

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

KATHERINE E. OWEN\*, JOHN TENHUNEN\*, MARKUS REICHSTEIN†, QUAN WANG‡, EVA FALGE\*, RALF GEYER\*, XIANGMING XIAO§, PAUL STOY¶, CHRISTOF AMMANN||, ALTAFA ARAIN\*\*, MARC AUBINET††, MIKA AURELA‡‡, CHRISTIAN BERNHOFER§§, BOGDAN H. CHOJNICKI¶¶, ANDRÉ GRANIER|||, THOMAS GRUENWALD§§, JULIAN HADLEY\*\*\*, BERNARD HEINESCH††, DAVID HOLLINGER†††, ALEXANDER KNOHL†, WERNER KUTSCH†, ANNALEA LOHILA‡‡, TILDEN MEYERS‡‡‡, EDDY MOORS§§§§, CHRISTINE MOUREAUX††, KIM PILEGAARD¶¶¶, NOBUKO SAIGUSA|||, SHASHI VERMA\*\*\*\*, TIMO VESALA†††† and CHRIS VOGEL‡‡‡‡

\*Department of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany, †Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Strasse 10, 07745 Jena, Germany, ‡Institute of Silviculture, Faculty of Agriculture, Shizuoka University, Ohya 836, Shizuoka 422-8529, Japan, §Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824, USA, ¶Nicholas School of the Environment and Earth Sciences, Duke University, A328 LSRC, Durham, NC 27708-0328, USA, ||Swiss Federal Research Station for Agroecology and Agriculture of Zurich-Reckenholz, Reckenholzstrasse 191, 8046 Zürich, Switzerland, \*\*School of Geography and Earth Sciences, McMaster University, 1280 Main Street West, Hamilton, ON, Canada L8S 4K1, ††Unité de Physique des Biosystèmes, Faculté universitaire des Sciences agronomiques de Gembloux, B-5030 Gembloux, Belgique, ‡‡Finnish Meteorological Institute, Climate and Global Change Research, PO Box 503, FI-00101 Helsinki, Finland, §§Technische Universität Dresden, IHM-Meteorologie, Piennerstrasse 9, 01737 Tharandt, Germany, ¶¶Department of Agrometeorology, Agricultural University of Poznań, 60-637 Poznań, Poland, |||INRA, Unité d'Ecophysiologie Forestière, F-54280 Champenoux, France, \*\*\*Harvard University, Harvard Forest, PO Box 68, 324 N. Main Street, Petersham, MA 01366, USA, †††USDA Forest Service, Northern Research Station, 271 Mast Rd, PO Box 640, Durham, NH 03824, USA, ‡‡‡NOAA/ARL, Atmospheric Turbulence and Diffusion Division, PO Box 2456, 456 South Illinois Avenue, Oak Ridge, TN 37831-2456, USA, §§§Alterra – Centre for Water and Climate, Wageningen University, 6700 AA Wageningen, The Netherlands, ¶¶¶Risø National Laboratory, Biosystems Department, PO Box 49, DK-4000 Roskilde, Denmark, ||||National Institute of Advanced Industrial Science and Technology, 16-1 Onogawa, Tsukuba, Ibaraki 305-8569, Japan, \*\*\*\*School of Natural Resources, University of Nebraska – Lincoln, 244 L.W. Chase Hall, PO Box 830728, Lincoln, NE 68583-0728, USA, ††††Department of Physical Sciences, University of Helsinki, FIN-00014, Helsinki, Finland, ‡‡‡‡NOAA Air Resources Laboratory, Canaan Valley Institute, PO Box 673, Davis, WV 26260, USA

## 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**

Correspondence: Katherine E. Owen, fax +49 0921 552564, e-mail: katie\_e\_owen@yahoo.com

Data additionally provided by: Christian Bernhofer/Thomas Gruenwald/Barbara Koestner; Eddy Moors/Jan Elbers/Wilma Jans; Timo Vesala/Michael Boy/Nuria Altimir; Tuomas Laurila/Mika Aurela/Juha-Pekka Tuovinen/Annalea Lohila; Marc Aubinet/Bernard Heinesch/Christine Moureaux; Riccardo Valentini/Giorgio Matteucci/Nicola Arriga/Mazzenga Francesco/Paolo Stefani; André Granier/Bernard Longdoz; Corinna Rebmann/Werner Kutsch/Alexander Knohl; Lise Lotte Soerensen/Andreas Ibrom/Kim Pilegaard; Bogdan Chojnicki/Janusz Olejnik/Marek Urbaniak; Christof Ammann/Juerg Fuhrer; Gabriel Katul/David Ellsworth/Ram Oren/Paul Stoy; Altaf Arain; David Hollinger/Eric Davidson/Bob Evans/Mike Goltz/Monique Leclerc/John Lee/Kevin Tu; T. Andrew Black/Michael Novak/Hiroaki Kondo/Nobuko Saigusa/Shohei Murayama; Steven Wofsy/Julian Hadley/Patrick Crill/David Fitzjarrald/Michael Goulden/Kathleen Moore/J. (Bill) Munger; Walter Oechel/Joe Verfaillie, Jr./George Vourlitis/Rommel Zulueta; Tilden Meyers/Chris Vogel; Lawrence Flanagan; Shashi Verma/Todd Schimelfenig/Andrew Suyker.

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

*Received 23 August 2006; revised version received 4 October 2006 and accepted 11 October 2006*

## Introduction

Networks of eddy covariance sites have been established worldwide to observe the long-term characteristics of carbon dioxide (CO<sub>2</sub>), water vapour and energy fluxes associated with different ecosystem types along climate gradients (Baldocchi *et al.*, 1996, 2001). With respect to CO<sub>2</sub>, such studies allow only direct measurements and comparisons of net ecosystem CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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 ( $V_{c_{max}}$ ), 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](http://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<sub>2</sub> exchange parameters obtained for different ecosystem types, (2) examine patterns in CO<sub>2</sub> uptake or loss as

related to climate factors, LAI, and canopy and leaf physiology, (3) determine whether convergence occurs in CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> and H<sub>2</sub>O (Aubinet *et al.*, 2000), accounting for correction of CO<sub>2</sub> storage and filtering for low-turbulence night con-

ditions 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  $R_{\text{ref}}$ , 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):

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

where NEE is ungap-filled NEE ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $\alpha$  is the initial slope of the light response curve and an approximation of the canopy light utilization efficiency ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / (\mu\text{mol photon m}^{-2} \text{ s}^{-1})$ ),  $\beta$  is the maximum CO<sub>2</sub> uptake rate of the canopy ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $Q$  is the PPFD ( $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ),  $\gamma$  is an estimate of the average daytime ecosystem respiration occurring during the observation period ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $(\alpha/\beta)$  is the radiation required for half-maximal uptake rate, and  $(\beta + \gamma)$  is the theoretical maximum uptake capacity ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) 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 ( $Q = 2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  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  $\alpha$ ,  $\beta$ , and  $\gamma$  were estimated with

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  $\alpha$ , 100 for  $\beta$ , or 15 for  $\gamma$ . 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  $\text{PAI} = \text{SAI} + \text{LAI}$ . Needle leaves were modelled with projected leaf area. Total shortwave radiation on sunlit leaves ( $S_{\text{sunlit}}$ ) is the sum of direct ( $S_{\text{beam}}$ ), sky diffuse ( $S_{\text{sky}}$ ), and multiple scattered radiation ( $S_{\text{scat}}$ ). Total shortwave radiation on shaded leaves ( $S_{\text{shade}}$ ) includes only the sum of  $S_{\text{sky}}$  and  $S_{\text{scat}}$ . Direct radiation on leaves is calculated according to Norman (1982)

$$S_{\text{beam}} = S_{\text{dir}} G / \cos \theta, \quad (2)$$

where  $S_{\text{dir}}$  is the direct component of global solar radiation above the canopy,  $\theta$  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  $\phi$ ). For canopies with spherical leaf angle distribution  $\phi = 60^\circ$  (Norman, 1979); this was found to be a good approximation for canopies when  $\theta$  ranges between 30 and  $60^\circ$  (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

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

where  $S_{\text{dif}}$  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 ( $\Omega$ )

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

where  $\bar{\theta}$  is a representative zenith angle for diffuse radiation transmission, dependent on canopy elements ( $\cos \bar{\theta} = 0.537 + 0.025 \text{PAI}$ ).  $\Omega$  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)

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

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

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

The term  $\text{LAI} / \text{PAI}$  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  $\text{CO}_2$  fixation is limited by either the regeneration of Ribulose-1,5-bisphosphate (RuBP) (at low light intensity and/or high internal  $\text{CO}_2$  concentration) or by Rubisco activity and  $\text{CO}_2/\text{O}_2$ -concentration (at saturated light and low internal  $\text{CO}_2$  concentration; Reichstein, 2001).

Net photosynthesis,  $P_{\text{net}}$  is obtained using

$$P_{\text{net}} = \left(1 - \frac{\Gamma^*}{c_i}\right) \min(w_c; w_j) - 0.5 R_d, \quad (7)$$

where  $\Gamma^*$  is the  $\text{CO}_2$  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

light, and  $c_i$  is the internal CO<sub>2</sub> concentration expressed by Eqn (8) based on Fick's Law for molecular diffusion of CO<sub>2</sub> through the stomata and boundary layer.

$$c_i = c_s - \frac{1.6 P_{\text{net}}}{g_s}, \quad (8)$$

where  $c_s$  is the CO<sub>2</sub> 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)).

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

where  $g_{s:\text{min}}$  is the minimum stomatal conductance for water vapour,  $g_{\text{fac}}$  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

$$w_c = \frac{V_c c_i}{c_i + K_c(1 + O/K_o)}, \quad (10)$$

where  $V_c$  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<sup>3</sup> O<sub>2</sub> (L air)<sup>-1</sup>]. The temperature dependency of carboxylation is described as

$$V_c = \frac{V_{c:\text{max}} e^{\Delta H_a(T_K - 298)/298RT_K}}{1 + e^{(\Delta ST_K - \Delta H_d)/RT_K}} \left( 1 + e^{(298\Delta S - \Delta H_d)/298R} \right), \quad (11)$$

where  $V_{c:\text{max}}$  is the average leaf carboxylation capacity at 25 °C,  $\Delta H_a$  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  $\Delta H_d$  is the deactivation enthalpy of carboxylation.

