

Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe

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Abstract

This paper develops a statistical model for daily gross primary production (GPP) in boreal and temperate coniferous forests. The model applies the light use efficiency (LUE) approach, which estimates the conversion efficiency of daily absorbed photosynthetically active radiation (APAR) into daily GPP as a product of potential LUE and modifying factors. The latter were derived from daily total APAR and daily mean temperature, vapour pressure deficit (VPD) and soil water content (SWC). Modelling data came from five European eddy covariance measurement towers over 2–8 years. The model was tested against independent data from two AmeriFlux stations. The model with the APAR, temperature and VPD modifiers worked well in almost all the site–year combinations, but the SWC modifier only improved the fit in few cases. Geographical variation was found in the modifiers and potential LUE in site-specific models. When a model was fitted to pooled data, differences between sites could be explained by potential LUE, leaf area and environmental conditions. The test against the AmeriFlux data corroborated this finding. The potential LUE varied from 1.9 to 3.1 g C MJ⁻¹, and a weak correlation was found between foliar nitrogen concentration and potential LUE. Some year-to-year variation remained which could be captured by neither the pooled nor the site-specific models.

Keywords: APAR, gross primary production, light use efficiency, photosynthesis, soil water, statistical model, temperature acclimation, VPD

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Introduction

Gross primary production (GPP) is the origin of carbon in all ecosystem fluxes, and a key component of the carbon balance between the biosphere and the atmosphere. The biological basis of GPP is well understood; however, because of its dependence on a variety of environmental and internal drivers at several time scales, its quantification for different biomes is not straightforward. Quantitative information about GPP and its environmental control is crucial for predictions of ecosystem response to climate change. It is the central

driver of ecosystem growth models (Mäkelä *et al.*, 2000), and it is also being increasingly used in remote sensing applications to predict global carbon fluxes (Still *et al.*, 2004; Xiao *et al.*, 2005).

Biologically, GPP is a product of photosynthesis, which is composed of fast, light-driven biochemical reactions in the leaves (Farquhar & von Caemmerer, 1982), stomatal control that regulates the diffusion rate of CO₂ (Leuning, 1995), and slower acclimation processes that are particularly important for conifers in relation with the annual cycle of temperature (Pelkonen & Hari, 1980; Bergh *et al.*, 1998). Physiologically based canopy photosynthesis models have been developed to describe these processes, together with the distribution

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of phytomass and light attenuation in canopies (Law *et al.*, 2000; Kramer *et al.*, 2002; Medlyn *et al.*, 2003), but they generally require detailed input information at a high temporal resolution, impractical for large-scale applications.

An alternative approach is based on models that summarize the fast, leaf-level responses at a longer-term, whole-canopy scale, taking longer-term average weather data as their input. Daily-time-step models include the widely used Forest-BGC and Biome-BGC (Running & Gower, 1991; Running & Hunt, 1993; Kennedy *et al.*, 2006), while a monthly time step is used in the 3-PG model (Landsberg & Waring, 1997). Moving from faster time-steps compatible with the usual shoot-level measurements of photosynthesis, to a coarser scale requires integration over time and space to relate the available measurements with the summary model parameters. Because of uncertainties in the method of summarizing, calibration of parameter values is required to make the model predictions agree with observation (Law *et al.*, 2000; Kramer *et al.*, 2002). However, the increasing availability of canopy-level estimates of GPP from eddy covariance (EC) measuring stations has made the calibration process more feasible than ever.

The increasing availability of empirical canopy-level estimates of GPP from different regions and biomes also allows us to develop canopy-level photosynthesis models using statistical fitting procedures. A few studies have already been conducted using hourly (van Dijk *et al.*, 2005), daily (Yuan *et al.*, 2007) and monthly (Maselli *et al.*, 2006) time scales. Of course the fitted models will have little value unless they portray the environmental responses sufficiently generally to be applicable more widely both temporally and spatially. In order for the statistical fit to be as generally applicable as possible, the model structure and parameters should be based on our biological understanding of the process. Formulations used in the summary type photosynthesis models that have been shown to be consistent with canopy level measurements (Landsberg & Waring, 1997; Thornton *et al.*, 2002) would, therefore, seem good candidates for empirical model fitting.

A widely used summary model of GPP is based on the concept of light use efficiency (LUE) reduced by modifying factors (McMurtrie *et al.*, 1994; Landsberg & Waring, 1997). It assumes a linear dependence of GPP on absorbed photosynthetically active radiation (APAR), modified by a parabolic effect of temperature and exponential-type reductions caused by increasing vapour pressure deficit (VPD) and/or decreasing soil water content (McMurtrie *et al.*, 1994; Landsberg & Waring, 1997). However, although fairly linear with respect to APAR over monthly or annual time periods, GPP has been found to be strongly nonlinear with

respect to APAR at the daily scale (Medlyn *et al.*, 2003; Turner *et al.*, 2003). Secondly, there is indication that the parabolic temperature response may lead to underestimation of photosynthetic production during the warm season (Thornton *et al.*, 2002), suggesting that a saturating effect might be more appropriate. The main effect of temperature on photosynthesis in boreal and temperate conifers has been proposed to be through acclimation to the annual cycle, described as a temperature-dependent dynamic delay process (Mäkelä *et al.*, 2004; van Dijk *et al.*, 2005).

The objective of this paper is to develop an empirical model consistent with process knowledge for the GPP of coniferous forests, using daily values of environmental driving variables and information about canopy leaf area as input. Daily values of GPP estimated with standard techniques from five European EC measurement towers during 2–8 years each are used as the response variables. The model applies the LUE approach, analysing the significance of APAR, temperature, VPD and soil water content as potential modifying factors. It is hypothesized that the same parameterization can be applied to all sites and years, and this is tested (1) by comparing site-specific fitted parameters with those in the pooled data set, and (2) by testing the model in an independent data set from two AmeriFlux stations. Finally, the ability of the model to capture regional and year-to-year variability in GPP, and the major remaining caveats for doing so, are discussed.

Materials and methods

Model

The summary model used in this study is a LUE-type model of daily photosynthetic production of the canopy:

$$P_k = \beta \Phi_k \prod_i f_{ik} + \varepsilon_k, \quad (1)$$

where P_k is canopy GPP (g C m^{-2}) during day k , β is potential daily LUE (g C mol^{-1}), Φ_k is APAR (mol m^{-2}) during day k , $f_{ik} \in [0, 1]$ are modifying factors accounting for suboptimal conditions in day k , and ε_k is random error during day k . The actual LUE of the canopy in day k is the product of β and the current values of the modifiers.

To account for the nonlinearity in the response to APAR, a light modifier f_L was defined so as to yield the rectangular hyperbola when multiplied with the linear response included in the LUE model, Eqn (1):

$$f_L(\Phi_k) \equiv \frac{1}{\gamma \Phi_k + 1}, \quad (2)$$

where γ ($\text{m}^2 \text{mol}^{-1}$) is an empirical parameter (Fig. 1).

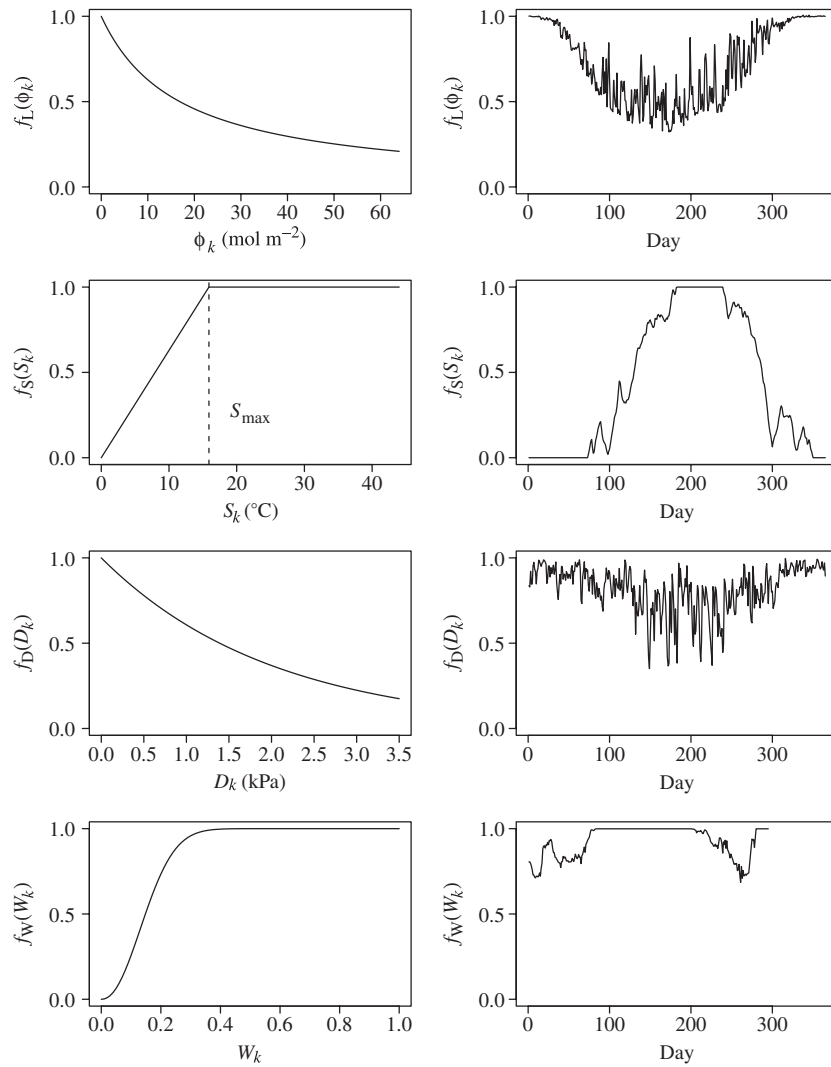


Fig. 1 Schematic illustrations of the functional forms and annual course of the light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)], VPD [f_D ; Eqn (5)] and soil water [f_W ; Eqn (7a)] modifiers. VPD, vapour pressure deficit.

