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Linking flux network measurements to continental scale simulations: ecosystem carbon dioxide exchange capacity under non-water-stressed conditions

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Abstract

This paper examines long-term eddy covariance data from 18 European and 17 North American and Asian forest, wetland, tundra, grassland, and cropland sites under non-water-stressed conditions with an empirical rectangular hyperbolic light response model and a single layer two light-class carboxylase-based model. Relationships according to ecosystem functional type are demonstrated between empirical and physiological parameters, suggesting linkages between easily estimated parameters and those with greater potential for process interpretation. Relatively sparse documentation of leaf area index

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dynamics at flux tower sites is found to be a major difficulty in model inversion and flux interpretation. Therefore, a simplification of the physiological model is carried out for a subset of European network sites with extensive ancillary data. The results from these selected sites are used to derive a new parameter and means for comparing empirical and physiologically based methods across all sites, regardless of ancillary data. The results from the European analysis are then compared with results from the other Northern Hemisphere sites and similar relationships for the simplified process-based parameter were found to hold for European, North American, and Asian temperate and boreal climate zones. This parameter is useful for bridging between flux network observations and continental scale spatial simulations of vegetation/atmosphere carbon dioxide exchange.

Keywords: carbon dioxide exchange, crops, eddy covariance, forest, grassland, gross primary production, model inversion, net ecosystem exchange, up-scaling, wetland

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Introduction

Networks of eddy covariance sites have been established worldwide to observe the long-term characteristics of carbon dioxide (CO_2), water vapour and energy fluxes associated with different ecosystem types along climate gradients (Baldocchi *et al*., 1996, 2001). With respect to CO_2, such studies allow only direct measurements and comparisons of net ecosystem CO_2 exchange (NEE). Nevertheless, consensus views on processing of data from such networks are being developed to (1) provide estimates of the flux components associated with canopy photosynthesis [gross primary production (GPP)] and ecosystem respiration (Reco) (cf. Falge *et al*., 2001, 2002a; Reichstein *et al*., 2005), (2) reveal seasonal changes in CO_2 exchange potentials (Falge *et al*., 2002b; Reichstein *et al*., 2002; Gilmanov *et al*., 2003), and (3) support the derivation of model parameters for use in spatial generalizations of vegetation/atmosphere CO_2 exchange (Reichstein *et al*., 2003b; Wang *et al*., 2003).

Parameters that define the capacity of ecosystems for carbon uptake (GPP) and loss (Reco) are key components in models of carbon dynamics, and both empirical and physiologically based parameters have been examined. Empirical analyses based on light response curves for NEE (Tamiya, 1951; Gilmanov *et al*., 2003) are advantageous, especially for those focusing research attention on additional data analysis problems (e.g. remote sensing), since seasonal patterns in the direct observations are revealed, results are rapidly obtained, and no other ecosystem structural information from flux tower sites is required.

Physiologically based analyses of GPP, on the other hand, attempt to identify process components that regulate fluxes, with the hope that these may be linked in modelling to an overall understanding of ecosystem physiology and biogeochemistry. Critical parameters linking observations at flux tower sites with process-based models for estimation of carbon exchange at regional to global scales, including leaf area index (LAI), average carboxylase capacity of the leaves (Vc_{max}), average leaf light utilization efficiency (*alpha*), length of the active season for carbon uptake, and sensitivity of stomata to changes in soil water availability can be used to express the potential of an ecosystem to acclimate to changing constraints. While various strategies have been applied to describe spatial and temporal variation in these parameters at large scales (Potter *et al*., 1993; Running & Hunt, 1993; Bonan, 1995; Sellers *et al*., 1996; Liu *et al*., 1997, 1999; Chen *et al*., 1999), consistent or standardized methodologies based on flux network observations have not yet been demonstrated.

This paper describes results from the first of two analyses focused on comparative derivation of critical ecosystem carbon exchange parameters along a European transect from Mediterranean to Arctic climatic zones, using both empirical and physiologically based models. NEE data from all major ecosystem types studied within the network project CarboEurope (www.carboeurope.org) are analysed, but this first summary describes vegetation response in situations where soil water availability is nonlimiting. A subsequent paper focuses on the additional complexity confronted with the occurrence of water stress, (e.g. where relationships between relative extractable water in the rooting zone (Granier *et al*., 2006) and/or measured meteorological variables (i.e. latent heat and air temperature) at eddy covariance tower sites allow clear definition of the water stress period).

Our goals are to (1) demonstrate relationships between calculated empirical and process-based CO_2 exchange parameters obtained for different ecosystem types, (2) examine patterns in CO_2 uptake or loss as

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related to climate factors, LAI, and canopy and leaf physiology, (3) determine whether convergence occurs in CO_2 uptake characteristics of the ecosystems studied, (i.e. whether 'functional ecosystem types' may be identified), and (4) search for ways in which process-based descriptions may be simplified for continental scale spatial simulations of vegetation/atmosphere CO_2 exchange. We conduct a sensitivity analysis on critical leaf level and canopy structure parameters to obtain accurate simplifications for model applications. In summary, we attempt to reduce a relatively complex physiologically based model to the level of empirical descriptions, at least in terms of the number of critical parameters, while maintaining the capacity for response to factors such as remotely sensed LAI, fertilization, management, and canopy water use. The resulting model may be viewed as a prototype for bridging between observations within flux tower networks and simulations of carbon exchange at continental scale.

Materials and methods

Site descriptions and eddy covariance fluxes

The research programme EUROFLUX ('Long-term carbon dioxide and water vapor fluxes of European forests and interactions with the climate system') was established as a network of 15 forest sites to examine NEE along European continental gradients from western oceanic to eastern continental zones, and from boreal to Mediterranean climates (Baldocchi *et al.*, 1996; Tenhunen *et al.*, 1998, 1999; Papale & Valentini, 2003). The network has been extended in the current European Union Integrated Project CarboEurope to include measurement sites within croplands, grasslands, wetlands, and additional Mediterranean woodland and shrubland vegetation formations. Eddy covariance flux measurements from 18 sites consisting of 27 years of data including the major ecosystem types of Central and Northern European vegetation and distributed along a north–south transect were selected for analysis (Table 2), including four coniferous, one mixed and five deciduous forests, two wetlands, three nongrazed grasslands, and four cropland sites. To examine generality of the derived approaches, similar analysis of data from 17 North American and Asian sites with a total of 37 years of observations was later carried out for comparison (Table 6).

Half-hourly averaged global radiation and photosynthetic photon flux density (PPFD); air temperature and humidity; rainfall; and wind speed and direction were used together with eddy covariance fluxes of CO_2 and H_2O (Aubinet *et al.*, 2000), accounting for correction of CO_2 storage and filtering for low-turbulence night conditions using a friction velocity (u^*)-threshold criterion according to Reichstein *et al.* (2005). The same procedure of gap filling, using the marginal distribution sampling method, and partitioning of the observed NEE into GPP and Reco, using a short-term temperature dependent method based on Lloyd & Taylor (1994), was applied at all sites using the method of Reichstein *et al.* (2005). One modification of the published method was made. In order for R_{ref}, the reference ecosystem respiration at 15 °C, to be comparable with remote sensing indices, it was estimated using a window of 8 days with a 4-day time step (i.e. 4 days of overlap). Errors and uncertainties introduced in the process of gap filling and flux partitioning have been discussed by Reichstein *et al.* (2005). While our objective was to use a single method across many sites, a danger remains that important individual site characteristics may be overlooked, and problems with reported measurements are difficult to assess. Furthermore, the annual sums of GPP, Reco, and NEE from this standardized processing may differ from other published values for the same sites (Barford *et al.*, 2001; Hadley & Schedlbauer, 2002; Lohila *et al.*, 2004; Stoy *et al.*, 2006).

Hyperbolic light response model

Empirical description of the measured daytime NEE fluxes was accomplished via a nonlinear least squares fit of the data to the hyperbolic light response model, also known as the rectangular hyperbola or the Michaelis–Menten type model (Tamiya, 1951; Gilmanov *et al.*, 2003):

$$\mathrm{NEE} = -\frac{\alpha\beta Q}{\alpha Q + \beta} + \gamma, \qquad (1)$$

where NEE is ungap-filled NEE (μmol CO_2 m^{-2} s^{-1}), α is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency (μmol CO_2 m^{-2} s^{-1})/(μmol photon m^{-2} s^{-1}), β is the maximum CO_2 uptake rate of the canopy (μmol CO_2 m^{-2} s^{-1}), Q is the PPFD (μmol photon m^{-2} s^{-1}), γ is an estimate of the average daytime ecosystem respiration occurring during the observation period (μmol CO_2 m^{-2} s^{-1}), (α/β) is the radiation required for half-maximal uptake rate, and $(\beta+\gamma)$ is the theoretical maximum uptake capacity (μmol CO_2 m^{-2} s^{-1}) as sometimes the rectangular hyperbola saturates very slowly in terms of light. $\alpha\beta Q/(\alpha Q+\beta)$ evaluated at a reasonable level of high light ($Q = 2000\,\mu$mol m^{-2} s^{-1} is used in this study) is an approximation of GPP and can be thought of as the average maximum canopy uptake capacity, notated here as $(\beta+\gamma)_{2000}$. Ungap-filled NEE data were used to avoid effects of the gap-filling routine on the parameters. The parameters α, β, and γ were estimated with

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daytime data for three periods in each month, including data from days 1 through 10, 11 through 20, and 21 to the end of the month. At least five half-hourly data points with high-quality ungap-filled NEE were required to fit the parameters in each period. Parameters were not included in further analysis when the relative standard error was >0.6 or when parameter values were negative or above 0.17 for α, 100 for β, or 15 for γ. These thresholds were primarily used during dormant winter months to eliminate periods when NEE is near zero and, correspondingly, the rectangular hyperbola is not an appropriate model.

Carboxylase-based model

The physiologically based model applied to describe light interception and leaf gas exchange is single layered and defines sun and shade light classes for canopy foliage. Thus, it is similar to several other models developed for crop and forest stands (e.g. Williams *et al.*, 1996; dePury & Farquhar, 1997; Wang & Leuning, 1998).

Light interception. Radiation distribution onto sunlit and shaded leaves is described according to Chen *et al.* (1999). The equations for light interception in Chen *et al.* (1999), Eqns (21–24) were based on LAI only. As stems and branches also intercept light, we expanded all occurrences of LAI to plant area index (PAI) with the assumption that the stem area index (SAI) is 14% of the LAI and that PAI = SAI+LAI. Needle leaves were modelled with projected leaf area. Total shortwave radiation on sunlit leaves (S_{sunlit}) is the sum of direct (S_{beam}), sky diffuse (S_{sky}), and multiple scattered radiation (S_{scat}). Total shortwave radiation on shaded leaves (S_{shade}) includes only the sum of S_{sky} and S_{scat}. Direct radiation on leaves is calculated according to Norman (1982)

$$S_{\mathrm{beam}} = S_{\mathrm{dir}}\ G/\cos\theta, \tag{2}$$

where S_{dir} is the direct component of global solar radiation above the canopy, θ is the solar zenith angle, and G is the foliage orientation function ($G = 0.5$, i.e. the cosine of the mean leaf-sun angle ϕ). For canopies with spherical leaf angle distribution $\phi = 60^\circ$ (Norman, 1979); this was found to be a good approximation for canopies when θ ranges between 30 and 60° (Chen, 1996b). Hence, this relationship was used for all sites in this study. Sky diffuse radiation on leaves is calculated from the average of total intercepted sky diffuse radiation for the total PAI

$$S_{\mathrm{sky}} = (S_{\mathrm{dif}} - S_{\mathrm{dif,\,under}})/\mathrm{PAI}, \tag{3}$$

where S_{dif} is the diffuse component of global solar radiation above the canopy. Diffuse radiation reaching the ground below the canopy is calculated with a simple exponential extinction, modified to consider the influence of clumping (Ω)

$$S_{\mathrm{dif,\,under}} = S_{\mathrm{dif}}\ \exp(-G\ \Omega\ \mathrm{PAI}/\cos\bar{\theta}), \tag{4}$$

where $\bar{\theta}$ is a representative zenith angle for diffuse radiation transmission, dependent on canopy elements ($\cos\bar{\theta} = 0.537 + 0.025\,\mathrm{PAI}$). Ω was assumed to be 0.5 for coniferous forests, 0.7 for deciduous forests, and 0.9 for grasslands, wetlands, and crops (Chen & Cihlar, 1995; Chen, 1996a; Chen *et al.*, 2003). Multiple scattered radiation is based on Norman (1982)

$$S_{\mathrm{scat}} = 0.07\,\Omega\,S_{\mathrm{dir}}(1.1 - 0.1\ \mathrm{LAI})\exp(-\cos\theta). \tag{5}$$

The average proportion of sunlit leaves, A_{sunlit}, is calculated as

$$A_{\mathrm{sunlit}} = \cos\theta/G(1 - \exp(-G\ \Omega\ \mathrm{LAI}/\cos\theta))\mathrm{LAI}/\mathrm{PAI}. \tag{6}$$

The term LAI/PAI corrects for the effects of stems.

