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Light use efficiency based GPP models

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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. Diagnostic models, based on the theory of light use efficiency (LUE) have emerged as one method to estimate ecosystem GPP. However, problems have been noted particularly when applying global results at regional levels. We hypothesize that accounting for non-linear light response and temperature acclimation of daily GPP in boreal regions 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 four eddy covariance sites within Russia for the years 2002–2004, for a total of 10 site years. Model evaluation was performed via 10-out cross-validation.

This study presents a methodology for comparing diagnostic modeling approaches. Cross validation clearly demonstrates the improvement in model performance that temperature acclimation makes in modeling GPP at strongly temperature controlled sites in Russia. Additionally, the inclusion of a non-linear light response function is shown to further improve performance. Furthermore we demonstrate the parameterization of the big leaf model, incorporating environmental modifiers for temperature and VPD.

1 Introduction

A variety of methods have been developed to estimate ecosystem carbon fluxes. This includes flux towers (e.g. Friend et al., 2007), carbon accounting techniques (e.g. Shvidenko and Nilsson, 2003), process-based vegetation models (e.g. Quegan et al., 2011), atmospheric measurements (e.g. Stephens et al., 2007) and diagnostic satellite-based techniques as explained by Running et al. (2004), with each methodology.

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offering advantages and shortcomings. Satellite-based models in particular, have been developed to monitor primary production – with the advantage that they can model the globe at high temporal/spatial frequency using remotely sensed products 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 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 results at regional levels (Pan et al., 2006; Turner et al., 2006; Shvidenko et al., 2010; McCallum et al., 2009). 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). Beer et al. (2010) show that in particular, LUEs in boreal regions are strongly climate controlled, with temperature being the most dominant factor. Due to the acclimation of canopies (in terms of both light capture and physiology, Franklin, 2007) LUE may remain fairly constant with respect to absorbed radiation over monthly or annual time periods. However, on a daily time-scale such acclimation is not possible resulting in a variable LUE because instantaneous photosynthesis is nonlinear with respect to absorbed radiation (Makela et al., 2008). We hypothesize that accounting for non-linear light response and temperature acclimation of daily GPP will largely improve model performance compared to a standard linear LUE model.

To test this hypothesis, we have chosen four diagnostic models for comparison, namely: (1) the LUE approach parameterized according to (Running, 2000), (2) the LUE approach parameterized according to (Makela et al., 2008) but without a light modifier, (3) the LUE approach parameterized according to (Makela 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). 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 model also includes two

environmental modifiers for temperature and VPD, but is non-linear in its light response. Initially, all models are calibrated against four eddy covariance sites within Russia for the years 2002–2004. Model evaluation is performed via 10-out cross-validation, allowing us to compare the ability of each model to estimate daily GPP across the four sites for three consecutive years.

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 (Shvidenko et al., 2007). In addition vast areas are characterized by tundra ecosystems, dominated by shrubs, grasses and sedges, mostly above permafrost. 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 disturbances including 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).

This study focuses in particular on four locations across Russia where ecosystem flux measurements using the eddy covariance (EC) technique were undertaken (Fig. 1). The Cherskii 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 vapour pressure deficit at midday: 28 hPa) and low rainfall of 50 mm during summer (July–September) (Corradi et al., 2005). The Chokurdakh tower is located on

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a tundra ecosystem in the far east of Russia, underlain by continuous permafrost. It is characterized by a continental climate, that 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 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 typically being below 0°C between November and March (Milyukova et al., 2002). The Zotino tower is located in a Central Siberia 200 yr old Pine forest, with no permafrost, however it experiences heavy snowfall in winter ($> 1\text{ m}$). The long-term average length of the growing season is 132 days, lasting roughly from early May to late September (Tchebakova et al., 2002).

2.2 Model description

The models compared in this study are briefly described below. All parameters are listed in Table A1.

