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Improved light and temperature responses for light-use-efficiency-based GPP models

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Abstract. Gross primary production (GPP) is the process by which carbon enters ecosystems. Models based on the theory of light use efficiency (LUE) have emerged as an efficient method to estimate ecosystem GPP. However, problems have been noted when applying global parameterizations to biome-level applications. In particular, model–data comparisons of GPP have shown that models (including LUE models) have difficulty matching estimated GPP. This is significant as errors in simulated GPP may propagate through models (e.g. Earth system models). Clearly, unique biome-level characteristics must be accounted for if model accuracy is to be improved. We hypothesize that in boreal regions (which are strongly temperature controlled), accounting for temperature acclimation and non-linear light response of daily GPP will improve model performance.

To test this hypothesis, we have chosen four diagnostic models for comparison, namely an LUE model (linear in its light response) both with and without temperature acclimation and an LUE model and a big leaf model both with temperature acclimation and non-linear in their light response. All models include environmental modifiers for temperature and vapour pressure deficit (VPD). Initially, all models were calibrated against five eddy covariance (EC) sites within Russia for the years 2002–2005, for a total of 17 site years. Model evaluation was performed via 10-out cross-validation.

Cross-validation clearly demonstrates the improvement in model performance that temperature acclimation makes in modelling GPP at strongly temperature-controlled sites in Russia. These results would indicate that inclusion of temperature acclimation in models on sites experiencing cold temperatures is imperative. Additionally, the inclusion of a non-linear light response function is shown to further improve performance, particularly in less temperature-controlled sites.

1 Introduction

Terrestrial plants fix carbon dioxide (CO_2) as organic compounds through photosynthesis, a carbon flux also known at the ecosystem level as gross primary production (GPP) (Beer et al., 2010). A variety of methods have been developed to estimate ecosystem carbon fluxes. These include flux towers (e.g. Friend et al., 2007), carbon accounting techniques (e.g. Shvidenko and Nilsson, 2003), process-based vegetation models (e.g. Sitch et al., 2003), atmospheric measurements (e.g. Stephens et al., 2007) and diagnostic satellite-based techniques (e.g. Running et al., 2004), with each methodology having advantages and shortcomings. Satellite-based models in particular have been developed to monitor gross primary production – with the advantage that they can model the globe at high temporal frequency using remotely sensed products of fine resolution and may be calibrated against flux tower data. These models are generally based on the theory of light use efficiency (LUE), which states that a relatively constant relationship exists between photosynthetic carbon uptake (GPP) and absorbed photosynthetically

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active radiation (APAR) at the canopy level (Anderson et al., 2000; Sjoestroem et al., 2011).

Problems have however been noted with the LUE approach, particularly when applying global parameterizations to local applications (Pan et al., 2006; Turner et al., 2006; Shvidenko et al., 2010; McCallum et al., 2009). This is not surprising as temperature, radiation, and water interact to impose complex and varying limitations on vegetation activity and LUE in different parts of the world (Churkina and Running, 1998). A recent model–data comparison of GPP from 26 models (including LUE models) noted that none of the models matched estimated GPP within observed uncertainty (Schaefer et al., 2012). On average, models over-predicted GPP under dry conditions and for temperatures below 0 °C. This occurs for many reasons, including the following: (1) the majority of models have not been calibrated with flux tower data and hence can not replicate the detailed in situ estimates; (2) models generally operate at much coarser spatial resolution than flux tower measurements; and (3) models are designed to be generally applicable at the continental or global level, and thus often do not include certain biome-level specificities which may be captured in flux tower estimates.

The recent increasing availability of empirical canopy-level estimates of GPP from eddy covariance (EC) measuring stations (FLUXNET) is however making the calibration process more feasible (Mäkelä et al., 2008), potentially leading to improved models. We now have the ability both to create statistically fitted models (e.g. van Dijk et al., 2005; Jung et al., 2008) and to parameterize more general summary-type photosynthesis models. Several recent studies have demonstrated model calibration of summary-type LUE models at continental (Mäkelä et al., 2008; King et al., 2011) and global (Beer et al., 2010) scales.

The objective of this paper is to calibrate four GPP models (of increasing complexity) simultaneously across five Russian boreal EC stations and evaluate their performance. As Russia represents a large land mass that is strongly climate controlled with relatively few in situ measurements, such analysis can improve our ability to model GPP across the Eurasian continent. We hypothesize that accounting for temperature acclimation and to a lesser extent non-linear light response of daily GPP will largely improve model performance.

2 Methods

2.1 Study region

Russia comprises almost one fourth of the world's forest cover, making these boreal forests a unique natural phenomenon at the global scale. In addition vast areas are characterized by tundra ecosystems, dominated by shrubs, grasses and sedges, mostly above permafrost. Furthermore, significant agricultural and grassland areas occur outside of permafrost regions. This large land area undergoes great annual changes in albedo and productivity as seasonal temperatures swing well above and below 0 °C. Large regions lie in various stages of permafrost and the area is prone to catastrophic disturbance in the form of fire (Goldammer, 1996; Kajii et al., 2002; Balzter et al., 2005). Furthermore, the climate of both the boreal forests and the tundra ecosystems in eastern Siberia can resemble that of a boreal/arctic desert during long periods of the growing season (Vygodskaya et al., 1997).

2.2 Model description

Four diagnostic models were chosen for comparison in this study, namely (1) the LUE approach parameterized according to Running (2000), (2) the LUE approach parameterized according to Mäkelä et al. (2008) but without a light modifier, (3) the LUE approach parameterized according to Mäkelä et al. (2008) with a light modifier and (4) a non-rectangular hyperbola (big leaf) model (e.g. Hirose and Werger, 1987; Hirose et al., 1997). All parameters are listed in Table 1. The LUE models follow the standard approach, each including two environmental modifiers for temperature and vapour pressure deficit (VPD), and in the third instance a non-linear light modifier. The big leaf (BL) model also includes two environmental modifiers for temperature and VPD, and is inherently non-linear in its light response. Initially, all models are calibrated against five EC sites within Russia for the years 2002–2005. Model evaluation is performed via 10-out cross-validation.