Canopy gas exchange. The light interception of the sunlit and shaded leaves is used along with absorption and emission of long-wave radiation, convective heat loss and latent heat loss through transpiration to calculate the energy balance of leaves in two classes (sunlit and shaded). Owing to the iterative process of solving for stomatal conductance and leaf temperature, the energy balance is calculated separately for sunlit and shaded leaves, which are summed to obtain total canopy fluxes. The simulation of gross photosynthesis follows Farquhar & von Caemmerer (1982) as modified for field applications by Harley & Tenhunen (1991). Model inversions for parameter estimation are based on Ribulose-1,5-bisphosphate-carboxylase-oxygenase (Rubisco) enzyme reactions where the rate of CO_2 fixation is limited by either the regeneration of Ribulose-1,5-biphosphate (RuBP) (at low light intensity and/or high internal CO_2 concentration) or by Rubisco activity and CO_2/O_2-concentration (at saturated light and low internal CO_2 concentration; Reichstein, 2001).

Net photosynthesis, P_{net}, is obtained using

$$P_{\mathrm{net}} = \left(1 - \frac{\Gamma^*}{c_{\mathrm{i}}}\right)\min(w_{\mathrm{c}};\ w_{\mathrm{j}}) - 0.5\ R_{\mathrm{d}}, \tag{7}$$

where Γ^* is the CO_2 compensation point in the absence of mitochondrial respiration, w_{c} is the carboxylation rate supported by the Rubisco enzyme expressed by Eqn (10), w_{j} is the carboxylation rate supported by the actual electron transport rate expressed by Eqn (12), R_{d} is the respiration occurring in mitochondria without

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light, and c_i is the internal CO_2 concentration expressed by Eqn (8) based on Fick's Law for molecular diffusion of CO_2 through the stomata and boundary layer.

$$c_i = c_s - \frac{1.6\ P_{net}}{g_s}, \tag{8}$$

where c_s is the CO_2 concentration at the surface of the leaf and g_s is the stomatal conductance for water vapour according to Ball *et al*. (1987; cf. Eqn (9)).

$$g_s = g_{s:min} + gfac\frac{(P_{net} + 0.5R_d)rH}{c_s}, \tag{9}$$

where $g_{s:min}$ is the minimum stomatal conductance for water vapour, *gfac* is a proportionality constant evaluated in chamber experiments, R_d is the mitochondrial dark respiration, and *rH* is the relative humidity at the leaf surface.

w_c is the carboxylation rate supported by the Rubisco enzyme at a specific temperature

$$w_c = \frac{Vc\ c_i}{c_i + K_c(1 + O/K_O)}, \tag{10}$$

where *Vc* is the maximum rate of carboxylation, K_c is the Michaelis constant for carboxylation, K_O is the Michaelis constant for oxygenation, and *O* is the oxygen concentration of the air [210 $cm^3 O_2$ (L air)$^{-1}$]. The temperature dependency of carboxylation is described as

$$Vc = \frac{Vc_{max} e^{\Delta H_a (T_K - 298)/298RT_K}}{1 + e^{(\Delta ST_K - \Delta H_d)/RT_K}} \left(1 + e^{(298\Delta S - \Delta H_d)/298R}\right), \tag{11}$$

where Vc_{max} is the average leaf carboxylation capacity at 25 °C, ΔH_a is activation enthalpy of carboxylation, T_K is the estimate of the leaf temperature in the current model iteration, *R* is the universal gas constant, *S* is an entropy term for deactivation and ΔH_d is the deactivation enthalpy of carboxylation.

w_j is the carboxylation rate supported by the actual electron transport rate

$$w_j = \frac{P_m c_i}{c_i + 2.0\ \Gamma^*}, \tag{12}$$

where P_m is the maximum potential rate of RuBP production and is calculated using the Smith equation (cf. Tenhunen *et al*., 1976)

$$P_m = \frac{alpha\ I}{\sqrt{1 + (alpha^2 I^2 / P_{ml}^2)}}, \tag{13}$$

where *alpha* is the average leaf light utilization efficiency without photorespiration, *I* is the incident PPFD, and P_{ml} is the CO_2 and light saturated temperature dependent potential RuBP regeneration rate as described in Falge (1997).

Table 1 Values used for leaf physiological parameters and their definitions that determine the temperature-dependent response of leaves as well as stomatal conductance

Parameter	Conifer forests	Deciduous forests	Grasslands and crops	Unit
$\Delta H_a(J_{max})$	47 170	47 170	40 000	J mol^{-1}
$\Delta H_d(J_{max})$	2 45 000	2 00 000	2 00 000	J mol^{-1}
$\Delta S(J_{max})$	643	643	655	J mol^{-1} K^{-1}
$E_a(R_d)$	63 500	63 500	58 000	J mol^{-1}
$E_a(K_O)$	36 000	36 000	35 900	J mol^{-1}
$f(K_O)$	159.597	159.597	248	—
$E_a(K_c)$	65 000	65 000	59 500	J mol^{-1}
$f(K_c)$	299.469	299.469	404	—
$\Delta H_a(Vc_{max})$	75 750	75 750	69 000	J mol^{-1}
$\Delta H_d(Vc_{max})$	2 00 000	2 00 000	1 98 000	J mol^{-1}
$\Delta S(Vc_{max})$	656	656	660	J mol^{-1}K^{-1}
$f(\tau)$	2339.53	2339.53	2339.53	—
$E_a(\tau)$	−28 990	−28 990	−28 990	J mol^{-1}
gfac	9.8	9.8	12	—

ΔH_a	Activation enthalpy for enzymatic reactions
ΔH_d	Deactivation enthalpy for enzymatic reactions
ΔS	Entropy term for the deactivation of enzymes
J_{max}	Maximum rate of electron transport
E_a	Activation energy
R_d	Rate of CO_2 evolution from processes other than photorespiration
K_O	Michaelis–Menten constant for oxygenation
f	Scaling factor
K_c	Michaelis–Menten constant for carboxylation
Vc_{max}	Maximum rate of carboxylation
τ	Enzyme specificity factor
gfac	Bell–Berry stomatal conductance factor

Parameter values are generalized from (Harley *et al*., 1986; Harley & Tenhunen, 1991; Falge *et al*., 1996; Ryel *et al*., 2001; Falge *et al*., 2003; Fleck *et al*., 2004). Acclimation over the season for the parameters listed is not considered.

Parameter estimation – complex model. Leaf physiological parameters determining the temperature dependent response of leaves and stomates were held constant at generalized values established in leaf gas exchange studies (under conditions without water limitation) as shown in Table 1. Seasonal variation of *alpha*, the average leaf light utilization efficiency without photorespiration, and Vc_{max}, the average leaf carboxylation capacity at 25 °C, were estimated via model inversion studies with individual site GPP data (cf. Wang *et al*., 2003). We used the Levenberg–Marquardt method for minimizing our objective functions to calculate these critical parameters. The capacity for RuBP regeneration, *c*, and the capacity for leaf respiration, *d*, were

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considered proportional to the leaf carboxylation capacity at 25 °C, $Vc_{\max}$, as in Eqns (14) and (15) (Wilson *et al.*, 2000).

$$c = \frac{Vc_{\max}}{2.1}, \tag{14}$$

$$d = 0.025Vc_{\max}. \tag{15}$$

Parameter determinations also require information with respect to seasonal variation in LAI (described in detail with respect to the presented results below), except in the case of evergreen and coniferous forests where LAI was considered constant. The parameters *alpha* and $Vc_{\max}$ were estimated, as in the case with the empirical hyperbolic light response model, for three periods in each month. Parameters were not included in further analysis when the relative standard error was >0.6 or when parameter values were negative or above 0.17 for *alpha* or 350 for $Vc_{\max}$.

The total estimated canopy assimilation obtained with first guess parameter estimates was compared with the gap-filled GPP in an iterative process to determine best parameter values. As GPP contains many uncertainties, such as periods of unusually high or low carbon uptake due to gaps in measurements (further discussed below) and/or effects from flux partitioning and gap filling, parameters were first estimated with 0% and 10% of GPP values trimmed. A comparative analysis (not shown) showed that better parameter estimation with higher r^2 values, fewer outliers and lower root-mean-square errors occurred when GPP data were trimmed. Therefore, a nonlinear least-trimmed squares regression technique was used (Stromberg, 1997; Reichstein *et al.*, 2003a) that seeks to minimize the sum of squared residuals as ordinary nonlinear regression, but with exclusion of the largest 10% of residuals that are assumed to be due to contaminated data or due to data inconsistent with the model. The technique is able to objectively identify outliers, or more precisely data points that are inconsistent with the model assumptions (Reth *et al.*, 2005). The objective function that was minimized is the trimmed sum of squared errors (TSSE):

$$\mathrm{TSSE} = \sum_{i \le 0.9N} r_i^2, \tag{16}$$

where r_i is the ith smallest residual, N is the total number of data points, and 0.9 is the fraction of residuals to be kept. Recent analyses (Hollinger & Richardson, 2005; Richardson *et al.*, 2006) indicate that flux data measurement errors are not Gaussian, but are instead characterized by a peaked distribution with long tails. An alternative objective function would be the sum of the absolute value of the residuals

$$\omega = \sum |r_i|. \tag{17}$$

Parameter estimation – simplified model. Given the difficulty of describing spatial variation of multiple parameters for a process-based model at continental scales, we tested two simplifying assumptions with respect to critical parameters to which the models are sensitive: (1) eliminating seasonal variation in LAI and assuming LAI equal to the observed maximum, and (2) assuming *alpha* to be proportional to $Vc_{\max}$ [i.e. like c and d in Eqns (14) and (15)] rather than independent. While $Vc_{\max}$ in terms of the complex model is defined in relation to the carboxylation capacity of the average leaf, it is, in fact, influenced by experimental errors in the measurement of NEE, assumptions made in the estimation of GPP, our inability to obtain detailed spatial estimates of LAI and associate these with variations in NEE, the lack of information on potential time-dependent changes in LAI, particularly in conifer stands, and assumptions of the models, such as lack of acclimation along light gradients and nonoccurrence of water stress (see Wang *et al.*, 2003 for additional discussion). Hence, estimates of $Vc_{\max}$ from the simplified inversions are subject to interpretation as it becomes a lumped parameter. To call attention to this, we refer to the derived values as Vc_{uptake2^*} when *alpha* and $Vc_{\max}$ are independent, and as Vc_{uptake1^*} when *alpha* depends on $Vc_{\max}$. Additionally, we define whether LAI varies or is held constant. In the case of Vc_{uptake1^*}, LAI is always constant at the observed seasonal maximum.