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

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

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

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

where  $\alpha$  is the average leaf light utilization efficiency without photorespiration,  $I$  is the incident PPFD, and  $P_{\text{ml}}$  is the CO<sub>2</sub> 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
$\Delta H_a(J_{\text{max}})$	47 170	47 170	40 000	J mol <sup>-1</sup>
$\Delta H_d(J_{\text{max}})$	2 45 000	2 00 000	2 00 000	J mol <sup>-1</sup>
$\Delta S(J_{\text{max}})$	643	643	655	J mol <sup>-1</sup> K <sup>-1</sup>
$E_a(R_d)$	63 500	63 500	58 000	J mol <sup>-1</sup>
$E_a(K_o)$	36 000	36 000	35 900	J mol <sup>-1</sup>
$f(K_o)$	159.597	159.597	248	—
$E_a(K_c)$	65 000	65 000	59 500	J mol <sup>-1</sup>
$f(K_c)$	299.469	299.469	404	—
$\Delta H_a(V_{c:\text{max}})$	75 750	75 750	69 000	J mol <sup>-1</sup>
$\Delta H_d(V_{c:\text{max}})$	2 00 000	2 00 000	1 98 000	J mol <sup>-1</sup>
$\Delta S(V_{c:\text{max}})$	656	656	660	J mol <sup>-1</sup> K <sup>-1</sup>
$f(\tau)$	2339.53	2339.53	2339.53	—
$E_a(\tau)$	-28 990	-28 990	-28 990	J mol <sup>-1</sup>
$g_{\text{fac}}$	9.8	9.8	12	—

$\Delta H_a$	Activation enthalpy for enzymatic reactions
$\Delta H_d$	Deactivation enthalpy for enzymatic reactions
$\Delta S$	Entropy term for the deactivation of enzymes
$J_{\text{max}}$	Maximum rate of electron transport
$E_a$	Activation energy
$R_d$	Rate of CO <sub>2</sub> evolution from processes other than photorespiration
$K_o$	Michaelis–Menten constant for oxygenation
$f$	Scaling factor
$K_c$	Michaelis–Menten constant for carboxylation
$V_{c:\text{max}}$	Maximum rate of carboxylation
$\tau$	Enzyme specificity factor
$g_{\text{fac}}$	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  $V_{c:\text{max}}$ , 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

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

$$c = \frac{V_{c_{\max}}}{2.1}, \quad (14)$$

$$d = 0.025V_{c_{\max}}. \quad (15)$$

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  $V_{c_{\max}}$  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  $V_{c_{\max}}$ .

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):

$$\text{TSSE} = \sum_{i \leq 0.9N} r_i^2, \quad (16)$$

where  $r_i$  is the  $i$ th 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

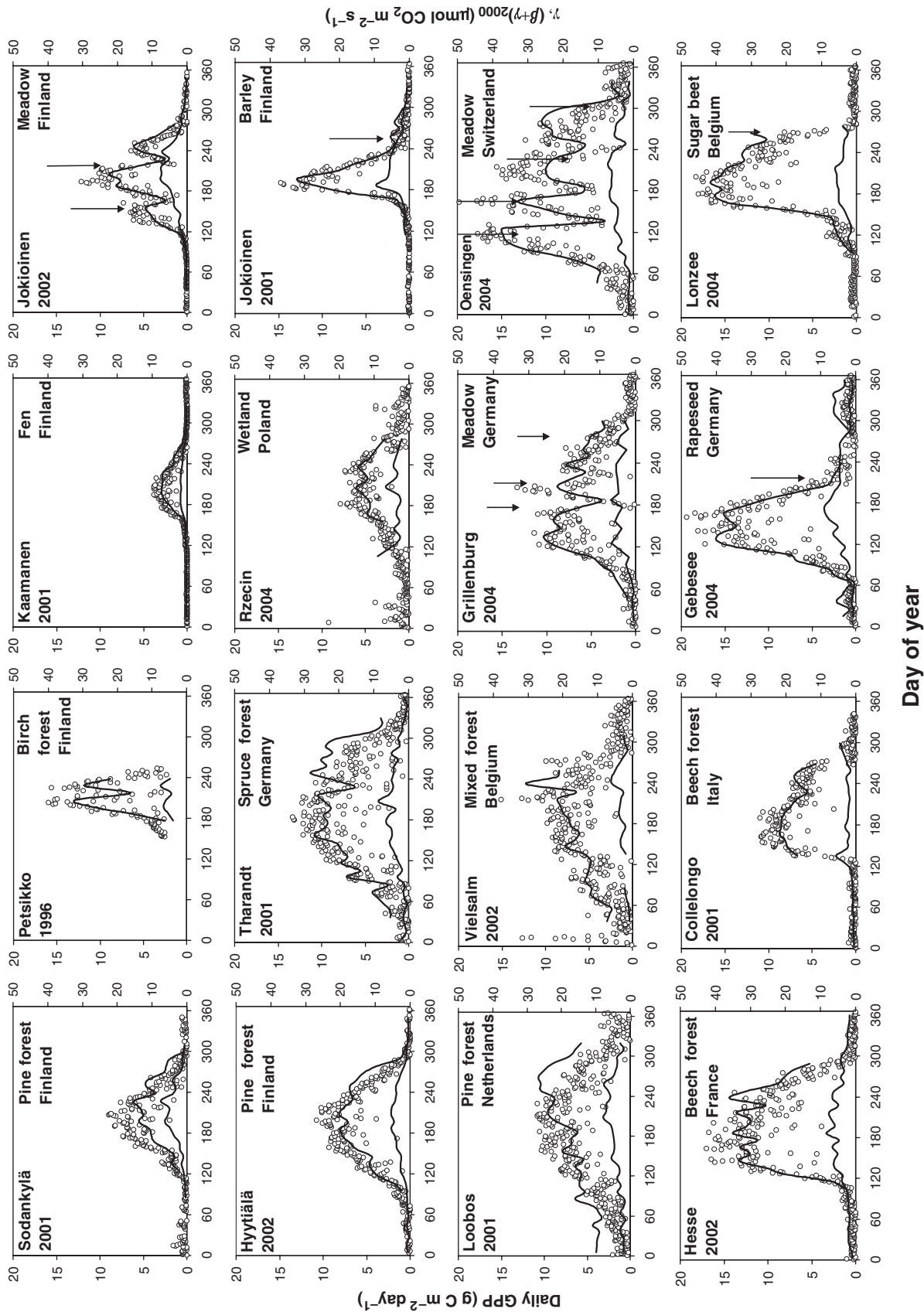
$$\omega = \sum |r_i|. \quad (17)$$

*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  $V_{c_{\max}}$  [i.e. like  $c$  and  $d$  in Eqns (14) and (15)] rather than independent. While  $V_{c_{\max}}$  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  $V_{c_{\max}}$  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  $V_{c_{\text{uptake}2^*}}$  when  $\alpha$  and  $V_{c_{\max}}$  are independent, and as  $V_{c_{\text{uptake}1^*}}$  when  $\alpha$  depends on  $V_{c_{\max}}$ . Additionally, we define whether LAI varies or is held constant. In the case of  $V_{c_{\text{uptake}1^*}}$ , 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<sub>2</sub> 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 So-dankylä), 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<sub>2</sub> by wetlands, crops, and grasslands is



**Fig. 1** Results of inverting the simple hyperbolic light response model based on net ecosystem CO<sub>2</sub> exchange observations for the parameters  $(\beta + \gamma)_{2000}$ , the upper solid line, and  $\gamma$ ; 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.

quite variable with obvious responses to season length, nutrient availability (compare maximum daily rates for wetlands with the intensively fertilized grassland Oenningen), 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  $\gamma$  superimposed on the daily observations of GPP in Fig. 1 ( $\gamma$  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  $\alpha$ ,  $\beta$ , and  $\gamma$  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.  $\alpha$  and  $\beta$  are negatively correlated with an upper quartile, average, and lower quartile of  $-0.73$ ,  $-0.51$ , and  $-0.36$ , respectively.  $\alpha$  and  $\gamma$  are very positively correlated with an upper quartile, average, and lower quartile of  $0.88$ ,  $0.82$ , and  $0.81$ , respectively.  $\beta$  and  $\gamma$  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  $\gamma$  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  $R_{\text{ref}}$  is derived and similarly provides an estimate of seasonal changes in ecosystem respiratory capacity based on the evaluation of temperature response during night-time.  $\gamma$  and  $R_{\text{ref}}$  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  $V_{\text{C}_{\text{uptake2*}}}$  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 Lonze and Klingenberg were studied as indicated in Fig. 4.  $V_{\text{C}_{\text{uptake2*}}}$  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,  $V_{\text{C}_{\text{uptake2*}}}$  as in the case of  $(\beta + \gamma)_{2000}$  was linearly related to GPP (cf. Table 4) even though more scattered.

The relationship of  $V_{\text{C}_{\text{uptake2*}}}$  to the parameter  $(\beta + \gamma)_{2000}$  from the hyperbolic light response model (noting both provide an estimate of total canopy  $\text{CO}_2$



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

\*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  $V_{c_{uptake2^*}}$  is predicted. The differences in  $V_{c_{uptake2^*}}$  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

**Table 3** Annual sums of CO<sub>2</sub> and latent heat exchange for the sites in Table 2

Site	Year	Annual NEE (g C m <sup>-2</sup> )	Annual GPP (g C m <sup>-2</sup> )	Annual Reco (g C m <sup>-2</sup> )	Latent heat exchange (mm)	Spring NEE decrease (day)	Fall NEE increase (day)	Negative NEE season (days)
<i>Coniferous forest</i>								
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
<i>Mixed forest</i>								
Vielsalm, Belgium	2002	-355	1528	1173	268	56	287	232
<i>Deciduous forest</i>								
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
<i>Wetland</i>								
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
<i>Grasslands and meadows</i> <sup>†</sup>								
Oensingen (intensively managed), Switzerland	2004	-630	2345	1715	684	32	315	284
Grillenbourg, Germany	2004	-260	1233	973	437	72	276	205
Jokioinen, Finland	2002	73	782	855	422	119	207	89
<i>Crops</i>								
Gebesee (rapeseed), Germany	2004	-200	1419	1219	372	67	199	133
Lonze (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.