The effect of temperature on daily GPP was modelled using the concept of state of acclimation, S_k (°C) (Mäkelä *et al.*, 2004), a piecewise linear function of X_k (°C) calculated from the mean daily ambient temperature, T_k (°C), using a first-order dynamic delay model:

$$X_k = X_{k-1} + \frac{1}{\tau}(T_k - X_{k-1}), X_1 = T_1, \quad (3a)$$

$$S_k = \max\{X_k - X_0, 0\}, \quad (3b)$$

where τ (days) is the time constant of the delay process and X_0 (°C) is a threshold value of the delayed temperature. The modifying function f_S is defined as

$$f_S(S_k) \equiv \min\left\{\frac{S_k}{S_{\max}}, 1\right\}, \quad (4)$$

where the empirical parameter $S_{\max}$ (°C) determines the value of S_k at which the temperature modifier attains its saturating level (Fig. 1).

Following Landsberg & Waring (1997), the VPD modifier was defined as

$$f_D(D_k) \equiv e^{\kappa D_k}, \quad (5)$$

where D_k (kPa) is VPD in day k and κ (kPa⁻¹) is an empirical parameter assuming typically negative values (Fig. 1).

The soil water modifier was based on the relative extractable water (REW), W , defined as

$$W_k \equiv \min\left\{\frac{\theta_k - \theta_{WP}}{\theta_{FC} - \theta_{WP}}, 1\right\}, \quad (6)$$

where θ_k is volumetric soil water content (SWC) ($\text{m}^3 \text{m}^{-3}$), and θ_{WP} and θ_{FC} are SWC at permanent wilting point and at field capacity, respectively. Dependent on soil type, θ_{WP} and θ_{FC} were determined for each site using water retention curves obtained either from measurements or from the literature. Two different modifiers were fitted, one following Landsberg & Waring (1997):

$$f_W(W_k) \equiv \left[1 + \left(\frac{1 - W_k}{\alpha} \right)^v \right]^{-1}, \quad (7a)$$

and the other the Weibull function:

$$f_W(W_k) \equiv 1 - \exp(-\alpha W_k^v), \quad (7b)$$

where α and v are empirical parameters (Fig. 1).

Data

The data for model fitting came from five European coniferous forest sites with EC micrometeorological measurement towers: Sodankylä, Finland; Hyytiälä, Finland; Norunda, Sweden; Tharandt, Germany; and Bray, France (Table 1).

Half-hourly measurements of photosynthetic photon flux density (PPFD) above the canopy ($\mu\text{mol m}^{-2} \text{s}^{-1}$), air temperature ($^{\circ}\text{C}$), VPD (kPa) and SWC in the layer of 0–30 cm (but 0–80 cm in Bray) ($\text{m}^3 \text{m}^{-3}$) were used to derive daily totals (PPFD) and averages (all other variables). The daily values were computed from gap-filled half-hourly observations. If more than 30% (14/48) of the half-hourly observations were gap-filled, the daily value was coded missing.

Ecosystem GPP was estimated as the difference between measured net ecosystem exchange (NEE) and estimated total ecosystem respiration (TER) (Falge *et al.*, 2001). Half-hourly TER was modelled from the friction-velocity-filtered night-time NEE measurements as an Arrhenius type function of soil organic layer temperature (Sodankylä, Hyytiälä), air temperature (Norunda, Tharandt) or their mean (Bray); in each site, the temperature sensitivity parameter was first estimated over each year, after which the absolute level parameter was estimated in windows of 9–11 days. The temperature dependence of night-time TER was generalized to daytime, and the half-hourly daytime GPP was computed by subtracting the estimated TER from the measured NEE. When NEE was not measured or the measurement was rejected, either NEE gap-filled with the look-up tables method (Falge *et al.*, 2001; Wang *et al.*, 2003) was used (Tharandt), or GPP was directly estimated as a saturating function of PPFD (Sodankylä, Hyytiälä, Bray) or global radiation (Norunda). For Sodankylä, Hyytiälä and Bray, the estimation procedure is docu-

mented in Mäkelä *et al.* (2006). The daily totals of GPP (g C m^{-2}) were summed from the half-hourly estimates.

The daily canopy APAR, Φ (mol m^{-2}), was taken to be a site-specific fraction of daily total PPFD (Table 1), constant over time. In Tharandt, the fraction was estimated from daily measurements of PPFD taken above and below canopy in the EC mast. In Norunda, the estimation was based on below-canopy PPFD measurements taken with PAR sensors placed randomly or on a portable ramp at several plots near the mast (Lagergren *et al.*, 2005). In the other sites, the fraction was estimated with the Lambert–Beer law using all-sided canopy leaf area and previously estimated site-specific extinction coefficients (0.23, 0.19 and 0.27 for Sodankylä, Hyytiälä and Bray, respectively). Ground vegetation was not accounted for.

The number of missing daily values was notable in some site-year-variable combinations: In Bray 2001 and 2002, the SWC data were very sparse, with not more than a few dozen daily values per each year. In Norunda, there were no SWC observations available in 1995 and no PPFD measurements available for the first half of 1998. In Sodankylä 2001 and 2002, more than half of the GPP values were missing due to poor quality of NEE data.

Data for model validation were obtained from the coniferous AmeriFlux sites in northern Manitoba, Canada (NOBS for Northern Old Black Spruce) (Gower *et al.*, 1997; Dunn *et al.*, 2007), and in Metolius, OR, USA (Law *et al.*, 2003; Schwarz *et al.*, 2004) (Table 1). Half-hourly gap-filled data including the required input variables and GPP were retrieved from the free WWW sites (NOBS: ftp://ftp.as.harvard.edu/pub/nigec/Boreas_OBS/; Metolius: http://blg.oce.orst.edu/data_info/sisters.index.html). The flux and GPP computation methods are documented for NOBS by Dunn *et al.* (2007) and for Metolius by Schwarz *et al.* (2004) and Vickers *et al.* (2007); for Metolius, only data with less than nine gap-filled half-hourly NEE values per day were used. The percentage PPFD absorbed by the canopy was obtained from previous publications for the sites (Dang *et al.*, 1997; Turner *et al.*, 2003 for NOBS; Law *et al.*, 2001a for Metolius); the very low value for Metolius relative to its leaf area index (LAI) (Table 1) relates to the large openness of the canopy in the site.

The annual ecosystem GPP correlates with location and indicators of annual weather in the data sets (Fig. 2).

Method of model fitting

The models were first estimated separately for each site and year (site-year-specific models), as well as for all years in each site (site-specific models); the idea in these

Table 1 Site information

Site	Location	Elevation (m)	Dominant species	Age (a)	H _{dom} (m)	N (ha ⁻¹)	T _{av} (°C)	ETS (dd)	Precipitation (mm)	Soil	LAI _{proj} (m ² m ⁻²)/ LAI _{tot} (m ² m ⁻²)	fAPAR	Years of data	References
Sodankylä	67°22'N 26°38'E	180	<i>Pinus sylvestris</i>	50–160	12	2100	–1.0	1000	500	Sand	1.7/4.0	0.60	2001–2002	Aurela (2005)
Hyytiälä	61°51'N 24°18'E	170	<i>Pinus sylvestris</i>	42	14	1450	2.9	1350	640	Till	2.9/7.0	0.75	2001–2003	Ilvesniemi & Liu (2001), Sumi <i>et al.</i> (2003)
Norunda	60°05'N 17°29'E	45	<i>Picea abies</i> + <i>Pinus sylvestris</i>	105	28	890	5.5	1500	530	Sandy till	4.3/11.7	0.87	1995–2002	Lundin <i>et al.</i> (1999)
Tharandt	50°58'N 13°34'E	375	<i>Picea abies</i>	110	28	440	7.5	2000	820	Brown earth	7.6/22.8	0.94	2001–2003	Grünwald (2003)
Bray	44°42'N 0°46'W	61	<i>Pinus pinaster</i>	32	21	410	13.0	3200	970	Podzol	1.7/4.0	0.66	2001–2002	Delzon <i>et al.</i> (2004)
Manitoba (NOBS)	55°53'N 98°29'W	259	<i>Picea mariana</i>	160	10	5450	–3.2	1200	510	Peat (30–50 cm) over clay	4.2/10.1	0.85	2000–2002	Gower <i>et al.</i> (1997), Dunn <i>et al.</i> (2007)
Metolius	44°27'N 121°33'W	1232	<i>Pinus ponderosa</i>	60*	20	325	8.6	1550	550	Sandy loam	3.0/8.0	0.45	2002–2004	Law <i>et al.</i> (2001b, 2003, 2006), Schwarz <i>et al.</i> (2004)

H_{dom}, dominant height; N, stand density; T_{av}, mean annual temperature; ETS, effective temperature sum; LAI_{proj}, projected leaf area index; LAI_{tot}, all-sided leaf area index; fAPAR, proportion of PAR intercepted by the canopy.

*Mean age; mean age of the oldest 10% is 90 years.