Results

Ecosystem fluxes

Results of the flux separation for the European sites are illustrated in Fig. 1 and summarized for all sites and years in Table 3. Reduced CO_2 uptake during winter at coniferous forest sites is influenced by the degree of continentality (cf. Tharandt) as well as latitude influences on growing season length (cf. Hyytiälä and Sodankylä), where the long cold periods in northern Europe lead to strong dormancy (Suni *et al.*, 2003b). The Loobos maritime coniferous site remains active throughout the year. In the case of deciduous forest sites, there is a general decrease in annual GPP from south to north in response to growing season length with the exception of Collelongo (1560 m a.s.l.), which is influenced by altitude. Further details of forest site comparisons have been discussed for earlier periods in Papale & Valentini (2003) and Valentini (2003). The uptake of CO_2 by wetlands, crops, and grasslands is

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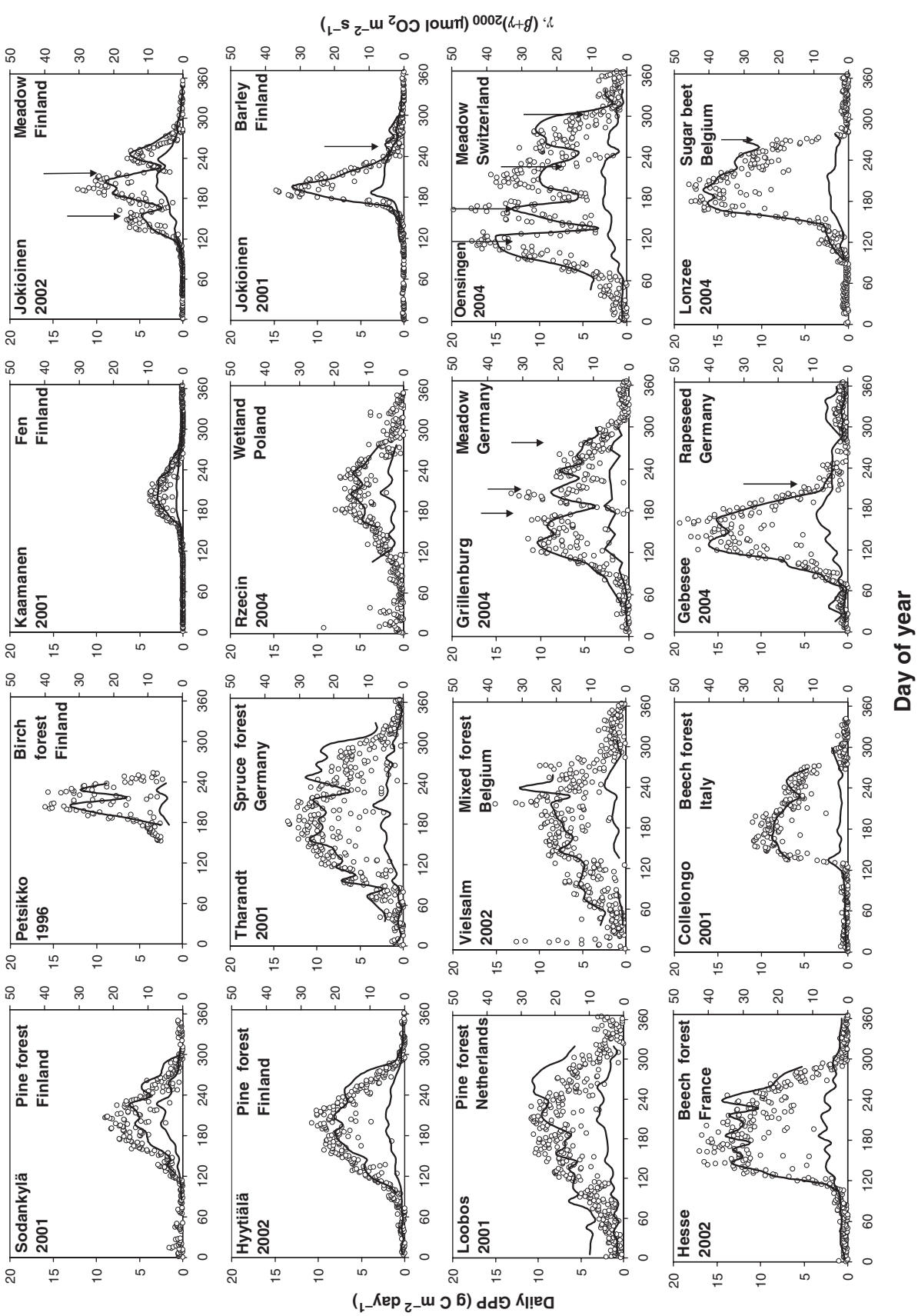

Fig. 1 Results of inverting the simple hyperbolic light response model based on net ecosystem CO_2 exchange observations for the parameters $(\beta + \gamma)_{2000}$, the upper solid line, and γ, the lower solid line, superimposed on the daily observations of gross primary production (GPP), shown as open circles, derived according to Reichstein *et al.* (2005). The arrows indicate crop harvest or grassland cut dates.

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quite variable with obvious responses to season length, nutrient availability (compare maximum daily rates for wetlands with the intensively fertilized grassland Oensingen), and management measures (crop rotation schemes and harvests). Annual NEE was near zero or positive (i.e. source of carbon) at the subarctic fen in Kaamanen, depending on snow melt (Laurila *et al.*, 2001), at the Jokioinen site with both barley and grassland due to high respiratory fluxes from the underlying peat soil, and at the Sodankylä pine forest. Latent heat exchange estimated at each site is summarized in Table 3 for reference.

Hyperbolic light response parameters

All sites and years were analysed with respect to the reported results (not shown), but in order to enhance the readability of the graphs and as results were similar, only 1 year per site is shown on the comparison figures. The year that was chosen provided the best fit (highest r^2 values). Results of inverting the simple hyperbolic light response model based on NEE observations are shown for the parameters $(\beta+\gamma)_{2000}$ and γ superimposed on the daily observations of GPP in Fig. 1 (γ is the lower curve in each figure). As seen in the individual site seasonal courses in Fig. 1 and in the regressions in Fig. 2, daily GPP is highly correlated with the average maximum canopy uptake capacity, $(\beta+\gamma)_{2000}$, observed for 10-day periods (r^2 in Fig. 2 between 0.57 and 0.94) for all ecosystem types. Nevertheless, there are some periods, for example late in the season at Hyytiälä, Loobos, and Tharandt, where the apparent relationship shifts. This shift depends on the relative length of time the canopy performs under high or low light conditions, which changes over the course of a season. Such shifts contribute to the scatter in relationships shown in Fig. 2 and reduce the r^2 values of the correlations. Other differences stem from the comparison between the estimates of α, β, and γ obtained using ungap-filled NEE data and the gap-filled daily GPP data. Vielsalm, a mixed forest, was included in the analysis of both the dense coniferous and deciduous forests.

Given the simplicity of the hyperbolic light response model, the inversion solutions are obtained in a very dependable fashion with few difficulties arising in the statistical fitting of light response curves. α and β are negatively correlated with an upper quartile, average, and lower quartile of -0.73, -0.51, and -0.36, respectively. α and γ are very positively correlated with an upper quartile, average, and lower quartile of 0.88, 0.82, and 0.81, respectively. β and γ are not correlated with an upper quartile, average, and lower quartile of 0.17, -0.01, and -0.27, respectively. All regressions shown in the scatter plot figures use the geometric mean regression (also known as the Reduced Major Axis or the Model II regression) which considers the errors in both x and y (Sokal & Rohlf, 1995). The slopes of the regressions shown for different ecosystem types in Fig. 2 are similar. The importance of maintaining the suggested grouping is discussed further below in relation to physiological model inversions.

The parameter γ provides an estimate of average observed daytime ecosystem respiration during 10-day periods as obtained from the fitting of the canopy light response curve and on the basis of half-hour eddy flux measurements. In the process of flux partitioning, the value for R_{ref} is derived and similarly provides an estimate of seasonal changes in ecosystem respiratory capacity based on the evaluation of temperature response during night-time. γ and R_{ref} are related with r^2 values between 0.46 and 0.86 (Fig. 3). Thus, the parameters provide a consistent picture of seasonal influences on Reco even though different data (daytime vs. night-time) were used.

Process-based model parameters

Inversions to estimate the parameters *alpha* and $Vc_{\mathrm{uptake2^*}}$ for the physiological model were carried out for those sites where confidence in estimates and measurements of LAI were best. This was especially of concern for summer active ecosystems with strong seasonal change in LAI. Thus, three pine sites, the Tharandt dense spruce forest, the Hesse beech forest, grasslands at Jokioinen and Grillenburg, and the crop sites Lonzee and Klingenberg were studied as indicated in Fig. 4. $Vc_{\mathrm{uptake2^*}}$ and *alpha* are negatively correlated with an upper quartile, average, and lower quartile of -0.29, -0.54, and -0.77, respectively, so a certain degree of noise was associated with the seasonal courses for the two parameters as they varied with respect to preference in the search for minimizing residual errors. On the other hand, general seasonal trends were recognizable in all cases and were compatible with trends found for the more restricted one-parameter fits discussed below. Reasons for the sensitivity in parameter estimates may have to do with the change in importance of limiting and high light conditions during individual periods, or may be related to the imposition of defined temperature response curves based on previous cuvette gas exchange experimentation that are not ideal for describing overall gas exchange of the canopy, or may relate to time-dependent change in measurement errors. Nevertheless, $Vc_{\mathrm{uptake2^*}}$ as in the case of $(\beta+\gamma)_{2000}$ was linearly related to GPP (cf. Table 4) even though more scattered.

The relationship of $Vc_{\mathrm{uptake2^*}}$ to the parameter $(\beta+\gamma)_{2000}$ from the hyperbolic light response model (noting both provide an estimate of total canopy CO_2

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Table 2 Eddy covariance flux measurement sites according to vegetation type included in the comparison of GPP, Reco and model parameters

Site location and dominant species	Latitude (°N)	Longitude (°E)	Measurement methods*
Coniferous forest			
Tharandt, Germany	50.96	13.57	Bernhofer *et al*. (2003)
Picea abies			
Loobos, the Netherlands	52.17	5.74	Dolman *et al*. (2002)
Pinus sylvestris			
Hyytiälä, Finland	61.85	24.29	Rannik *et al*. (2004, 2002), Suni *et al*. (2003a, b)
Pinus sylvestris			
Sodankylä, Finland	67.36	26.64	Aurela (2005), Suni *et al*. (2003b)
Pinus sylvestris			
Mixed forest			
Vielsalm, Belgium	50.31	6.00	Aubinet *et al*. (2002, 2001)
Pseudotsuga menziesii, *Fagus sylvatica*			
Deciduous forest			
Collelongo, Italy	41.85	13.59	Valentini *et al*. (2000, 1996)
Fagus sylvatica			
Hesse, France	48.67	7.07	Granier *et al*. (2002, 2000a, b), Lebaube *et al*. (2000)
Fagus sylvatica			
Hainich, Germany	51.08	10.45	Anthoni *et al*. (2004), Knohl *et al*. (2003)
Fagus sylvatica			
Soroe, Denmark	55.49	11.65	Pilegaard *et al*. (2003, 2001)
Fagus sylvatica			
Petsikko, Finland	69.47	27.23	Aurela *et al*. (2001b), Laurila *et al*. (2001)
Betula pubescens			
Wetlands			
Rzecin, Poland	52.77	16.30	*
Scirpus, *Carex*, shrubs and moss			
Kaamanen, Finland	69.14	27.30	Aurela *et al*. (2002, 2001a), Laurila *et al*. (2001)
Carex spp., *Betula nana*, shrubs and moss			
Grasslands and meadows			
Oensingen (intensively managed), Switzerland	47.29	7.73	Ammann *et al*. (2007), Flechard *et al*. (2005)
Alopecurus pratensis, *Lollium perenne*			
Grillenburg, Germany	50.95	13.51	*
Festuca pratensis, *Alopecurus pratensis*, *Phleum pratensis*			
Jokioinen, Finland	60.90	23.51	Lohila *et al*. (2004)
Poa pratense, *Festuca pratensis*			
Crops			
Gebesee, Germany	50.10	10.91	Anthoni *et al*. (2004)
Brassica Napus Napus			
Lonzee, Belgium	50.55	4.75	Moureaux *et al*. (2006)
Beta vulgaris l.			
Klingenberg, Germany	50.89	13.52	*
Hordeum vulgaris			
Jokioinen, Finland	60.90	23.51	Lohila *et al*. (2004)
Hordeum vulgaris			

*All sites except Jokioinen and Petsikko are described in the CarboEurope database.

uptake capacity) is shown in Fig. 4 (r^2 varying between 0.48 and 0.70). The slope of the relationships are quite similar for all ecosystem types except pine forests where much higher $Vc_{uptake2^*}$ is predicted. The differences in $Vc_{uptake2^*}$ in the pine forests could suggest that different functional types exist among coniferous stands, especially as higher activity of needles of pine as compared with Norway spruce in Central Europe has been noted previously (Ryel *et al*., 2001; Falge *et al*., 2003). However, inaccurate values of LAI may also contribute, as

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Table 3 Annual sums of CO_2 and latent heat exchange for the sites in Table 2