2.2.1 Light use efficiency (LUE)

The basic LUE approach is as follows,

$$\text{GPP} = \text{PAR} \cdot f_{\text{APAR}} \cdot \text{LUE} \cdot f_1(T) \cdot f_2(\text{VPD}) \quad (1)$$

where GPP represents daily gross primary productivity (gC m^{-2}), PAR is photosynthetic active radiation (MJ m^{-2}), f_{APAR} is the fraction of absorbed PAR and LUE is the potential LUE in terms of GPP (gC 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 $f_2(\text{VPD})$, both of which are defined as linear ramp functions $[0,1]$ as per (Running, 2000). $f_1(T)$ is 0 when daily minimum temperature ($^{\circ}\text{C}$) is less than or equal to $T_{\text{min}_{\text{min}}}$ ($^{\circ}\text{C}$) and increases linearly to 1 at temperature $T_{\text{min}_{\text{max}}}$ ($^{\circ}\text{C}$).

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 allowed to fluctuate with optimization. $f_2(\text{VPD})$ has a value of 1 when VPD is less than or equal to VPD_{\min} (Pa) and declines linearly to 0 as VPD increases to VPD_{\max} (Pa) (Running, 2000).

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 $f_2(\text{VPD})$ were parameterized differently. The effect of temperature on daily GPP was modelled using the concept of acclimation, calculated from the mean daily ambient temperature, using a first-order dynamic delay model where t (days) is the time constant of the delay process and X_0 ($^{\circ}\text{C}$) is a threshold value of the delayed temperature (Makela et al., 2008). The modifying function $f_1(T)$ is defined here as (Makela et al., 2008)

$$f_1(T) = \min \left\{ \frac{S_k}{S_{\max}}, 1 \right\}, \quad (2)$$

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

$$f_2(\text{VPD}) = e^{KD} \quad (3)$$

where K is an empirical parameter (see Table A1) 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

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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 (Makela et al., 2008)

$$f_3(L) = \frac{1}{\gamma \text{APAR} + 1} \quad (4)$$

where γ ($\text{m}^2 \text{mol}^{-1}$) is an empirical parameter (see Table A1) defined according to (Makela 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 (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

$$\text{GPP} = \frac{h}{2\theta} \left[\phi I_a + E_a A_{\text{max}} - \sqrt{(\phi I_a + E_a A_{\text{max}})^2 - 4\phi I_a E_a A_{\text{max}} \theta} \right] \quad (5a)$$

where

$$E_a = f_1(T) \cdot f_2(\text{VPD}) \quad (5b)$$

defined as h day length; θ convexity of leaf photosynthesis; ϕ quantum efficiency; I_a absorbed photosynthetically active radiation; E_a environmental modifier for temperature $f_1(T)$ and VPD $f_2(\text{VPD})$; 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 (Makela et al., 2008). The effect of VPD $f_2(D)$ on A_{max} was estimated according to (Landsberg and Waring, 1997).

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2.3 Eddy covariance and meteorological data

Data for model calibration was obtained from www.fluxdata.org for four sites with eddy covariance flux measurements in Russia: Cherskii (RU-Che), Chokurdakh (RU-Cho), Fyodorovskoe (RU-Fyo) and Zotino (RU-Zot) (Table 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 footprint of typically 1 km² (especially if 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 (usually) highly dynamic in space and time depending on friction velocity, sensible heat flux, temperature, and wind direction. For all sites, gap-filled and flux-partitioned daily data was obtained, having been treated according to standard procedures (Papale et al., 2006; Reichstein et al., 2005). In particular, the partitioning of net ecosystem exchange into GPP and terrestrial ecosystem respiration was done according to (Reichstein et al., 2005). See individual tower references for a description of the methodology applied at each tower (Table 1).

Daily GPP (g C m⁻² d⁻¹) from each site was selected with a quality flag = 1 (i.e. the daily value was calculated from half-hourly measurements or those which originate from very reliable gap-filling). 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 (hPa) 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).

