Seasonal fluctuations of photosynthetic parameters for light use efficiency models and the impacts on gross primary production estimation

Xiaofeng Lin ^{a, b}, Baozhang Chen ^{a, b, c*}, Jing Chen ^d, Huifang Zhang ^a, Shaobo Sun ^{a, b}, Guang Xu ^{a, b},
Lifeng Guo ^{a, b}, Mengyu Ge ^c, Junfeng Qu ^c, Lijuan Li ^e, Yawen Kong ^{a, b}

^a State Key Laboratory of Resources and Environment Information System, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 11A, Datun Road, Chaoyang District, Beijing, 100101, China

^b University of Chinese Academy of Sciences, No. 19A, Yuquan Road, Beijing 100049, China

^c School of environment science and spatial informatics, China University of Mining and Technology, Xuzhou 221116, China

^d Meteorological Information Center of Beijing, Beijing Meteorological Bureau, No. 44, Zizhuyuan Road, Haidian District, Beijing 100089, China

^e China University of Geosciences, No. 29, Xueyuan Road, Beijing 100083, China

* Corresponding author. Tel.: +86 10 64889574.

E-mail addresses: baozhang.chen@igsnr.ac.cn (B. Chen)

16 Abstract

17 How parameterization improves Light-use efficiency (LUE) models by taking into account the seasonal
18 variations of the maximum LUE ($\varepsilon_{\max}$) has been rarely investigated. The LUE models include two
19 categories which are the one-leaf LUE model (SL-LUE) and the two-leaf LUE model (TL-LUE) with
20 separation of sunlit and shaded leaves (ε_{msu} and ε_{msh}). In this study, the SL-LUE and TL-LUE models
21 were parameterized for 46 towers (176 site-years data) representing eighteen typical plant functional
22 types (PFTs) by using the Metropolis-Hasting algorithm at monthly time scales. The results indicate
23 that the maximum LUE parameters varied seasonally for most PFTs having a significant positive linear
24 correlation with leaf area index (LAI) and ambient temperature changes. The relationships of ε_{msu} and
25 ε_{msh} with $\varepsilon_{\max}$ can be well described by linear equations, indicating the existence of general patterns
26 across biomes. And as expected, The LUE models with the seasonal fluctuations of $\varepsilon_{\max}$, ε_{msu} and
27 ε_{msh} significantly improved GPP estimation except for needleleaf evergreen forests in mid- and low-
28 latitude regions. The improvements of both the SL-LUE and TL-LUE models were most significant in
29 summer for tropical and Mediterranean climate regions, while most evident in spring and winter for
30 temperate and boreal climate regions. Even with seasonal parameters, both the LUE models still cannot
31 well capture GPP dynamics in cold season for some PFTs in Mediterranean and tropical regions (e.g.,
32 Tropical-BEF, C3-C4 grass). This study suggests that further improvement of modelling GPP requires
33 taking into account seasonal variations of the key parameters.

34 **Keywords:** light use efficiency (LUE) models; seasonal variations of maximum LUE parameters;
35 Capacity of gross primary production; Metropolis-Hasting algorithm; eddy covariance

36 1. Introduction

37 Terrestrial carbon storage and its variation play a significant role in the global carbon cycle ([Gao](#)
38 [and Liu, 2008](#)). Gross primary production (GPP) determines the thermal, hydrologic and

39 biogeochemical cycles in terrestrial ecosystems (Odum et al., 2009). Quantitative estimation of GPP at
40 various temporal and spatial scales is important for understanding the interactions between ecosystems
41 and climate change (Grace et al., 2007; Cheng et al., 2014). Many approaches were developed to
42 estimate GPP (Monteith, 1972; Farquhar et al., 1980; Baldocchi, 2001; Beer et al., 2007). One of the
43 widely accepted concepts is the light use efficiency (LUE) (Monteith, 1972, 1977), because of both its
44 theoretical basis and practicality (Running et al., 2000; Yuan et al., 2007) and its utility for connecting
45 eddy covariance observations of carbon fluxes (e.g., Thurner et al., 2014; He et al., 2013; Yuan et al.,
46 2014) and remotely sensed data (e.g., Xiao et al., 2005; Yuan et al. 2007; Wu et al., 2010). LUE,
47 defined as the CO₂ uptake per unit photons absorbed by vegetation, is straightforward and
48 physiologically based (Field et al., 1994; Haxeltine and Prentice 1996; Medlyn, 1998; Goetz and Prince,
49 1999). It has been used in many production efficiency models at different spatial and temporal scales
50 (Running et al., 2004; Heinsch et al., 2003; Yuan et al., 2007; Zhao et al., 2010; He et al., 2013).
51 However, even though the eddy covariance (EC) flux data and remotely sensed data are conjunctively
52 introduced into various LUE models, the uncertainties in GPP estimation are still large (Chen et al.,
53 2014).