2.2.1 Light use efficiency (LUE)

The basic LUE approach is as follows:

$$\mathrm{GPP} = \mathrm{PAR}\ f_{\mathrm{APAR}}\ \mathrm{LUE}\ f_1(T)\ f_2(\mathrm{VPD}), \tag{1}$$

where GPP represents daily gross primary productivity ($\mathrm{g\,C\,m^{-2}}$), PAR is photosynthetic active radiation ($\mathrm{MJ\,m^{-2}}$), f_{APAR} is the fraction of absorbed PAR and LUE is the potential LUE in terms of GPP ($\mathrm{g\,C\,MJ^{-1}}$). Potential LUE is the maximum LUE attainable on a site without environmental constraints. Potential LUE is reduced to actual LUE via the environmental scalars for daily minimum temperature $f_1(T)$ and daily vapour pressure deficit $f_2(\mathrm{VPD})$, both of which are defined as linear ramp functions [0,1] as per Running (2000). $f_1(T)$ is 0 when daily minimum temperature (°C) is less than or equal to $T\mathrm{min}_{\mathrm{min}}$ (°C) and increases linearly to 1 at temperature $T\mathrm{min}_{\mathrm{max}}$ (°C). As a global generalization, the algorithm truncates GPP on days when the minimum temperature is below −8 °C (Running et al., 2004); however in our study, this value was optimized for each site year. $f_2(\mathrm{VPD})$ has a value of 1 when VPD is less than or equal to $\mathrm{VPD}_{\mathrm{min}}$ (Pa) and declines linearly to 0 as VPD increases to $\mathrm{VPD}_{\mathrm{max}}$ (Pa) (Running, 2000).

Table 1. Parameters required for LUE, LUE-TA, LUE-TAL and BL models.

Symbol	Description	Unit	Model	Parameter Values		Increment	Reference
				Min	Max		
$T\,\mathrm{min}_{\mathrm{min}}$	Minimum temperature: minimum	°C	LUE	−11	−2	2	King et al. (2011)
$T\,\mathrm{min}_{\mathrm{max}}$	Minimum temperature: maximum	°C	LUE	4	13	2	King et al. (2011)
V_{min}	Minimum VPD	Pa	LUE	0	2500	500	King et al. (2011)
V_{max}	Maximum VPD	Pa	LUE	1500	4500	500	King et al. (2011)
LUE	Light use efficiency (Maximum)	$\mathrm{g\,C\,MJ^{-1}}$	LUE, LUE-TA, LUE-TAL	0.5	4	0.1	King et al. (2011)
S_{max}	Saturating level	°C	LUE-TA, LUE-TAL, BL	15	30	3	Mäkelä et al. (2008)
t	Time constant	days	LUE-TA, LUE-TAL, BL	1	22	3	Mäkelä et al. (2008)
X_0	Threshold value	°C	LUE-TA, LUE-TAL, BL	−10	5	3	Mäkelä et al. (2008)
K	VPD	$\mathrm{kPa^{-1}}$	LUE-TA, LUE-TAL, BL	−0.1	−0.9	−0.2	Landsberg and Waring (1997)
γ	Light	$\mathrm{m^2\,mol^{-1}}$	LUE-TAL	0	0.12	0.03	Mäkelä et al. (2008)
A_{max}	Light saturated photosynthesis	$\mathrm{umol\,CO_2\,m^{-2}\,s^{-1}}$	BL	0	40	2	Ruimy et al. (1996)
θ	Convexity of leaf photosynthesis	–	BL	0.8		–	Hirose et al. (1997)
ϕ	Photosynthetic quantum efficiency	$\mathrm{ug\,C\,J^{-1}}$	BL	2.73		–	Wong et al. (1979)
h	Day length	$\mathrm{h\,d^{-1}}$	BL	12		–	Estimated

2.2.2 Light use efficiency – temperature acclimation (LUE-TA)

The basic LUE approach (Eq. 1) was again employed; however both $f_1(T)$ and $f_2(\mathrm{VPD})$ were parameterized differently. The effect of temperature on daily GPP was modelled using the concept of acclimation S_k (°), a piecewise linear function of X_k (°) calculated from the mean daily ambient temperature T_k (°), using a first-order dynamic delay model:

$$X_k = X_{k-1} + \frac{1}{t}\left(T_k - X_{k-1}\right), \quad X_1 = T_1, \tag{2}$$

$$S_k = \max\left\{X_k - X_0, 0\right\}, \tag{3}$$

where t (days) is the time constant of the delay process and X_0 (°C) is a threshold value of the delayed temperature (Mäkelä et al., 2008). The modifying function $f_1(T)$ is defined here as (Mäkelä et al., 2008)

$$f_1(T) = \min\left\{\frac{S_k}{S_{\mathrm{max}}}, 1\right\}, \tag{4}$$

where the empirical parameter S_{max} (°C) determines the value of S_k (°C) at which the temperature modifier attains its saturating level. The effect of VPD f_2 (VPD) was estimated according to Landsberg and Waring (1997):

$$f_2(\mathrm{VPD}) = e^{KD}, \tag{5}$$

where K is an empirical parameter (see Table 1) assuming typically negative values and D (kPa) is vapour pressure deficit.

2.2.3 Light use efficiency – temperature acclimation and light (LUE-TAL)

Again the basic LUE approach (Eq. 1) was used, parameterized according to LUE-TA. In addition, to account for non-linearity in the photosynthetic response to APAR, a light modifier $f_3(L)$ was defined to yield the rectangular hyperbola light response function when multiplied with the linear response included in the LUE-TA model (Mäkelä et al., 2008):

$$f_3(L) = \frac{1}{\gamma\,\mathrm{APAR} + 1}, \tag{6}$$

where γ ($\mathrm{m^2\,mol^{-1}}$) is an empirical parameter (see Table 1) defined according to Mäkelä et al. (2008). Because this light response function does not vary with environmental modifiers, it differs from the non-rectangular BL model (described below), in which the light response interacts (changes shape) with the environmental modifiers.

2.2.4 Non-rectangular hyperbola/big leaf (BL)

Leaf photosynthesis is described with the non-rectangular hyperbola model (Hirose and Werger, 1987; Hirose et al., 1997). Leaf level photosynthesis is up-scaled to daily canopy photosynthesis by integration over the canopy (Franklin, 2007) using canopy f_{APAR} to determine the amount of absorbed incoming radiation. Daily gross primary production GPP is thus defined here according to

$$\mathrm{GPP} = \frac{h}{2\theta}\Big[\phi I_{\mathrm{a}} + E_{\mathrm{a}} A_{\mathrm{max}} - \sqrt{\left(\phi I_{\mathrm{a}} + E_{\mathrm{a}} A_{\mathrm{max}}\right)^2 - 4\phi I_{\mathrm{a}} E_{\mathrm{a}} A_{\mathrm{max}}\theta}\Big], \tag{7}$$

where

$$E_{\mathrm{a}} = f_1(T)\, f_2(\mathrm{VPD}), \tag{8}$$

h is day length; θ convexity of leaf photosynthesis; Ø quantum efficiency; I_{a} absorbed photosynthetically active radiation; E_{a} environmental modifier for temperature $f_1(T)$ and

VPD f_2(VPD); and A_{max} light-saturated canopy photosynthesis. The effect of temperature $f_1(T)$ on daily A_{max} was modelled using the concept of state of acclimation (Mäkelä et al., 2008); i.e. it acclimates dynamically to temperature with a time delay. The effect of VPD $f_2(D)$ on A_{max} was estimated according to Landsberg and Waring (1997).

