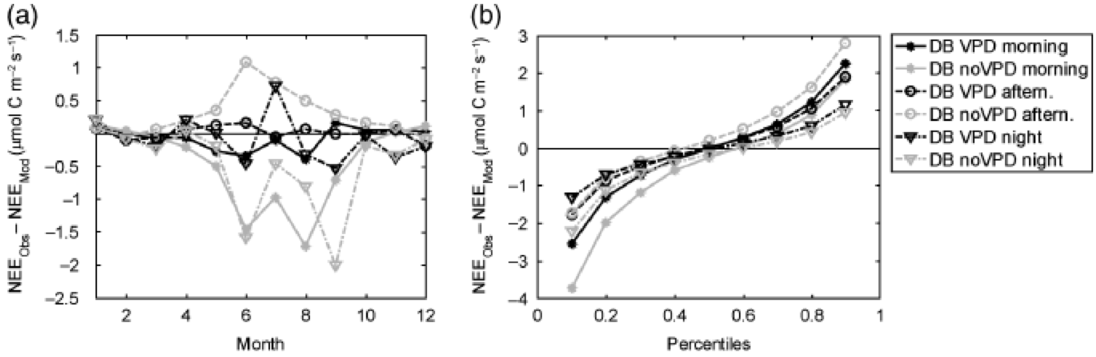

Fig. 3 Seasonal cycle of the morning, afternoon and night biases of the DB VPD and DB noVPD estimate (a), percentiles of the morning, afternoon and night biases of the DB VPD and DB noVPD half hourly estimates (b). Data: US-Ib2.

the flux magnitude in Fig. 1 and the difference in sign in Fig. 3 and Table 2). Comparing the biases observed during morning, afternoon and nighttime on annual time scales (Table 2) shows that the NEE of the DB noVPD is more negative in the afternoon and more positive at night and during morning hours compared with the observations.

The NEE predictions of the DB noVPD approach are more positive in the morning as the model fails to replicate the negative peak in NEE before noon. Values are more negative in the afternoon as DB noVPD does not account for the decrease in NEE magnitude likely due to higher afternoon VPD (at similar levels of radiation compared with morning hours). Without accounting for the VPD the parameter estimation routine increases *rb* to mimic the more positive NEE during the afternoon. This in turn results in higher nighttime respiration estimates. The biases are larger during the growing season (Fig. 3a; similar results are found for the other sites) as VPD itself and the flux rates are higher, e.g. GPP is small or zero outside the growing season. The residuals of the DB noVPD method show a similar pattern with respect to VPD across all sites analyzed here. Modeled NEE is lower (more negative) than observations at low and high VPD, and is higher than measurements in the intermediate VPD range (Fig. 2). The largest difference between model and observations occurs at high VPD.

Using the 'DB noVPD all' method, the asymmetry of the diurnal cycle can be mimicked by compensating for the absence of a VPD limitation term by increasing the parameter estimate of respiration in the afternoon, caused by an unrealistically high estimate of temperature sensitivity (E_0) up to more than 1000. Such a high value corresponds to a Q_{10} of 15 between 10 °C and 20 °C. When extrapolated to nighttime periods, the higher E_0 can cause a strong, temperature-related decrease of R_{eco} during the night (BW-Ma1, CA-Oas, US-Ib2, Fig. 1), which is inconsistent with the observed data (Fig. 1, where nighttime NEE equals R_{eco}). While the pattern in the residuals with respect to VPD is reduced compared with the DB noVPD method (Fig. 2), the residuals using the 'DB noVPD all' method are biased with respect to R_g and T_{air} (Fig. 5).

Table 2 Mean annual bias between modeled and observed NEE (μmol m^{-2} s^{-1})

	Morning		Afternoon		Night	
Site	*HBLR*	*HBLR VPD*	*HBLR*	*HBLR VPD*	*HBLR*	*HBLR VPD*
FR-Pue	−0.66	−0.31	0.16	0.07	−0.28	0.00
US-IB2	−0.53	−0.09	0.33	0.01	−0.53	−0.12
US-Bo1	−0.03	0.22	0.05	−0.04	−0.39	−0.26
DE-Hai	−0.36	0.03	0.17	−0.05	−0.38	−0.26
CA-Sj1	−0.25	−0.06	0.04	0.04	−0.20	0.05
CA-Oas	−0.54	0.05	0.00	−0.03	−0.27	0.00
BW-Ma1	−0.29	0.16	0.23	0.00	0.11	0.46
BR-Ma2	2.01	2.83	−0.79	−0.90	−0.76	−0.57

Only measured high-quality data were used in the comparison.

Different estimates of the temperature sensitivity (E_0) also result in different diurnal amplitudes of R_{eco}; this may explain the earlier reported large disagreement of diurnal R_{eco} courses in the intercomparison of statistical flux-partitioning algorithms (Desai *et al.*, 2008). Our results strongly caution against confounding VPD effects on GPP with temperature effects on R_{eco}; these are fundamentally different mechanisms and must be treated separately. Given the high temperature-dependence of VPD, such confounding effects may be not always easily resolved from the daytime data, we here prefer to derive E_0 (the temperature response of R_{eco}) from nighttime data and the magnitude (*rb*) from daytime data (cf. Appendix A). Contrary to Reichstein *et al.* (2005) we hence do not rely on the problematic nighttime data for estimation of the R_{eco} magnitude. However, our ap-

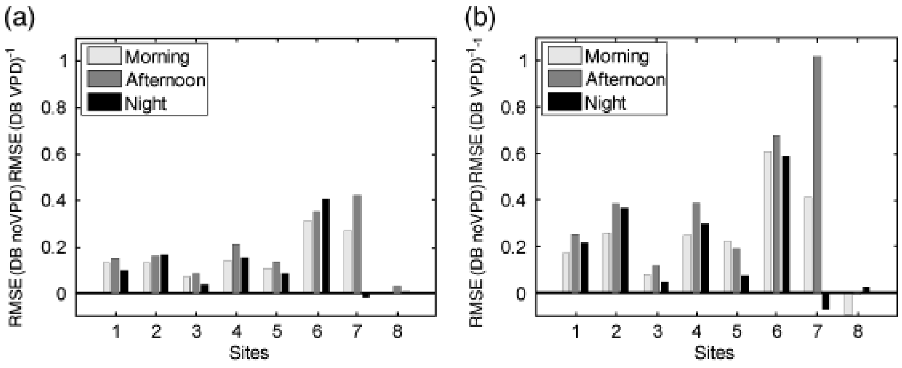

Fig. 4 Relative changes in RMSE when including VPD on halfhourly (a) and daily (b) timescale, for the sites 1, FR-Pue; 2, US-IB2 3,US-Bo1; 4, DE-Hai; 5, CA-Sj1; 6, CA-Oas; 7, BW-Ma1; 8, BR-Ma2; positive values indicate a lower RMSE for the DB VPD model.