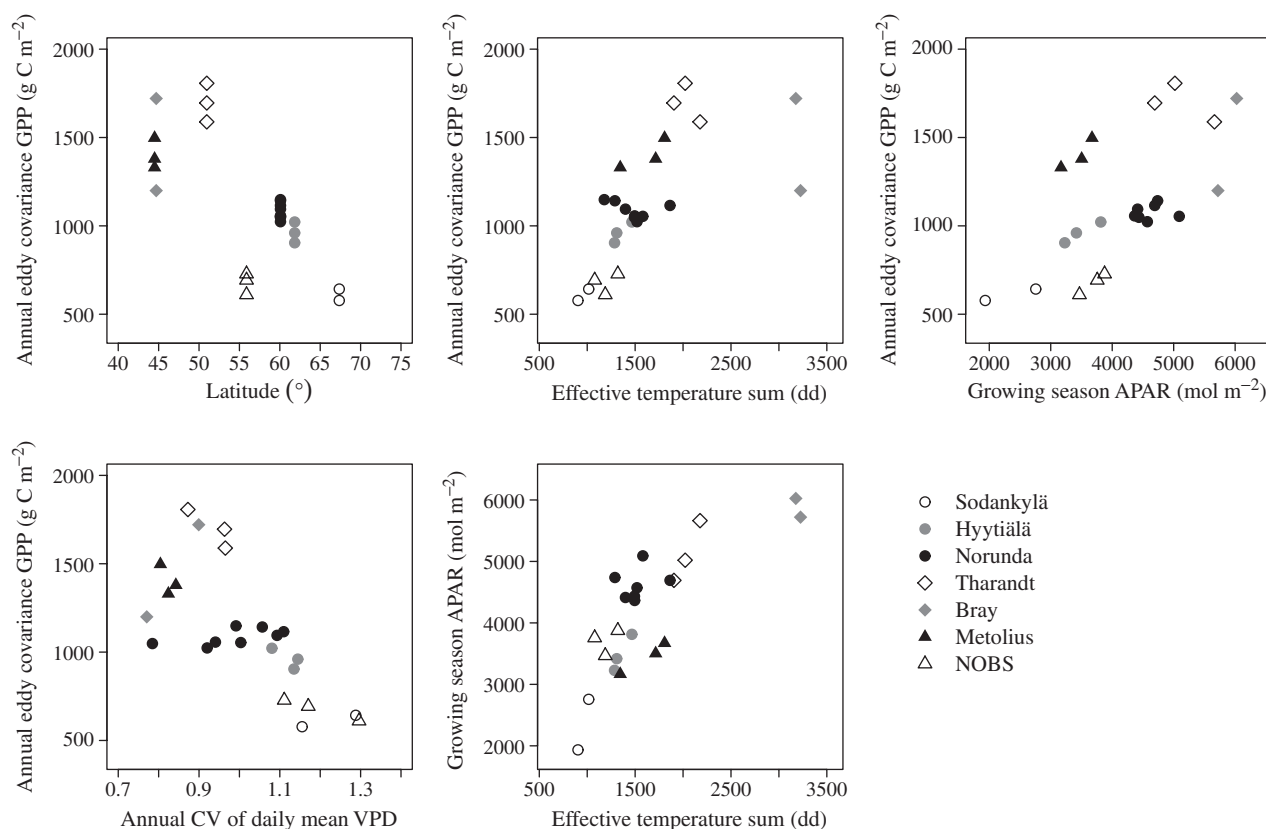


Fig. 2 Annual eddy covariance GPP vs. indicators of location and annual weather in the estimation sites (Sodankylä, Hyttiälä, Norunda, Tharandt and Bray) and in the AmeriFlux test sites (Metolius and NOBS). CV, coefficient of variation; GPP, gross primary production; NOBS, Northern Old Black Spruce; APAR, absorbed photosynthetically active radiation.

fittings was to study the significance of the different modifiers and to investigate the between-years and between-sites variation in the parameter estimates. A set of common parameters for all the sites and years was then sought by fitting the model with the significant modifiers over the whole data set (whole-data model). Finally, a modification of the whole-data model was fitted where the LUE parameter, β , was allowed to vary between sites while the other parameters were shared (variable-LUE model).

Least squares estimates of the parameters were found using a combination of (1) the Gauss–Newton method (Bates & Watts, 1988) and (2) experimental screening of the parameter space. The latter was necessary because the temperature modifier was not differentiable with respect to its parameters. The following steps were used:

1. Assign τ , X_0 and $S_{\max}$ a set of values in a sparse grid covering the whole parameter space.
2. For each combination of values, estimate the other model parameters with the Gauss–Newton method.

3. On the basis of 20 fits with the smallest RMSEs, choose an appropriate subset of the parameter space, and assign τ , X_0 and $S_{\max}$ a set of values in a finer grid covering this subset.
4. For each combination of values, estimate the other model parameters with the Gauss–Newton method; select the model with the smallest RMSE as the final model.

RMSE was computed as $[SSE/(n-p)]^{1/2}$, where SSE is the residual sum of squares, n is the number of observations and p is the number of parameters in the model.

If the random error terms have zero expectation and constant variance and are mutually independent, the Gauss–Newton method produces biased but consistent parameter estimates and approximate estimates for their variance–covariance matrix and error variance. In our data, however, the observations in each site were temporally dependent, and the constant error variance was not a realistic assumption either (in days with large GPP the variation of the residuals tends to be large compared with days with small GPP). With these violations, the parameter estimates still remained

consistent, but their variances became underestimated, which could result in too optimistic significance tests.

The iterative method does not provide any quantitative information on the uncertainty of the τ , X_0 and $S_{\max}$ estimates. These were studied with contour plots of RMSE (or R^2_{adj}) for each pair of the parameters.

The variable-LUE model was obtained from the whole data set by reformulating the model using an indicator variable to incorporate site-specific LUE parameters:

$$P_k = \sum_j \left[\beta_j \delta_k(j) \Phi_k \prod_i f_{ik} \right] + \varepsilon_k, \quad (8)$$

where $\delta_k(j) = 1$ if observation k was made in site j , and otherwise $\delta_k(j) = 0$. The site-specific LUE parameters β_j were then estimated simultaneously with the shared parameters γ , τ , X_0 , $S_{\max}$ and κ (α , v were not estimated as soil water modifier f_W was not included in the variable-LUE model).

Model diagnostics and comparison

Model diagnostics were based on the analysis of residuals (EC GPP–estimated GPP). The fit was appraised with the adjusted coefficient of determination

$$R^2_{\text{adj}} = 1 - \frac{\text{MSE}}{\text{Var}(\text{GPP})}, \quad (9)$$

which proportions the estimate of the error term variance ($\text{MSE} = \text{SSE}/(n-p)$) to the sample variance of GPP in the data.

The statistical significance of each modifier (set of modifiers) f_i was assessed with a likelihood ratio test, where the partial model without the modifier(s) was compared with the full model containing the modifier(s), the null hypothesis being that $f_{ik} = 1$ for all k . With the assumption of the (multivariate) normal distribution of the random error terms and the nonlinear regression function, the test becomes an approximate F test involving the residual sums of squares (SSE_p for the partial model with p_p parameters in it, SSE_f for the full model with p_f parameters in it, n being the number of observations):

$$F = \frac{(\text{SSE}_p - \text{SSE}_f)/(p_f - p_p)}{\text{SSE}_f/(n - p_f)}, \quad (10)$$

which is approximately F -distributed with the degrees of freedom $(p_f - p_p)$ and $(n - p_f)$.

For comparing the site-specific and site-and-year-specific models to the whole-data and variable-LUE models, the key question was what is the gain from estimating the parameters separately for each site and year, compared with one set of parameters for the whole data set. This was examined by comparing the

model fits in terms of residual means and standard deviations in each year in each site.

Results

Site-specific models

The model with the light (f_L), temperature (f_S) and VPD (f_D) modifiers was statistically significant in almost all cases (site–years, sites), but the soil water modifier (f_W) improved the fit significantly only in a few cases. We will, therefore, first report the results without f_W , then describe the cases where f_W was significant.

The model with the f_L , f_S and f_D modifiers fitted best in the Sodankylä and Hyytiälä data, fairly well in Norunda and Tharandt, and clearly most poorly in Bray (Fig. 3, Table 2). No large between-years variation in the fit was seen at any site, with the exception of Bray ($R^2_{\text{adj}} = 0.79$ in 2001 vs. $R^2_{\text{adj}} = 0.71$ in 2002) and Norunda ($R^2_{\text{adj}} = 0.83$ in 2002 vs. $0.8 \leq R^2_{\text{adj}} \leq 0.93$ in the other years). The year-specific models did not perform much better than the model estimated over the whole time period, except for Bray 2002 (Fig. 4).

The model fit to the Bray data was generally poor, which was manifested as (1) difficulties in fitting the temperature modifier, and (2) no statistical significance of the light modifier. It turned out that the temperature modifier was at its maximum value most of the time, and the result was not sensitive to any of the related parameters τ , X_0 or $S_{\max}$, so a wild variation of values with no apparent optimum was obtained in the fitting procedure. The temperature modifier nevertheless remained significant.

The site-specific parameter estimates showed geographical trends (Fig. 5). The reducing effect of large VPD became more pronounced (κ in f_D decreased) from north to south, while the nonlinearity of the GPP response to light decreased (γ in f_L decreased). At the same time, the delay time τ of the temperature acclimation decreased from north to south while the difference between $S_{\max}$ and X_0 [Eqns (3) and (4)] increased. The potential LUE, β , decreased (although not statistically significantly) from north to south in the pine stands, but was larger in the spruce stand in Tharandt. In all sites, there was considerable variation in the year-specific parameter estimates (Fig. 5). The large β estimate in Sodankylä 2002 resulted from unusually large GPP values towards the end of the growing season. No patterns related to stand characteristics (LAI, age, stand density, dominant height, basal area, mean diameter) were found in the parameters.

Incorporating the soil water modifier f_W improved R^2_{adj} in Norunda 1999, Bray 2001 and Bray 2001–2002, and Tharandt 2003 and Tharandt 2001–2003 (Table 3).