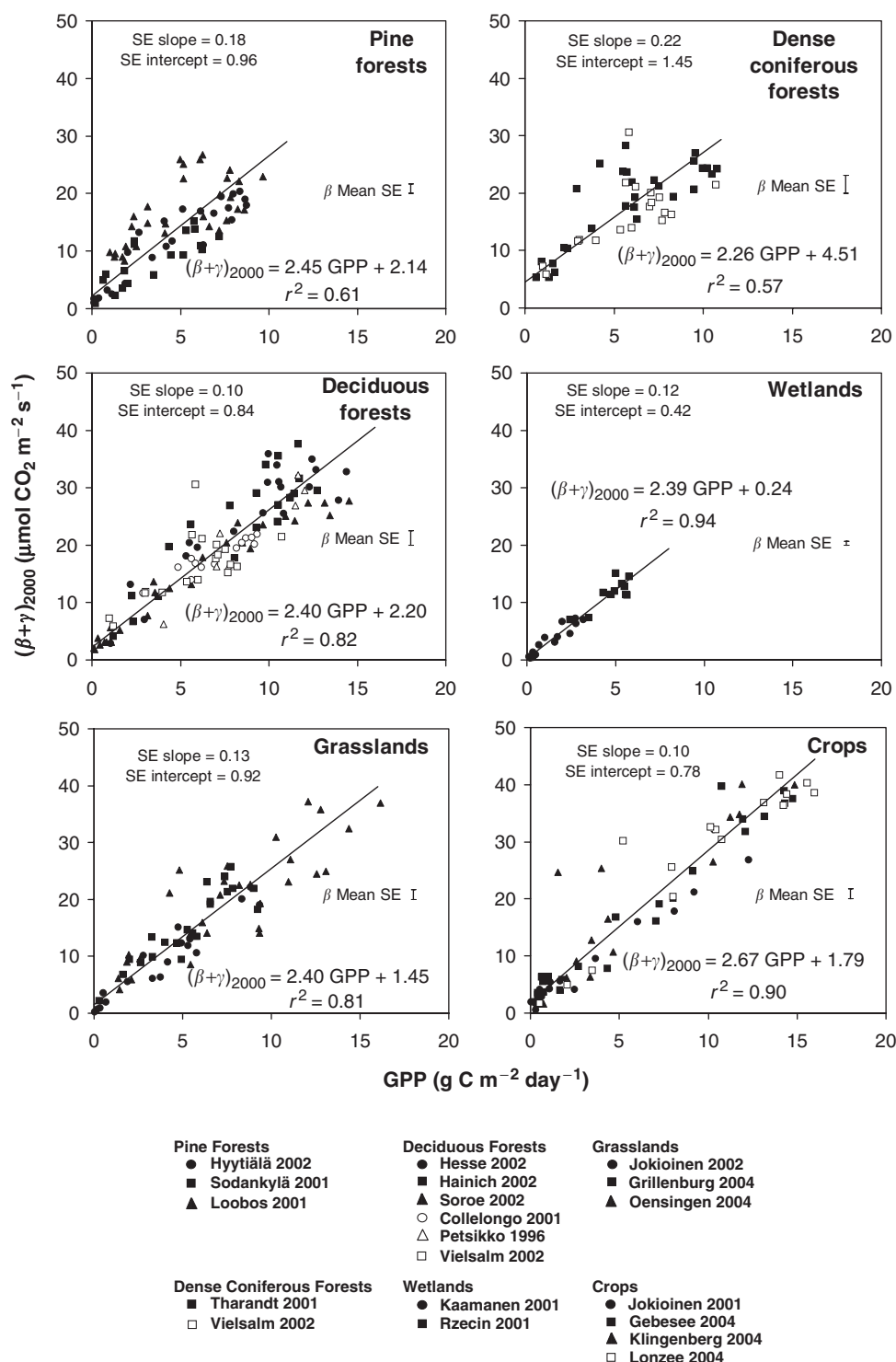
‡Measurements for Klingenberg were started on day of year 92 in 2004.

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.

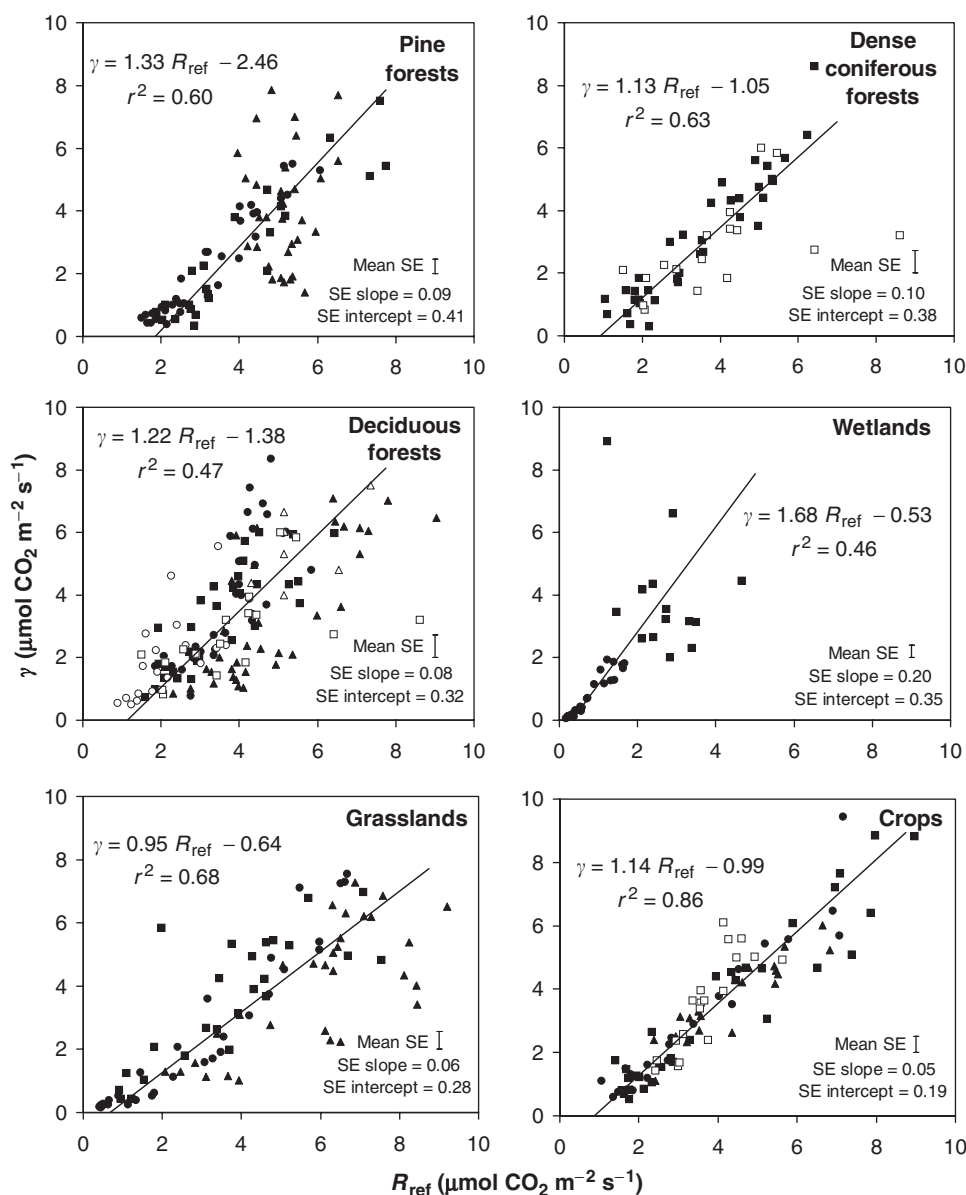
NEE, net ecosystem CO<sub>2</sub> exchange; GPP, gross primary production; Reco, ecosystem respiration.

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  $\alpha$  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  $\Omega$  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  $r^2$ .



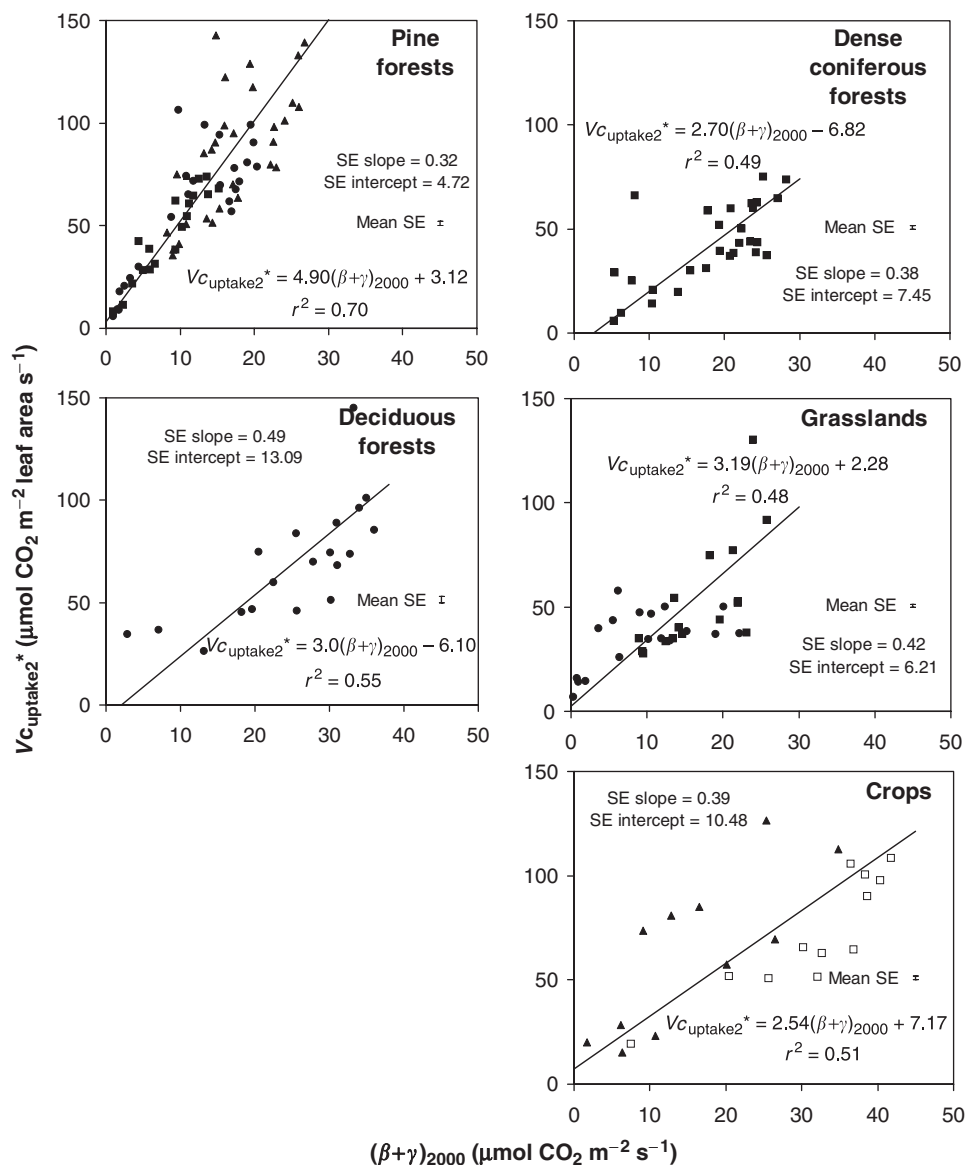
**Fig. 2** Relationships and linear regressions for the results shown in Fig. 1 between daily gross primary production (GPP) from flux partitioning and ( $\beta + \gamma$ )<sub>2000</sub>, the average maximum rate of canopy CO<sub>2</sub> uptake capacity, observed for 10-day periods for different functional ecosystem types. The mean standard error of  $\beta$ , which is a conservative estimate of the standard error of the ( $\beta + \gamma$ )<sub>2000</sub> 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.