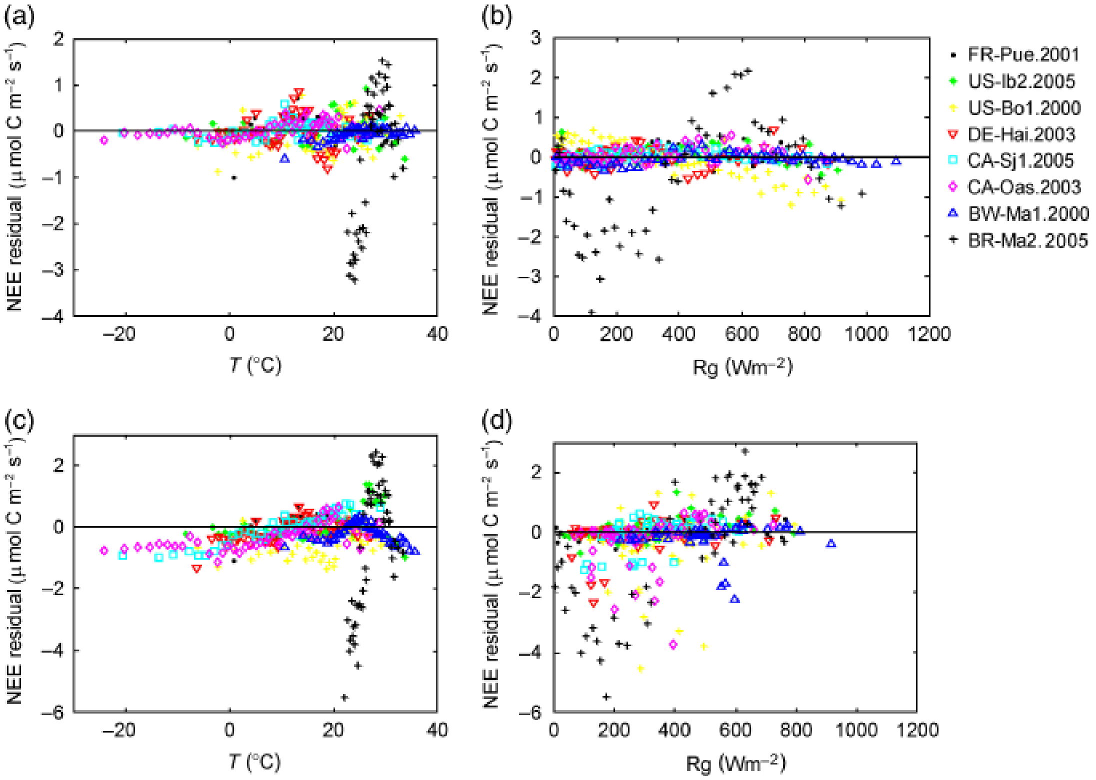

Fig. 5 Residuals of the DB VPD derived NEE vs. the model drivers, air temperature (a) and global radiation (b). Residuals of the DB noVPD all vs. air temperature (c) and global radiation (d).

proach did not overcome all issues (see 'Limitations of the algorithm').

Including a VPD limitation of GPP in the model (DB VPD) generally improves the ability of the model to reproduce the peak before noon and the decrease in the afternoon across the selected sites (Fig. 1). The site BR-Ma2 is an exception here, see 'Limitations' section below for a discussion.

The annual RMSE is reduced when including VPD in the model, on both half hourly and daily time scales (Fig. 4). The model including VPD eliminates the clear systematic bias for the different periods of the day (Table 2). The median of the error distribution is closer to zero and the range of the bias is reduced (Fig. 3b). Small biases of the model compared with the NEE observations used for fitting can be caused by the weighting in the cost function, and the interpolation of fluxes between the different parameter sets.

For DB VPD, the residuals are not correlated with VPD (e.g. maximum $R^2 = 0.02$ even for a third degree polynomial for BR-Ma2) and there is no consistent pattern across sites, indicating that systematic biases associated with the revised model tend to be minimal (Fig. 2). The bias of the residuals with respect to VPD was reduced by estimating the temperature sensitivity with daytime data: in some sites (FR-Pue and DE-Hai) this bias was removed entirely. At first sight both methods result in similar NEE estimates, however, residual analysis shows that the DB noVPD all method is biased with respect to T_{air} and global radiation (Fig. 5). This indicates that the asymmetry in the diurnal cycle is mainly caused by the VPD limitation of GPP. When modeling this behavior by increased respiration, the estimates are biased, with respect to temperature and the temperature sensitivity is too high.

The residuals of the two drivers of the model, temperature and global radiation, do not show consistent patterns across sites for the DB VPD method (Fig. 5). As VPD is partly a function of temperature, including the VPD limitation reduces the pattern in the relation between residuals and temperature (not shown). Owing to this strong correlation it is not possible to differentiate statistically between VPD-driven and temperature-driven decreases in GPP (Doughty & Goulden, 2008). There is no systematic bias in the residuals for high temperature (Fig. 5), suggesting that adding VPD limitation is a logical step for improving estimation of GPP and R_{eco} from daytime data across globally distributed ecosystems.