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2.4 Model calibration

Each model was first estimated separately for each site and year and additionally for all years at each site. Thus parameters were estimated by means of a search on a coarse grid (see Table A1 for parameter ranges and increments). Model diagnostics were based on the regression of EC tower based GPP against modeled GPP. The minimum residual sum of squares (RSS) has been used as the calibration criteria. It was further appraised using both the coefficient of determination (r^2) and root mean square error (RMSE).

2.5 Model evaluation

Evaluation of the performance of the four 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). For each site, measured GPP values were dropped 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 error (MSE), which were used to evaluate the model's ability to predict GPP, averaged for all data.

3 Results and discussion

3.1 Model calibration and results

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 2, 3, 4 and 5,

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respectively). The LUE model (Table 2) showed clear discrepancies in obtaining a good fit in the far north, obtaining generally low coefficients of determination and high RMSE values at both sites, Cherskii (except in 2002, N is however low) and Chokurdakh. This is in part due to the low values of T_{\min} selected during optimization, which allow 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 3), demonstrating the importance of accounting for temperature acclimation in the northern regions. At the remaining two sites the models performed equally well. Both the LUE-TAL and BL models (Tables 4, 5) 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.

Site-specific parameter estimates in the BL model demonstrated geographical trends (i.e. latitude) when all site-years were considered (Fig. 2), keeping in mind that only four sites and 10 site years were included. In all cases except A_{\max} , these trends agree with previous findings of (Makela et al., 2008). In particular, the reducing effect of large VPD strengthened moving from north to south while t , the delay time of the temperature acclimation also decreased moving from north to south. Figure 2 also demonstrates that the majority of the parameter estimates (see Table A1) do not lie on the edge of the parameter space, indicating successful optimization. The identification of a geographical trend in several of the parameters could potentially aid in the application of this approach at the regional level.

In addition, scatterplots, annual flux and environmental scalars are presented for two sites with low (Cherskii) and high (Fyodorovskoe) productivity, in Figs. 3 and 4, respectively. 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. 3), as noted previously. Both the scatterplot and annual flux indicates that the LUE approach is not able to capture the daily measurements, while the LUE-TA, LUE-TAL and BL approaches are more

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successful (see Sect. 3.1 above for explanation). 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 non-limiting. Furthermore, the scatterplots (top row) in Fig. 3 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. 4), situated in evergreen needleleaf forest, all models generally capture the seasonal GPP flux, with the LUE-TAL and BL models performing best. Here again, the environmental scalars are vastly different 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. 4, there appears to be consistent underestimation all over and for all models, which is also evidenced by fairly similar r^2 and RMSE values. In particular, it seems that all models underestimate the latter half of the growing season.

3.2 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 6). For the majority of site-year combinations (with the exception of RU-Che 2004), 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 3 of the 10 site-year combinations, along with the lowest overall mean MSE. The BL model records the lowest MSE in 6 of the 10 site-year combinations, and records a low mean overall MSE.

4 Conclusions

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 to experience significant forms of environmental change. Previous efforts to focus on this region demonstrated a need for refinement in measurements (Quegan et al., 2011; Beer et al., 2006; Potter et al., 2005).

In this study we present a methodology for comparing diagnostic modeling approaches. The results presented here (using cross validation) clearly demonstrate that not accounting for temperature acclimation at northern sites leads to a very poor fit of modeled versus eddy covariance derived daily GPP values. These results would indicate that inclusion of temperature acclimation on sites experiencing cold temperatures is imperative. Furthermore, models with a non-linear light response outperform models with a linear light response. Additionally we demonstrate the parameterization of the big leaf model, incorporating environmental modifiers for temperature acclimation and VPD.