**Fig. 3** Relationships and linear regressions between 10-day average  $R_{ref}$ , the reference ecosystem respiration at 15 °C, and  $\gamma$ , an estimate of the average ecosystem respiration, observed for 10-day periods for different functional ecosystem types. The mean standard error of the  $\gamma$  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  $\text{CO}_2$  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  $V_{c_{uptake2^*}}$ , 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  $V_{c_{uptake2^*}}$  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



**Fig. 4** Relationships and linear regressions between  $(\beta + \gamma)_{2000}$ , the average maximum rate of canopy  $\text{CO}_2$  uptake capacity, and  $V_{c_{\text{uptake}2^*}}$ , related to the average leaf carboxylation capacity at  $25^\circ\text{C}$ , for different functional ecosystem types using those sites where confidence in estimates of leaf area index were best. The mean standard error of the  $V_{c_{\text{uptake}2^*}}$  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  $V_{c_{\text{uptake}}}$  along with many modifying factors [Eqn (18)].

$$\alpha = \begin{matrix} 0.0008V_{c_{\text{uptake}2^*}} & V_{c_{\text{uptake}2^*}} \leq 75 \\ 0.06 & V_{c_{\text{uptake}2^*}} \geq 75. \end{matrix} \quad (18)$$

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  $V_{c_{\text{uptake}}}$  with LAI maintained at the reported site seasonal maximum value. To overcome the overly sensitive trade-offs in estimation of light utilization efficiency vs.  $V_{c_{\text{uptake}}}$ ,

**Table 4** The linear regression between 10-day period average GPP and  $V_{\text{C}_{\text{uptake}2^*}}$ , 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	$V_{\text{C}_{\text{uptake}2^*}} = 13.27 \times \text{GPP} + 9.46$	0.50
Dense coniferous forest	$V_{\text{C}_{\text{uptake}2^*}} = 6.35 \times \text{GPP} + 5.29$	0.38
Deciduous forest	$V_{\text{C}_{\text{uptake}2^*}} = 7.16 \times \text{GPP} + 5.31$	0.59
Grassland	$V_{\text{C}_{\text{uptake}2^*}} = 7.76 \times \text{GPP} + 9.08$	0.42
Cropland	$V_{\text{C}_{\text{uptake}2^*}} = 6.93 \times \text{GPP} + 12.55$	0.41

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

we also examined inversions with  $\alpha$  dependent on  $V_{\text{C}_{\text{uptake}}}$  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  $V_{\text{C}_{\text{uptake}}}$  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  $V_{\text{C}_{\text{uptake}}}$  and  $\alpha$  were investigated for Hesse (not shown). As expected, a lower LAI results in higher  $V_{\text{C}_{\text{uptake}}}$  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  $V_{\text{C}_{\text{uptake}}}$ . In fact, the independent fits ( $V_{\text{C}_{\text{uptake}2^*}}$ ) have up to 85% higher relative standard errors during individual periods during the active vegetation season as compared with the  $\alpha$  dependent fits ( $V_{\text{C}_{\text{uptake}1^*}}$ ). 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

**Table 5** The linear regression between  $\alpha$  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)

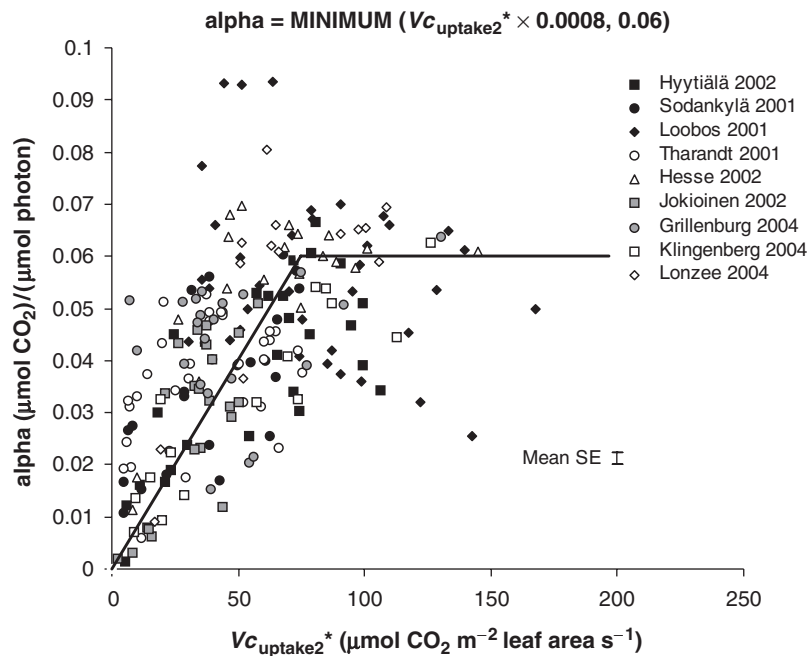
Ecosystem	Relationship	$r^2$
Pine forest	$\alpha = 1.05 \times \alpha + 0.010$	0.66
Dense coniferous forest	$\alpha = 0.62 \times \alpha + 0.012$	0.44
Deciduous forest	$\alpha = 0.37 \times \alpha + 0.035$	0.34
Grassland	$\alpha = 0.80 \times \alpha + 0.013$	0.49
Cropland	$\alpha = 0.97 \times \alpha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

LAI, leaf area index.

fit has higher  $r^2$  values during the spring and fall periods than the  $\alpha$ -dependent fits.

The parameter  $V_{\text{C}_{\text{uptake}1^*}}$  is a robust indicator of the canopy  $\text{CO}_2$  uptake capacity which allows effective comparisons across the data set (Fig. 7, solid lines). Nevertheless, some caution is required, as  $V_{\text{C}_{\text{uptake}1^*}}$  is a lumped parameter influenced by several factors. Comparing Fig. 7 with Fig. 1, one sees that  $V_{\text{C}_{\text{uptake}1^*}}$  more poorly follows the seasonal trend in GPP. While  $(\beta + \gamma)_{2000}$  directly reflects average maximum  $\text{CO}_2$  uptake capacity rates during each 10-day period,  $V_{\text{C}_{\text{uptake}1^*}}$  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,  $V_{\text{C}_{\text{uptake}1^*}}$  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  $\text{CO}_2$  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  $\text{CO}_2$  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



**Fig. 5** Scattergram of the relationship of light utilization efficiency,  $\alpha$ , with canopy  $\text{CO}_2$  uptake capacity,  $V_{c_{\text{uptake2}}^*}$ , 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  $V_{c_{\text{uptake}}}$  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  $V_{c_{\text{uptake1}}^*}$  using constant annual maximum LAI with North American and Asian sites superimposed as clear open symbols on the European data.

## Discussion

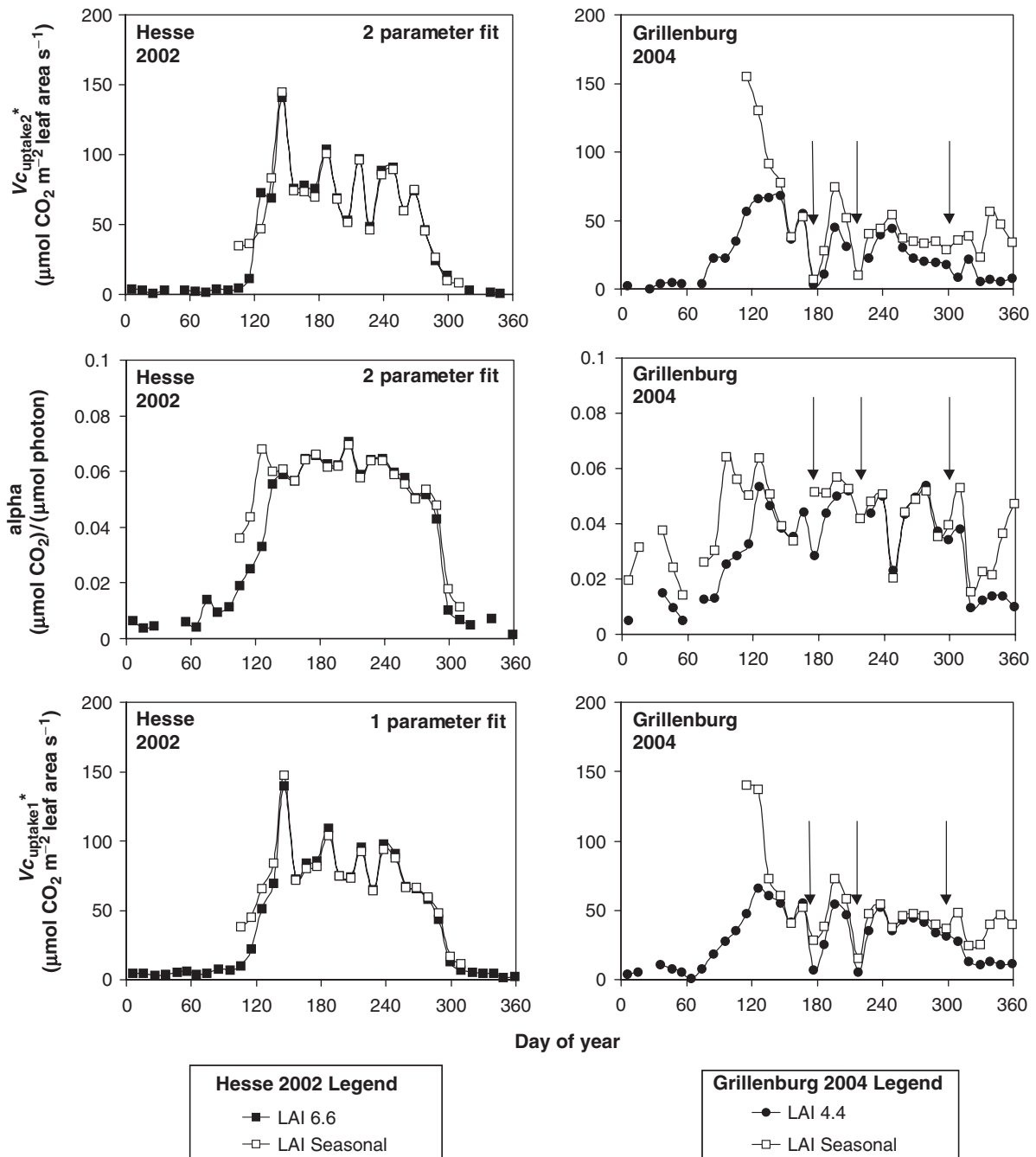
Many studies (Peat, 1970; Johnson & Thornley, 1984; Boote & Loomis, 1991; Gilmanov *et al.*, 2003) have shown that using the nonrectangular hyperbola [Eqn (19)], which contains an additional curvature parameter,  $\eta$ , provides less biased, more representative and different estimates of the  $\alpha$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