Limitations of the algorithm. We chose to use a simple, empirical model for this analysis. These models can be applied across a wide range of sites and vegetation types without the need for side-specific data on vegetation structure or C pools. However, complex interactions among physiological processes cannot necessarily be described by a simple equation. Hence, despite the achievement of a good and almost unbiased description of the diurnal NEE course through the inclusion of VPD effects on GPP there remain a number of limitations of the light-response curve approach, namely:

1. It has been reported that canopy assimilation is not only affected by the overall short wave radiation flux density, but also by its 'source' i.e. whether dominated by diffuse or direct radiation. With diffuse radiation higher assimilation rates have been observed at the same overall radiation flux density (Hollinger *et al.*, 1994; Baldocchi *et al.*, 1997; Gu *et al.*, 2003; Niyogi *et al.*, 2004; Jenkins *et al.*, 2007; Knohl & Baldocchi, 2008). This effect is not reflected in our light-response curve. However, two issues remain uncertain: First, the magnitude of the direct effect and the effect of the background correlation of high diffuse radiation with low VPD values (Rodriguez & Sadras, 2007; Wohlfahrt *et al.*, 2008a), second, and practical limitation that relatively few FLUXNET sites measure diffuse radiation. Currently a specific analysis on this topic is being carried out as part of the FLUXNET synthesis activities (A. Cescatti *et al.* unpublished data).
2. Circadian rhythms of stomatal conductance are not considered in our approach. They are either endogenous or caused by hydraulic limitations in the afternoon. These patterns in the diurnal cycle can persist for more than a week independent of environmental influences (Hennessey & Field, 1991). Although this effect has been widely observed (Gorton *et al.*, 1993; Hennessey *et al.*, 1993; Nardini *et al.*, 2005), the degree to which they affect the carbon exchange under field conditions is less clear. Williams & Gorton (1998) suggested by using a modeling approach that theses circadian rhythms do not significantly affect photosynthesis and stomatal conductance in field conditions.
3. The respiration model is only driven by temperature, but the overall signal of ecosystem respiration originates from different parts of the ecosystem which experience different temperatures. It is not clear which temperature is the appropriate driver for ecosystem respiration; studies suggest that this can vary between sites (Richardson *et al.*, 2006). We used air temperature as it often explains more variance of the ecosystem respiration (Reichstein *et al.*, 2005, but see Richardson *et al.*, 2006) and using air temperature more consistent temperature-respiration relationships have been found in some ecosystems (Van Dijk & Dolman, 2004). A large part of soil respiration can be assumed to be derived near the surface across ecosystems, which is better characterized by air temperature than soil temperature at deeper soil layers. Diurnal hysteresis effects are found for respiration when plotted against soil temperature (Bahn *et al.*, 2008; Vargas &Allen, 2008), this hysteresis increases with increasing soil depth (Bahn *et al.*, 2008). Moisture limitation has an significant effect on soil respiration (Irvine & Law, 2002). This limitation is not explicitly included in the model and few FLUXNET sites measure soil moisture, limiting its potential for widespread application at the present. However, parameter estimation may account for it by varying *rb*. Diel patterns in respiration that are not

driven by temperature but by soil moisture (Carbone *et al.*, 2008), are not reflected in the model.

4. As the light response curves are fit to daytime NEE, errors in GPP can always be compensated by errors in R_{eco}, resulting in incorrect estimates for both GPP and R_{eco} without compromising NEE model fit. Desai *et al.* (2008) showed this to occur for synthetic data. This problem occurs in particular if VPD is not included in the model, as the afternoon decrease in NEE is then ascribed to a higher respiration instead of a limited GPP and consequently leads to biased estimates. We reduced this confounding effect by extending the light response approach with a VPD limitation and estimating the temperature sensitivity using nighttime data independent of the NEE response to VPD.
5. The algorithm, as well as other flux partition algorithm strongly depends on the quality of the NEE measurements and an accurate quality assessment (Foken & Wichura, 1996). The positive peak in measured NEE during the morning at the Brazilian site (Fig. 1) and the strong bias in the residuals for low VPD (Fig. 2) likely occurs as a result of an incomplete storage correction as documented earlier for this site (Araujo *et al.*, 2008, 2002). Such problems arising from the complexity of site need to be addressed before such simple algorithms can be applied successfully.

Comparison of nighttime and daytime based estimates

We compared annual sums of GPP and R_{eco} of the updated DB VPD and conventional NB partitioning approach for all FLUXNET site-years with sufficient available data (417 site-years, 145 sites, see Appendix B). For NEE we compared the DB VPD estimate with the gap-filled annual sum of observations. The two estimates were strongly correlated [$R^2(\mathrm{NEE}) = 0.83$, $R^2(\mathrm{GPP}) = 0.97$, $R^2(\mathrm{R_{eco}}) = 0.86$], but deviations exceeded $52\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for NEE, $47\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for GPP $87\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for R_{eco} in over 50% of site-years (see Figs 6 and 7). These numbers are in a comparable range of the uncertainties reported for the u^* threshold, that remain below $100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for NEE (Papale *et al.*, 2006).

Comparing the gapfilled observations with the DB VPD method does not show systematic differences for the annual NEE estimates throughout the FLUXNET database (Figs 6 and 7). For GPP and R_{eco}, the confidence intervals of the regression parameters include a slope of one and an offset of zero, thus there is no systematic bias. For NEE the DB VPD estimate is slightly more negative compared with the observations, indicating greater biosphere C uptake by the model than is apparent in the data. The 95% confidence interval of the NEE offset does not include zero, but the slope is not significantly different from one.

The NB approach produces slightly higher R_{eco} estimates than the DB VPD approach, but the differences are not significant on the annual timescale. Despite being insignificant, differences were thought to be caused by a difference in the diurnal vs. seasonal temperature sensitivities of R_{eco} (Gaumont-Guay *et al.*, 2006); the NB approach overestimates daytime R_{eco} because it effectively characterizes the seasonal temperature sensitivity.

The higher NB estimates of R_{eco} are contrary to expectations that are based on the assumption that nighttime fluxes would be underestimated due to, e.g. insufficient turbulent exchange or missing low frequency contributions. Possibly, on average, the use of a nighttime u^* filter effectively addresses this problem. Nighttime-based approaches could also overestimate daytime R_{eco} because of a reduction of leaf respiration in the light (Brooks & Farquhar, 1985; Atkin *et al.*, 1998), thus the relationship derived from nighttime data could overestimate respiration during daytime and vice versa for the daytime data based estimate, although this daytime reduction of respiration is highly controversial among plant physiologists (Loreto *et al.*, 2001; Pinelli & Loreto, 2003).