Site	Year	Annual NEE ($g C m^{-2}$)	Annual GPP ($g C m^{-2}$)	Annual Reco ($g C m^{-2}$)	Latent heat exchange (mm)	Spring NEE decrease (day)	Fall NEE increase (day)	Negative NEE season (days)
Coniferous forest								
Tharandt, Germany	2001	−534	1681	1147	490	56	318	263
	2002	−685	1930	1245	386	25	337	313
Loobos, the Netherlands	2001	−255	1622	1367	556	72	285	214
	2002	−566	1755	1189	519	1	360	360
Hyytiälä, Finland	2001	−176	1011	836	302	95	260	166
	2002	−237	1102	866	337	90	283	194
Sodankylä, Finland	2001	80	652	732	300	125	200	76
	2002	0	742	742	307	107	220	114
Mixed forest								
Vielsalm, Belgium	2002	−355	1528	1173	268	56	287	232
Deciduous forest								
Collelongo, Italy	2000	−751	1434	684	*	119	300	182
	2001	−455	1039	585	321	125	283	159
Hesse, France	2001	−538	1706	1168	369	119	299	181
	2002	−539	1772	1233	374	123	283	161
Hainich, Germany	2002	−490	1597	1107	281	129	290	162
Soroe, Denmark	2001	−166	1590	1424	224	121	274	154
	2002	−202	1570	1369	218	119	277	159
Petsikko, Finland	1996	−230	740	510	126	180	242	63
Wetland								
Rzecin, Poland	2004	−255	829	573	471	1	345	345
Kaamanen, Finland	2001	−37	231	194	238	152	245	94
	2002	−54	298	244	258	141	243	103
Grasslands and meadows†								
Oensingen (intensively managed), Switzerland	2004	−630	2345	1715	684	32	315	284
Grillenburg, Germany	2004	−260	1233	973	437	72	276	205
Jokioinen, Finland	2002	73	782	855	422	119	207	89
Crops								
Gebesee (rapeseed), Germany	2004	−200	1419	1219	372	67	199	133
Lonzee (sugar beet), Belgium	2004	−564	1576	1013	588	139	275	137
Klingenberg (winter barley), Germany	2004	−484	1454	970	294	‡	316	‡
Jokioinen (summer barley), Finland	2001	187	603	790	443	162	214	53

*No latent heat measurements were made in 2000 at Collelongo.
†All grassland sites are nongrazed.
‡Measurements for Klingenberg were started on day of year 92 in 2004.
The start and end of the active NEE season is defined as where NEE (smoothed using the negative exponential method) changes from positive to negative and vice versa.
NEE, net ecosystem CO_2 exchange; GPP, gross primary production; Reco, ecosystem respiration.

understory components were not included in LAI estimates. The light utilization efficiency of the canopy, *alpha*, determined in two-parameter inversions is linearly related to α obtained in hyperbolic light response inversions (cf. Table 5; r^2 between 0.34 and 0.93). The efficiency of the pine stand canopy is found to be almost twice as large as that of the dense conifer stands. Caution must be taken with interpreting this statement, as an Ω value of 0.5 for both pine and dense conifer stands was used, although this alone could not account for the differences. When $\Omega = 0.3$ for pine stands, estimates of *alpha* are approximately 35–45% higher than when $\Omega = 0.5$. Oppositely, when $\Omega = 0.7$, estimates of *alpha* are approximately 15–20% lower than when $\Omega = 0.5$. It should be noted that the process-based model fits parameters better in general than the hyperbolic light response model with on average for each period an 18% higher r^2.

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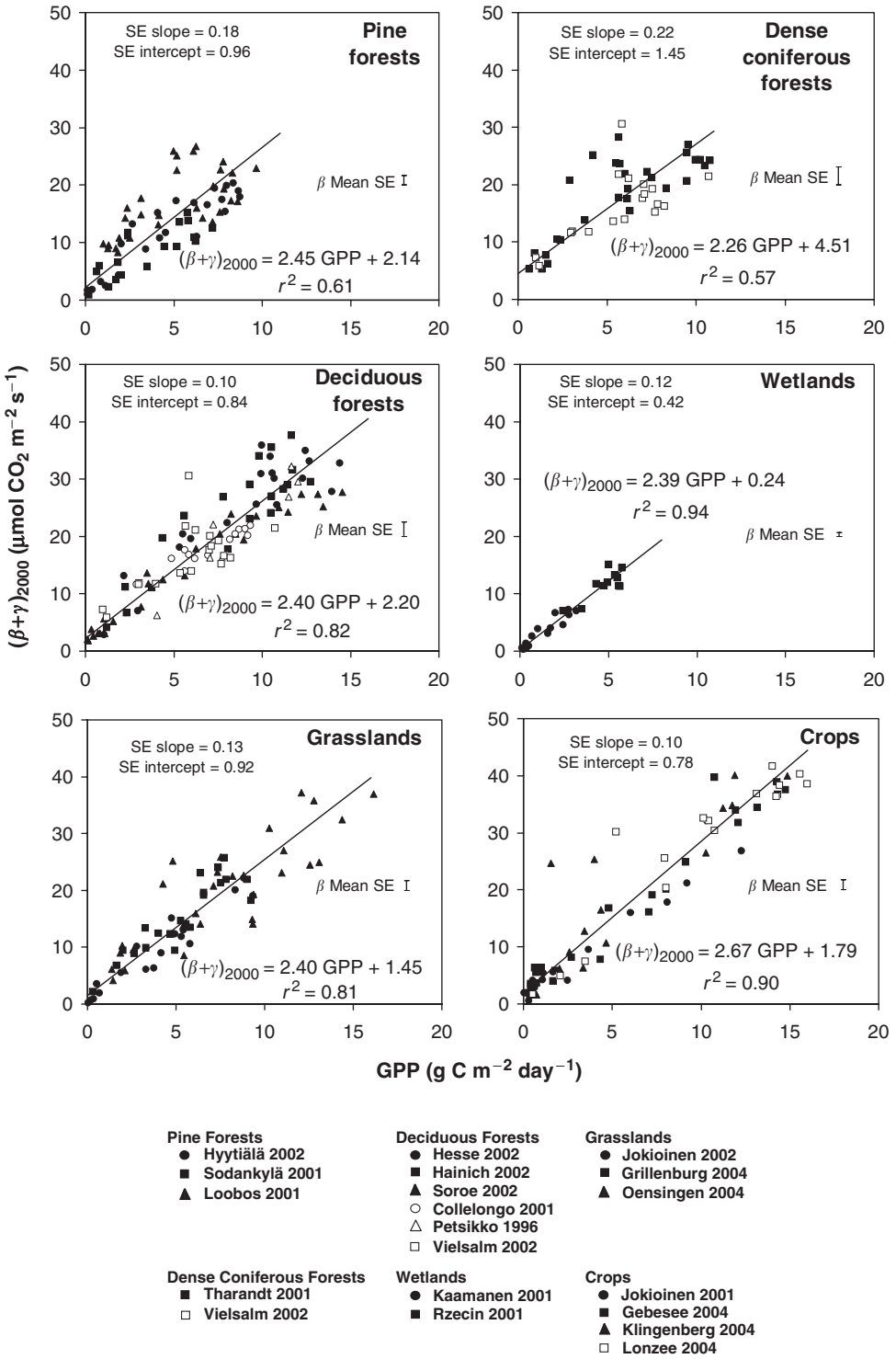

Fig. 2 Relationships and linear regressions for the results shown in Fig. 1 between daily gross primary production (GPP) from flux partitioning and $(\beta+\gamma)_{2000}$, the average maximum rate of canopy CO_2 uptake capacity, observed for 10-day periods for different functional ecosystem types. The mean standard error of β, which is a conservative estimate of the standard error of the $(\beta+\gamma)_{2000}$ parameter, is given on the right side of each graph. The standard error of each regression is shown. The legend is valid for Figs 2–4.

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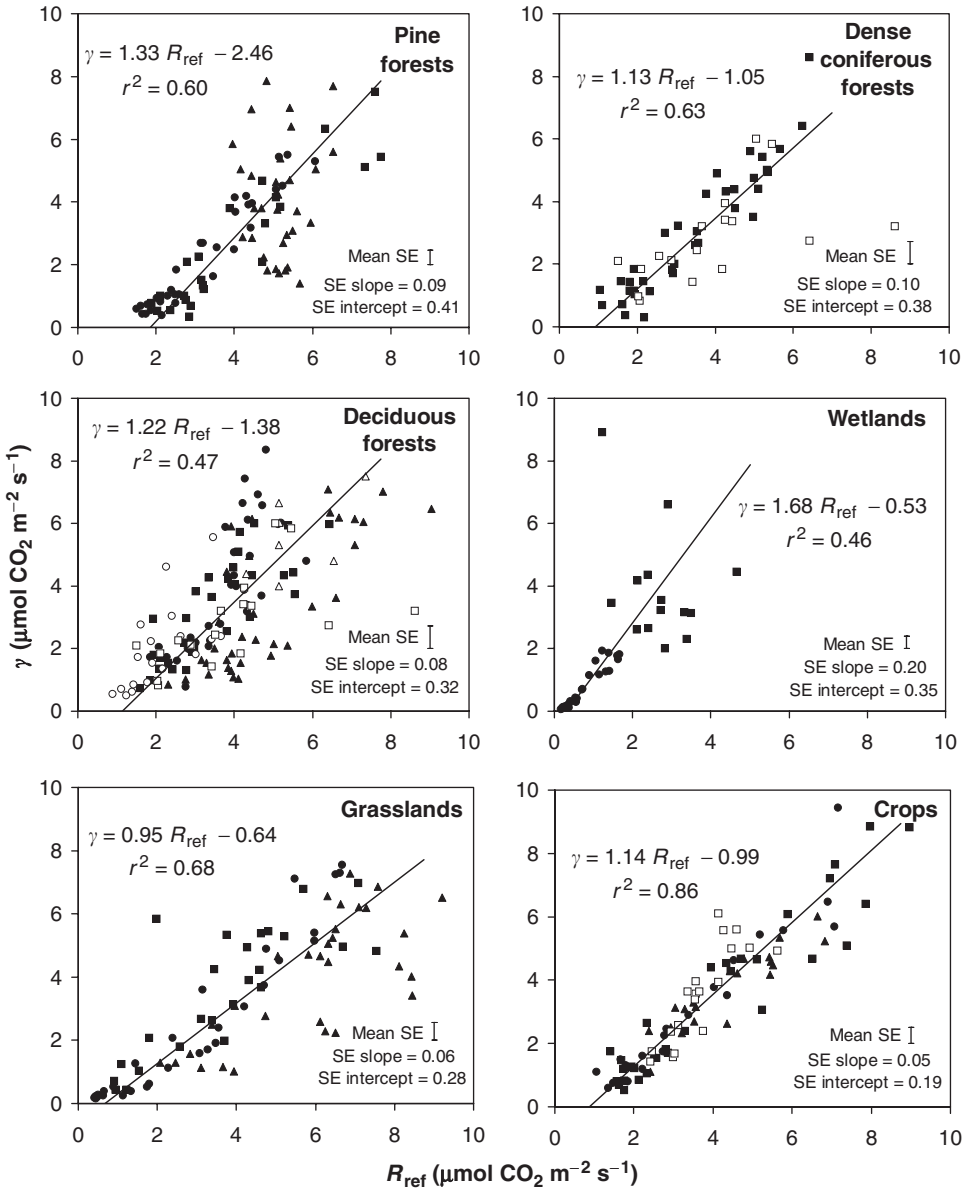

Fig. 3 Relationships and linear regressions between 10-day average R_{ref}, the reference ecosystem respiration at 15 °C, and γ, an estimate of the average ecosystem respiration, observed for 10-day periods for different functional ecosystem types. The mean standard error of the γ parameter is given on the right side of each graph. The standard error of each regression is shown. Symbols indicate sites as in legend of Fig. 2.