Various studies have pointed to difficulties, in particular, when examining results from global diagnostic LUE models at regional levels (Pan et al., 2006; Turner et al., 2006; Shvidenko et al., 2010). In recent years, several continental scale diagnostic approaches have been produced, parameterized with eddy covariance data (King et al., 2011; Makela et al., 2008; Jung et al., 2008; Sjoestroem et al., 2011). Results from those efforts have shown that a regionally specific approach yields plausible results. This study presents new results comparing several diagnostic approaches

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parameterized with eddy covariance data over Russia. Results from this and earlier studies elsewhere suggest that regionally parameterized models may in fact better capture processes not possible by a single global model. Thus developing models that address unique regional properties and integrating these into a global framework may improve overall accuracy of the results.

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 is a key goal within the scientific community. Future efforts should focus on up-scaling the results presented here and in similar studies to the regional level. The relationship between latitude and several of the parameters used in the models could aid in this process.

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Table 1. A description of the four FLUXNET towers used in this study.

Site	Location (°)	Data years	Land cover	References
Cherskii (RU-Che)	68.61° N 161.34° E	2002–2004	Tundra – Grass	(Merbold et al., 2009; Corradi et al., 2005)
Chokurdakh (RU-Cho)	70.61° N 147.89° E	2003–2004	Tundra – Grass	(van der Molen et al., 2007)
Fyodorovskoe (RU-Fyo)	56.46° N 32.92° E	2003–2004	Evergreen Needleleaf Spruce Forest	(Milyukova et al., 2002)
Zotino (RU-Zot)	60.80° N 89.35° E	2002–2004	Evergreen Needleleaf Pine Forest	(Tchebakova et al., 2002)

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Table 2. Parameter estimates and regression diagnostics for the LUE model.

Site	Year	LUE (gCMJ ⁻¹)	$T_{\min_{\min}}$ (°C)	$T_{\min_{\max}}$ (°C)	Vmin (Pa)	Vmax (Pa)	r^2	RMSE	<i>N</i>
RU-Che	2002	2	-11	4	0	3500	0.91	0.45	53
	2003	2	-5	13	0	2500	0.42	1.2	82
	2004	1.25	-2	4	0	2000	0.55	0.91	105
	All Years	1.5	-2	4	0	3000	0.51	1.2	240
RU-Cho	2003	1.5	-8	10	0	1500	0.51	1.1	117
	2004	1.75	-11	7	0	1500	0.73	0.52	64
	All Years	1.5	-5	4	0	1500	0.54	0.99	181
RU-Fyo	2003	2.75	-11	7	0	2000	0.77	1.6	202
	2004	2.25	-11	7	0	2000	0.83	1.4	247
	All Years	2.5	-11	10	0	2000	0.77	1.6	575
RU-Zot	2002	1.75	-5	13	0	3500	0.8	0.99	98
	2003	2	-11	4	0	2500	0.64	0.87	62
	2004	1.75	-5	7	0	4500	0.83	0.95	91
	All Years	1.75	-5	7	0	4000	0.75	1.1	251

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Table 3. Parameter estimates and regression diagnostics for the LUE-TA model.

Station	Year	S_{\max} (°C)	t (days)	X_0 (°C)	K (kPa ⁻¹)	LUE (gC MJ ⁻¹)	r^2	RMSE	N
RU-Che	2002	24	7	-10	-0.5	2.5	0.9	0.47	53
	2003	24	22	2	-0.3	3.75	0.87	0.57	82
	2004	15	22	-1	-0.5	2.5	0.87	0.5	105
	All Years	21	10	2	-0.5	3.25	0.61	1.1	240
RU-Cho	2003	18	22	-1	-0.9	3.25	0.89	0.54	117
	2004	15	22	-7	-0.9	1.5	0.68	0.56	64
	All Years	21	22	-1	-0.9	3.75	0.85	0.56	181
RU-Fyo	2003	27	22	-10	-0.9	4	0.77	1.6	191
	2004	24	16	-10	-0.7	2.5	0.85	1.3	247
	All Years	18	1	-7	-0.9	2.75	0.77	1.6	575
RU-Zot	2002	15	19	-4	-0.5	2	0.86	0.82	98
	2003	15	1	-10	-0.7	2.25	0.62	0.89	62
	2004	15	10	-4	-0.3	1.75	0.84	0.92	91
	All Years	18	13	-4	-0.3	1.75	0.8	0.98	251

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Table 4. Parameter estimates and regression diagnostics for the LUE-TAL model.