The NB and DB VPD estimates of GPP are more strongly correlated than those of R_{eco}, because both approaches estimate GPP from daytime NEE, while NB R_{eco} is estimated independently of the daytime NEE data. While the correlations of R_{eco} and GPP are comparable, the lower correlations for NEE are caused by the smaller range of the data (-1000 to 500 compared with 0–4000 $\mathrm{gC\,m^{-2}\,yr^{-1}}$), but with the same amount of scatter. This is also reflected in the histograms of the annual differences between nighttime and daytime based estimate in Fig. 7.

The median deviation of NEE and GPP are within the same range, while the spread of the differences in R_{eco} is much wider. We chose the median and median deviation to characterize the histogram, as the distribution is not Gaussian but more leptokurtic and the SD does not characterize such distributions appropriately. The median of all three histograms is close to zero, supporting the conclusion that there is no overall systematic difference between daytime- and nighttime-based annual carbon flux estimates.

The deviations between NB and DB VPD represent the uncertainty in the annual estimates caused by inconsistent nighttime data and the choice of the partitioning method. Inconsistencies between day and nighttime data can be caused by low turbulence, advection,

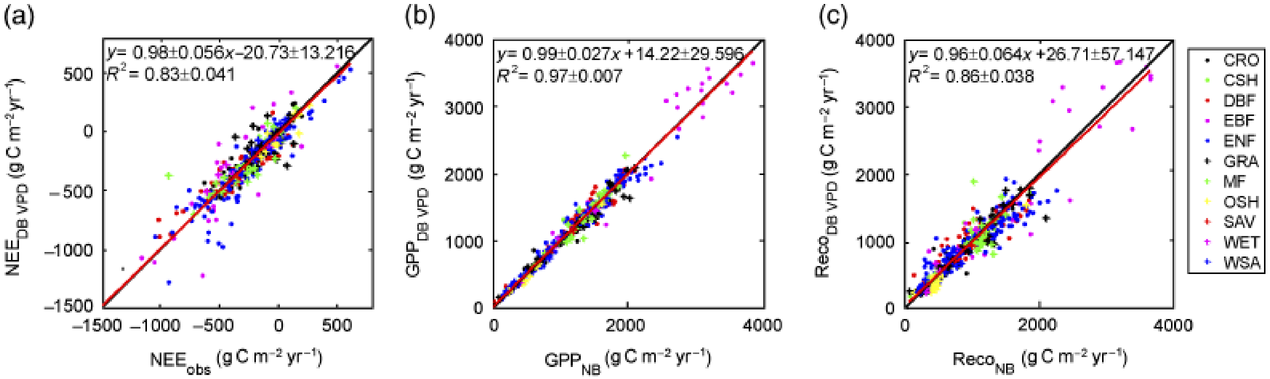

Fig. 6 Scatter plots of (a) annual sums of gapfilled observations (*x*-axis) and DB VPD (*y*-axis) estimates of NEE, annual sums of nighttime data based (*x*-axis) and DB VPD (*y*-axis) estimates of (b) GPP and (c) R_{eco}. CRO, cropland; CSH, closed shrubland; DBF, deciduous broadleaf forest; EBF, evergreen broadleaf forest; ENF, evergreen needleleaf forest; GRA, grassland; MF, mixed forest; OSH, open shrubland; SAV, savanna; WET, wetland; WSA, woody savanna.

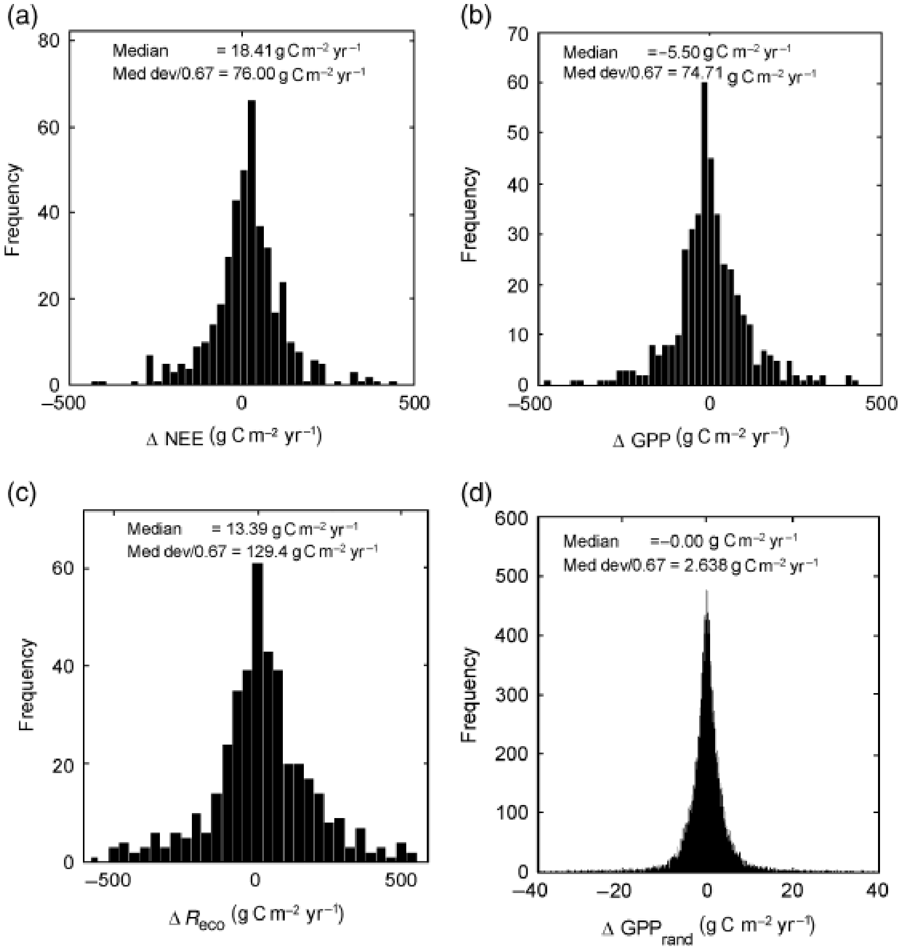

Fig. 7 Histograms of the difference between gapfilled annual observations and the daytime data based estimate of NEE (a), annual nighttime data based estimate and daytime data based estimate for (b) GPP, (c) R_{eco}. The Median deviation/0.67 is a robust estimate for the SD, a positive difference denotes a more positive nighttime based estimate. (d) Histogram of the expected difference between GPP estimates based on the statistical uncertainty of GPP caused by the half-hourly random errors.

insufficient *u**-filtering, decoupling of the flow or a difference in the footprint; at night the footprint is smaller than during the day. Comparing the deviations arising from such systematic errors, the deviations arising from statistical uncertainty, is small, in most cases below $20\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for GPP (Fig. 7). The statistical uncertainty is mainly caused by the random error of the data and is relatively small on an annual basis. The uncertainties due to inconsistencies in the data and the partitioning method is one order of magnitude larger (see also Richardson *et al*. (2006).