2.3 Eddy covariance, meteorological and satellite data

Eddy covariance data for model calibration was obtained from http://www.fluxdata.org for five sites (Table 2, Fig. 1). The eddy covariance method, a micrometeorological technique, provides a direct measure of the net exchange of carbon and water between vegetated canopies and the atmosphere (Baldocchi et al., 2001). Although flux tower data represent point measurements with a maximum footprint of 1 km^2 (dependent upon whether sensor height was selected to observe such a dimension), they can be used to validate models and to spatialize biospheric fluxes at regional and continental scales (Papale and Valentini, 2003). In reality however, the footprint is highly dynamic in space and time depending on friction velocity, sensible heat flux, temperature, and wind direction.

The Cherskii (RU-Che) tower was situated in an arctic wet tundra ecosystem in the far east of Russia. The site was characterized by late thawing of permafrost soils in June and periodic spring floods with a stagnant water table below the grass canopy (Merbold et al., 2009). The climate is continental with average daily temperature in the warmest months of 13 °C (maximum temperature at midday: 28 °C by the end of July), dry air (maximum VPD at midday: 28 hPa) and low rainfall of 50 mm during summer (July–September) (Corradi et al., 2005). The Chokurdakh (RU-Cho) tower is located on a tundra ecosystem in the far east of Russia, underlain by continuous permafrost. It is characterized by a continental climate, which is reflected in low winter soil temperatures (−14 °C) and short, relatively warm summers, stimulating high photosynthesis rates (van der Molen et al., 2007). The Fyoderovskoe (RU-Fyo) tower is located in a 150 yr old European Russia spruce forest, with no permafrost. In general, air temperatures increase from March until June, remaining relatively warm up until late September, after which a rapid decline occurs. Air temperatures is typically below 0 °C between November and March (Milyukova et al., 2002). The Hakasia (RU-Ha1) tower is located in a natural steppe ecosystem in southern Siberia (Marchesini et al., 2007). The climate at the site is semi-arid cool, continental, with an annual mean temperature of 0.4 °C and annual precipitation of 304 mm. The steppe was managed as a pasture until 2001, but with low grazing pressure. The Zotino (RU-Zot) tower is located in a 200 yr old pine forest in central Siberia, without permafrost though experiencing heavy snowfall in winter ($>$ 1 m). The long-term average length of the growing season is 132 days, lasting from approximately early May to late September (Tchebakova et al., 2002). Permission was not obtained to include further sites in this study.

GPP data are commonly derived by flux-partitioning methods due to the fact that eddy covariance fluxes are only capable of measuring the net ecosystem exchange (NEE) of carbon dioxide and water vapour amongst other trace gases. NEE, a combination of the two counteracting processes, ecosystem respiration (R_{eco}) and GPP, is commonly separated by applying statistical flux-partitioning methods (e.g. Falge et al., 2001; Reichstein et al., 2005; Moffat et al., 2007; Stoy et al., 2006) in order to fill data gaps in NEE. A study comparing 23 gap-filling methods for a ten-year record of NEE data revealed a good agreement among the different methods with a variation of about 10 % when comparing annual flux values (Desai et al., 2008). Furthermore, the choice of the driving variables to model R_{eco}, e.g. air temperature or soil temperature, may be of importance (Lasslop et al., 2012). To date there has been no agreement on a general method to partition CO_2 fluxes. Therefore we chose the available data products from the FLUXNET synthesis database including gap-filled and flux-partitioned daily data for all sites used in this study. Gap filling and flux partitioning are based on the procedures given by Papale et al. (2006) and Reichstein et al. (2005).

Daily GPP (g C m^{-2} d^{-1}) from each site was selected with a quality flag = 1 (i.e. highest quality). This resulted in variable amounts of data being available for calibration for each site year. Additionally, the following meteorological data recorded at each site were used: mean air temperature (°C), minimum air temperature (°C), vapour pressure deficit (kPa) and global radiation (MJ m^{-2} d^{-1}). PAR was set to half of global radiation (Stanhill and Fuchs, 1977). Finally, f_{APAR} was retrieved from http://fapar.jrc.ec.europa.eu/ (Gobron et al., 2006).

2.4 Parameter optimization

Each model was estimated separately for each site and year. Parameters were optimized by means of a search on a coarse grid (see Table 1 for parameter ranges and increments). Model diagnostics were based on the regression of EC tower based GPP against modelled GPP. The minimum residual sum of squares (RSS) has been used as the calibration criteria. Fit was further appraised using both the coefficient of determination (r^2) and root mean square error (RMSE).

All possible combinations of parameters were tested. The initial parameter range and increment was conceived by consulting the existing literature (see Table 1 for references). The step width is the increment listed in Table 1. We generally applied a rather coarse increment as RMSE has been found to be generally insensitive to the parameters close to the optimum (King et al., 2011) and use of a finer increment greatly increased computing time.

Table 2. A description of the five flux towers used in this study.