In the interest of reducing the number of model parameters, the relationship of light utilization efficiency, *alpha*, was studied with respect to possible dependency on canopy CO_2 uptake capacity. Pooling all of the information from these stands where seasonal changes in LAI are best known, one obtains the scattergram shown in Fig. 5. Substantial variation in *alpha* could be explained with a linear dependency on $Vc_{uptake2^*}$, but the general impression obtained is that *alpha* increases rapidly to values near 0.06 and is then limited. In addition, unexplained variations in *alpha* occur which may depend on real changes in processes or on the model inversion procedures. However, as $Vc_{uptake2^*}$ and *alpha* are negatively statistically correlated, this makes the positive correlation in Fig. 5 more pronounced. Numerous regressions, including the rectangular hyperbolic, polynomial and logarithmic regression, were fitted to these data and had a maximum r^2 value of 0.35. All regressions saturated at values close to 0.06. For the polynomial regression, only the linear and quadratic

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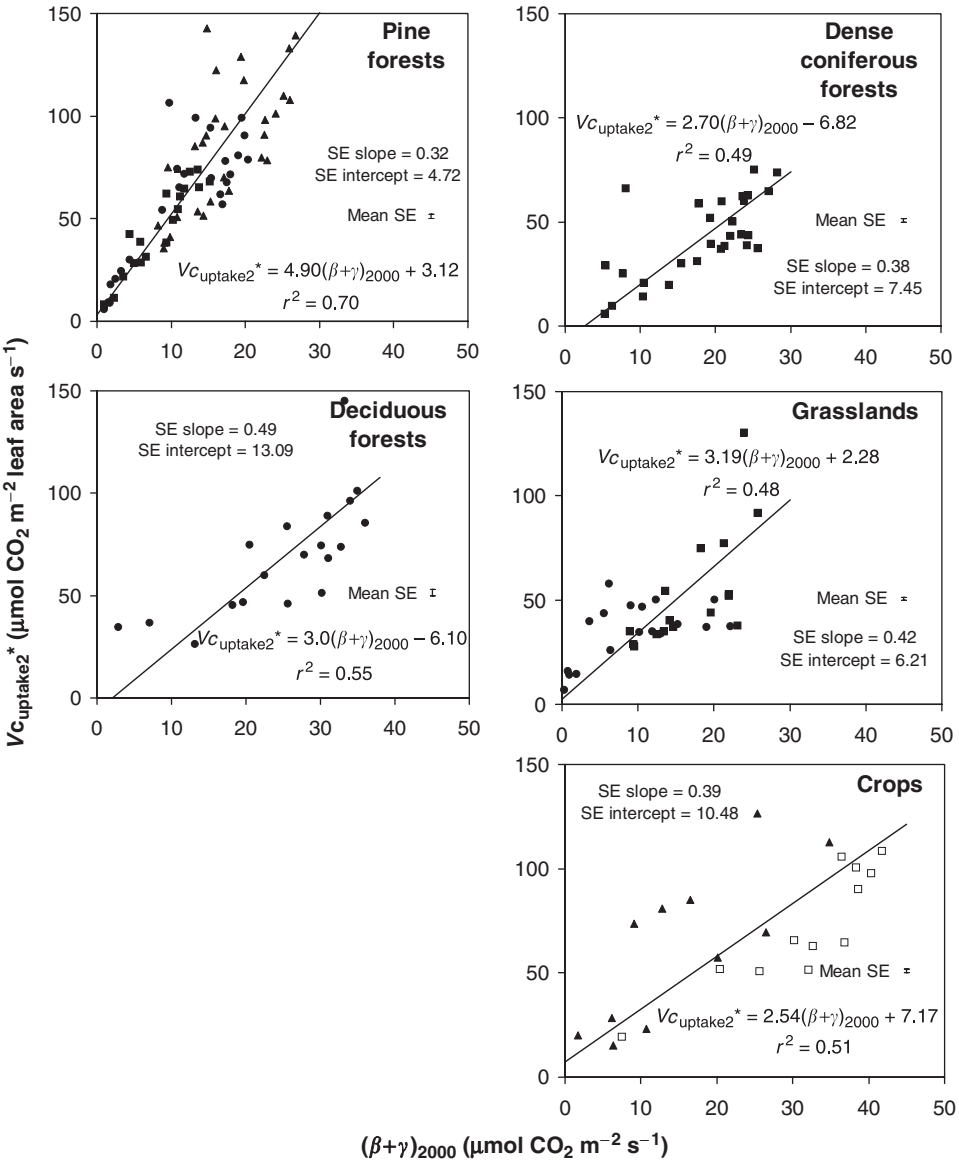

Fig. 4 Relationships and linear regressions between $(\beta+\gamma)_{2000}$, the average maximum rate of canopy CO_2 uptake capacity, and $Vc_{uptake2^*}$, related to the average leaf carboxylation capacity at 25 °C, for different functional ecosystem types using those sites where confidence in estimates of leaf area index were best. The mean standard error of the $Vc_{uptake2^*}$ parameter is given on the right side of each graph. The standard error of each regression is shown. Symbols indicate sites as in legend of Fig. 2.

term were found to be significant and justify a non-linear approximation. This threshold type relationship gives a slightly higher r^2 value. For simplification we interpreted this scatter as the linear solid line in Fig. 5, assuming that there is a general relationship of *alpha* to Vc_{uptake} along with many modifying factors [Eqn (18)].

$$alpha = \begin{matrix} 0.0008Vc_{uptake2^*} & Vc_{uptake2^*} \leq 75 \\ 0.06 & Vc_{uptake2^*} \geq 75. \end{matrix} \quad (18)$$

The consequences of making this assumption are discussed in the next section.

Process-based model simplification

Among studies of the summer active ecosystems, few observers have quantified seasonal changes in LAI. As a broad set of observations is required to support spatial modelling of carbon balances at regional to continental scales, we relaxed the data requirements for model inversions, obtaining parameter estimates for Vc_{uptake} with LAI maintained at the reported site seasonal maximum value. To overcome the overly sensitive trade-offs in estimation of light utilization efficiency vs. Vc_{uptake},

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Table 4 The linear regression between 10-day period average GPP and $Vc_{uptake2^*}$, related to the average leaf carboxylation capacity at 25 °C, for different functional ecosystem types using those sites where confidence in estimates of LAI were best (see Fig. 5 for sites)

Ecosystem	Relationship	r^2
Pine forest	$Vc_{uptake2^*} = 13.27 \times GPP + 9.46$	0.50
Dense coniferous forest	$Vc_{uptake2^*} = 6.35 \times GPP + 5.29$	0.38
Deciduous forest	$Vc_{uptake2^*} = 7.16 \times GPP + 5.31$	0.59
Grassland	$Vc_{uptake2^*} = 7.76 \times GPP + 9.08$	0.42
Cropland	$Vc_{uptake2^*} = 6.93 \times GPP + 12.55$	0.41

GPP, gross primary production; LAI, leaf area index.

Table 5 The linear regression between α obtained from the hyperbolic light response curve and *alpha* the average leaf light utilization efficiency without photorespiration determined from two-parameter inversions, for different functional ecosystem types using those sites where confidence in estimates of LAI were best (see Fig. 5 for sites)

Ecosystem	Relationship	r^2
Pine forest	$alpha = 1.05 \times \alpha + 0.010$	0.66
Dense coniferous forest	$alpha = 0.62 \times \alpha + 0.012$	0.44
Deciduous forest	$alpha = 0.37 \times \alpha + 0.035$	0.34
Grassland	$alpha = 0.80 \times \alpha + 0.013$	0.49
Cropland	$alpha = 0.97 \times \alpha + 0.007$	0.93

LAI, leaf area index.

we also examined inversions with *alpha* dependent on Vc_{uptake} according to the solid line function shown in Fig. 5.

The new assumptions with respect to LAI had little influence with respect to coniferous stands. The effect of constant LAI on summer active ecosystems is shown for the Hesse beech forest and Grillenburg grassland in Fig. 6. Assuming a constant LAI of 4.4 in Grillenburg or 6.6 in Hesse led to an underestimate in the parameter values for only very short periods during initial increases in LAI with leaf expansion in spring and after each cut of the grassland sites and during the senescence period in fall. As LAI increases above ca. 3 or 4, no further influence on the parameter values occurs, considering either the two-parameter or one-parameter model inversions. Eliminating free determination of *alpha* also had little influence (e.g. seasonal changes in Vc_{uptake} obtained for either the two-parameter or one-parameter model were quite similar). The effects of varying constant LAI between values of 3 and 9 on Vc_{uptake} and *alpha* were investigated for Hesse (not shown). As expected, a lower LAI results in higher Vc_{uptake} and *alpha* parameters as the carboxylase is compensating for lack of leaf area for the calculated production and vice versa. The annual maximum LAI provides a reasonable approximation of the seasonally varying LAI over relatively long periods.

The fit of the physiological model does not suffer by setting *alpha* dependent to Vc_{uptake}. In fact, the independent fits ($Vc_{uptake2^*}$) have up to 85% higher relative standard errors during individual periods during the active vegetation season as compared with the *alpha* dependent fits ($Vc_{uptake1^*}$). But in terms of r^2, the independent fits have on average over all periods a 6% higher r^2 than the *alpha*-dependent fit, although for some sites the highest maximum r^2 value occurs with the *alpha*-dependent fits. Additionally, the independent fit has higher r^2 values during the spring and fall periods than the *alpha*-dependent fits.

The parameter $Vc_{uptake1^*}$ is a robust indicator of the canopy CO_2 uptake capacity which allows effective comparisons across the data set (Fig. 7, solid lines). Nevertheless, some caution is required, as $Vc_{uptake1^*}$ is a lumped parameter influenced by several factors. Comparing Fig. 7 with Fig. 1, one sees that $Vc_{uptake1^*}$ more poorly follows the seasonal trend in GPP. While $(\beta + \gamma)_{2000}$ directly reflects average maximum CO_2 uptake capacity rates during each 10-day period, $Vc_{uptake1^*}$ is the activity required at 25 °C to allow the observed maximum rates. If high rates are required at low temperatures during winter, cf. Loobos pine forest, $Vc_{uptake1^*}$ may increase in order to obtain a high carboxylation capacity in the low temperature range, because temperature dependencies used in the model inversions currently remain constant over the course of the year. Data to support inclusion of acclimation in the temperature response do not exist for the many species considered in this work (e.g. systematic leaf gas exchange measurements over the course of the year are seldom available from individual flux tower sites). Additional problems will occur if the maximum LAI used does not appropriately account for all CO_2 sinks within the ecosystem, such as moss or lichen layers, loss of needles during autumn in certain pine sites or stem photosynthesis.

To determine whether convergence occurs in CO_2 uptake characteristics of the ecosystems studied and whether the relationships of the 'functional ecosystem types' identified for Europe are applicable to other temperate and boreal zone regions across the world, additional sites from North America and Asia were analysed (Table 6). Results of the flux separation are summarized for all sites and years in Table 7. Figure 8 shows the linear regressions between daily GPP and $(\beta + \gamma)_{2000}$, with the non-European sites superimposed

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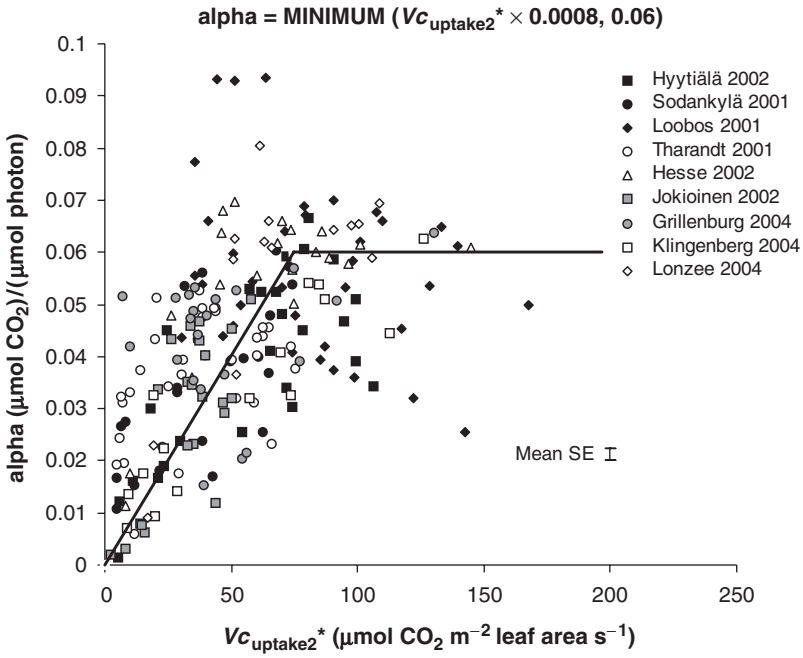

Fig. 5 Scattergram of the relationship of light utilization efficiency, *alpha*, with canopy CO_2 uptake capacity, $Vc_{uptake2*}$, for sites where confidence in estimates of leaf area index were best. Our interpretation of the scatter is indicated as the linear solid line assuming that there is a general relationship of *alpha* to Vc_{uptake} along with many modifying factors (see discussion of Eqn (18) in text). The mean standard error of the *alpha* parameter is shown.

in clear open symbols on the results from Fig. 2. Figure 9 shows the linear regressions between daily GPP and $Vc_{uptake1*}$ using constant annual maximum LAI with North American and Asian sites superimposed as clear open symbols on the European data.