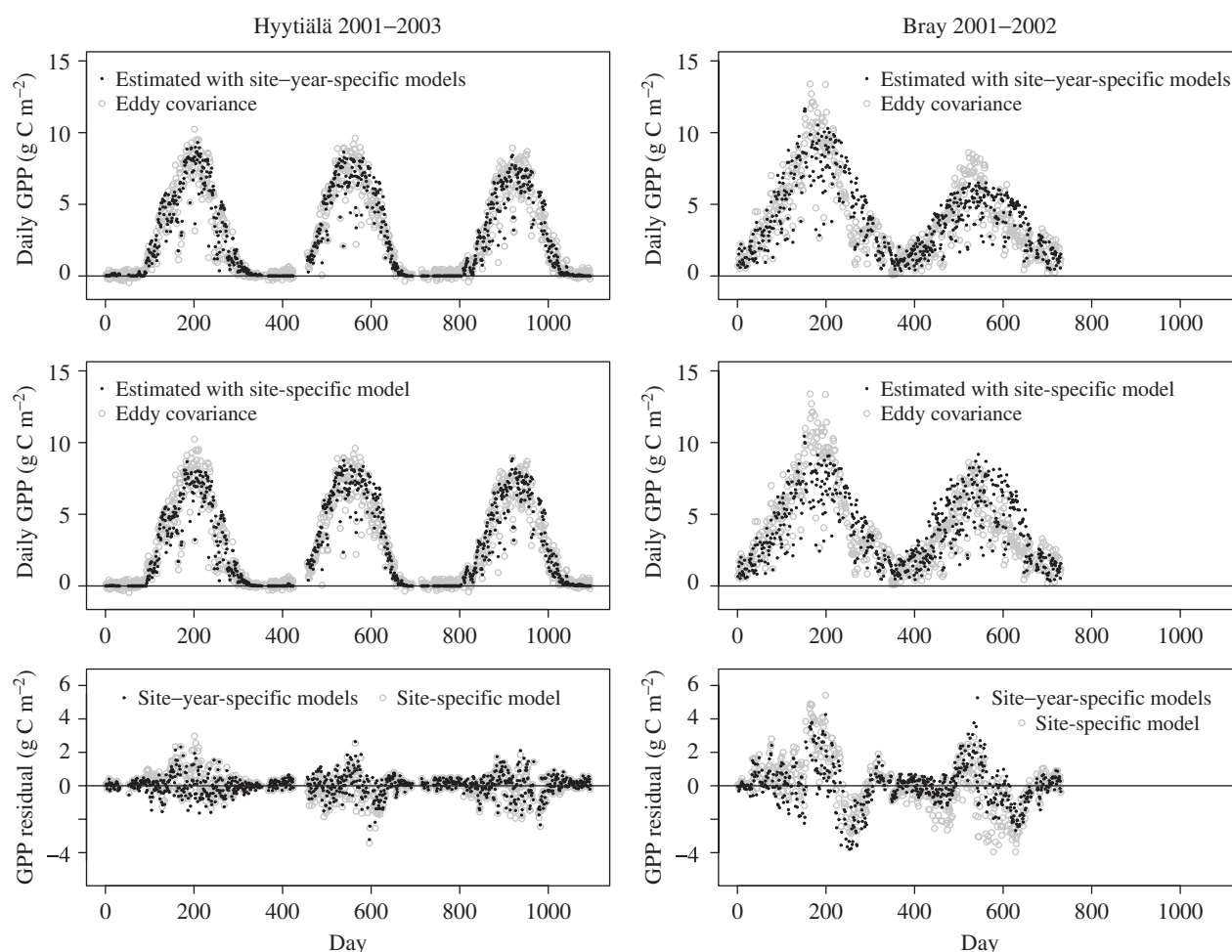


Fig. 3 The best (Hyytiälä) and the worst (Bray) fits of the site-year-specific and site-specific models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers. GPP, gross primary production; VPD, vapour pressure deficit.

Otherwise, f_W was not statistically significant or in many cases not even estimable from the data. When f_W was included in the model, the estimate of β increased, the nonlinearity of the light response became stronger (but remained statistically nonsignificant in Bray), and the effect of VPD weakened. In Bray, including f_W also appeared to make f_S more realistic, but the results remain uncertain due to the modest number of SWC data points (Table 3).

Models fitted to the whole data

Although coherent differences in the estimated parameter values could be found between the sites, the parameter estimates in each site were strongly correlated with each other. The largest correlations occurred between β and γ (≈ 0.9) and between γ and κ (≈ 0.7). The site-specific estimates also showed correlation across sites (0.86 between β and γ , 0.85 between γ and κ).

This suggests that a 'global' parameter set could be found that would provide nearly as good fits as the site-specific parameters (although perhaps losing some of the biological insight). The whole-data estimations were carried out using f_L , f_S and f_D only.

The whole-data parameters were closest to those of the Norunda site-specific model (years 1995–2002), which was expected as the Norunda data constituted nearly half of all the data (Table 2). When only data from the years 2001 and 2002 (observed at every site) were considered, the parameter values perhaps most resembled the values of Hyytiälä (not shown). Using the whole-data parameters increased the prediction error and error variation most in Tharandt and Bray and least in Sodankylä and Hyytiälä (Figs 4 and 6). Nevertheless, the predictions still followed the temporal pattern of the EC values, except in Bray where the whole-data model underestimated GPP in summer 2001 and severely overestimated it in the latter half of 2002.

Table 2 Parameter estimates and regression diagnostics for the site-specific, whole-data and variable-LUE models containing light (f_L), temperature (f_S) and VPD (f_D) modifiers

Model	All sites		Sodankylä		Hyytiälä		Norunda		Tharandt		Bray	
	Whole-data	Variable-LUE	Variable-LUE/		Variable-LUE/		Variable-LUE/		Variable-LUE/		Variable-LUE/	
			Whole-data	Site-specific	Whole-data	Site-specific	Whole-data	Site-specific	Whole-data	Site-specific	Whole-data	Site-specific
β (SE)	0.513 (0.00855)		0.495 (0.0142)	0.831 (0.0538)	0.541 (0.00963)	0.579 (0.0174)	0.504 (0.00886)	0.500 (0.0124)	0.643 (0.0114)	0.742 (0.0237)	0.505 (0.00875)	0.459 (0.0195)
γ (SE)	0.0196 (0.00121)	0.0223 (0.00125)		0.0650 (0.0101)		0.0303 (0.00283)		0.0220 (0.00178)		0.0267 (0.00259)		-0.000669 (0.00221)
κ (SE)	-0.389 (0.0161)	-0.403 (0.0149)		-0.150 (0.0712)		-0.235 (0.0281)		-0.391 (0.0213)		-0.512 (0.0287)		-0.560 (0.0568)
τ	7.2	6.3		10.2		11.1		5.7		1.8		2.6
X_0	-4.0	-3.9		-0.9		-3.1		-4.0		-5.2		-17.6
$S_{\max}$	17.3	17.1		16.4		17.3		17.6		18.5		45.0
RMSE	1.24	1.15		0.47		0.67		1.04		1.31		1.503
R^2_{adj}	0.84	0.86		0.96		0.95		0.87		0.86		0.71
n	5071	5071	200	200	936	936	2319	2319	1028	1028	588	588

Whole-data model: model estimated from the whole data, i.e. from the observations of all the sites and years pooled together; Variable-LUE model: parameter β estimated separately for each site by reformulating the whole-data model; Site-specific model: model estimated for each site from all the observations available for that site.

Letting β vary between the sites considerably reduced the bias at all sites but had practically no effect on the residual standard deviation (Fig. 4). The variable-LUE model fitted to the data almost as well as the site-specific models: while the site-specific models were superior in Sodankylä and Bray (Table 2), the effect of estimating parameters other than β site-wise was negligible in Hyytiälä, Tharandt and Norunda (Table 2, Fig. 4). However, neither the site-specific nor the variable-LUE models were able to capture some of the year-to-year variation in GPP, which was incorporated as year-to-year differences in fitted parameter values in the site-year-specific models (Fig. 4). The findings were similar when only the years 2001 and 2002 were considered.

Compared with the site-specific models, fixing the values of the rest of the parameters in the variable-LUE model reduced the variation in the β estimates (Table 2). A geographical trend could no more be found in the pine-stand β estimates, while the Tharandt spruce stand still had a relatively higher estimate for β .

Comparison with independent data

The prediction performance of (1) the whole-data model and (2) the variable-LUE model was studied with the independent data. In the latter case, the LUE parameter β was estimated for each test site conditional on the values obtained from the European data for the rest of the parameters (Table 2); the β estimates were hence found through simple linear regression with zero intercepts.

The whole-data model somewhat overpredicted the daily GPP at the NOBS site and severely underpredicted it at the Metolius site, especially in 2003 (Figs 7 and 4). This was reflected in the β estimates in the variable-LUE model (0.428 for NOBS, 0.696 for Metolius). The prediction performance of the variable-LUE model in the test sites was comparable to the fit of the model in the estimation sites (Fig. 4). The temporal pattern of the residuals at Metolius (Fig. 7) resembled that of Bray (Fig. 3), the only European site where water was likely to be limited.

Annual totals of GPP

On an annual basis, the GPP values summed up from the daily model estimates corresponded well with the sums of the EC values (Fig. 8). The estimates from the site-specific models were not considerably better than those from the variable-LUE model, but both of these were clearly more accurate than the estimates from the whole-data model.