Station	Year	S_{\max} (°C)	t (days)	X_0 (°C)	K (kPa ⁻¹)	LUE (gC MJ ⁻¹)	γ (m ² mol ⁻¹)	r^2	RMSE	N
RU-Che	2002	21	4	-10	-0.3	3	0.09	0.93	0.39	53
	2003	15	19	2	-0.1	3.5	0.12	0.91	0.47	82
	2004	15	16	2	-0.5	3.75	0.06	0.88	0.47	105
	All Years	15	10	2	-0.3	3.5	0.12	0.65	1	240
RU-Cho	2003	15	16	-1	-0.7	4	0.12	0.92	0.45	117
	2004	15	4	-10	-0.5	2.25	0.12	0.82	0.46	68
	All Years	15	19	-1	-0.5	4	0.12	0.9	0.46	181
RU-Fyo	2003	21	22	-10	-0.5	4	0.06	0.81	1.5	191
	2004	18	22	-7	-0.1	4	0.12	0.89	1.1	247
	All Years	18	1	-7	-0.5	4	0.09	0.8	1.5	575
RU-Zot	2002	15	10	-1	-0.3	3	0.09	0.89	0.71	98
	2003	15	7	-4	-0.5	3.75	0.12	0.73	0.75	62
	2004	15	10	-4	-0.1	3.25	0.12	0.89	0.77	91
	All Years	15	13	-1	-0.1	3.25	0.12	0.85	0.85	251

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Table 5. Parameter estimates and regression diagnostics for the BL model.

Site	Year	S_{\max} (°C)	t (days)	X_0 (°C)	K (kPa ⁻¹)	A_{\max} ($\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$)	r^2	RMSE	N
RU-Che	2002	27	1	-4	-0.7	28	0.9	0.46	53
	2003	18	10	5	-0.1	20	0.92	0.44	82
	2004	15	13	5	-0.3	20	0.8	0.6	105
	All Years	15	10	5	-0.3	20	0.64	1	240
RU-Cho	2003	27	10	2	-0.5	32	0.93	0.41	117
	2004	15	1	-10	-0.3	8	0.82	0.42	64
	All Years	15	16	-1	-0.1	12	0.88	0.5	181
RU-Fyo	2003	18	22	-4	-0.5	40	0.8	1.5	191
	2004	15	10	-1	-0.3	28	0.89	1.1	247
	All Years	18	1	-1	-0.7	36	0.79	1.5	575
RU-Zot	2002	15	7	2	-0.3	16	0.9	0.69	98
	2003	15	10	-1	-0.5	16	0.75	0.73	62
	2004	15	7	-1	-0.1	16	0.89	0.77	91
	All Years	15	7	2	-0.1	16	0.86	0.83	251

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Table 6. Cross validation results (mean square error) 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	0.429	0.405	0.242	0.369
	2003	2.053	0.385	0.272	0.214
	2004	1.271	0.424	0.479	0.685
RU-Cho	2003	1.842	0.577	0.401	0.392
	2004	0.635	0.828	0.427	0.296
RU-Fyo	2003	3.836	3.946	2.68	2.643
	2004	2.482	2.409	1.421	1.59
RU-Zot	2002	1.874	0.844	0.85	0.738
	2003	1.518	1.335	0.859	0.831
	2004	1.56	1.579	0.713	1.03
Mean		1.75	1.27	0.83	0.88

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Table A1. Parameters required for LUE, LUE-TA, LUE-TAL and BL models.