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

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 focus-

ing 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 day-time data are shown for Hesse beech forest and Grillenburg meadow in Fig. 10. The models produce very different estimates of  $\beta$ , 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.  $3 \text{ gC m}^{-2} \text{ day}^{-1}$ . Further detailed study must be carried out to explain these characteristics, which appear to be



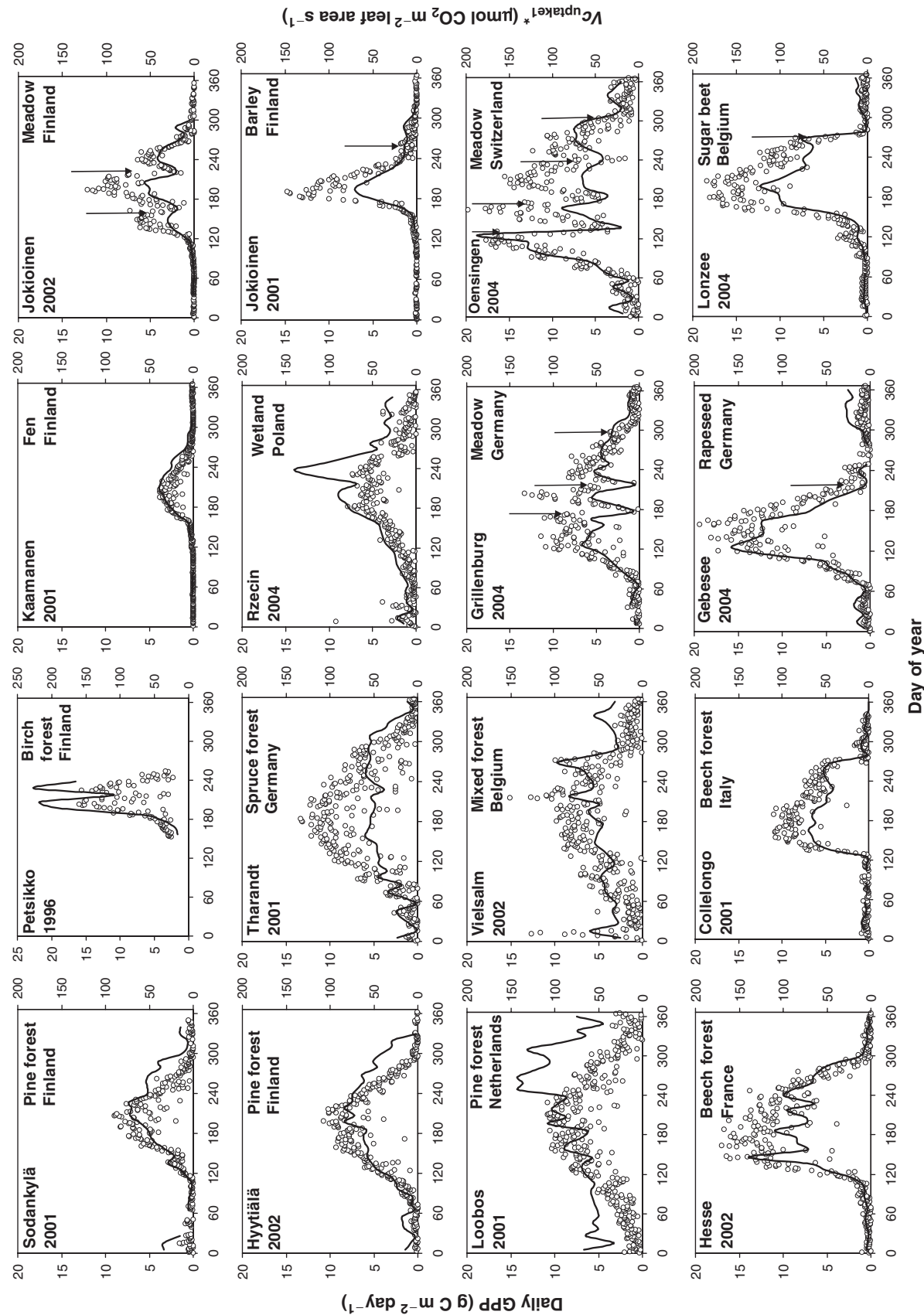
**Fig. 6** Comparison between seasonally changing leaf area index (LAI) and constant annual maximum LAI on model inversions for summer active ecosystems for the Hesse beech forest in 2002 and Grillenburg grassland in 2004. The arrows show dates of grass cutting in Grillenburg.

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

These results between  $V_{C_{uptake1}^*}$  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  $V_{C_{uptake1}^*}$  is a robust indicator of the canopy  $CO_2$  uptake capacity useful in simula-

tions 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  $V_{C_{uptake1}^*}$  and GPP at ca.  $2\text{--}3\text{ g C m}^{-2}\text{ day}^{-1}$ . Some pine stands seem to exhibit similar behaviour to those stands classified as dense





**Fig. 7** Values derived for the parameter  $V_{cuptake1*}$  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.

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

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

**Table 7** Annual sums of CO<sub>2</sub> and latent heat exchange for the North American and Asian sites in Table 6

Site	Year	Annual NEE (g C m <sup>-2</sup> )	Annual GPP (g C m <sup>-2</sup> )	Annual Reco (g C m <sup>-2</sup> )	Latent heat exchange (mm)	Spring NEE decrease (day)	Fall NEE increase (day)	Negative NEE season (day)
<i>Coniferous forest</i>								
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
Campbell River, BC, Canada	2003	-239	1306	1067	321	93	301	209
	1999	-469	1405	936	418	1	305	305
	2000	-434	1803	1368	415	8	266	259
	2001	-474	1695	1221	382	17	307	291
<i>Deciduous forest</i>								
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
Harvard, MA, USA	2004	-327	638	311	160	137	288	152
	2000	-325	1237	912	*	144	287	144
	2003	-320	1242	922	*	140	287	148
<i>Tundra and wetland</i>								
Upad, Alaska, USA	1994 <sup>‡</sup>	-16	75	59	123	176	220	45
Barrow, AK, USA	1998	-54	147	93	99	§	239	§
	1999 <sup>¶</sup>	-87	150	63	111	190	243	54
	2000	-72	155	83	76		246	
<i>Grasslands and prairies</i>								
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
<i>Crop</i>								
Bondville (maize/soybean), IL, USA	1998**	87	426	513	643	178	253	76
	1999 <sup>††</sup>	-497	1272	775	624	152	252	101
	2000**	51	628	678	588	171	246	76
	2001 <sup>††</sup>	-444	964	520	733	143	251	109
	2002**	-237	693	456	565	179	261	83
	2003 <sup>††</sup>	-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.

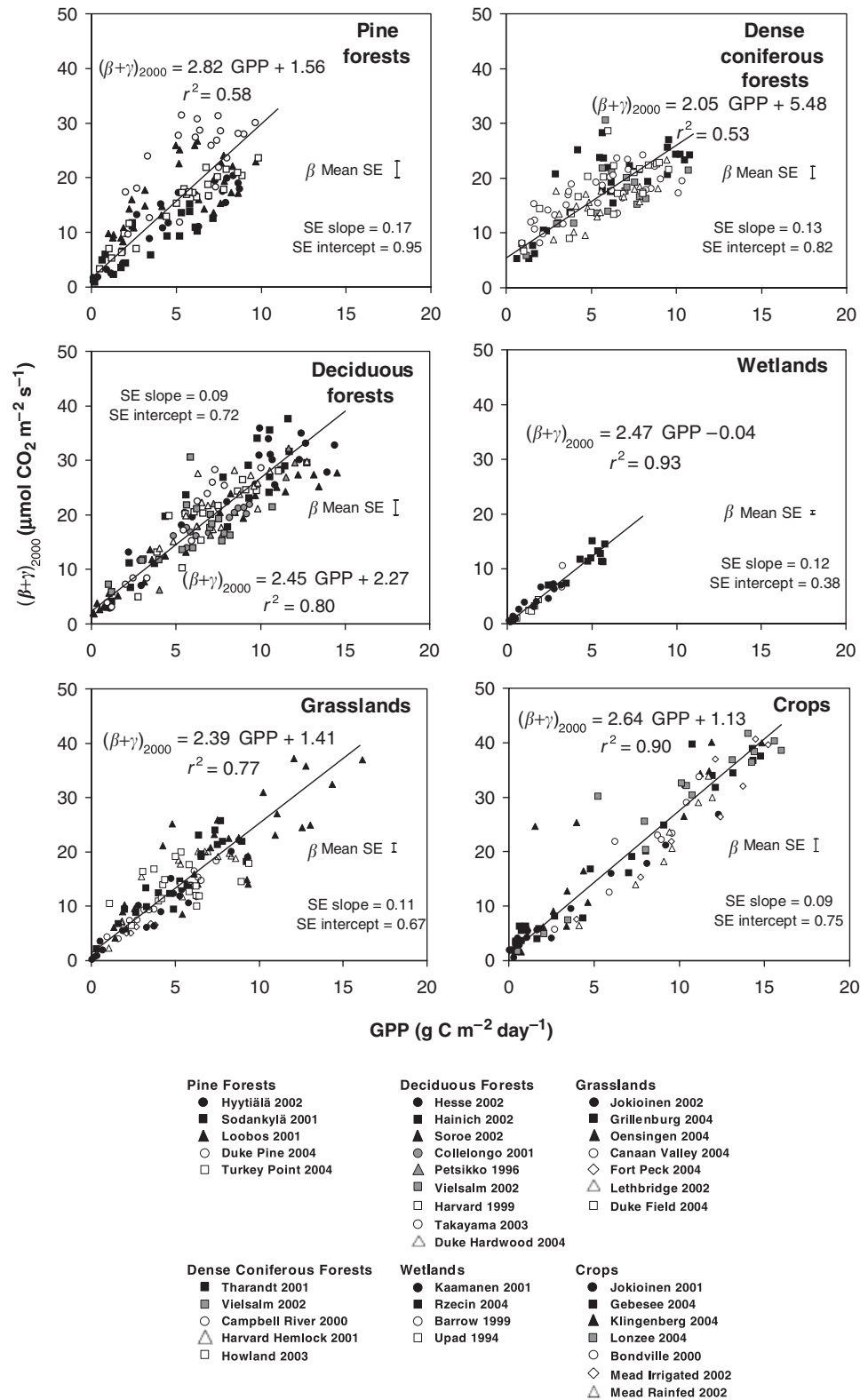
||Measurements for Barrow were made from day of year 92 to 250 in 2000.