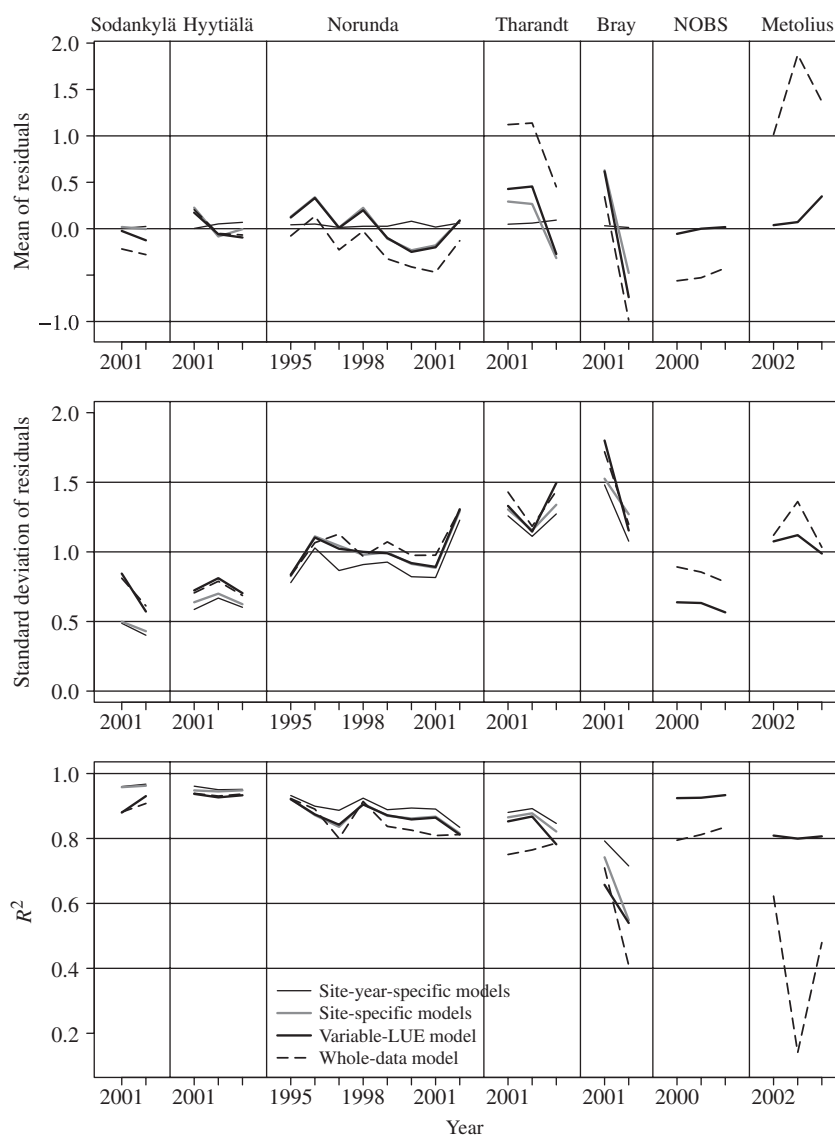


Fig. 4 GPP residual ($\text{g C m}^{-2} \text{ day}^{-1}$) diagnostics for the models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers in all the years in the estimation and test sites. R^2 , unadjusted coefficient of determination. GPP, gross primary production; VPD, vapour pressure deficit; NOBS, Northern Old Black Spruce; LUE, light use efficiency.

Discussion

The present study has shown that a simple LUE-based model, with intercepted light, state of temperature acclimation, and VPD as input variables, can explain a major part of the day-to-day variation in the GPP of boreal and temperate coniferous forests. The explanation seemed more robust in the more boreal, less drought-limited sites, but no definite improvement was gained in this study by including the relative soil water content as an additional explanatory variable. However, this lack of response may be not because of a lack of effect, but because of the sparse data available on soil water.

The results indicate that while the same response to the environmental driving variables can be assumed across different sites and species, the level of GPP is still site-specific. Assuming that the biochemical mechanism of photosynthetic production is universal and largely independent of species (Landsberg & Waring, 1997), this suggests that some site-specific factors affecting the level of LUE have not been included, or have been misrepresented, in the model. An obvious candidate for such a factor is foliar nitrogen which was not generally available for the sites but has been suggested in many studies to be a key determinant of canopy photosynthesis (Ågren, 1996; Smith *et al.*, 2002). Indeed, when plotting the variable-LUE model estimates of β against

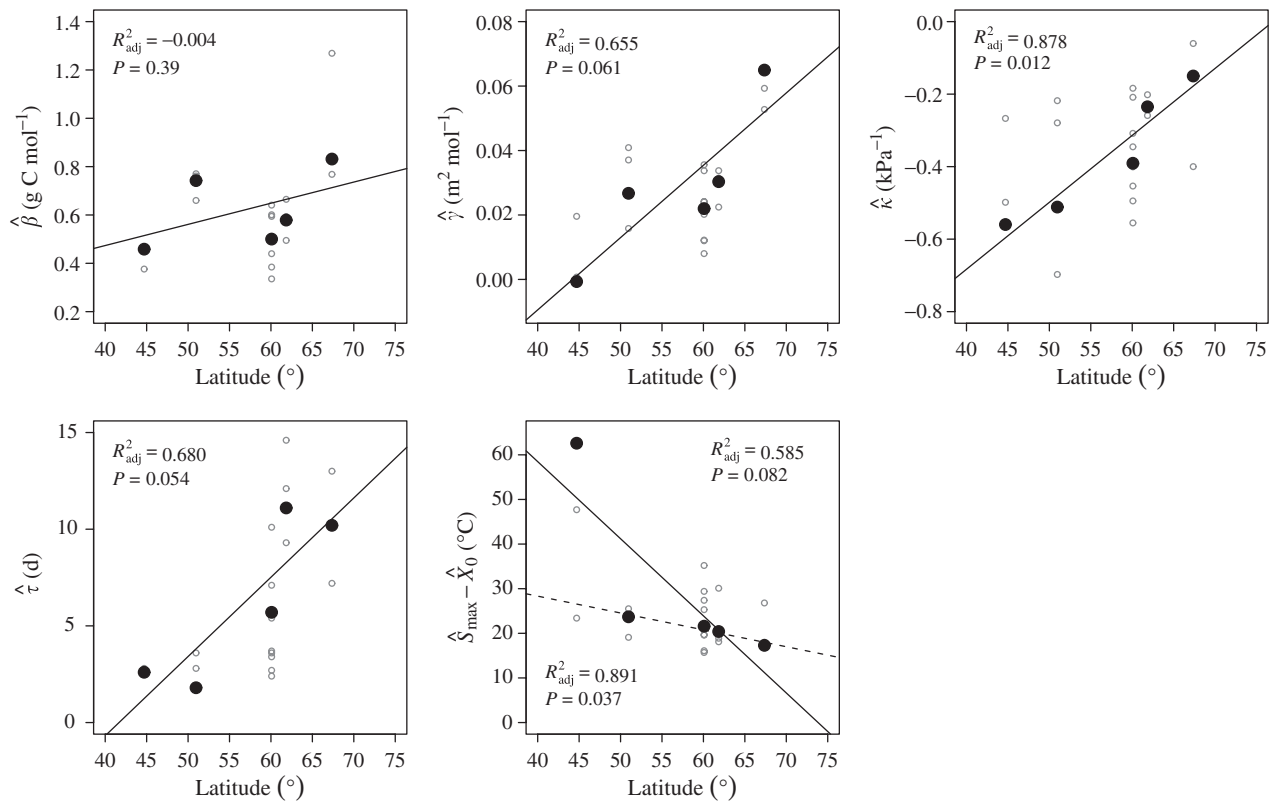


Fig. 5 Variation in the parameter estimates of the site-year-specific models (○) and site-specific models (●) containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers. Linear regressions were fitted to site-specific estimates with (solid line) and without (dashed line) Bray. The P values refer to the F tests of the null hypothesis that the regression coefficient is zero. Note: The estimate $\hat{\tau} = 80$ obtained in Bray 2002 is not shown. VPD, vapour pressure deficit.

Table 3 Parameter estimates and regression diagnostics for the models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)], VPD [f_D ; Eqn (5)] and soil water [f_W ; Eqn (7a)] modifiers in the site-year combinations where f_W was statistically significant. For comparison, results for the models not containing f_W ($f_L f_S f_D$) and fitted to the same data (i.e., to the points where SWC was available) are given. Statistically nonsignificant estimates are in *italics*.

	Norunda 1999		Tharandt 2003		Tharandt 2001–2003		Bray 2001		Bray 2001–2002	
Model	$f_L f_S f_D f_W$	$f_L f_S f_D$	$f_L f_S f_D f_W$	$f_L f_S f_D$	$f_L f_S f_D f_W$	$f_L f_S f_D$	$f_L f_S f_D f_W$	$f_L f_S f_D$	$f_L f_S f_D f_W$	$f_L f_S f_D$
β (SE)	0.700 (0.0771)	0.488 (0.0466)	0.988 (0.0784)	0.659 (0.0369)	0.843 (0.0300)	0.732 (0.0243)	1.158 (0.367)	0.493 (0.196)	0.561 (0.0846)	0.387 (0.0681)
γ (SE)	0.0437 (0.00971)	0.00191 (0.00571)	0.0437 (0.00734)	0.0155 (0.00349)	0.0393 (0.00343)	0.0265 (0.00267)	0.0397 (0.0326)	0.0218 (0.0349)	0.00700 (0.00865)	0.00757 (0.0111)
κ (SE)	-0.617 (0.0561)	-0.390 (0.0633)	-0.484 (0.0428)	-0.699 (0.0467)	-0.370 (0.0278)	-0.510 (0.0293)	-0.161 (0.219)	-0.0602 (0.409)	-0.202 (0.137)	-0.298 (0.174)
α (SE)	1.062 (0.0262)		1.002 (0.00143)		1.003 (0.00154)		0.843 (0.0652)		0.913 (0.112)	
ν (SE)	11.27 (3.120)		442.7 (262.7)		362.3 (193.6)		2.756 (0.940)		1.509 (0.525)	
τ	6.1	5.0	3.0	2.0	3.0	2.0	11.0	2.0	24.3	1.0
X_0	-7.6	-10.0	-4.0	-5.0	-4.6	-5.0	-1.1	-1.0	1.6	-15.0
S_{max}	27.1	29.0	18.3	19.5	17.7	18.0	24.2	19.0	11.4	34.0
RMSE	1.06	1.24	1.14	1.29	1.20	1.30	1.26	2.16	1.31	1.73
R^2_{adj}	0.79	0.71	0.88	0.84	0.88	0.86	0.87	0.61	0.79	0.64
N	172	172	347	347	971	971	21	21	57	57