The deviations between the methods vary across vegetation types. Table 3 characterizes the distribution of differences between daytime data based and nighttime data based estimates of GPP and R_{eco}, and between daytime data based and gapfilled NEE for the different vegetation types. The strongest deviation of the median from zero is found for vegetation types with a small number of sites available, suggesting that increasing the number of sites may remove the apparent bias. The median deviation appears to be higher for tall vegetations (forests). The NEE observations are higher (positive median) for all vegetation types, except wetlands compared with the daytime data based estimates, and the nighttime data based R_{eco} estimate is higher for most vegetation types. For GPP no clear pattern emerged. The strong differences in the median deviation between vegetation types suggest a strongly varying uncertainty between sites. This result supports the necessity of a site and year specific uncertainty estimate, incorporating all sources of uncertainty, to enable scientists to use the data properly to fully exploit the information inherent to the database.

Global relationship between carbon fluxes in the FLUXNET database

For the first time, we can now compare quasi-independent estimates of GPP and R_{eco} across a large data set, since we can use GPP derived from daytime data and R_{eco} derived from nighttime data only. Previous studies including Reichstein *et al*. (2007), Wang *et al*. (2008), Baldocchi (2008) relied on GPP and R_{eco} estimates which were ultimately derived from the same data. To some extent this may cause spurious correlation between R_{eco} and GPP, since GPP is inferred as R_{eco} minus NEE (Vickers *et al*. (2009); but see comment by Lasslop *et al*. submitted to Agricultural & Forest Meteorology). Here, we do not compute GPP as a difference, but moreover derive R_{eco} and GPP from quasi-disjoint NEE data subsets. Hence, we minimize spurious correlations and still find a strong and highly significant positive relation between annual GPP and R_{eco} (Fig. 8). These results give further evidence to Janssens *et al*. (2001), Reichstein *et al.* (2003a, b, 2007), Baldocchi (2008) – now across and separated into different biomes – that ecosystem assimilation and respiration are strongly coupled on the annual time scale. The overall relationship shown in Fig. 8 is dominated by spatial (= between-site) variability – e.g. the spatial coefficient of variation of mean site GPP is 53% while the temporal coefficient of inter-annual GPP variation reaches only 2–57%, with a median of 9%. This overall between-site correlation of GPP and R_{eco} can be relatively easily explained by typical ecosystem model concepts that involve carbon pools that are built up by photosynthesis and allocation and subsequently decomposed by autotrophic and heterotrophic respiration (Sitch *et al*., 2003;

Table 3 The median, median deviation/0.67 (med dev, i.e. an estimate of the SD) and kurtosis (kurt) of the annual differences between NB and *DB VPD* estimate (GPP and R_{eco}) and between daytime data based estimate and gapfilled observations (NEE) for different vegetation types

	NEE			GPP			R_{eco}			
	Median	med dev	kurt	Median	med dev	kurt	Median	med dev	kurt	*N*
CRO	14.62	79.31	2.66	−9.90	52.00	6.46	11.15	81.22	6.29	37
CSH	33.07	93.19	1.98	−50.61	69.76	3.58	−51.52	153.10	3.21	8
DBF	15.14	76.11	3.68	−15.95	101.66	3.46	−0.62	144.38	3.40	79
EBF	14.36	163.05	3.61	9.21	269.59	2.44	19.25	420.62	2.72	30
ENF	21.43	83.78	6.32	−9.63	77.33	4.07	18.64	147.04	3.74	148
GRA	17.40	59.76	5.72	7.82	55.53	7.54	26.41	82.33	11.78	49
MF	26.32	84.87	10.93	3.53	67.05	5.36	16.83	142.69	8.13	29
OSH	63.46	41.73	3.92	20.66	60.28	1.42	84.12	103.15	2.31	14
SAV	33.05	6.36	1.00	27.28	13.17	1.00	60.33	19.52	1.00	2
WET	−58.49	120.75	1.45	−2.34	20.27	2.76	−60.66	97.39	1.92	6
WSA	4.04	37.96	2.75	−30.73	40.23	2.52	−25.11	85.97	2.61	15

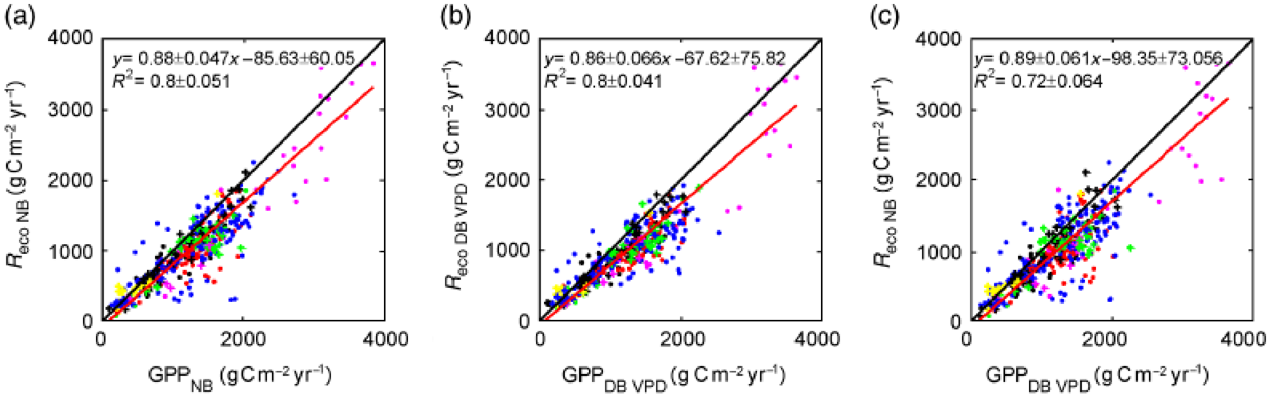

Fig. 8 Scatter plot of the annual sums (a) of the nighttime data based estimate of R_{eco} and GPP, (b) of the daytime data based estimate of R_{eco} and GPP, (c) of the daytime data based GPP and the nighttime data based R_{eco}, data: FLUXNET database, legend see Fig. 6.