\*\*Soybean rotation years.

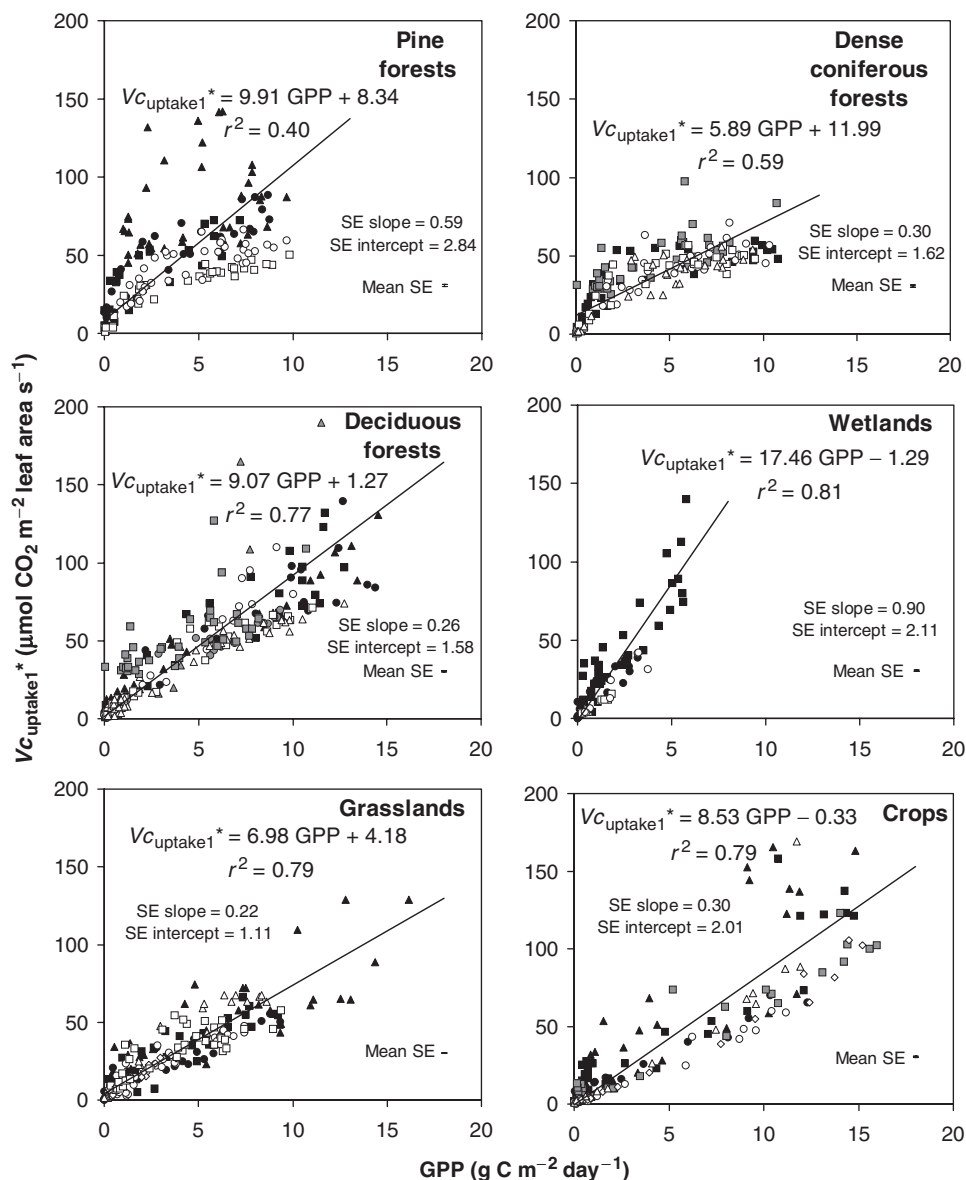
††Maize rotation years.

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<sub>2</sub> exchange; GPP, gross primary production; Reco, ecosystem respiration.



**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  $\text{CO}_2$  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  $\beta$ , 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.



**Fig. 9** Relationships and linear regressions for the results between daily gross primary production (GPP) from flux partitioning and  $V_{c_{uptake1}}^*$ , which is a robust indicator of the canopy CO<sub>2</sub> 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  $V_{c_{uptake1}}^*$  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  $V_{c_{uptake1}}^*$ , 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  $V_{c_{uptake1}}^*$  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  $V_{c_{uptake1}}^*$  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,

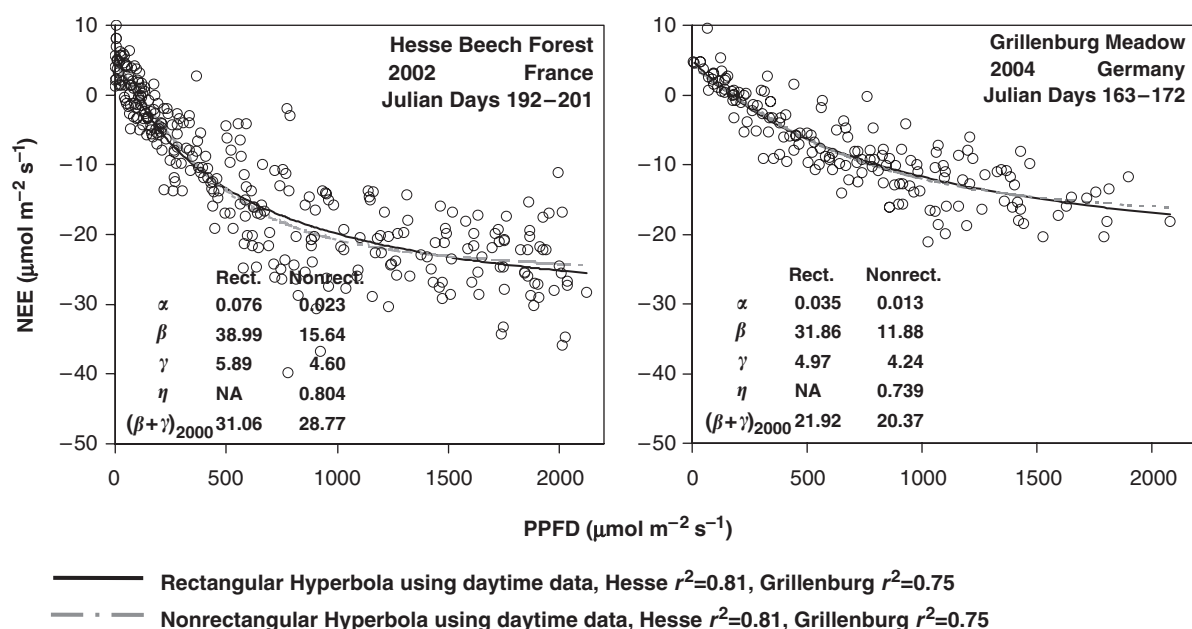


Fig. 10 Example light response curves and parameters for one inversion period for the Hesse beech forest in 2002 and Grillenburg grassland in 2004. The lines compare results of inverting the rectangular hyperbola and the nonrectangular hyperbola using daytime data.

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  $\alpha$ ,  $\beta$  and  $\gamma$  are obtainable by simple optimization, while  $\alpha$  and  $V_{C_{uptake}}$  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  $V_{C_{uptake1}}$  parameter is sensitive to nitrogen availability and manage-

ment measures as seen in Fig. 7 for the nonfertilized Grillenburg and heavily fertilized Oensingen meadows. Finally,  $V_{\text{C}_{\text{uptake1}}^*}$  is a 'property' of the canopy, independent of meteorological conditions, and thus contains more generality than  $\alpha$ ,  $\beta$ , and  $\gamma$  (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 ( $V_{\text{C}_{\text{uptake1}}^*}$ ) 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  $V_{\text{C}_{\text{uptake1}}^*}$  increase, the period with relatively constant  $\text{CO}_2$  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  $V_{\text{C}_{\text{uptake1}}^*}$  when it is evaluated as described in the above analysis. In these cases,  $V_{\text{C}_{\text{uptake1}}^*}$  should be evaluated with LAI obtained over the season, for example as obtained from remote sensing. Again, a springtime increase in  $V_{\text{C}_{\text{uptake1}}^*}$  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  $V_{\text{C}_{\text{uptake1}}^*}$  includes the influences of average leaf carboxylase, changes in LAI during certain periods (leaf expansion, leaf senescence, harvest times, etc.), undefined sinks for  $\text{CO}_2$  (underscoring 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  $V_{\text{C}_{\text{uptake1}}^*}$  (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, ( $V_{\text{C}_{\text{uptake1}}^*}$ ), 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  $V_{\text{C}_{\text{uptake1}}^*}$  parameter along with remotely sensed LAI can be used in modeling approaches at continental scale.

## Acknowledgements

Data collection was funded by CarboEurope, Fluxnet-Canada Research Network, AmeriFlux, and AsiaFlux under the umbrella organization of Fluxnet as well as individual flux stations. The authors would like to thank all the project investigators and their staff and graduate students for providing ancillary data. We would like to thank Martin Heimann for his comments and support of the modelling and three anonymous reviewers for their helpful remarks on the manuscript. The modelling work was funded by the CarboEurope Integration Project Work Package.

## References

- Ammann C, Flechard CR, Leifeld J, Neftel A, Fuhrer J (2007) The carbon budget of newly established grassland depends on management intensity. *Agriculture, Ecosystems and Environment*, in press.
- Anthoni PM, Knohl A, Rebmann C, Freibauer A, Mund M, Ziegler W, Kolle O, Schulze ED (2004) Forest and agricultural land-use-dependent  $\text{CO}_2$  exchange in Thuringia, Germany. *Global Change Biology*, **10**, 2005–2019.