Symbol	Parameter	Unit	Parameter Values	Increment	Reference
$T_{\min_{\min}}$	Minimum (minimum temperature)	°C	−11 : −2	−3	(King et al., 2011)
$T_{\min_{\max}}$	Maximum (minimum temperature)	°C	4 : 13	3	(King et al., 2011)
V_{\min}	Minimum VPD	Pa	0 : 2500	500	(King et al., 2011)
V_{\max}	Maximum VPD	Pa	1500 : 4500	500	(King et al., 2011)
LUE	Light use efficiency (maximum)	gCMJ^{-1}	0.5 : 4	0.25	(King et al., 2011)
S_{\max}	Saturating level	°C	15 : 30	3	(Makela et al., 2008)
t	Time constant	days	1 : 22	3	(Makela et al., 2008)
X_0	Threshold value	°C	−10 : 5	3	(Makela et al., 2008)
K	VPD	kPa^{-1}	−0.1 : −0.9	−0.2	(Landsberg and Waring, 1997)
A_{\max}	Light saturated photosynthesis	$\mu\text{molCO}_2 \text{m}^{-2} \text{s}^{-1}$	0 : 40	4	(Ruimy et al., 1996)
θ	Convexity of leaf photosynthesis	–	0.8	–	(Hirose et al., 1997)
ϕ	Photosynthetic quantum efficiency	μgCJ^{-1}	2.73	–	(Wong et al., 1979)
h	Day length	hd^{-1}	12	–	Estimated
γ	Light	$\text{m}^2 \text{mol}^{-1}$	0 : 0.12	0.03	(Makela et al., 2008)

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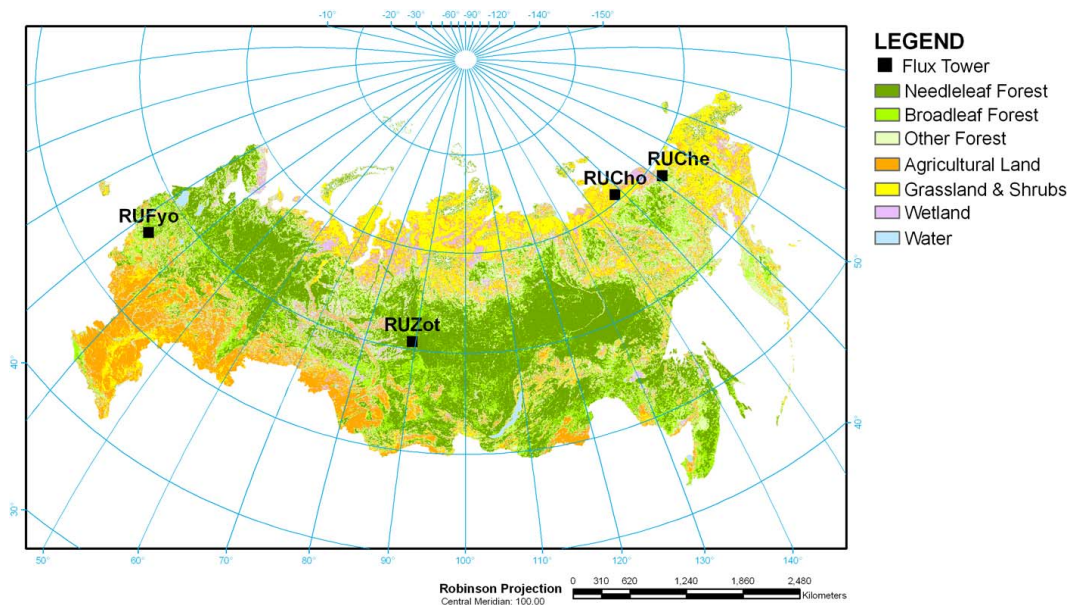


Fig. 1. Map of dominant Russian land cover (Schepaschenko et al., 2011), along with locations of the four flux towers used in this study.