Discussion

Many studies (Peat, 1970; Johnson & Thornley, 1984; Boote & Loomis, 1991; Gilmanov *et al.*, 2003) have shown that using the nonrectangular hyperbola [Eqn (19)], which contains an additional curvature parameter, η, provides less biased, more representative and different estimates of the α, β, and γ parameters of the light response of flux data.

$$\mathrm{NEE} = -\frac{1}{2\eta}\left(\alpha Q + \beta - \sqrt{(\alpha Q + \beta)^2 - 4\alpha\beta\eta Q}\right) + \gamma. \tag{19}$$

However, we chose the rectangular hyperbola [Eqn (1)], as one of the goals in this study is to simplify models for use at continental scale, and the rectangular hyperbola is a simplification of the nonrectangular hyperbola with $\eta = 0$. Many studies continue to use the rectangular hyperbola (Wofsy *et al.*, 1993; Aubinet *et al.*, 2001; Pilegaard *et al.*, 2001) including those focusing on remote sensing (Ruimy *et al.*, 1995; Xiao, 2006). By using 10-day periods for parameter estimation, one loses the hysteresis effect and can mask the curvature of the diurnal light response (Biscoe *et al.*, 1975; Ham *et al.*, 1995; Gilmanov *et al.*, 2003) but, again, if using the results presented here in continental scale models, only a restricted amount of information can be incorporated and as few parameters as possible is desirable. An example of the differences between the rectangular hyperbola and the nonrectangular hyperbola using daytime data are shown for Hesse beech forest and Grillenburg meadow in Fig. 10. The models produce very different estimates of β, but analysis in this paper is done with $(\beta + \gamma)_{2000}$ which have very similar values.

The comparison demonstrates that the relationships between $(\beta + \gamma)_{2000}$ to GPP based on functional ecosystem type for European sites (Fig. 2) are valid for the other temperate and boreal sites examined in the Northern Hemisphere (Fig. 8). The differences in the slopes of the regressions in Figs 2 and 8 are small with essentially little change in r^2 values. Among coniferous sites, Loobos, Duke Pine, Tharandt, and Howland exhibited large annual changes in the apparent relationship of $(\beta + \gamma)_{2000}$ to GPP. A different relationship seems to apply below and above daily GPP values of ca. $3\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$. Further detailed study must be carried out to explain these characteristics, which appear to be

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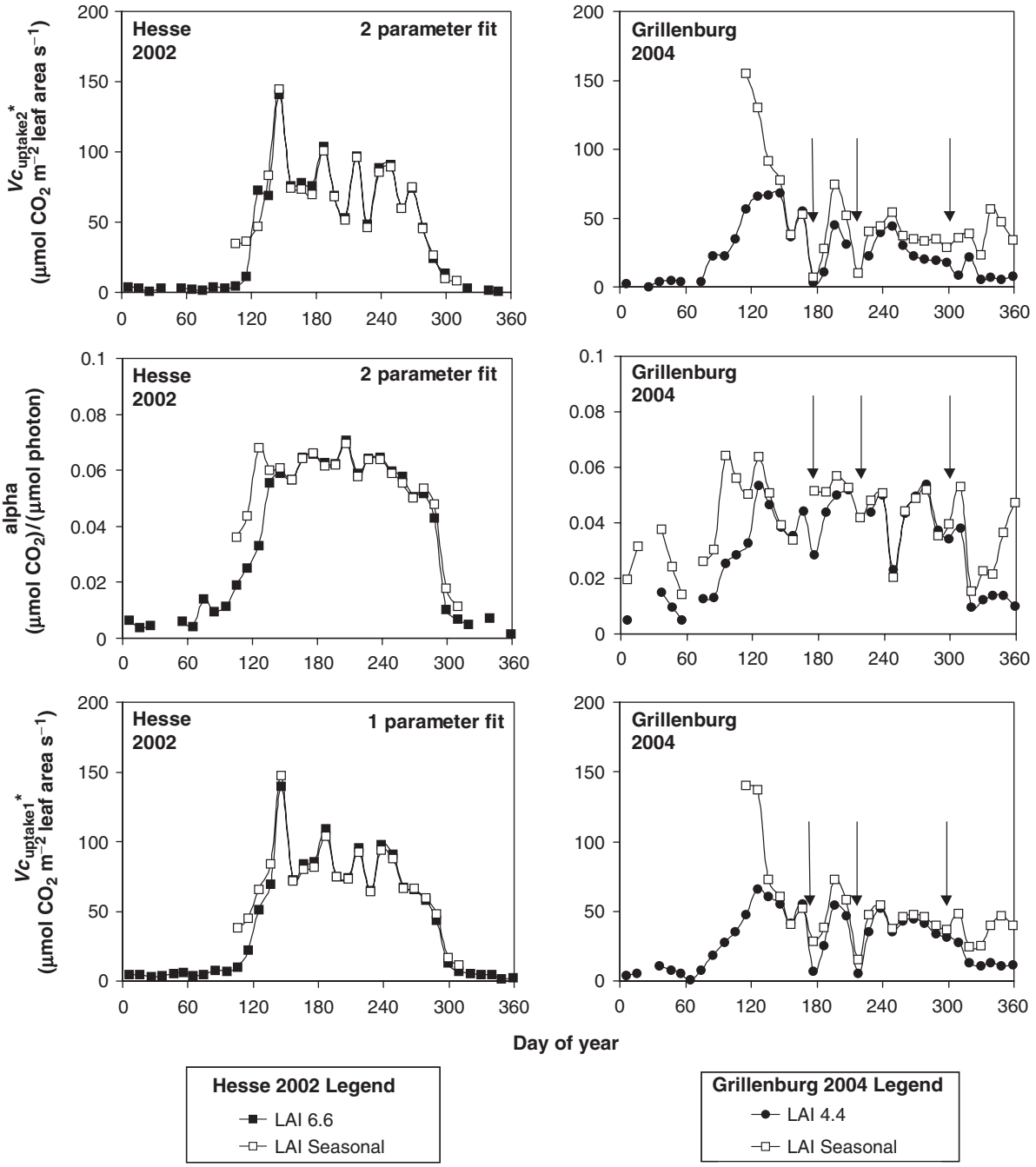

Fig. 6 Comparison between seasonally changing leaf area index (LAI) and constant annual maximum LAI on model inversions for summer active ecosystems for the Hesse beech forest in 2002 and Grillenburg grassland in 2004. The arrows show dates of grass cutting in Grillenburg.

an integral component of conifer ecosystem gas exchange (related to seasonal adjustments).

These results between $Vc_{\mathrm{uptake1^*}}$ and GPP (Fig. 9) using a larger data set clearly demonstrate several principles for consideration in future studies, and they support the basic idea that $Vc_{\mathrm{uptake1^*}}$ is a robust indicator of the canopy CO_2 uptake capacity useful in simulations at large scales. Broad agreement is found at European, North American, and Asian sites within the indicated categories. Dense conifer forests appear to have two phases of response, with a separation in the correlation between $Vc_{\mathrm{uptake1^*}}$ and GPP at ca. 2–3 g C m^{-2} day^{-1}. Some pine stands seem to exhibit similar behaviour to those stands classified as dense

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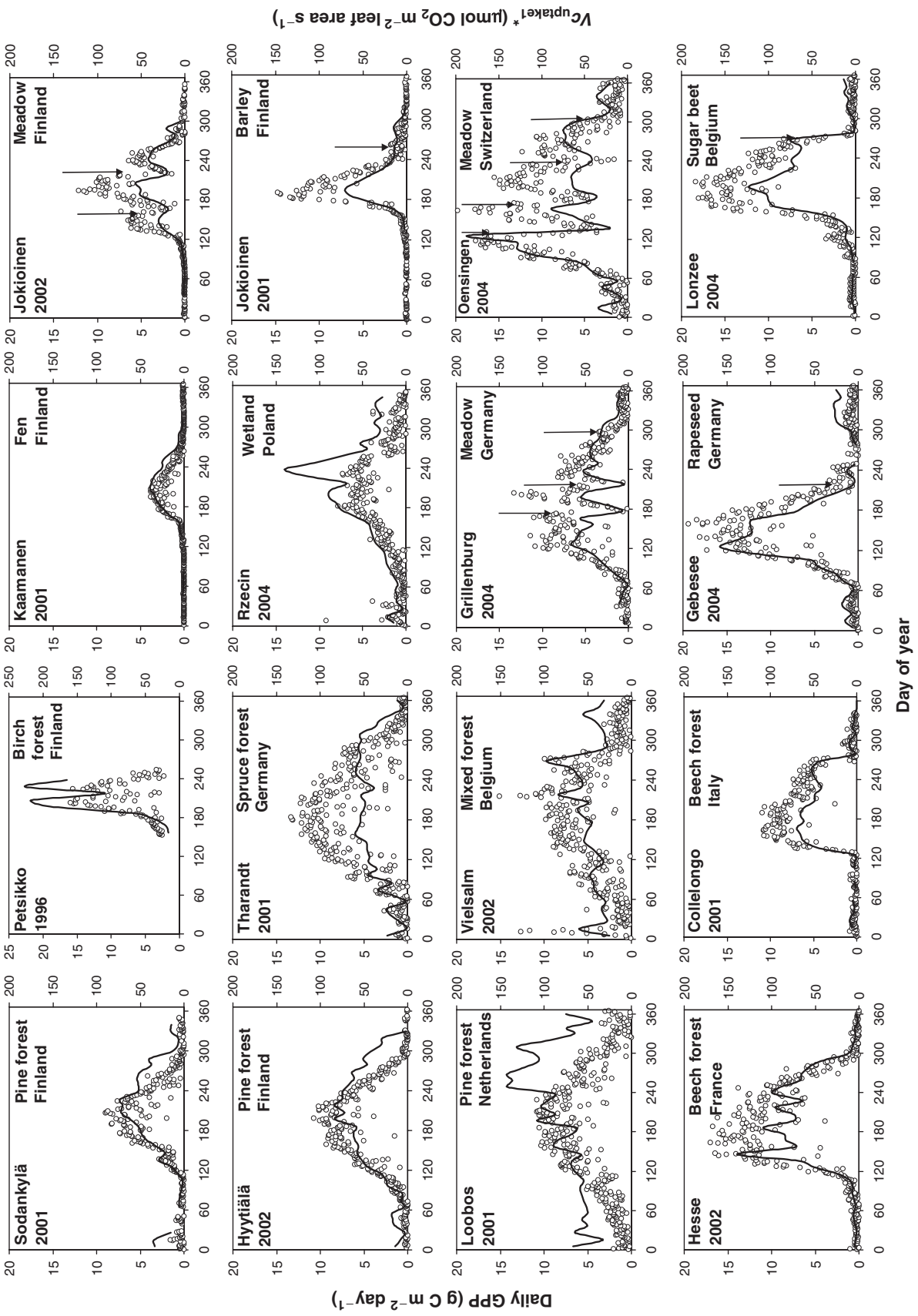

Fig. 7 Values derived for the parameter $Vc_{uptake1*}$ using constant annual maximum leaf area index (solid line) superimposed on the daily observations of gross primary production (GPP) (○) derived according to Reichstein *et al.* (2005). The arrows indicate crop harvest or grassland cut dates.