- Arain AA, Restrepo-Coupe N (2005) Net ecosystem production in a temperate pine plantation in southeastern Canada. *Agricultural and Forest Meteorology*, **128**, 223–241.
- Aubinet M, Chermaine B, Vandenhaute M, Longdoz B, Yernaux M, Laitat E (2001) Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agricultural Forest Meteorology*, **108**, 293–315.
- Aubinet M, Grelle A, Ibrom A *et al.* (2000) Estimates of the annual net carbon and water exchange of forests: the euroflux methodology. *Advances in Ecological Research*, **30**, 113–175.
- Aubinet M, Heinesch B, Longdoz B (2002) Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. *Global Change Biology*, **8**, 1053–1071.
- Aurela M (2005) *Carbon dioxide exchange in subarctic ecosystems measured by a micrometeorological technique*. Finnish Meteorological Institute Contributions, 51, Helsinki, Finland.
- Aurela M, Laurila T, Tuovinen JP (2001a) Seasonal CO<sub>2</sub> balances of a subarctic mire. *Journal of Geophysical Research*, **106**, 1623–1637.
- Aurela M, Laurila T, Tuovinen JP (2002) Annual CO<sub>2</sub> balances of a subarctic fen in northern Europe: importance of the winter-time efflux. *Journal of Geophysical Research*, **107**, 1–12.
- Aurela M, Tuovinen JP, Laurila T (2001b) Net CO<sub>2</sub> exchange of a subarctic mountain birch ecosystem. *Theoretical and Applied Climatology*, **70**, 135–148.
- Baldocchi DD, Falge E, Gu LH *et al.* (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2434.
- Baldocchi DD, Valentini R, Running S, Oechel W, Dahlman R (1996) Strategies for measuring and modeling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology*, **2**, 159–168.
- Ball JT, Woodrow IE, Berry JA (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: *Progress in Photosynthesis Research. Vol. IV.5, Proceedings of the VII International Photosynthesis Congress* (ed. Biggins I), pp. 221–224. Martinus Nijhoff, Leiden, the Netherlands.
- Barford CC, Wofsy SC, Goulden ML *et al.* (2001) Factors controlling long- and short-term sequestration of atmospheric CO<sub>2</sub> in a mid-latitude forest. *Science*, **294**, 1688–1691.
- Bernhofer C, Aubinet M, Clement R *et al.* (2003) Spruce forests (Norway and Sitka spruce, including Douglas fir): carbon and water fluxes and balances, ecological and ecophysiological determinants. In: *Fluxes of Carbon, Water and Energy of European Forests. Vol. 163. Ecological Studies Series* (ed. Valentini R), pp. 99–123. Springer-Verlag, Heidelberg.
- Biscoe PV, Soctt RK, Monteith JL (1975) Barley and its environment: III. Carbon budget of the stand. *Journal of Applied Ecology*, **12**, 269–293.
- Bonan GB (1995) Land-atmosphere CO<sub>2</sub> exchange simulated by a land surface process model coupled to an atmospheric general circulation model. *Journal of Geophysical Research*, **100**, 2817–2831.
- Boote KJ, Loomis RS (1991) The prediction of canopy assimilation. In: *Modeling Crop Photosynthesis – from Biochemistry to Canopy*, **19** (eds Boote KJ, Loomis RS), pp. 109–137. Crop Science Society of America Special Publication, Madison, WI.
- Chen JM (1996a) Optically-based methods for measuring seasonal variation in leaf area index of boreal conifer forests. *Agricultural and Forest Meteorology*, **80**, 135–163.
- Chen JM (1996b) Canopy architecture and remote sensing of the fraction of photosynthetically active radiation in boreal conifer stands. *IEEE Transactions on Geoscience and Remote Sensing*, **34**, 1353–1368.
- Chen JM, Cihlar J (1995) Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *IEEE Transactions on Geoscience and Remote Sensing*, **33**, 777–787.
- Chen JM, Liu J, Cihlar J, Goulden ML (1999) Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications. *Ecological Modelling*, **124**, 99–119.
- Chen JM, Liu J, Leblanc SG, Lacaze R, Roujean JL (2003) Angular optical remote sensing for assessing vegetation structure and carbon absorption. *Remote Sensing of the Environment*, **84**, 516–525.
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, **113**, 3–19.
- Davidson EA, Richardson AD, Savage KE, Hollinger DY (2006) A distinct seasonal pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest. *Global Change Biology*, **12**, 230–239.
- DePury D, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment*, **20**, 537–557.
- Dolman AJ, Moors EJ, Elbers JA (2002) The carbon uptake of a mid latitude pine forest growing on sandy soil. *Agricultural and Forest Meteorology*, **111**, 157–170.
- Drewitt GB, Black TA, Nesic Z *et al.* (2002) Measuring forest floor CO<sub>2</sub> fluxes in a Douglas-fir forest. *Agricultural and Forest Meteorology*, **110**, 299–317.
- Falge E (1997) Die Modellierung der Kronendachtranspiration von Fichtelbeständen (*Picea abies* (L.) Karst.). In: *Bayreuther Forum Ökologie*, Vol. 48. Bayreuther Institut für Terrestrische Ökosystemforschung (eds.), Bayreuth, Germany, 221 pp.
- Falge E, Baldocchi D, Olson RJ *et al.* (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural Forest Meteorology*, **107**, 43–69.
- Falge E, Baldocchi DD, Tenhunen JD *et al.* (2002a) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, **113**, 53–74.
- Falge E, Graber W, Siegwolf R, Tenhunen JD (1996) A model of the gas exchange response of *Picea abies* to habitat conditions. *Trees*, **10**, 277–287.
- Falge E, Tenhunen J, Aubinet M *et al.* (2003) A model-based study of carbon fluxes at ten European forest sites. In: *Fluxes of Carbon, Water and Energy of European Forests Vol. 163. Ecological Studies Series* (ed. Valentini R), pp. 151–177. Springer-Verlag, Heidelberg, Germany.



- Falge E, Tenhunen J, Baldocchi D *et al.* (2002b) Phase and amplitude of ecosystem carbon release and uptake potential as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, **113**, 75–95.
- Farquhar GD, von Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In: *Encyclopedia of Plant Physiology, New Series*, Vol. 12b (eds Lange OL, Nobel PS, Osmond CB, Ziegler H), pp. 549–587. Springer-Verlag, Germany.
- Flanagan LB, Johnson BG (2005) Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology*, **130**, 237–253.
- Flanagan LB, Wever LA, Carlson PJ (2002) Seasonal and inter-annual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology*, **8**, 599–615.
- Flechard CR, Neftel A, Jocher M, Ammann C, Fuhrer J (2005) Bi-directional soil/atmosphere N<sub>2</sub>O exchange over two mown grassland systems with contrasting management practices. *Global Change Biology*, **11**, 2114–2127.
- Fleck S, Schmidt M, Köstner B, Faltin W, Tenhunen JD (2004) Impacts of canopy internal gradients on carbon and water exchange of beech and oak trees. In: *Biogeochemistry of Forested Catchments in a Changing Environment. Ecological Studies Series* (ed. Matzner E), pp. 99–126. Springer Verlag, Heidelberg, Germany.
- Gilmanov TG, Tieszen LL, Wylie BK *et al.* (2005) Integration of CO<sub>2</sub> flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. *Global Ecology and Biogeography*, **14**, 271–292.
- Gilmanov TG, Verma S, Sims P, Meyers T, Bradford J, Burba G, Suyker A (2003) Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO<sub>2</sub>-flux tower measurements. *Global Biogeochemical Cycles*, **17**, 1071.
- Granier A, Biron P, Lemoine D (2000a) Water balance, transpiration and canopy conductance in two beech stands. *Agricultural and Forest Meteorology*, **100**, 291–308.
- Granier A, Ceschia E, Damesin C *et al.* (2000b) The carbon balance of a young Beech forest. *Functional Ecology*, **14**, 312–325.
- Granier A, Pilegaard K, Jensen NO (2002) Similar net ecosystem exchange of beech stands located in France and Denmark. *Agricultural and Forest Meteorology*, **114**, 75–82.
- Granier A, Reichstein M, Bréda N *et al.* (2006) Water and carbon fluxes over European forest ecosystems during an extremely dry year: 2003. *Agricultural and Forest Meteorology*, **143**, 123–145.
- Hadley JL, Schedlbauer JL (2002) Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England. *Tree Physiology*, **15**, 1079–1092.
- Ham JM, Owensby CE, Coyne PI, Bremer DJ (1995) Fluxes of CO<sub>2</sub> and water vapour from a prairie ecosystem exposed to ambient and elevated atmospheric CO<sub>2</sub>. *Agricultural and Forest Meteorology*, **77**, 73–93.
- Harley PC, Tenhunen JT (1991) Modeling the photosynthetic response of C3 leaves to environmental factors. In: *Modeling Crop Photosynthesis – from Biochemistry to Canopy* (eds Boote KJ, Loomis RS), pp. 17–39. Crop Science Society of America Inc. and American Society of Agronomy Inc., Madison, WI.
- Harley PC, Tenhunen JD, Lange OL (1986) Use of an analytical model to study limitations to net photosynthesis in *Arbutus unedo* under field conditions. *Oecologia*, **70**, 393–401.
- Hollinger DY, Aber J, Dail B *et al.* (2004) Spatial and temporal variability in forest-atmosphere CO<sub>2</sub> exchange. *Global Change Biology*, **10**, 1689–1706.
- Hollinger SE, Bernacchi CJ, Meyers TP (2005) Carbon budget of mature no-till ecosystem in North Central Region of the United States. *Agricultural and Forest Meteorology*, **130**, 59–69.
- Hollinger DY, Goltz SM, Davidson EA, Lee JT, Tu K, Valentine HT (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.
- Hollinger DY, Richardson AD (2005) Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiology*, **25**, 873–885.
- Johnson IR, Thornley JHM (1984) A model of instantaneous and daily canopy photosynthesis. *Journal of Theoretical Biology*, **10**, 531–545.
- Knohl A, Schulze ED, Kolle O, Buchmann N (2003) Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agricultural and Forest Meteorology*, **118**, 151–167.
- Laurila T, Soegaard H, Lloyd CR, Aurela M, Tuovinen JP, Nordstroem C (2001) Seasonal variations of net CO<sub>2</sub> exchange in European Arctic ecosystems. *Theoretical and Applied Climatology*, **70**, 183–201.
- Lebaube S, LeGoff N, Ottorini JM, Granier A (2000) Carbon balance and tree growth in a *Fagus sylvatica* stand. *Annals of Forest Science*, **57**, 49–61.
- Liu J, Chen JM, Cihlar J, Park WM (1997) A process-based boreal ecosystem productivity simulator using remote sensing inputs. *Remote Sensing of Environment*, **62**, 158–175.
- Liu J, Chen JM, Cihlar J, Chen W (1999) Net primary productivity distribution in the BOREAS region from a process model using satellite and surface data. *Journal of Geophysical Research*, **104**, 27735–27754.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Lohila A, Aurela M, Tuovinen JP, Laurila T (2004) Annual CO<sub>2</sub> exchange of a peat field growing spring barley or perennial forage grass. *Journal of Geophysical Research-Atmospheres*, **109**, D18116.
- Meyers TP, Hollinger SE (2004) An assessment of storage terms in the surface energy balance of maize and soybean. *Agricultural and Forest Meteorology*, **125**, 105–115.
- Moureaux C, Debacq B, Bodson B, Heinesch B, Aubinet M (2006) Annual net ecosystem carbon exchange by a sugar beet crop. *Agricultural and Forest Meteorology*, **139**, 25–39.
- Norman JM (1979) Modeling the complete crop canopy. In: *Modification of the Aerial Environment of Crops* (eds Barfield BJ, Gerber JF), pp. 249–277. American Society of Agricultural Engineers, St. Joseph, Michigan.