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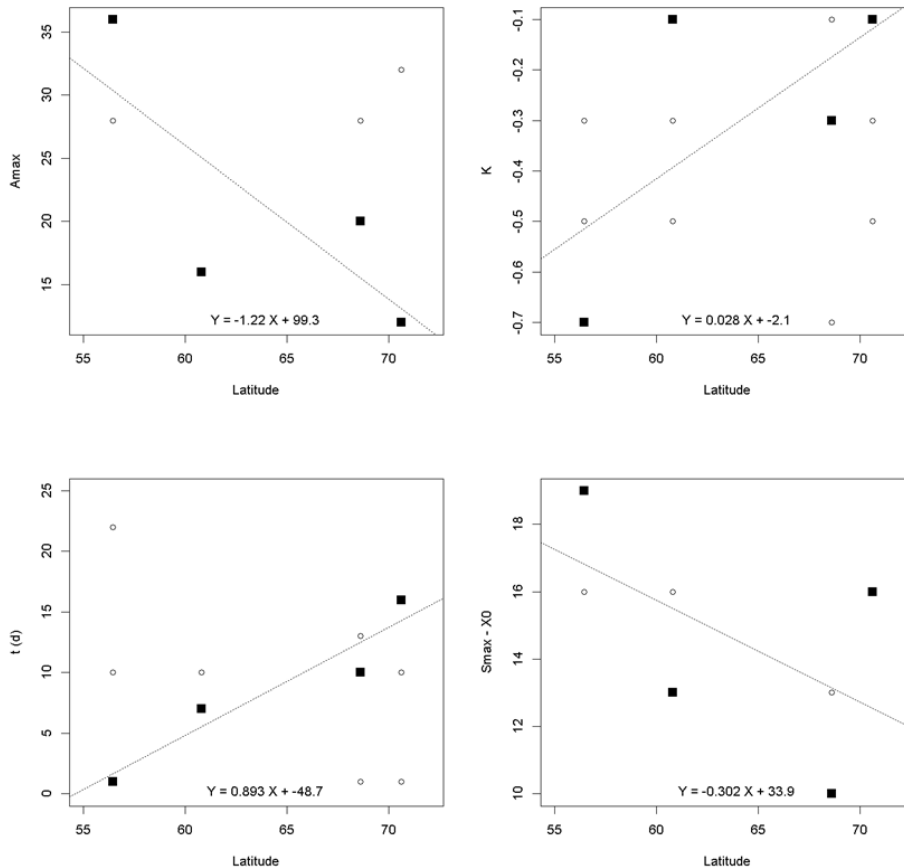


Fig. 2. Resulting optimized parameter values from the BL model (open circles are individual years, closed squares are average of all years). Linear regression (dashed line) fitted to the four average site-year parameter values.

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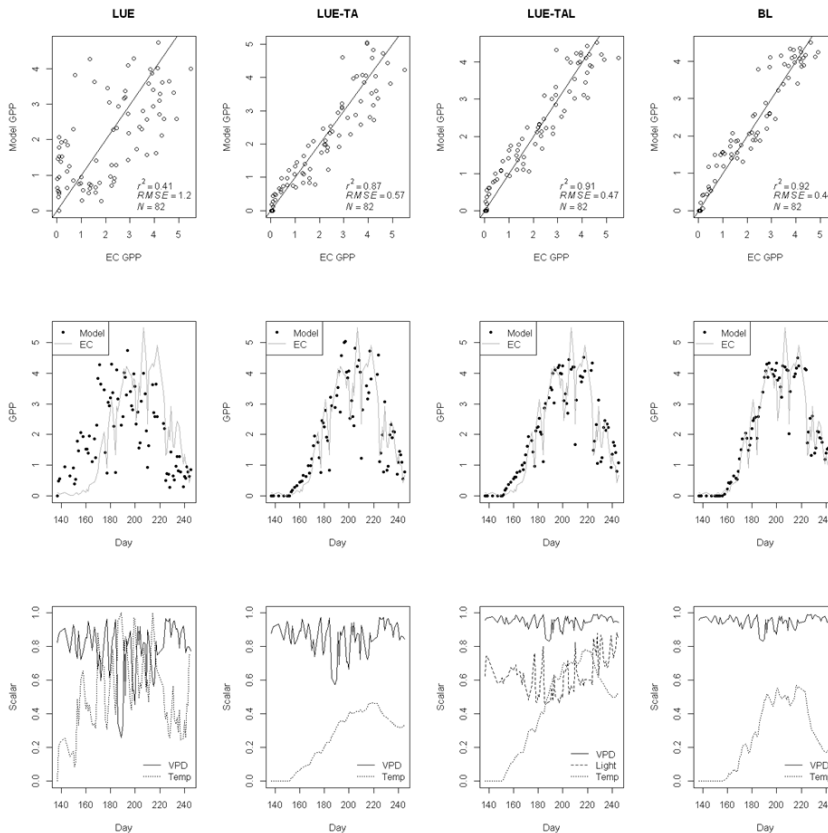