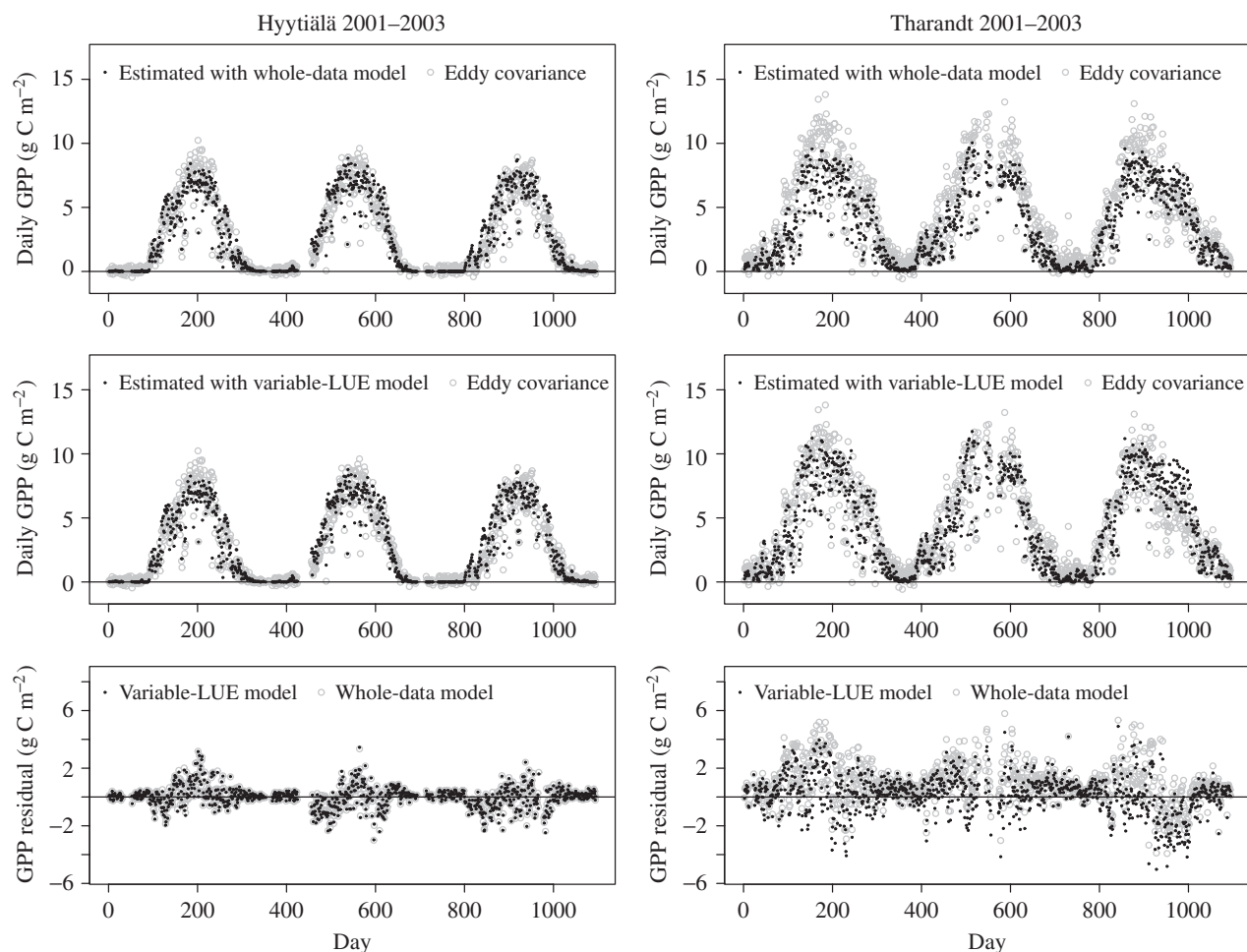


Fig. 6 The best (Hyytiälä) and the second worst (Tharandt) fits of the whole-data and variable-LUE models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers. LUE, light use efficiency; GPP, gross primary production; VPD, vapour pressure deficit.

available information on foliar N per leaf area in the sites, a clear relationship was detected (Fig. 9).

Other factors causing differences in β could be (1) differences in ground vegetation and (2) uncertainty in estimating the fraction of absorbed PAR (fAPAR) in the sites. The significance of ground vegetation varies from site to site according to stand density, soil type and other factors. For example, in Tharandt the canopy was dense with virtually nonexistent ground vegetation, while in Bray, the ground vegetation LAI was comparable with that of the tree canopy and had a pronounced annual pattern. fAPAR was estimated using nonstandard, site-specific methods. Its uncertainty is difficult to assess, yet the estimate of β is very sensitive to errors in fAPAR because the two parameters are multiplicative in the model. A weak negative correlation was found between fAPAR and β ($r = -0.34$, $n = 7$).

The variation in β was reduced from the site-specific models to the variable-LUE model. This was because

there were strong correlations between the site-specific β , γ and κ . When γ and κ were fixed, the variation in β was also reduced. Had β been fixed, these differences would likely have materialised in the other parameters.

Different functional forms for the modifiers were not compared in this study, except for the soil water modifier [Eqn (7)], the two variants of which gave virtually identical results in terms of model predictions and diagnostics. However, the choice of a saturating light function instead of a linear one appeared important, as in all sites but one the nonlinear parameter γ was statistically significant. Similarly, delayed temperature appeared a better explanatory variable than current temperature, as the time constant $\tau > 1$ in most cases. Given these basic qualitative choices, different functional forms would likely have provided very similar results.

Many previous studies have reported values for monthly or daily based LUE; however, the magnitudes

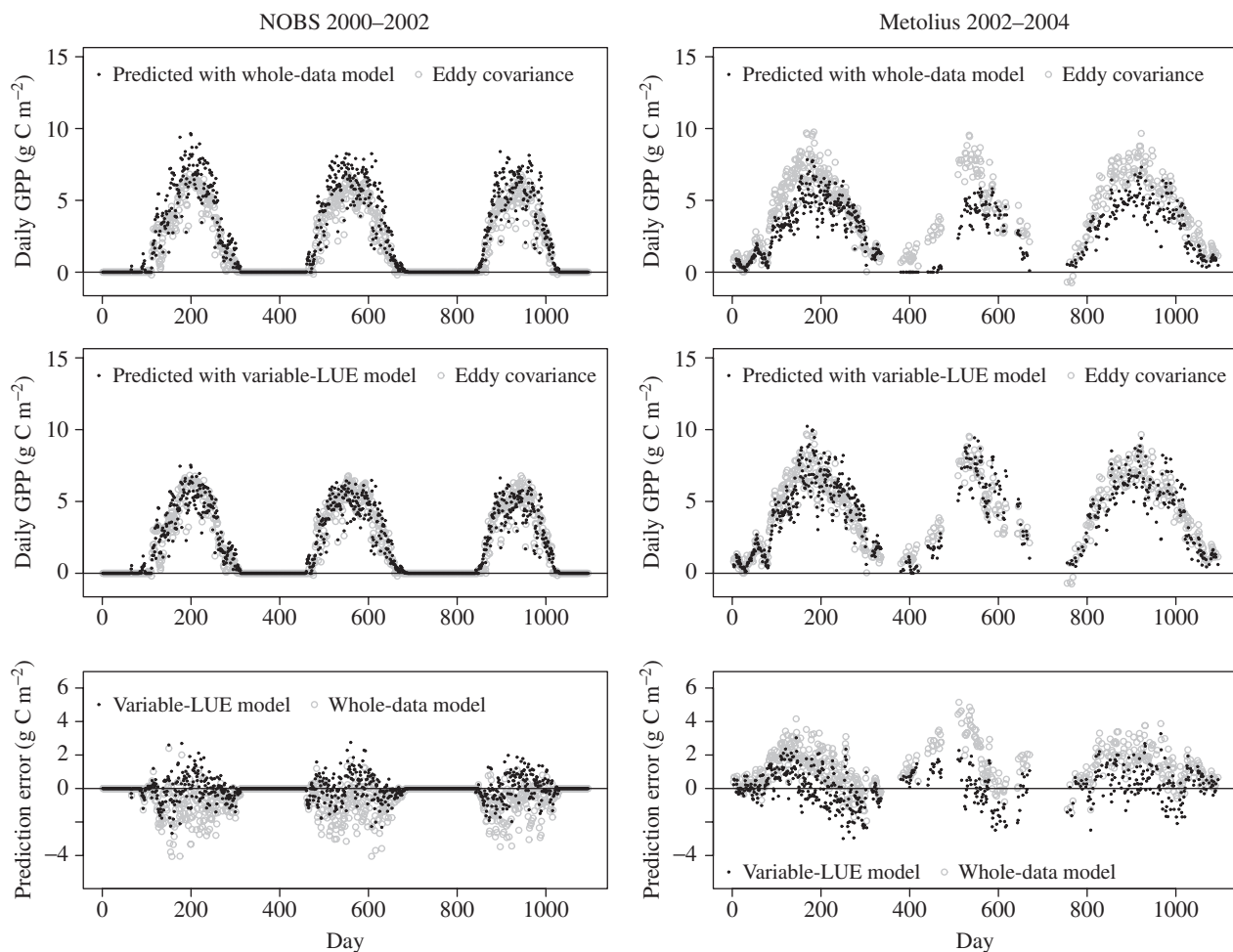


Fig. 7 Daily GPP predictions with the whole-data and the variable-LUE models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers against daily eddy covariance GPP in the two AmeriFlux test sites. LUE, light use efficiency; GPP, gross primary production; NOBS, Northern Old Black Spruce; VPD, vapour pressure deficit.

are only comparable if the same modifying factors are applied. In this study, the LUE estimates without SWC ($\beta \approx 1.9\text{--}3.1\text{ g C MJ}^{-1}$) were, as expected, lower than those obtained when SWC was included ($\beta \approx 2.5\text{--}5.2\text{ g C MJ}^{-1}$). The latter are similar to the range $4.2\text{--}5\text{ g C MJ}^{-1}$ reported for the overall maximum LUE (Russell *et al.*, 1989). Lagergren *et al.* (2005) observed a conversion efficiency of 0.9 g C MJ^{-1} for NPP at Norunda which, assuming about 50% respiratory costs (Waring *et al.*, 1998), is well comparable with the present 2.2 g C MJ^{-1} for GPP.