Site Name	Location (°)	Tower Height (m)	Data Years Used	Dominant Land Cover	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)	Tower References
Cherskii (RU-Che)	68.61° N 161.34° E	5.3	2002–2004	Tundra-grass	−12.5	200–215	Merbold et al. (2009), Corradi et al. (2005)
Chokurdakh (RU-Cho)	70.61° N 147.89° E	4.7	2003–2004	Tundra-grass	−10.5	212	van der Molen et al. (2007)
Fyodorovskoe (RU-Fyo)	56.46° N 32.92° E	31.0	2003–2004	Evergreen needle-leaf spruce forest	3.7	584.3	Milyukova et al. (2002)
Hakasia (RU-Ha1)	54.72° N 90.00° E	4.5	2002–2004	Steppe	0.4	304	Marchesini et al. (2007)
Zotino (RU-Zot)	60.80° N 89.35° E	27.0	2002–2004	Evergreen needle-leaf pine forest	−1.5	593	Tchebakova et al. (2002), Arneth et al. (2002)

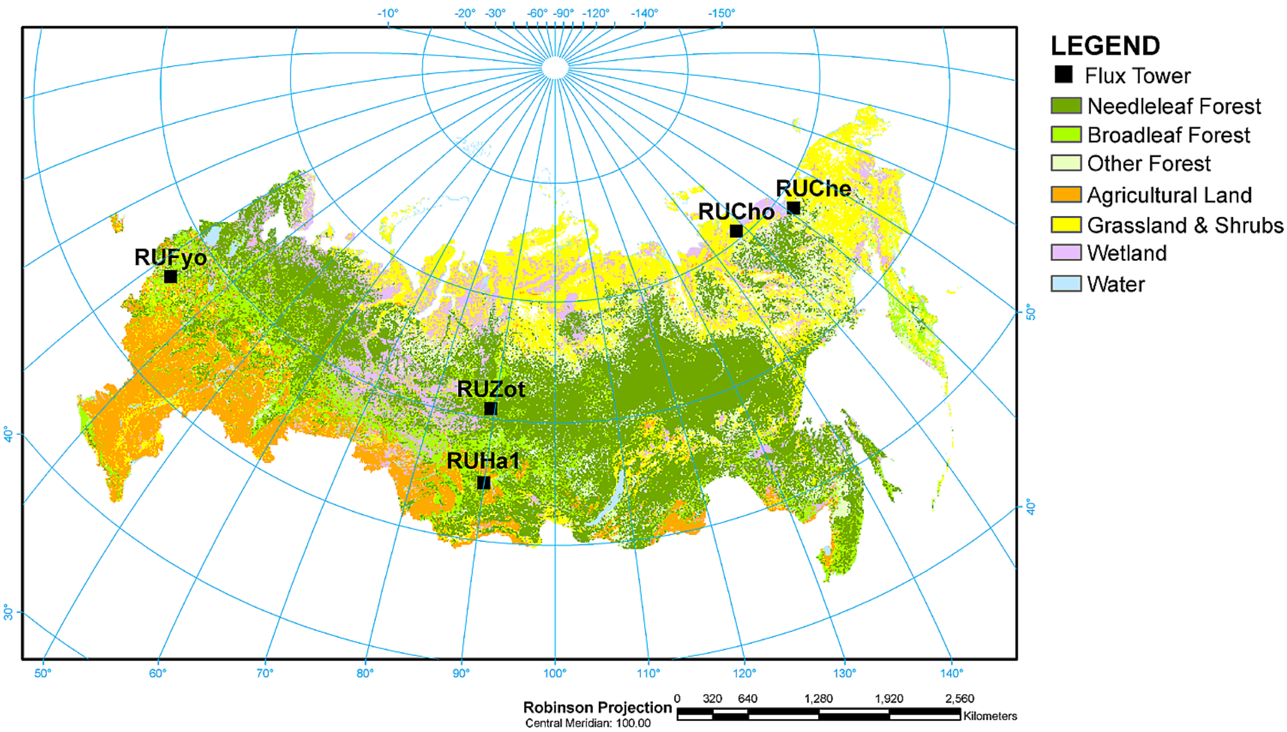

Fig. 1. Map of dominant Russian land cover (Schepaschenko et al., 2011), along with locations of the flux towers used in this study.

2.5 Cross-validation

Evaluation of the performance of the models used in this study utilized 10-out cross-validation. Cross-validation is a widely used method for estimating prediction error. It allows comparison of completely different models and is independent of the number of parameters and possible correlation between them as well as of the distributional assumptions (Hastie et al., 2001). Furthermore cross-validation was selected as we are actually interested in predictive power more than explanatory power. Cross-validation implicitly takes parsimony into consideration: although a higher number of parameters might mean a better fit, it does not necessarily mean better prediction due to resulting volatility of the estimates. Various methods exist for model selection (Forster, 2000), with cross-validation and AIC being noted as asymptotically equivalent (Stone, 1977).

For each site, measured GPP values were dropped (consecutively) ten at a time, while the remaining values were used to estimate the parameters. The estimated parameter values were then used to predict GPP of the dropped data points (i.e. those not used in the parameter estimation). The differences between these predictions (of the dropped data points) and the measured data were used to calculate the mean square

Table 3. Resulting optimized model parameters and regression diagnostics for the LUE model by site and year.

Site	Year	Optimized Parameters					Diagnostics		
		LUE ($g\,C\,MJ^{-1}$)	$T\min_{min}$ (°C)	$T\min_{max}$ (°C)	V_{min} (Pa)	V_{max} (Pa)	r^2	RMSE ($g\,C\,m^{-2}\,d^{-1}$)	n
RU-Che	2002	2	−10	4	0	3500	0.91	0.44	53
	2003	1.7	−6	12	0	3000	0.42	1.2	82
	2004	1.4	−2	4	0	2000	0.55	0.91	105
	2005	1.7	−2	10	0	2500	0.37	0.91	21
RU-Cho	2003	0.9	−6	4	1000	1500	0.48	1.2	117
	2004	1.2	−10	4	1000	1500	0.62	0.61	64
	2005	1	−10	4	1000	1500	0.4	0.48	58
RU-Fyo	2002	1.9	−10	12	0	3000	0.72	1.6	125
	2003	2.8	-8	6	0	2000	0.76	1.6	183
	2004	2.3	-10	8	0	2000	0.82	1.4	217
	2005	3.1	-10	10	0	1500	0.88	1.5	196
RU-Ha1	2002	1.3	−10	4	0	2000	0.81	0.59	106
	2003	1.3	−10	6	0	2500	0.73	0.65	148
	2004	1.5	−10	12	0	3000	0.91	0.69	182
RU-Zot	2002	1.7	−6	12	0	3500	0.79	1	98
	2003	2.1	−10	4	0	2500	0.64	0.87	62
	2004	1.9	−6	8	0	4000	0.83	0.95	91

error (MSE), which was used to evaluate the model's ability to predict GPP, averaged for all data. The leave-10-out cross-validation was performed a similar amount of times for each model for every site year.