Fig. 3. Results for Cherskii, 2003 from the LUE (1st column), LUE-TA (2nd column), LUE-TAL (3rd column) and BL (4th column) models where the top row depicts scatterplots of eddy covariance (EC) GPP vs. model GPP, the middle row depicts the daily course of GPP (EC and model) and the bottom row depicts the environmental scalars for temperature, light and VPD.

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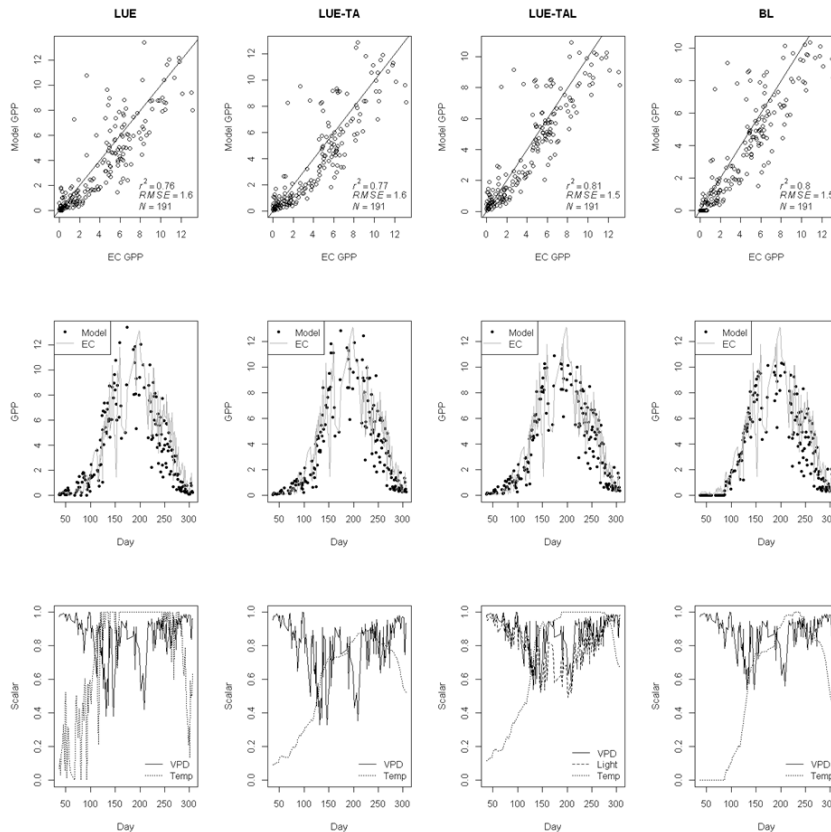


Fig. 4. Results for Fyodorovskoe, 2003 from the LUE (1st column), LUE-TA (2nd column), LUE-TAL (3rd column) and BL (4th column) models where the top row depicts scatter plots of EC GPP vs. model GPP, the middle row depicts the daily course of GPP (EC and model) and the bottom row depicts the environmental scalars for temperature, light and VPD.