There was variation in GPP at each site between years that was not captured by the non-year-specific models (Fig. 4). Part of this may be due to interannual variation of leaf area which was not included in the model. In Bray, some trees and ground vegetation were removed in 2002, and the same year also suffered from severe drought (Duursma *et al.*, 2007). The Hyytiälä

(Vesala *et al.*, 2005) and Tharandt stands were thinned in 2002. Generally, leaf area varies between years because growth and leaf shedding do. Models including within-year leaf area dynamics, such as 3-PG and Forest-BGC, could predict such variations from the preceding weather conditions; however, the trade-off would be the need of more detailed input information.

Some variation not captured by the model may be due to systematic features in the EC measurements that can only be explained by factors not entering the photosynthesis model. These include the variation of footprint area of NEE with wind direction and turbulence regime (e.g. Rannik *et al.*, 2006), the temporal and spatial variation in the proportions in which trees vs. ground vegetation and soil contribute to NEE (e.g. Davidson *et al.*, 2006), and the error related to the estimation of TER from night-time measurements and

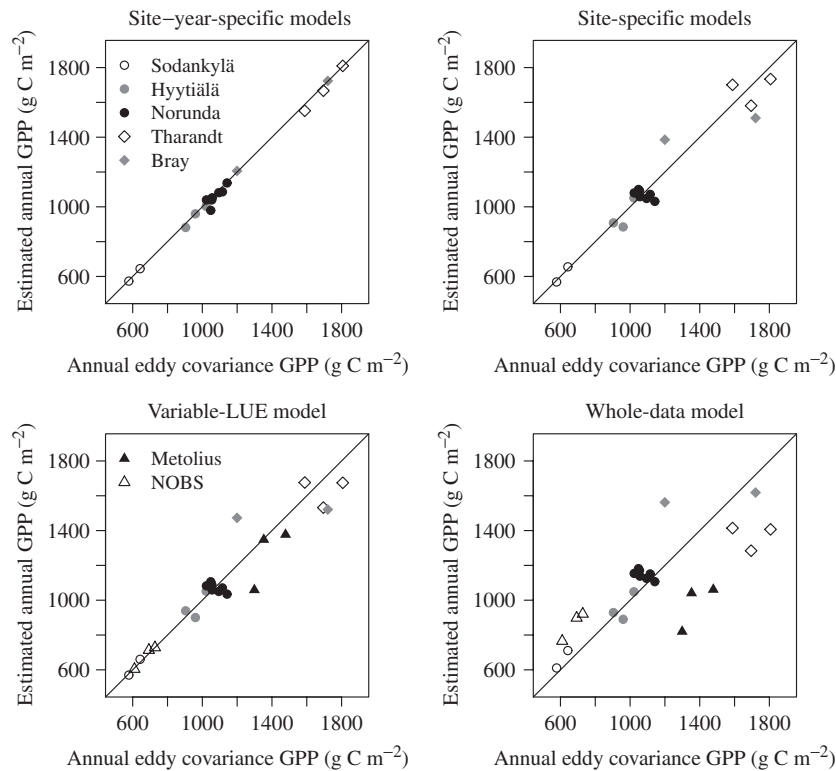


Fig. 8 Annual GPP estimated with the models containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers against annual eddy covariance GPP in the estimation and test sites. The lines indicate the one-to-one relationships. LUE, light use efficiency; GPP, gross primary production; NOBS, Northern Old Black Spruce; VPD, vapour pressure deficit.

soil organic layer or air temperature (Mäkelä *et al.*, 2006).

The form of the TER model, the environmental driving factors included in it and the way of estimating its parameters affect not just the absolute level but also the temporal patterns, the magnitude of variation and the apparent behaviour of TER and GPP with respect to the driving factors. Whenever available, we used soil organic layer temperature as the explanatory variable. Mechanistically, it should explain TER better than air temperature, because a large part of forest respiratory CO_2 emanates from soil surface; soil, stem and shoot chamber data from Hyytiälä also support this approach. The processes controlling night-time and daytime respiration differ from each other and change in time; consequently, the actual short-term temperature response of TER may be different from the long-term response estimated from night-time NEE (Reichstein *et al.*, 2005). However, the short-term response is difficult to determine accurately from EC data, as in the time scale of days or weeks the random noise in EC fluxes is large compared with the range of temperature. Also, water stress affects respiration, which calls for soil moisture as a driving factor in the TER model in the sites subject to drought.

We think that the temperature dependence of GPP in our models is real and not an artefact caused by TER estimation. Soil organic layer temperature varies diurnally and annually less than air temperature, and hence its use in TER estimation is unlikely to cause a seeming dependence between GPP and air temperature. Using air temperature tends to exaggerate the amplitude of diurnal variation in TER: GPP estimated with air temperature can be up to 20% higher than GPP estimated without any temperature dependence (assuming daytime TER simply equal to night-time TER; Mäkelä *et al.*, 2006). Even in the worst case, at least 80% of the observed GPP-temperature relationship is real. Seasonal variation in GPP is much larger than what extrapolating daytime TER from air temperature can introduce.

It was against our expectation that soil water did not become significant in the model. The model without SWC described a large proportion of variation in GPP in Bray and Metolius which are usually characterized as water limited (Berbigier *et al.*, 2001; Schwarz *et al.*, 2004). Part of the soil water effect was probably embedded in VPD, as drought periods tend to be accompanied by high VPD. Landsberg & Waring (1997) suggested that VPD and soil water be alternative, not simultaneous

limiting factors. Both Bray and Metolius had relatively low leaf areas, probably an acclimation to recurring droughts. The drought effect could, therefore, have been explained implicitly through a combination of VPD and leaf area. On the other hand, these sites did manifest the largest relative prediction errors (Fig. 4), suggesting that drought may play a role not foreseen by the model.

The detection of drought was difficult in the data set because SWC measurements were relatively sparse. Secondly, SWC has substantial spatial variation, so measurements taken in a few spots may not reflect the whole footprint area. Thirdly, the 0–30 cm soil layer may not fully reflect water availability throughout the rooting depth (cf. Schwarz *et al.*, 2004). Furthermore, trees may actually respond to soil water potential rather than REW. Physiological research suggests that conifers react with abrupt stomatal closure when soil water potential reaches a threshold value (Duursma *et al.*, 2007). This threshold is difficult to estimate from data with large uncertainties.

In this study, a statistical approach was chosen to determine the parameter values of a physiologically meaningful model. Although the parameters have a phenomenological interpretation, this approach does not provide information about the 'true' magnitude of the parameters, and the values can only be compared among models with exactly the same structure. This was clearly demonstrated in this study by the fact that the parameter values varied between the different model formulations and that the parameters were strongly correlated with each other. These correlations reflect the interdependence between PAR and the driving variables in the modifiers. Thus, adding a new modifier affects the estimability and parameter estimates of the other modifiers.

Although the individual parameter estimates cannot be interpreted as 'true' values, the full model may still accurately represent the response of GPP to the combination of driving variables. In this sense, the result may be more reliable than in models where the response has been carefully identified for each factor at a time, as small errors in parameter estimates may lead to larger errors in the prediction when combined with other model components. The combined model will then need to be calibrated, as is the case with many physiologically based models (Law *et al.*, 2000; Kramer *et al.*, 2002).

This study has shown that the day-to-day variation of GPP over a wide geographical range of temperate and boreal coniferous forests can be rather generally explained by the variation in absorbed PAR, temperature acclimation and VPD. The absorbed PAR is a function of total PAR and LAI, possibly modified to some extent by

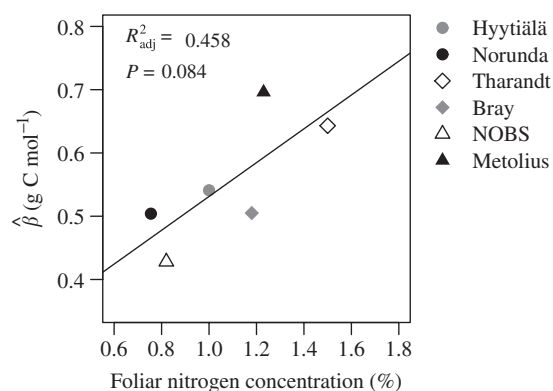


Fig. 9 Estimates of the site-specific β in the variable-LUE model containing light [f_L ; Eqn (2)], temperature [f_S ; Eqn (4)] and VPD [f_D ; Eqn (5)] modifiers against foliar nitrogen concentration in the six sites where the nitrogen information was available (Hyttiälä: Palmroth & Hari, 2001; Tharandt: Ngo *et al.*, 2001; Bray: Porté & Loustau, 1998; NOBS: Middleton *et al.*, 1997; Metolius: Pierce *et al.*, 1994; Running, 1994; Law *et al.*, 2000; for Norunda, the value was measured by Fredrik Lagergren). The solid line is the linear regression fitted to the points. The P value refers to the F test of the null hypothesis that the regression coefficient is zero. LUE, light use efficiency; NOBS, Northern Old Black Spruce; VPD, vapour pressure deficit.

stand structure (Duursma & Mäkelä, 2007). However, after accounting for these three modifying factors, some site-specific variation remains in the potential LUE. For practical applications of the approach, this variation could relatively easily be calibrated if EC data were available. Understanding the causal factors underlying this between-sites variation remains a topic of further study. More systematic data on soil water and foliar nitrogen could prove enlightening in this respect.

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References

- Ågren GI (1996) Nitrogen productivity or photosynthesis minus respiration to calculate plant growth. *Oikos*, **76**, 529–535.