3 Results and discussion

Model calibration resulted in a set of optimized parameters for the four approaches compared in this study, namely LUE, LUE-TA, LUE-TAL and BL (Tables 3, 4, 5 and 6, respectively). The LUE model (Table 3) showed clear discrepancies in obtaining a good fit, obtaining generally low coefficients of determination and high RMSE values at both the Cherskii (except in 2002) and Chokurdakh sites. This is in part due to the low values of $T\min_{min}$ selected during optimization, which allowed the model to record positive values of the temperature scalar early in the season. For the more southern sites, however, the LUE model generally performed as well as the other models, with similar RMSE values. The LUE-TA model (accounting for temperature acclimation) clearly outperformed the LUE model at the two northern sites (RU-Che and RU-Cho) (Table 4), demonstrating the importance of accounting for temperature acclimation in the northern regions. At the remaining sites the models performed equally well. Both the LUE-TAL and BL models (Tables 5 and 6) generally achieved higher r^2 across all sites and years than the LUE and LUE-TA models, suggesting that the inclusion of a non-linear light response improved model performance.

In addition, scatterplots, annual flux and environmental scalars are presented for three sites, namely tundra (Cherskii), forest (Fyodorovskoe) and grassland (Hakasia), in Fig. 2–4, respectively, for the year 2003. For the Cherskii site, situated in the tundra, the LUE model performs poorly, in comparison with the LUE-TA, LUE-TAL and BL models (Fig. 2), as noted previously. Both the scatterplot and annual flux indicate that the LUE approach is not able to capture the daily measurements, while the LUE-TA, LUE-TAL and BL approaches are more successful. The environmental scalars used in the four approaches are notably different, with the LUE model scalars for temperature and VPD showing large variation over the year. In contrast, the scalars for the LUE-TA and in particular the BL approaches are smoother, with VPD showing negligible effect and temperature having a very strong effect. This is in contradiction to the clear response to VPD (but not to temperature) of half-hourly photosynthesis at the Cherskii site as noted by Merbold et al. (2009). In the case of the LUE-TAL model, the light scalar allows the temperature scalar to increase, while the VPD scalar remains largely non-limiting. Furthermore, the scatterplots in Fig. 2 (top row) imply that the LUE and BL models are the least biased. The LUE-TA and LUE-TAL models seem to have a clear problem with overestimation of low values of GPP.

For the Fyodorovskoe site (Fig. 3), situated in evergreen needleleaf forest, all models generally capture the seasonal GPP flux, with the LUE-TAL model performing marginally better. Here again, the environmental scalars are different

Table 4. Resulting optimized model parameters and regression diagnostics for the LUE-TA model by site and year.

Site	Year	Optimized Parameters					Diagnostics	
		S_{max} (°C)	t (days)	X_0 (°C)	K (kPa^{-1})	LUE ($g\,C\,MJ^{-1}$)	r^2	RMSE ($g\,C\,m^{-2}\,d^{-1}$)
RU-Che	2002	24	7	−10	−0.5	2.4	0.9	0.47
	2003	15	22	2	−0.3	2.4	0.87	0.57
	2004	15	22	−1	−0.5	2.5	0.87	0.5
	2005	15	1	2	−0.9	2.3	0.41	0.88
RU-Cho	2003	27	22	−1	−0.1	3.6	0.85	0.62
	2004	15	13	−10	−0.1	1.2	0.61	0.61
	2005	15	22	2	−0.1	3	0.56	0.41
RU-Fyo	2002	30	1	−7	−0.9	3.2	0.74	1.6
	2003	18	1	−7	−0.9	3.2	0.76	1.6
	2004	24	13	−10	−0.7	2.5	0.83	1.4
	2005	24	22	−10	−0.9	3.5	0.89	1.4
RU-Ha1	2002	15	16	−4	-0.9	1.5	0.8	0.6
	2003	15	16	−1	−0.9	1.8	0.78	0.59
	2004	15	10	−1	−0.5	1.5	0.92	0.64
RU-Zot	2002	15	19	−4	−0.5	2	0.86	0.82
	2003	15	1	−10	−0.7	2.3	0.62	0.89
	2004	15	10	−4	−0.3	1.9	0.84	0.92

Table 5. Resulting optimized model parameters and regression diagnostics for the LUE-TAL model by site and year.

Site	Year	Optimized Parameters						Diagnostics	
		S_{max} (°C)	t (days)	X_0 (°C)	K (kPa^{-1})	LUE ($g\,C\,MJ^{-1}$)	γ ($m^2\,mol^{-1}$)	r^2	RMSE ($g\,C\,m^{-2}\,d^{-1}$)
RU-Che	2002	21	4	−10	−0.3	3.1	0.09	0.93	0.39
	2003	15	19	2	−0.1	3.6	0.12	0.91	0.47
	2004	15	16	2	−0.5	3.7	0.06	0.88	0.47
	2005	15	1	2	−0.7	3.2	0.12	0.4	0.89
RU-Cho	2003	15	19	−1	−0.1	3.5	0.12	0.91	0.49
	2004	15	22	−7	−0.1	2.1	0.12	0.72	0.52
	2005	15	22	−1	−0.1	3.8	0.12	0.61	0.39
RU-Fyo	2002	30	1	−7	−0.7	3.7	0.03	0.73	1.6
	2003	18	22	−7	−0.5	4	0.06	0.79	1.5
	2004	21	22	−10	−0.1	4	0.12	0.87	1.2
	2005	24	10	−10	−0.3	4	0.06	0.92	1.2
RU-Ha1	2002	15	13	−4	−0.3	2.1	0.12	0.89	0.44
	2003	15	19	−1	−0.3	2.4	0.12	0.84	0.51
	2004	18	7	−1	−0.3	2.6	0.09	0.94	0.55
RU-Zot	2002	15	10	−1	−0.3	3.4	0.12	0.89	0.72
	2003	15	7	−4	−0.5	3.7	0.12	0.73	0.75
	2004	15	10	−4	−0.1	3.2	0.12	0.89	0.77

between the models. The temperature scalar for the LUE, LUE-TA and LUE-TAL models rapidly reach a non-limiting value, while in the BL model temperature is only briefly non-limiting late in the growing season. VPD has a similar but slightly stronger effect in the LUE and LUE-TA models as compared to the LUE-TAL and BL models. Additionally in Fig. 3, there appears to be consistent underestimation all over and for all models, which is also evidenced by fairly similar

Table 6. Resulting optimized model parameters and regression diagnostics for the BL model by site and year.