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Table 6 North American and Asian eddy covariance flux measurement sites according to vegetation type included in the comparison of GPP, Reco, and model parameters

Site location and dominant vegetation	Latitude (°N)	Longitude (°E)	Measurement methods*
Coniferous forest			
Duke, NC, USA *Pinus taeda*	35.98	−79.09	Oren *et al*. (2006), Palmroth *et al*. (2005), Stoy *et al*. (2005, 2006)
Harvard Hemlock, MA, USA *Tsuga canadensis* L.	42.54	−72.18	Hadley & Schedlbauer (2002)
Turkey Point, ON, Canada *Pinus strobus* L.	42.71	−80.36	Arain & Restrepo-Coupe (2005)
Howland, ME, USA *Picea rubens* Sarg., *Tsuga canadensis* (L.) Carr.	45.20	−68.74	Hollinger *et al*. (2004, 1999), Davidson *et al*. (2006)
Campbell river, BC, Canada *Pseudotsuga menezeisii* (Mirbel) Franco	49.87	−125.33	Drewitt *et al*. (2002)
Deciduous forest			
Duke Hardwood, NC, USA *Quercus*, *Carya*	35.98	−79.09	Palmroth *et al*. (2005), Stoy *et al*. (2005, 2006)
Takayama, Japan *Quercus crispula* Blume, *Betula ermanii* Cham., *Betula platyphylla Sukatchev* var. japonica *Hara*	36.13	137.42	Saigusa *et al*. (2005)
Harvard, MA, USA *Quercus rubra*, *Quercus alba*, *Quercus velutina*, *Tsuga canadensis*, *Betula lenta*, *Acer rubrum*	42.54	−72.17	Curtis *et al*. (2002), Barford *et al*. (2001), Wofsy *et al*. (1993)
Tundra			
Upad, AK, USA *Eriophorum angustifolium*, *Carex aquatilis*, *Carex bigelowii*	70.28	−148.88	Vourlitis & Oechel (1997)
Barrow, AK, USA *Carex aquatilis* ssp. *stans*, *Eriophorum angustifolium*, *Dupontia fisheri*, *Poa arctica*	71.32	−156.63	Walker *et al*. (2003), Oechel *et al*. (2000)
Grasslands and prairies			
Duke Old Field, NC, USA *Festuca arundinaria* Shreb	35.97	−79.09	Novick *et al*. (2004), Stoy *et al*. (2006)
Canaan Valley, WV, USA *Dactylis glomerata Phleum pratense*, *Anthoxanthenum odoratum*, *Poa palustris*, *Galium mallugo*	39.06	−79.42	Warren (2003)
Fort Peck, MT, USA *Agropyron cristatum*, *Pascopyron smithii*, *Stipa* spp., *Bouteloua gracilis*	48.31	−105.10	Gilmanov *et al*. (2005)
Lethbridge, AB, Canada *Agropyron dasystachyum* (Hook.) Scrib., *Pascopyronsmithii* Rydb., *Tragopogon dubius* Scop.	49.71	−112.94	Flanagan *et al*. (2002), Flanagan & Johnson (2005), Gilmanov *et al*. (2005), Wever *et al*. (2002)
Crops			
Bondville, IL, USA *Zea mays* L., *Glycine max* (L.) Merr.	40.01	−88.29	Meyers & Hollinger (2004), Hollinger *et al*. (2005)
Mead irrigated, NE, USA *Zea mays* L., *Glycine max* (L.) Merr.	41.16	−96.47	Suyker *et al*. (2005, 2004), Verma *et al*. (2005)
Mead rainfed, NE, USA *Zea mays* L., *Glycine max* (L.) Merr.	41.18	−96.44	Suyker *et al*. (2005, 2004), Verma *et al*. (2005)

*All sites are described on the Ameriflux, Fluxnet-Canada or Asiaflux websites

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Table 7 Annual sums of CO_2 and latent heat exchange for the North American and Asian sites in Table 6

Site	Year	Annual NEE ($g C m^{-2}$)	Annual GPP ($g C m^{-2}$)	Annual Reco ($g C m^{-2}$)	Latent heat exchange (mm)	Spring NEE decrease (day)	Fall NEE increase (day)	Negative NEE season (day)
Coniferous forest								
Duke Pine, NC, USA	2003	−745	1542	797	841	1	365	365
	2004	−909	1758	849	862	1	365	365
Harvard Hemlock, MA, USA	2001	−505	1220	715	*	88	†	†
Turkey Point, ON, Canada	2004	−162	1306	1144	373	94	299	206
Howland, ME, USA	1999	−204	1419	1215	447	81	311	231
	2000	−285	1541	1256	425	79	318	240
	2003	−239	1306	1067	321	93	301	209
Campbell River, BC, Canada	1999	−469	1405	936	418	1	305	305
	2000	−434	1803	1368	415	8	266	259
	2001	−474	1695	1221	382	17	307	291
Deciduous forest								
Duke Hardwood, NC, USA	2003	−538	1384	846	757	92	294	203
	2004	−667	1581	914	730	104	295	192
Takayama, Japan	2002	−482	1000	518	204	136	295	160
	2003	−352	931	579	221	138	299	162
	2004	−327	638	311	160	137	288	152
Harvard, MA, USA	2000	−325	1237	912	*	144	287	144
	2003	−320	1242	922	*	140	287	148
Tundra and wetland								
Upad, Alaska, USA	1994‡	−16	75	59	123	176	220	45
Barrow, AK, USA	1998	−54	147	93	99	§	239	§
	1999¶	−87	150	63	111	190	243	54
	2000	−72	155	83	76	‖	246	‖
Grasslands and prairies								
Duke Old Field, NC, USA	2003	−236	1505	1269	746	23	363	341
	2004	−101	1417	1316	677	12	366	355
Canaan Valley, WV, USA	2004	−261	1062	801	739	6	278	273
Fort Peck, MT, USA	2004	−25	329	304	348	99	220	122
Lethbridge, AB, Canada	2002	−287	787	499	263	151	284	134
	2003	−217	669	452	335	114	229	116
	2004	−96	582	485	349	130	226	97
Crop								
Bondville (maize/soybean), IL, USA	1998**	87	426	513	643	178	253	76
	1999††	−497	1272	775	624	152	252	101
	2000**	51	628	678	588	171	246	76
	2001††	−444	964	520	733	143	251	109
	2002**	−237	693	456	565	179	261	83
	2003††	−732	1355	622	515	149	245	97
	2004**	−371	1047	675	631	154	247	94
Mead irrigated (maize/soybean), NE, USA	2004**	133	766	899	556	190	262	73
Mead rainfed (maize/soybean), NE, USA	2004**	60	771	831	546	187	260	74

*No latent heat measurements were made.
†Measurements for Harvard Hemlock were ended on day of year 305 in 2001.
‡Measurements for Upad were made from day of year 154 to 243 in 1994.
§Measurements for Barrow were made from day of year 182 to 304 in 1998.
¶Measurements for Barrow were made from day of year 152 to 243 in 1999.
‖Measurements for Barrow were made from day of year 92 to 250 in 2000.
**Soybean rotation years.
††Maize rotation years.
The start and end of the active NEE season is defined as in Table 3 where the smoothed NEE curve changes from positive to negative and vice versa.
NEE, net ecosystem CO_2 exchange; GPP, gross primary production; Reco, ecosystem respiration.

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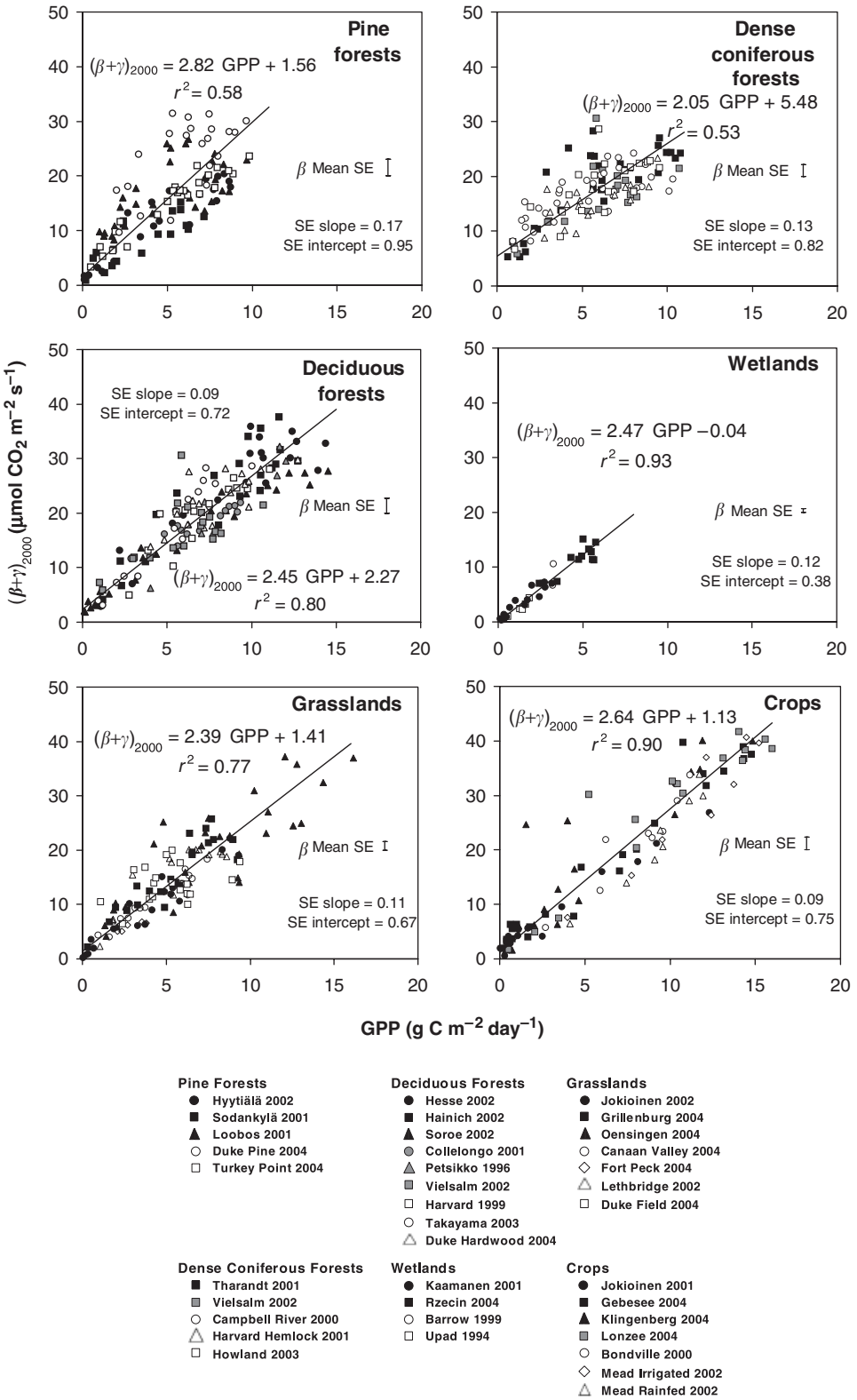

Fig. 8 Relationships and linear regressions for the results between daily gross primary production (GPP) from flux partitioning and $(\beta + \gamma)_{2000}$, the average maximum rate of canopy CO_2 uptake capacity, for European sites as in Fig. 2 and North American and Asian sites for 10-day periods for different functional ecosystem types. The mean standard error of β, which is a conservative estimate of the standard error of the $(\beta + \gamma)_{2000}$ parameter, is given on the right side of each graph. The standard error of each regression is shown. The legend is valid for Figs 8 and 9.