Krinner *et al.*, 2005). These concepts predict that after infinite time of constant conditions without disturbance the system will be in steady state and without lateral export of carbon, R_{eco} will consequently approximately equal GPP (i.e. be on the 1 : 1-line). Several factors may cause deviations from this theoretical state: (1) climate and environmental conditions are never constant, but vary at all time scales causing disequilibrium (e.g. CO_2 and N fertilization effect are thought to increase carbon sinks), (2) in many ecosystems anthropogenic export via wood or crop harvest plays an important role and leads to reduced on-site respiratory fluxes (Imhoff *et al.*, 2004; Ciais *et al.*, 2007), (3) disturbance events (clear cuts, wind throws, fires) temporally reduce productivity while soil carbon is continued to be respired (legacy effect) (Barford *et al.*, 2001; Saleska *et al.*, 2003). Hence the overall tendency of $R_{eco} > \text{GPP}$ (slope: 0.86–0.89) should be caused by factor categories (1) and (2), while the site years above the 1 : 1 line are likely to have been affected by recent disturbance, although also strong interannual variability maybe causes ecosystems to be sources during particular years when GPP is more strongly reduced than R_{eco} (or R_{eco} more strongly enhanced).

We still cannot fully exclude spurious correlation between our GPP and R_{eco} estimates, for instance if the errors in day and nighttime data are strongly correlated; this depends also on the temporal resolution used to compute the correlation. However, we can analyze the effect of the spurious correlation expected when using the same data and algorithm (e.g. only the nighttime data based estimate) for GPP and R_{eco} estimation (see above) which should be larger than spurious correlation derived from using different data sets (e.g. R_{eco} nighttime data based, extrapolating the daytime and GPP daytime data based), where the error of R_{eco} does not propagate into the GPP estimate. The relationships of different combinations of GPP and R_{eco} estimates (only nighttime based, daytime based or R_{eco} nighttime and GPP daytime based) are statistically indistinguishable (confidence bounds of the correlation coefficient and the regression parameters overlap). This shows that we can have an increased confidence in the derived global pattern and that the expected effect of the spurious correlation (Wang *et al.*, 2008; Vickers *et al.*, 2009) due to the dependency of R_{eco} and GPP when GPP is computed as the residual and the estimates are based on the same data is rather small on the annual timescale. Hence, from a methodological point of view the robustness of the relationship shows that despite uncertainties and statistical pitfalls inherent to the data global patterns of ecosystem-atmosphere CO_2 exchange can be derived from the eddy covariance method when deployed as a network with standardized processing schemes.

Concluding discussion

In this study, we introduced an algorithm that splits NEE into its main components GPP and R_{eco} using daytime data. Including VPD limitation of CO_2 uptake improved the model's ability to reproduce peak flux before noon and the afternoon decrease in NEE magnitude. Including the VPD limitation removed a systematic pattern in the residuals of the model and improved the models performance.

One important finding is that if VPD effects are not explicitly accounted for, they can be easily confounded with temperature effects on ecosystem respiration, resulting in a biased partitioning of the NEE flux into R_{eco} and GPP including unrealistic diurnal cycles of these quantities. Also our approach is not free of errors, as for instance the u* filtering threshold is uncertain.

We provide a R_{eco}/GPP dataset additional to the one generated according to Reichstein *et al.* (2005) where R_{eco} is based on nighttime respiration. We recommend the combined use of the two datasets to cross check flux estimates and point to sites and periods where carbon flux estimates remain uncertain. The application of further plausible algorithms would be desirable to obtain a better estimate of the possible range of flux estimates derived from eddy covariance flux data.

Yet, the comparison should be combined with additional quality and consistency checks based on the comparison with biometric measurements as an additional independent constraint (as for instance Luyssaert *et al.*, 2009; Stoy *et al.*, 2006).

The comparison of the two estimates shows a strong correlation and no significant biases for GPP and R_{eco}. Although the overall agreement is good, there can be large deviations for specific sites or years. Comparing these deviations with the deviation that could be caused by the formal statistical uncertainty of GPP arising from the random error of half-hourly values, shows that the uncertainty arising from systematic errors, such as advection, low turbulence, decoupling of the flow, differences in the footprint during the night compared with daytime or the choice of model and extrapolation, clearly dominates the overall uncertainty of the estimates. Hence, these uncertainties should be considered in any statistical analysis, process model evaluation and model data fusion based on the FLUXNET database. Although the annual sums of many sites must be expected to be biased or at least uncertain, the patterns derived from this global dataset, as for instance the correlation between R_{eco} and GPP, are reliable, increasing our confidence in analyses across sites based on the dataset. In spite of this we emphasize that more specific uncertainty estimates for individual sites and years are needed to strengthen the significance of more detailed statistical analysis and to fully exploit the information inherent in the FLUXNET database.

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Appendix A: Algorithm

The fit parameters of our models showed considerable seasonality to accommodate processes not included in the model. To account for this we use a moving window approach; parameters are estimated every two days with a 4-day moving window when using the daytime data and a 12-day moving window when using the nighttime data. Only the temperature sensitivity of the Lloyd & Taylor (1994) model is estimated with the nighttime data. The response of NEE measurements to temperature is assumed to be independent of systematic measurement errors during periods of poorly developed turbulence during nighttime. The parameter determining the magnitude of the respiration, *rb*, is estimated from daytime data and is thus independent of such biases.

The primary support for stable annual estimates of GPP and R_{eco} is a high number of estimates or small parameter gaps throughout the year. The settings for the parameters during the estimation procedure are summarized in Table A1. The estimation was sensitive to the chosen initial guess value of β the maximum carbon uptake rate, in the gradient-based parameter estimation routine. To deal with this problem we estimate the parameters three times, changing the initial guess value given in Table A1 to the half and double value for the second and third estimation. The parameter set with the lowest RMSE was then selected. The parameters were only accepted if they were within a reasonable range (ranges for each parameter are listed in Table A1). If parameters were outside the range certain parameters were fixed to values defined in the last column of Table A1 and the others were reestimated. Fluxes were computed for the two neighboring parameter sets and then linearly interpolated using the reciprocal of the distance to the parameter sets as weight.