Site	Year	Optimized Parameters					Diagnostics	
		S_{max} (°C)	t (days)	X_0 (°C)	K (kPa^{-1})	A_{max} (μmol CO_2 $m^{-2}s^{-1}$)	r^2	RMSE ($g\,C\,m^{-2}\,d^{-1}$)
RU-Che	2002	18	1	−4	−0.5	18	0.91	0.46
	2003	18	10	5	−0.1	20	0.92	0.44
	2004	15	13	5	−0.3	20	0.8	0.6
	2005	21	1	5	−0.7	16	0.41	0.88
RU-Cho	2003	21	10	2	−0.1	22	0.93	0.42
	2004	15	1	−10	−0.1	8	0.8	0.44
	2005	30	19	−10	−0.1	14	0.57	0.41
RU-Fyo	2002	30	1	−4	−0.7	38	0.68	1.8
	2003	18	22	−4	−0.5	38	0.76	1.6
	2004	15	10	−1	−0.3	28	0.88	1.2
	2005	15	4	−1	−0.5	40	0.91	1.2
RU-Ha1	2002	27	1	−7	−0.1	8	0.87	0.48
	2003	21	10	5	−0.1	16	0.78	0.6
	2004	27	4	5	−0.1	26	0.9	0.69
RU-Zot	2002	15	7	2	-0.3	16	0.9	0.69
	2003	15	10	−1	−0.3	14	0.74	0.73
	2004	15	7	−1	−0.1	16	0.89	0.77

r^2 and RMSE values. In particular, it seems that all models underestimate the latter half of the growing season.

At the Hakasia site (Fig. 4), situated on the southern steppe, the LUE-TAL model appears to best capture the seasonal GPP flux. The environmental scalars again display large discrepancies among models. There appears a consistent overestimation for all models in the early stages of the growing season, most apparent in the LUE-TA, LUT-TAL and BL models. This is the only site among the five sites studied which is potentially water-limited. As none of the models account for possible water constraints (aside from VPD), it may be that results at this site would benefit from the addition of a water-related environmental scalar.

3.1 Model evaluation

Mean square error was used as an indicator of performance resulting from cross-validation where the smaller of the MSE values is preferred (Table 7). For the majority of site year combinations (with the exception of RU-Che 2004/2005 and RU-Fyo 2002), the MSE values for the LUE and LUE-TA models are larger than those of the LUE-TAL and BL models. Hence, based on the 10-out cross-validation performed here, the LUE-TAL and BL models, accounting for temperature acclimation and a non-linear light response, generally outperform the LUE and LUE-TA approaches. In particular, the LUE-TAL records a lower MSE in 8 of the 17 site year combinations, along with the lowest overall mean MSE. The

Table 7. Cross-validation results (MSE) from the LUE, LUE-TA, LUE-TAL and BL models for all site years, and mean results for each model. Bold indicates lowest recorded MSE values per site year and model.

Site	Year	LUE	LUE-TA	LUE-TAL	BL
RU-Che	2002	0.451	0.43	**0.24**	0.309
	2003	2.152	0.377	0.269	**0.211**
	2004	1.269	**0.43**	0.452	0.672
	2005	1.646	**1.62**	1.806	1.804
RU-Cho	2003	1.873	0.743	0.573	**0.493**
	2004	0.907	0.844	0.381	**0.295**
	2005	3.522	1.86	1.069	**0.903**
RU-Fyo	2002	**5.393**	5.544	6.944	5.869
	2003	4.013	4.506	**3.116**	3.827
	2004	2.87	2.44	**1.543**	1.796
	2005	3.207	2.491	**1.534**	1.886
RU-Ha1	2002	0.505	0.458	**0.223**	0.289
	2003	0.732	0.557	**0.313**	0.492
	2004	0.589	0.477	**0.462**	0.576
RU-Zot	2002	1.783	0.879	0.785	**0.782**
	2003	1.591	1.431	0.96	**0.836**
	2004	1.422	1.281	**0.802**	1.03
Mean		1.996	1.551	**1.263**	1.298