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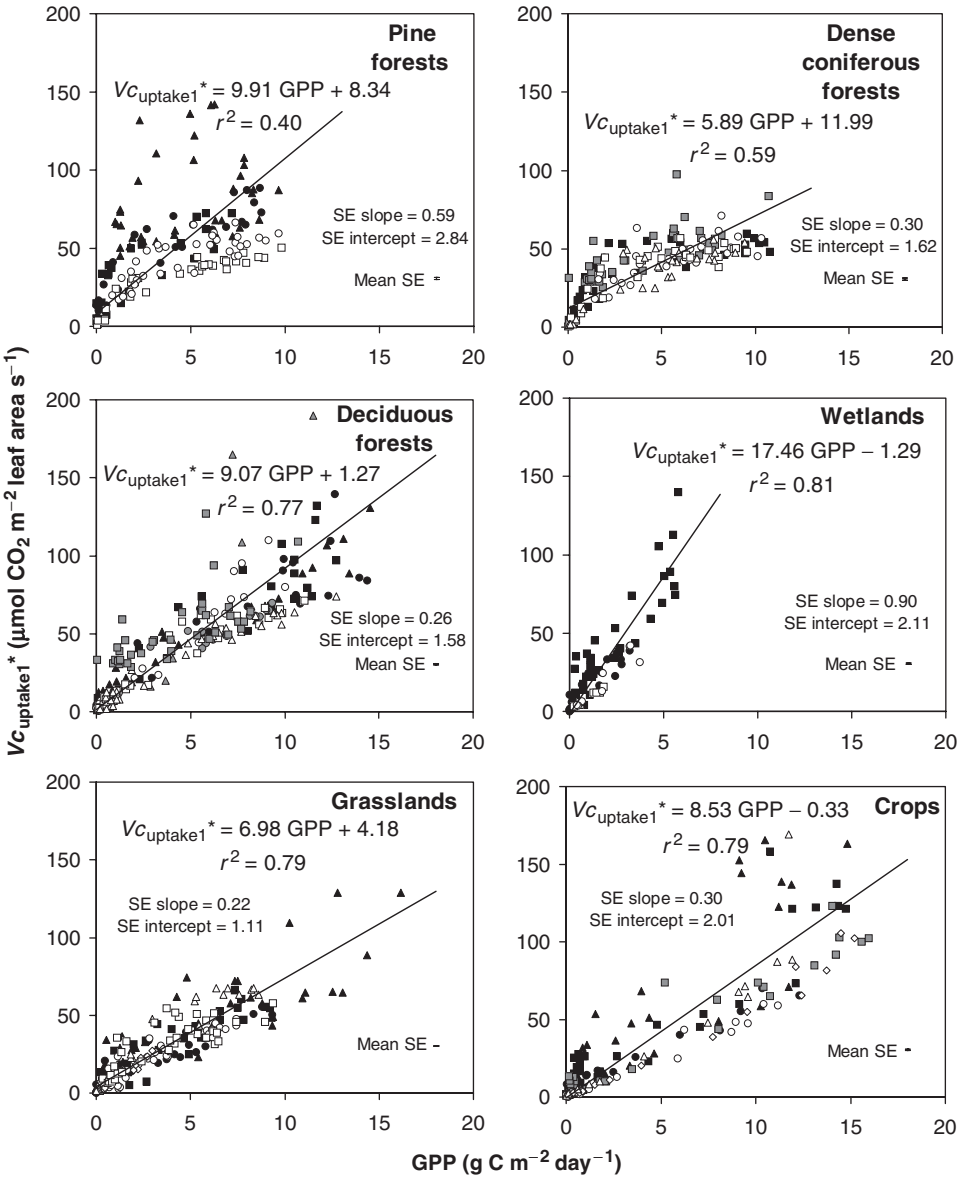

Fig. 9 Relationships and linear regressions for the results between daily gross primary production (GPP) from flux partitioning and $Vc_{uptake1*}$, which is a robust indicator of the canopy CO_2 uptake capacity, obtained using constant annual maximum leaf area index for European, North American and Asian sites for 10 day periods for different functional ecosystem types. The mean standard error of the $Vc_{uptake1*}$ parameter is given on the right side of each graph. The standard error of each regression is shown. Symbols indicate sites as in legend of Fig. 8.

conifers (e.g. Turkey Point) but the remaining pine stands exhibit larger $Vc_{uptake1*}$, suggesting that a separate functional type may be justified. Whether a clean separation of these groups by species type, influence of understory, or LAI is possible remains unclear.

All summer active ecosystems provide a linear correlation between $Vc_{uptake1*}$ and GPP. The slope of the relationships is fairly similar for deciduous forests, grasslands, and crops and much larger for wetlands. Daily GPP of northern or temperate wetlands remains very low at least in part due to small values of LAI. It is possible that the parameter values for wetlands as in the case of high outliers obtained with grass- and croplands result from the LAI restrictions imposed during analysis. On the other hand, lower values of $Vc_{uptake1*}$ would still be expected during certain periods.

The predicted relationships are similar independent of global region. The relatively wet Alaskan tundra sites fit well to the European wetland relationship. Drier tundra sites appeared to exhibit a different behaviour,

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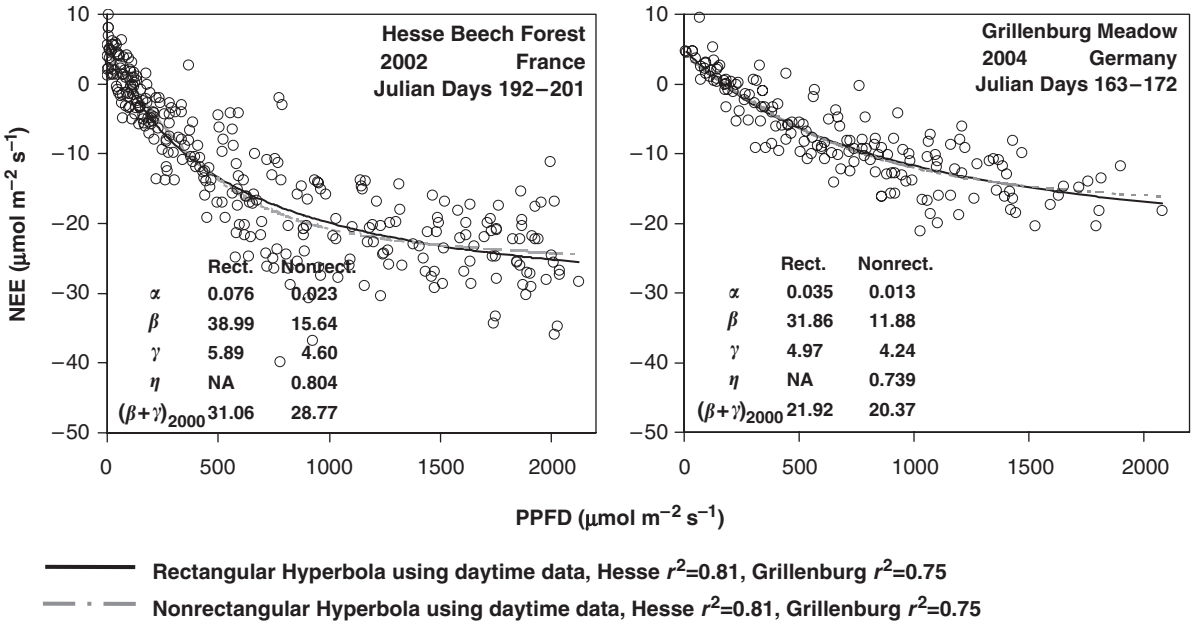

Fig. 10 Example light response curves and parameters for one inversion period for the Hesse beech forest in 2002 and Grillenburg grassland in 2004. The lines compare results of inverting the rectangular hyperbola and the nonrectangular hyperbola using daytime data.

but the data did not allow final conclusions. The mixed deciduous forest sites at Harvard Forest and Takayama were extremely similar to the European beech forest sites. The relationship obtained for C_3 crops fits both the North American legumes and the European grain and root crops. As discussed above, intensive management complicates parameter evaluations. A comparison of common management practices of similar ecosystems in different climate zones, or a comparison of different ecosystems under similar climates, would help to separate the influences of climate and management on important crop and grassland species.

One of the objectives of this paper was to demonstrate relationships between an empirical description of CO_2 exchange (rectangular hyperbolic light response model) that has been applied in several studies across sites (e.g. Hollinger *et al.*, 1999; Wohlfahrt *et al.*, 2005) and process-based parameters obtained with a carboxylase-based model of gas exchange. The relationships described in Figs 4 and 5 demonstrate that simple rules may be derived that permit, at least in the first approximation, translation of empirical canopy CO_2 uptake capacity and light utilization efficiency into their physiological counterparts. At the same time, the proportionalities depend on ecosystem type, as the physiological approach includes assumptions that differentiate among these (e.g. the treatment of light interception as influenced by leaf angles, clumping, assumed temperature responses, and characteristics of stomatal response).

As more data become available and with further careful study, we suggest that rules such as those found here will lead to a better understanding of the time-dependent changes in relationships between parameter sets. This may require more elaborate inversion schemes due to the necessity of including more realism into the physiological modelling approach (i.e. time dependent acclimation of gas exchange processes).

We have found that a parallel examination of data across sites with the two modelling approaches is extremely helpful, since α, β and γ are obtainable by simple optimization, while *alpha* and Vc_{uptake} are sensitive to the additional data required in physiological model inversions. One might ask whether the effort to simplify the physiological parameters is justifiable, since the final product departs from realism and recreates a simple description that needs additional input, namely maximum LAI for each location. However, the simplified physiological model provides a needed process-based link between carbon, water, and nutrient balances. While interception, throughfall, and soil evaporation will be shifted in a model with these simplifications, the problematic time periods may be short, and at many locations considered above, water is in excess throughout the growing season. Thus, we are faced with modelling trade-offs that must be critically examined in specific spatial model applications, rather than in the context of the current paper. The $Vc_{\mathrm{uptake1^*}}$ parameter is sensitive to nitrogen availability and manage-

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ment measures as seen in Fig. 7 for the nonfertilized Grillenburg and heavily fertilized Oensingen meadows. Finally, $Vc_{\text{uptake1*}}$ is a 'property' of the canopy, independent of meteorological conditions, and thus contains more generality than α, β, and γ (e.g. it may be viewed as a scientific advance). Improved ancillary data at network observation sites is desirable, particularly in the case of fundamentally important ecosystem variables such as seasonal change in LAI and, for example, leaf nutrient concentrations. In this study, only a small number of sites could be examined with respect to all aspects of the modelling.

The simplified model analysis illustrated in Fig. 7 is a first step toward deriving appropriate parameters upon which to base spatial simulations for large regions or continents. In the case of forests, where LAI either remains relatively constant (coniferous) or rapidly increases to a level in springtime that is nearly constant over the growing season (deciduous), the vegetation canopy may be conceptualized as having a constant LAI defined by the maximum evaluated from remote sensing and a variable uptake capacity ($Vc_{\text{uptake1*}}$) that follows a regular pattern as seen in the examples of Fig. 7. The subsequent task in continental scale modelling is to spatially describe the onset in springtime of $Vc_{\text{uptake1*}}$ increase, the period with relatively constant CO_2 uptake capacity, and the onset of autumn decrease in this critical parameter.

In the case of grasslands, and in the case of crops as well, management measures (harvesting) lead to large fluctuations in $Vc_{\text{uptake1*}}$ when it is evaluated as described in the above analysis. In these cases, $Vc_{\text{uptake1*}}$ should be evaluated with LAI obtained over the season, for example as obtained from remote sensing. Again, a springtime increase in $Vc_{\text{uptake1*}}$ is expected, a period during summer where the parameter remains relatively constant, and a decrease in parameter values with senescence of the vegetation in fall (Wilson *et al.*, 2001) or at times of harvest (hay meadows, multiple crops). Superimposed on this are the effects of management, which pose a significant challenge in spatial applications. Ultimately, in spatial model applications for grasslands and crops, LAI must be estimated seasonally via a growth model.

As described in Wang *et al*. (2003), one can only work towards defining useful 'lumped parameters' that aid the implementation of process-based approaches within the framework of limitations in both recorded site data and spatial data. The parameter $Vc_{\text{uptake1*}}$ includes the influences of average leaf carboxylase, changes in LAI during certain periods (leaf expansion, leaf senescence, harvest times, etc.), undefined sinks for CO_2 (understory vegetation, moss and lichen layers, stem photosynthesis, etc.), improper description of acclimation processes, impact of unrecognized stress due to cold temperatures and reduced water availability, and other influences. Nevertheless, general patterns in seasonal change in the effective parameter $Vc_{\text{uptake1*}}$ (Fig. 7) can support and guide further efforts directed at bridging between flux network observations and simulation modelling at large scales.

Conclusions

Radiation and temperature along with other environmental factors control seasonal changes in carbon uptake capacity in a complex fashion. The current paper attempts to derive relatively simple methods to describe these dynamic changes in physiology of ecosystems as revealed from flux tower network eddy covariance data. Two models, the rectangular hyperbola and a simplified Farquhar carboxylase-based process model, are used in the analysis. The comparison by necessity is carried out in stepwise fashion, examining relationships among empirical and physiologically based parameters from a subset of network sites found to have more extensive ancillary data, utilizing these results to simplify the physiological approach, and finally to derive a parameter, ($Vc_{\text{uptake1*}}$), and means for comparing empirical and physiologically based methods across all sites. We show that the proportionalities between the parameters depend on ecosystem type and hold for European, North American, and Asian temperate and boreal climate zones. We envision that the $Vc_{\text{uptake1*}}$ parameter along with remotely sensed LAI can be used in modeling approaches at continental scale.

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