- Aurela M (2005) Carbon dioxide exchange in subarctic ecosystems measured by a micrometeorological technique. PhD thesis. Finnish Meteorological Institute Contributions, 51, 39p. (<http://ethesis.helsinki.fi/julkaisut/mat/fysik/vk/aurela/>).
- Bates DM, Watts DG (1988) *Nonlinear regression analysis and its applications*. John Wiley & Sons, New York.
- Berbigier P, Bonnefond JM, Mellman P (2001) CO₂ and water vapour fluxes for 2 years above Euroflux forest site. *Agricultural and Forest Meteorology*, **108**, 183–197.
- Bergh J, McMurtrie RE, Linder S (1998) Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *Forest Ecology and Management*, **110**, 127–139.
- Dang QL, Margolis HA, Sy M, Coyea MR, Collatz GJ, Walthall CL (1997) Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: implications for scaling from leaf to canopy. *Journal of Geophysical Research*, **102**, 28845–28859.
- 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 temperate forest. *Global Change Biology*, **12**, 230–239.
- Delzon S, Sartore M, Burlett R, Dewar R, Loustau D (2004) Hydraulic responses to height growth in maritime pine trees. *Plant, Cell and Environment*, **27**, 1077–1087.
- Dunn AL, Barford CC, Wofsy SC, Goulden ML, Daube BC (2007) A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends. *Global Change Biology*, **13**, 577–590.
- Duursma R, Mäkelä A (2007) Summary models for light interception and light-use efficiency of non-homogeneous canopies. *Tree Physiology*, **27**, 859–870.
- Duursma RA, Kolari P, Perämäki M *et al.* (2007) Constant minimum leaf water potential assumption is successful in predicting the decline of maximum transpiration rate with drying soil. *Tree Physiology* (in review).
- Falge E, Baldocchi D, Olson RJ *et al.* (2001) Gap filling strategies for defensible annual sum of net ecosystem exchange. *Agricultural and Forest Meteorology*, **107**, 43–69.
- Farquhar GD, von Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In: *Physiological Plant Ecology. II. Water Relations and Carbon Assimilation. Encyclopaedia of Plant Physiology 12B* (eds Lange OL, Nobel PS, Osmond CB, Ziegler H), pp. 159–174. Springer Verlag, Berlin.
- Gower ST, Vogel JG, Norman JM, Kucharik CJ, Steele SJ, Stow TK (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research*, **102**, 29029–29041.
- Grünwald T (2003) Langfristige Beobachtungen von Kohlendioxidflüssen mittels Eddy-Kovarianz-Technik über einem Altfichtenbestand im Tharandter Wald. PhD thesis. Dresden University of Technology, Dresden, Germany (in German).
- Iivesniemi H, Liu C (2001) Biomass distribution in a young Scots pine stand. *Boreal Environment Research*, **6**, 3–8.
- Kennedy RE, Turner DP, Cohen WB, Guzy M (2006) A method to efficiently apply a biogeochemical model to a landscape. *Landscape Ecology*, **21**, 213–224.
- Kramer K, Leinonen I, Bartelink HH *et al.* (2002) Evaluation of six process-based forest growth models using eddy-covariance measurements of CO₂ and H₂O fluxes at six forest sites in Europe. *Global Change Biology*, **8**, 213–230.
- Lagergren F, Eklundh L, Lundblad M, Mölder M, Landkreijer H, Lindroth A (2005) Net primary production and light use efficiency in a mixed coniferous forest in Sweden. *Plant, Cell and Environment*, **28**, 412–423.
- Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.
- Law BE, Cescatti A, Baldocchi DD (2001a) Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange. *Tree Physiology*, **21**, 777–787.
- Law BE, Sun OJ, Campbell J, van Tuyl S, Thornton PE (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology*, **9**, 510–524.
- Law BE, Turner D, Lefsky M, Campbell J, Guzy M, Sun O, van Tuyl S, Cohen W (2006) Carbon fluxes across regions: observational constraints at multiple scales. In: *Scaling and Uncertainty Analysis in Ecology: Methods and Applications* (eds Wu J, Jones B, Li H, Loucks O), pp. 167–190. Springer, USA.
- Law BE, van Tuyl S, Cescatti A, Baldocchi DD (2001b) Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. *Agricultural and Forest Meteorology*, **108**, 1–14.
- Law BE, Waring RH, Anthoni PM, Aber JD (2000) Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology*, **6**, 155–168.
- Leuning R (1995) A critical-appraisal of a combined stomatal-photosynthesis model for C-3 plants. *Plant, Cell and Environment*, **18**, 339–355.
- Lundin LC, Halldin S, Lindroth A *et al.* (1999) Continuous long-term measurements of soil-plant-atmosphere variables at a forest site. *Agricultural and Forest Meteorology*, **98–99**, 53–73.
- Mäkelä A, Hari P, Berninger F, Hänninen H, Nikinmaa E (2004) Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. *Tree Physiology*, **24**, 369–376.
- Mäkelä A, Kolari P, Karimäki J, Nikinmaa E, Perämäki M, Hari P (2006) Modelling five years of weather-driven variation of GPP in a boreal forest. *Agricultural and Forest Meteorology*, **139**, 382–398.
- Mäkelä A, Landsberg J, Ek AR *et al.* (2000) Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology*, **20**, 289–298.
- Maselli F, Barbati A, Chiesi M, Chirici G, Corona P (2006) Use of remotely sensed and ancillary data for estimating forest gross primary productivity in Italy. *Remote Sensing of Environment*, **100**, 563–575.
- McMurtrie RE, Gholz HL, Linder S, Gower ST (1994) Climatic factors controlling the productivity of pine stands: a model-based analysis. *Ecological Bulletin (Copenhagen)*, **43**, 173–188.
- Medlyn B, Barrett D, Landsberg J, Sands P, Clement R (2003) Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology*, **30**, 153–169.

- Middleton EM, Sullivan JH, Bovard BD, DeLuca AJ, Chan SS, Cannon TA (1997) Seasonal variability in foliar characteristics and physiology for boreal forest species at the five Saskatchewan tower sites during the 1994 Boreal Ecosystem-Atmosphere study. *Journal of Geophysical Research*, **102**, 28831–28844.
- Ngo VT, Ringel C, Beer V, Wienhaus O (2001) Comparison of ascorbate, chlorophyll and starch contained in needles of Norway spruces (*Picea abies* [L.] Karst.) on sites exposed to various degrees of stress. *Forstwissenschaftliches Centralblatt*, **120**, 205–219.
- Palmroth S, Hari P (2001) Evaluation of the importance of acclimation of needle structure, photosynthesis, and respiration to available photosynthetically active radiation in a Scots pine canopy. *Canadian Journal of Forest Research*, **31**, 1235–1243.
- Pelkonen P, Hari P (1980) The dependence of the springtime recovery of CO₂ uptake in Scots pine on temperature and internal factors. *Flora*, **169**, 398–404.
- Pierce LL, Running SW, Walker J (1994) Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. *Ecological Applications*, **4**, 313–321.
- Porté A, Loustau D (1998) Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. *Tree Physiology*, **18**, 223–232.
- Rannik Ü, Kolari P, Vesala T, Hari P (2006) Uncertainties in measurement and modelling of net ecosystem exchange of a forest. *Agricultural and Forest Meteorology*, **138**, 244–257.
- 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.
- Running SW (1994) Testing Forest-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecological Applications*, **4**, 238–247.
- Running SW, Gower ST (1991) Forest-BGC, a general-model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*, **9**, 147–160.
- 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.
- Russell G, Jarvis PG, Monteith JL (1989) Absorption of radiation by canopies and stand growth. In: *Plant Canopies: Their Growth, Form and Function* (eds Russell G, Marshall B, Jarvis PG), pp. 21–39. Cambridge University Press, Cambridge.
- Schwarz PA, Law BE, Williams M, Irvine J, Kurpius M, Moore D (2004) Climatic versus biotic constraints on carbon and water fluxes in seasonally drought-affected ponderosa pine ecosystems. *Global Biogeochemical Cycles*, **18**, GB4007, doi: 10.1029/2004GB002234.
- Smith ML, Ollinger SV, Martin ME, Aber JD, Hallett RA, Goodale CL (2002) Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecological Applications*, **12**, 1286–1302.
- Still CJ, Randerson JT, Fung IY (2004) Large-scale plant light-use efficiency inferred from the seasonal cycle of atmospheric CO₂. *Global Change Biology*, **10**, 1240–1252.
- Suni T, Rinne J, Reissel A *et al.* (2003) Long-term measurements of surface fluxes above a Scots pine forest in Hyytiälä, southern Finland, 1996–2001. *Boreal Environment Research*, **4**, 287–301.
- Thornton PE, Law BE, Gholz HL *et al.* (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needle-leaf forests. *Agricultural and Forest Meteorology*, **113**, 185–222.
- Turner DP, Urbanski S, Bremer D, Wofsy SC, Meyers T, Gower ST, Gregory M (2003) A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biology*, **9**, 383–395.
- van Dijk AIJM, Dolman AJ, Schulze ED (2005) Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate European forests. *Global Biogeochemical Cycles*, **19**, GB2029, doi: 10.1029/2004GB002417.
- Vesala T, Suni T, Rannik Ü *et al.* (2005) Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochemical Cycles*, **19**, GB2001, doi: 10.1029/2004GB002316.
- Vickers D, Mahrt L, Law BE, Irvine J, Martin JG (2007) Net ecosystem exchange of carbon from a ponderosa pine ecosystem. *Agricultural and Forest Meteorology* (in review).
- Wang Q, Tenhunen J, Falge E, Bernhofer Ch, 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.
- Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forest: a constant fraction of primary production? *Tree Physiology*, **18**, 129–134.
- Xiao XM, Zhang QY, Hollinger D, Aber J, Moore B (2005) Modeling gross primary production of an evergreen needle-leaf forest using MODIS and climate data. *Ecological Applications*, **15**, 954–969.
- Yuan W, Liu S, Zhou G *et al.* (2007) Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. *Agricultural and Forest Meteorology*, **143**, 189–207.