Table A1: Settings for the parameters during the estimation procedure. If all parameter estimates meet the criteria listed in table, the estimate is accepted. If at least one is outside the predefined range, the value is set according to the last column and all other parameters for that time-window are reestimated.

Appendix B: Sites

A list of FLUXNET sites used in the global comparison is given in Table B1.

Table A1 Settings for the parameters during the estimation procedure

Parameter	Initial guess	Accepted values	If the parameter estimate is not acceptable
E_0	100	50–400	Set to value of previous window, if no previous window exists estimates <50 were set to 50, estimates >400 were set to 400
rb	Mean of nighttime NEE	>0	Whole parameter set is not used
α	0.01	$\geq 0, <0.22$	Set to value of previous window, if no previous window exists and <0, set to zero
β	Abs (0.03quantile – 0.97quantile) of NEE	$\geq 0, <250$ If >100 then $\sigma(\beta) < \beta$	If negative set to zero, else the whole parameter set is not used
k	0	≥ 0	Set to zero

If all parameter estimates meet the criteria listed in table, the estimate is accepted. If at least one is outside the predefined range, the value is set according to the last column and all other parameters for that time-window are reestimated or the parameter set is not used (see also last column).

Table B1 List of FLUXNET sites used in the global comparison

Site	Years	Vegetation type	References
AT-Neu	2003, 2006	GRA	Wohlfahrt *et al.* (2008b)
AU-Fog	2006	WET	–
AU-Tum	2002, 2003	EBF	van Gorsel *et al.* (2008)
AU-Wac	2006	EBF	Wood *et al.* (2008)
BE-Bra	2000, 2002, 2006	MF	Carrara *et al.* (2004)
BE-Lon	2005, 2006	CRO	Moureaux *et al.* (2006)
BE-Vie	97–03, 05–06	MF	Aubinet *et al.* (2001)
BR-Ban	2004	EBF	–
BR-Ji2	2001	GRA	Kruijt *et al.* (2004)
BR-Ma2	2004,05	EBF	Araujo *et al.* (2002)
BR-Sa1	2002–04	EBF	Saleska *et al.* (2003)
BR-Sa2	2001	CRO	Sakai *et al.* (2004)
BR-Sa3	2001–03	EBF	Goulden *et al.* (2004)
BR-Sp1	2001	WSA	Santos *et al.* (2004)
BW-Ma1	2000	WSA	Veenendaal *et al.* (2004)
CA-Ca1	1998–2005	ENF	Humphreys *et al.* (2006)
CA-Ca2	2001–2005	ENF	Humphreys *et al.* (2006)
CA-Ca3	2002–2005	ENF	Humphreys *et al.* (2006)
CA-Let	1999–2005	GRA	Flanagan *et al.* (2002)
CA-Man	1995,98,2000,01	ENF	Dunn *et al.* (2007)
CA-Mer	1999–2005	OSH	Lafleur *et al.* (2003)
CA-NS1	2003	ENF	Goulden *et al.* (2006)
CA-NS3	2002–2004	ENF	Goulden *et al.* (2006)
CA-NS6	2002–2004	OSH	Goulden *et al.* (2006)
CA-NS7	2003–2004	OSH	Goulden *et al.* (2006)
CA-Oas	1997–2005	DBF	Black *et al.* (2000)
CA-Obs	2000–2005	ENF	Bergeron *et al.* (2007)
CA-Ojp	2000–2005	ENF	Howard *et al.* (2004)
CA-Qcu	2002–2006	ENF	Giasson *et al.* (2006)
CA-Qfo	2004–2006	ENF	Bergeron *et al.* (2007)
CA-SJ1	2003	ENF	Zha *et al.* (2009)
CA-SJ2	2005	ENF	Zha *et al.* (2009)
CA-SJ3	2005	ENF	Zha *et al.* (2009)
CA-TP4	2004–2005	ENF	Arain & Restrepo-Coupe (2005)
CA-WP1	2004–2005	MF	Syed *et al.* (2006)
CH-Oe1	2003–2006	GRA	Ammann *et al.* (2007)
CH-Oe2	2005	CRO	Dietiker *et al.* (unpublished data)
CN-Cha	2003	MF	Guan *et al.* (2006)
CN-Do1	2005	WET	Yan *et al.* (2008)
CN-Do2	2005	WET	Yan *et al.* (2008)
CN-Do3	2005	WET	Yan *et al.* (2008)
CN-HaM	2002–2003	GRA	Kato *et al.* (2006)
CN-Xfs	2005	GRA	–
DE-Bay	1998–1999	ENF	Staudt & Foken (2007)
DE-Geb	2004–2006	CRO	Anthoni *et al.* (2004)
DE-Gri	2006	GRA	Gilmanov *et al.* (2007)
DE-Hai	2000–2005	DBF	Knohl *et al.* (2003)
DE-Har	2005–2006	ENF	Schindler *et al.* (2006)
DE-Kli	2005–2006	CRO	–
DE-Meh	2004–2006	MF	Don *et al.* (2009)
DE-Tha	1997–2006	ENF	Grünwald & Bernhofer (2007)
DE-Wet	2003–2006	ENF	Rebmann *et al.* (submitted)
DK-Lva	2005	GRA	Gilmanov *et al.* (2007)
DK-Ris	2004–2005	CRO	Houborg & Soegaard (2004)

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Table B1. (*Contd.*)