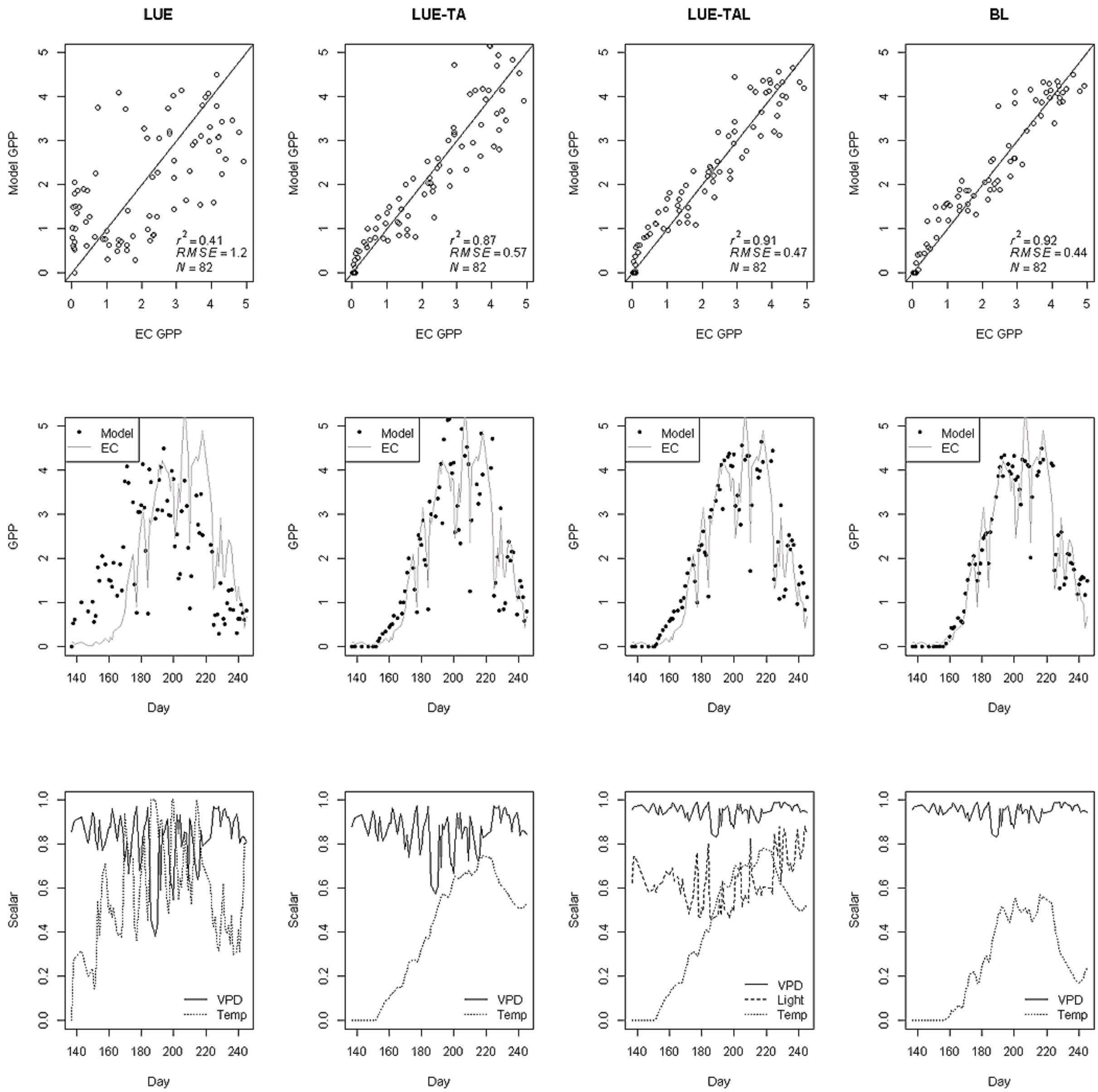

Fig. 2. Results for Cherskii, 2003, from the LUE (1st column), LUE-TA (2nd column), LUE-TAL (3rd column) and BL (4th column) models where the top row depicts scatterplots of eddy covariance (EC) GPP vs. model GPP, the middle row depicts the daily course of GPP (EC and model) and the bottom row depicts the environmental scalars for temperature and VPD. GPP in units of $\mathrm{g\,C\,m^{-2}\,d^{-1}}$.

BL model records the lowest MSE in 6 of the 17 site year combinations.

Based on this assessment, the LUE-TAL model appears to perform better in less environmentally stressful sites, while the BL model generally outperforms in more climate-controlled sites. On two occasions at the Cherskii site, the LUE-TA model outperforms the models with a non-linear light response, underscoring the effect of temperature at these locations.

The results of this study are novel in terms of the following:

1. The results compare the response of four diagnostic GPP models over Russia, clearly demonstrating the improvement that temperature acclimation makes when included in the models at strongly temperature-controlled high latitudes. Owing to the paucity of available flux tower data over Russia and its enormous size and unique biome characteristics, such a comparison is warranted.

2. The first of the non-linear models is actually the MODIS GPP algorithm. To our knowledge this is the first study to point to potential difficulties in

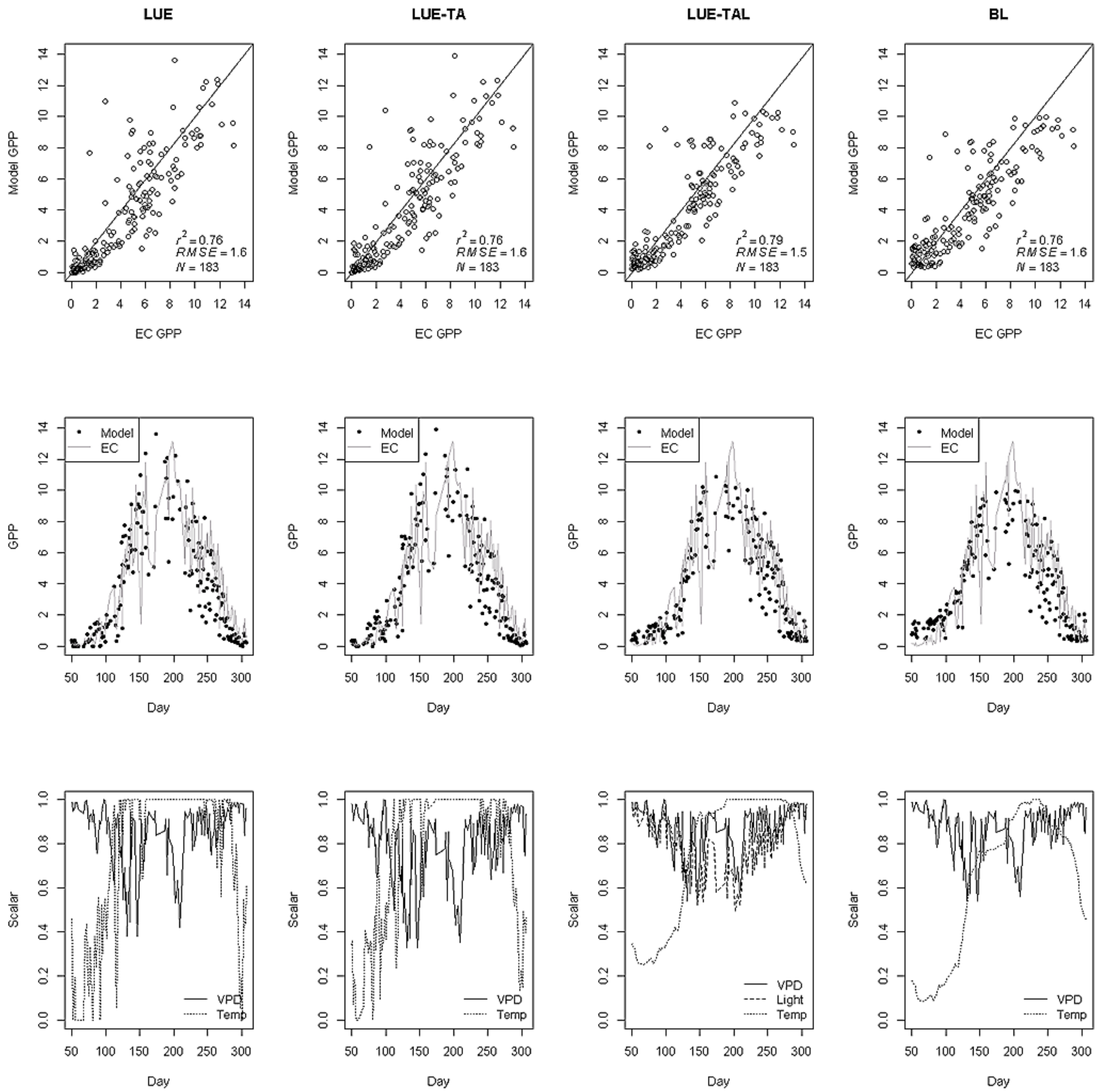

Fig. 3. Results for Fyodorovskoe, 2003, from the LUE (1st column), LUE-TA (2nd column), LUE-TAL (3rd column) and BL (4th column) models where the top row depicts scatter plots of EC GPP vs. model GPP, the middle row depicts the daily course of GPP (EC and model) and the bottom row depicts the environmental scalars for temperature and VPD. GPP in units of $\mathrm{g\,C\,m^{-2}\,d^{-1}}$.

the MODIS approach at flux tower sites in the far north, which could potentially be resolved by applying temperature acclimation. To date many studies have pointed to difficulties in comparing MODIS results with flux tower estimates; however they have largely identified problems with input data (f_{APAR}, meteo, etc) or a lack of a soil water modifier (Pan et al., 2006; Turner et al., 2006).