- Norman JM (1982) Simulation of microclimates. In: *Biometeorology in Integrated Pest Management* (eds Hatfield JL, Thomason IJ), pp. 65–99. Academic Press, New York.
- Novick KA, Stoy PC, Katul GG, Ellsworth DE, Siqueira MBS, Juang J, Oren R (2004) Carbon dioxide and water vapor exchange in a warm temperate grassland. *Oecologia*, **138**, 259–274.
- Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO<sub>2</sub> exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.
- Oren R, Hsieh CI, Stoy PC, Oishi AC, Kim H-S, Johnsen K, Katul GG, Oren R (2006) Estimating the uncertainty in annual net ecosystem carbon exchange: spatial variation in turbulent fluxes and sampling errors in eddy-covariance measurements. *Global Change Biology*, **12**, 883–896.
- Palmroth S, Maier CA, McCarthy HR, Oishi AC, Kim H-S, Johnsen K, Katul GG, Oren R (2005) Contrasting responses to drought of forest floor CO<sub>2</sub> efflux in a loblolly pine plantation and a nearby oak-hickory forest. *Global Change Biology*, **11**, 1–14.
- Papale D, Valentini R (2003) A new assessment of European forests carbon exchanges by eddy fluxes and artificial neural network spatialization. *Global Change Biology*, **9**, 525–535.
- Peat WE (1970) Relationships between photosynthesis and light intensity in the tomato. *Annals of Botany*, **34**, 319–328.
- Pilegaard K, Hummelshøj P, Jensen NO, Chen Z (2001) Two years of continuous CO<sub>2</sub> eddy-flux measurements over a Danish beech forest. *Agricultural and Forest Meteorology*, **107**, 29–41.
- Pilegaard K, Mikkelsen TN, Beier C, Jensen NO, Ambus P, Ro-Poulsen H (2003) Field measurements of atmosphere–biosphere interactions in a Danish beech forest. *Boreal Environment Research*, **8**, 315–333.
- Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA (1993) Terrestrial ecosystem production – a process model based on global satellite and surface data. *Global Biogeochemical Cycles*, **7**, 811–841.
- Rannik Ü, Altimir N, Raittila J *et al.* (2002) Fluxes of carbon dioxide and water vapour over Scots pine forest and clearing. *Agricultural and Forest Meteorology*, **111**, 187–202.
- Rannik Ü, Keronen P, Hari P, Vesala T (2004) Estimation of forest-atmosphere CO<sub>2</sub> exchange by eddy covariance and profile techniques. *Agricultural and Forest Meteorology*, **126**, 141–155.
- Reichstein M (2001) *Drought Effects on Carbon and Water Exchange in three Mediterranean Ecosystems*, Bayreuther Forum Oekologie, Band 89.
- Reichstein M, Dinh N, Running S, Tenhunen JT, Seufert G, Valentini B (2003a) Towards improved European carbon balance estimates through assimilation of MODIS remote sensing data and CARBOEUROPE eddy covariance observations into an advanced ecosystem and statistical modelling system. In: *Proceedings of the International Geoscience and Remote Sensing Symposium (IGARSS'03)*, Toulouse, France, July 21–25, 2003.
- Reichstein M, Falge E, Baldocchi D *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.
- Reichstein M, Tenhunen JD, Ourcival J-M *et al.* (2002) Severe drought effects on ecosystem CO<sub>2</sub> and H<sub>2</sub>O fluxes at three Mediterranean sites: revisions of current hypothesis? *Global Change Biology*, **8**, 999–1017.
- Reichstein M, Tenhunen JD, Ourcival J-M *et al.* (2003b) Inverse modelling of seasonal drought effects on canopy CO<sub>2</sub>/H<sub>2</sub>O exchange in three Mediterranean ecosystems. *Journal of Geophysical Research*, **108**, 4726, doi: 10.1029/2003JD003430.
- Reth S, Reichstein M, Falge E (2005) The effect of soil water content, soil temperature, soil pH-value and the root mass on soil CO<sub>2</sub> efflux – A modified model. *Plant and Soil*, **268**, 21–33.
- Richardson AD, Hollinger DY, Burba GG *et al.* (2006) A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology*, **136**, 1–18.
- Ruimy A, Jarvis PG, Baldocchi DD (1995) CO<sub>2</sub> fluxes over plant canopies and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–68.
- Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global scale models. In: *Scaling Physiological Processes: Leaf to Globe* (eds Ehleringer JR, Field CB), pp. 141–158. Academic Press, San Diego, CA.
- Ryel RJ, Falge E, Joss U, Geyer R, Tenhunen JD (2001) Penumbra and foliage distribution effects on *Pinus sylvestris* canopy gas exchange. *Theoretical Applied Climatology*, **68**, 109–124.
- Saigusa N, Yamamoto S, Murayama S, Kondo H (2005) Inter-annual variability of carbon budget components in an Asia-Flux forest site estimated by long-term flux measurements. *Agricultural and Forest Meteorology*, **134**, 4–16.
- Sellers PJ, Randall DA, Collatz GJ *et al.* (1996) A revised land surface parameterization (SiB<sub>2</sub>) for atmospheric GCMs, I, Model formulation. *Journal of Climate*, **9**, 676–705.
- Sokal RR, Rohlf FJ (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York.
- Stoy PC, Katul GG, Siqueira MBS *et al.* (2005) Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: a wavelet analysis. *Tree Physiology*, **25**, 887–902.
- Stoy PC, Katul GG, Siqueira MBS, Juang J-Y, Novick KA, Oren R (2006) An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agricultural and Forest Meteorology*, **141**, 2–18.
- Stromberg AJ (1997) Some software for computing robust linear or nonlinear regression estimators. *Communications in Statistics-Simulation and Computation*, **26**, 947–959.
- Sun T, Berninger F, Markkanen T *et al.* (2003a) Interannual variability and timing of growing-season CO<sub>2</sub> exchange in a boreal forest. *Journal of Geophysical Research*, **108**, 1–8.
- Sun T, Berninger F, Vesala T *et al.* (2003b) Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biology*, **9**, 1410–1426.
- Suyker AE, Verma SB, Burba GG, Arkebauer TJ, Walters DT, Hubbard KG (2004) Growing season carbon dioxide exchange in irrigated and rainfed maize. *Agricultural and Forest Meteorology*, **124**, 1–13.

- Suyker AE, Verma SB, Burba GG, Arkebauer TJ (2005) Gross primary production and ecosystem respiration of irrigated maize and irrigated soybean during a growing season. *Agricultural and Forest Meteorology*, **131**, 180–190.
- Tamiya H (1951) Some theoretical notes on the kinetics of algal growth. *Botanical Magazine*, **6**, 167–173.
- Tenhunen JD, Geyer R, Valentini R, Mauser W, Cernusca A (1999) Ecosystem studies, land-use change, and resource management. In: *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes* (eds Tenhunen JD, Kabat P), pp. 1–19. John Wiley & Sons, West Sussex, UK.
- Tenhunen JD, Valentini R, Köstner B, Zimmermann R, Granier A (1998) Variation in forest gas exchange at landscape to continental scales. *Annales des Sciences Forestières*, **55**, 1–12.
- Tenhunen JD, Weber JA, Yocum CS, Gates DM (1976) Development of a photosynthesis model with an emphasis on ecological applications. II. Analysis of a data set describing the PM surface. *Oecologia*, **26**, 101–119.
- Valentini R, (ed.) (2003) *Fluxes of Carbon, Water and Energy of European Forests*. Vol. 163. *Ecological Studies Series*. Springer-Verlag, Heidelberg.
- Valentini R, De Angelis P, Matteucci G, Monaco R, Dore S, Scarascia Mugnozza GE (1996) Seasonal net carbon dioxide exchange of a Beech forest with the atmosphere. *Global Change Biology*, **2**, 199–207.
- Valentini R, Matteucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.
- Verma SB, Dobermann A, Cassman KG *et al.* (2005) Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. *Agricultural and Forest Meteorology*, **131**, 77–96.
- Vourlitis GL, Oechel WC (1997) Landscape-scale CO<sub>2</sub>, H<sub>2</sub>O vapour, and energy flux of moist-wet coastal tundra ecosystems over two growing seasons. *Journal of Ecology*, **85**, 575–590.
- Walker DA, Jia GJ, Epstein HE (2003) Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes*, **14**, 103–123.
- Wang YP, Leuning R (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I. model description and comparison with a multi-layered model. *Agricultural and Forest Meteorology*, **91**, 89–111.
- Wang Q, Tenhunen J, Falge E, Bernhofer C, Granier A, Vesala T (2003) Simulation and scaling of temporal variation in gross primary production for coniferous and deciduous temperate forests. *Global Change Biology*, **10**, 37–51.
- Warren K (2003) *Summary of Region 5 Grassland Bird Management Project for Canaan Valley National Wildlife Refuge, Tucker County, West Virginia 2001–2003*. Internal Report. Canaan Valley National Wildlife Refuge, US Fish and Wildlife Service, 27 pp.
- Wever LA, Flanagan LB, Carlson PJ (2002) Seasonal and inter-annual variation in evapotranspiration, energy balance and surface conductance in a northern temperate grassland. *Agricultural and Forest Meteorology*, **112**, 31–49.
- Williams M, Rastetter EB, Fernandes DN *et al.* (1996) Modelling the soil–plant–atmosphere continuum in a Quercus-Acer stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment*, **19**, 911–927.
- Wilson KB, Baldocchi DD, Hanson PJ (2000) Quantifying stomatal and non-stomatal limitations to carbon assimilation resulting from leaf aging and drought in mature deciduous tree species. *Tree Physiology*, **20**, 787–797.
- Wilson KB, Baldocchi DD, Hanson PJ (2001) Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. *Plant, Cell and Environment*, **24**, 571–583.
- Wofsy SC, Goulden ML, Munger JW *et al.* (1993) Net exchange of CO<sub>2</sub> in a midlatitude forest. *Science*, **260**, 1314.
- Wohlfahrt G, Anfang C, Bahn M *et al.* (2005) Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling. *Agricultural and Forest Meteorology*, **128**, 141–162.
- Xiao X (2006) Light absorption by leaf chlorophyll and maximum light use efficiency. *IEEE Transactions on Geoscience and Remote Sensing*, **44**, 1933–1935.