Site	Years	Vegetation type	References
DK-Sor	1997–2002,05–06	DBF	Pilegaard *et al.* (2003)
ES-ES1	99–00,03,05–06	ENF	Reichstein *et al.* (2005)
ES-ES2	2006	CRO	–
ES-Lma	2004,05	SAV	–
ES-VDA	2004	GRA	Gilmanov *et al.* (2007)
FI-Hyy	1997–1999,2001–2004	ENF	Suni *et al.* (2003b)
FI-Sii	2005	GRA	Aurela *et al.* (2007)
FI-Sod	2001, 2005–2006	ENF	Suni *et al.* (2003a)
FR-Fon	2006	DBF	–
FR-Gri	2005	CRO	Hibbard *et al.* (2005)
FR-Hes	1998–1999, 2001–2006	DBF	Granier *et al.* (2000)
FR-LBr	1998	ENF	Berbigier *et al.* (2001)
FR-Lq1	2004–2005	GRA	Gilmanov *et al.* (2007)
FR-Lq2	2004	GRA	Gilmanov *et al.* (2007)
FR-Pue	2001–2006	EBF	Rambal *et al.* (2004)
GF-Guy	2004, 2006	EBF	Bonal *et al.* (2008)
HU-Bug	2006	GRA	Nagy *et al.* (2007)
HU-Mat	2006	GRA	Pinter *et al.* (2008)
ID-Pag	2002	EBF	Hirano *et al.* (2007)
IE-Dri	2003–2004	GRA	–
IL-Yat	2004–2006	ENF	Grünzweig *et al.* (2003)
IT-Amp	2003	GRA	Gilmanov *et al.* (2007)
IT-Bci	2005, 2006	CRO	Reichstein *et al.* (2003a)
IT-Cpz	1997, 2003, 2004, 2006	EBF	Garbulsky *et al.* (2008)
IT-Lav	2001, 2004, 2006	ENF	Marcolla *et al.* (2003)
IT-Lec	2006	EBF	–
IT-Mbo	2003–2006	GRA	Marcolla & Cescatti (2005)
IT-PT1	2003	EBF	Migliavacca *et al.* (2009)
IT-Ren	2002–2004	ENF	Montagnani *et al.* (2009)
IT-Ro1	2002–2006	DBF	Rey *et al.* (2002)
IT-Ro2	2002, 2003, 2006	DBF	Tedeschi *et al.* (2006)
IT-SRo	2001–2003, 2006	ENF	Chiesi *et al.* (2005)
JP-Mas	2002–2003	CRO	Saito *et al.* (2005)
JP-Tak	1999, 2002–2004	DBF	Ito *et al.* (2006)
JP-Tef	2002	MF	Takagi *et al.* (2009)
JP-Tom	2001–2003	MF	Hirata *et al.* (2007)
NL-Hor	2005–2006	GRA	Jacobs *et al.* (2007)
NL-Loo	1997, 2001–2006	ENF	Dolman *et al.* (2002)
PL-Wet	2004–2005	WET	Chojnicki *et al.* (2007)
PT-Mi1	2005	EBF	Pereira *et al.* (2007)
PT-Mi2	2005–2006	GRA	Pereira *et al.* (2007)
RU-Fyo	1999–2006	ENF	Kurbatova *et al.* (2008)
SE-Deg	2002, 2004	WET	Sagerfors *et al.* (2008)
SE-Fla	1997–1998, 2002	ENF	Lindroth *et al.* (2008)
SE-Nor	1996–1997,1999	ENF	Lagergren *et al* (2008)
UK-Gri	1998, 2001	ENF	Rebmann *et al.* (2005)
UK-Ham	2004	DBF	-
UK-PL3	2005	DBF	-
US-ARM	2003–2004	CRO	Fischer *et al.* (2007)
US-Aud	2004–2005	GRA	-
US-Bar	2004–2005	DBF	Jenkins *et al.* (2007)
US-Bkg	2005–2006	GRA	Gilmanov *et al.* (2005)
US-Blo	2000–2003, 2005–2006	ENF	Goldstein *et al.* (2000)
US-Bn2	2003	DBF	Liu *et al.* (2005)

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Table B1. (*Contd.*)

Site	Years	Vegetation type	References
US-Bo1	1997–2000, 2005–2006	CRO	Meyers & Hollinger (2004)
US-Bo2	2006	CRO	Meyers & Hollinger (2004)
US-Dk3	2004	MF	Pataki & Oren (2003)
US-Fpe	2004, 2006	GRA	–
US-FR2	2005	WSA	Heinsch *et al.* (2004)
US-Goo	2006	GRA	–
US-Ha1	1994–1996, 1998–2001	DBF	Urbanski *et al.* (2007)
US-Ho1	1996–2004	ENF	Hollinger *et al.* (2004)
US-Ho2	1999–2001, 2003–2004	MF	Hollinger *et al.* (2004)
US-IB1	2006	CRO	Allison *et al.* (2005)
US-IB2	2005–2006	GRA	Allison *et al.* (2005)
US-KS2	2002, 2004–2006	CSH	Powell *et al.* (2006)
US-LPH	2003–2004	DBF	Borken *et al.* (2006)
US-MMS	1999, 2001–2005	DBF	Schmid *et al.* (2000)
US-Moz	2005–2006	DBF	Gu *et al.* (2006)
US-Me4	1999	ENF	Law *et al.* (2001)
US-NC1	2006	OSH	Noormets *et al.* (2009)
US-NC2	2006	ENF	Noormets *et al.* (2009)
US-NR1	1999–2000, 2002–2003	ENF	Monson *et al.* (2002)
US-Ne1	2002–2004	CRO	Verma *et al.* (2005)
US-Ne2	2003–2004	CRO	Verma *et al.* (2005)
US-Ne3	2002–2004	CRO	Verma *et al.* (2005)
US-Pfa	1999	MF	Davis *et al.* (2003)
US-SO2	2004–2006	WSA	Lipson *et al.* (2005)
US-SO3	2005–2006	WSA	Lipson *et al.* (2005)
US-SO4	2004–2006	CSH	–
US-SP1	2005	ENF	Powell *et al.* (2008)
US-SP2	2001–2002, 2004	ENF	Clark *et al.* (2004)
US-SP3	2001–2004	ENF	Clark *et al.* (2004)
US-SRM	2004–2005	WSA	Scott *et al.* (2009)
US-Ton	2002–2006	WSA	Ma *et al.* (2007)
US-UMB	2000–2003	DBF	Gough *et al.* (2008)
US-Var	2001–2004, 2006	GRA	Xu & Baldocchi (2004)
US-WBW	1995–1999	DBF	Wilson & Baldocchi (2001)
US-WCr	2000, 2002–2003	DBF	Cook *et al.* (2004)
US-Wrc	2001–2002, 2004	ENF	Falk *et al.* (2008)
VU-Coc	2002–2003	EBF	Roupsard *et al.* (2006)