3. The model comparison includes the big leaf model, parameterized with modifiers for temperature acclimation and VPD. To our knowledge, our use of environmental modifiers in a big-leaf light absorption model is new.

4 Conclusions

In this study we present a comparison of four LUE-based GPP modelling approaches parameterized over five EC sites across Russia. This study focused on Russia, a vast country with large carbon pools and fluxes, properties unique to the northern hemisphere (i.e. permafrost which holds vast quantities of soil carbon; Tarnocai et al., 2009), and one predicted

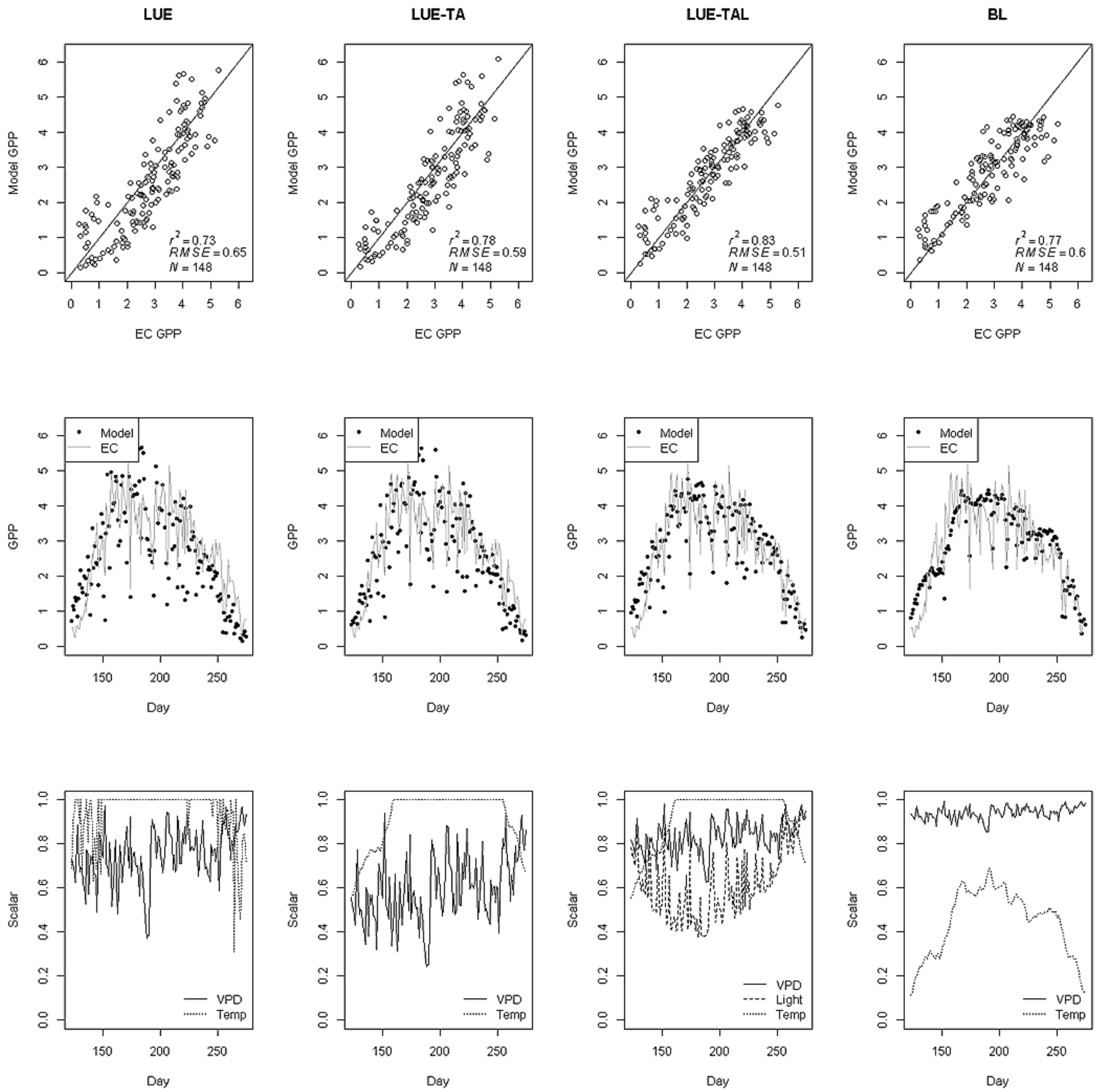

Fig. 4. Results for Hakasia, 2003, from the LUE (1st column), LUE-TA (2nd column), LUE-TAL (3rd column) and BL (4th column) models where the top row depicts scatter plots of EC GPP vs. model GPP, the middle row depicts the daily course of GPP (EC and model) and the bottom row depicts the environmental scalars for temperature and VPD. GPP in units of $\mathrm{g\,C\,m^{-2}\,d^{-1}}$.

to experience significant forms of environmental change. Various studies have pointed to difficulties when examining results from global diagnostic LUE models at the biome level (Pan et al., 2006; Turner et al., 2006; Shvidenko et al., 2010). The results presented here (using cross-validation) clearly demonstrate that accounting for temperature acclimation particularly at northern (temperature-controlled) sites significantly improves fit of modelled versus eddy-covariance-derived daily GPP values. These results indicate that inclusion of temperature acclimation on sites experiencing cold temperatures is imperative. Furthermore, models with a non-linear light response generally outperform models with a linear light response, increasingly so at the southern less temperature-controlled sites. Thus, developing models that address unique biome-level properties calibrated with EC data may help to improve the accuracy of global LUE-based models.

Findings from this study are important as vegetation productivity is a key input variable in many ecosystem models. These models require, among other datasets, an accurate depiction of vegetation productivity in order to address a variety of global land use issues. Hence, reducing uncertainty in gross primary productivity estimates is a key goal within the scientific community. Future efforts should focus on up-scaling the results presented here and in similar studies. In order to facilitate this, there is a need for a substantial expansion (by several orders of magnitude) of the ground-based observation network (Ciais et al., 2013). Finally, we think the findings from our study are useful for the modelling community in general, who are perhaps not entirely aware of the impacts that including (in particular) temperature acclimation may have on model results.

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