54 To reduce the GPP uncertainties in LUE models, parameter adjustment (e.g., Chen et al., 2014;
55 Zhou et al., 2015) and structural modification (e.g., He et al., 2013; Zhang et al., 2015) have been
56 developed. The former can compensate for errors derived from the latter (Kanniah et al., 2009; Chen et
57 al., 2010; Bonan et al., 2011; Chen et al., 2014). However, some studies note that parameter adjustment
58 by correcting parameters using flux tower observations or adding control factors still cannot capture the
59 photosynthetic dynamics in spring and fall for forests and shrubs and seasonal GPP change for
60 grasslands (Hashimoto et al., 2013; Chen et al., 2014). Little attention was given to the seasonal and
61 phenological variations of key parameters and variables in carbon assimilation. This issue must be
62 clarified and resolved to reduce the uncertainties in GPP estimates on regional and global scales.

Therefore, the purpose of this study is to determine the monthly values of LUE parameters ($\varepsilon_{\max}$, ε_{msu} and ε_{msh}) and to examine the seasonal response of these parameters for multiple plant functional types (PFTs). The specific objectives of this study are threefold: (1) to investigate seasonal variations of the LUE parameters, (2) to evaluate the response of GPP to seasonal LUE variations, and (3) to determine whether it is possible to estimate GPP for a given PFT for all phases with a single set of LUE parameters.

We hypothesize that incorporating the seasonal variations of LUE parameters can improve GPP estimation and can reasonably capture seasonally photosynthetic dynamics. We used EC measurements to optimize the maximum LUE with monthly-dataset. The selected EC towers represent 18 PFTs across 11 biome types in 4 main climate zones. Then we compared the adjusted estimations with the observations and simulations using default parameters.

2. Materials and methods

2.1. Data used

2.1.1 Eddy covariance data

The half-hourly meteorological and carbon fluxes data, acquired from the FLUXNET network (<http://fluxnet.ornl.gov/>), were used to parameterize and evaluate the one-leaf and two-leaf LUE models. The EC tower sites were selected based on data availability of key variables (Chen et al., 2014). In total, 176 site-years data from 46 sites were selected and all EC measurements were processed in a manner consistent with the FLUXNET project (Baldocchi et al., 2001; 2008). The observations spans the period from January 2000 to December 2010. And each site contains at least two years of data coverage. 92 of the 176 site-years observations were used for parameter optimization (two years for each site). And the remaining data were used for model validation. Detailed information of each site is shown in Fig. 1 and Table 1.

86 2.1.2 Leaf area index data

87 Global inventory modeling and mapping studies (GIMMS) LAI3g dataset (Zhu et al., 2013) were
88 used to drive the two LUE models. This dataset provides 15-day composite LAI values for each pixel
89 where flux towers locate in. The LAI values were extracted referring to Zhou et al., 2015, single-pixel
90 containing the coordinates for a tower was extracted. The resulting LAI time series of each site were
91 further smoothed using the locally adjusted cubic-spline capping (LACC) method (Chen et al., 2006) to
92 remove unrealistically short-term abrupt changes in LAI due to the contamination of the measurements
93 by clouds or the presence of ground snow or ice.

94 2.2. Model description

95 2.2.1. One-leaf light use efficiency model

96 The one-leaf LUE model (SL-LUE) model is based on the radiation conversion efficiency concept of
97 Monteith (1972) and described as follows:

$$98 \quad GPP = \varepsilon_{\max} \times APAR \times f(VPD) \times g(T_a) \quad (1)$$

99 Where $\varepsilon_{\max}$ is the maximum LUE (gC MJ^{-1}) without environment stress, which relates to plant
100 functional type, $APAR$ is the incident photosynthetically active radiation (PAR) absorbed by the
101 vegetation, $f(VPD)$ and $g(T_a)$ are the scalars of vapor pressure deficit (VPD) and the minimum air
102 temperature (T_a), respectively, both of which range from 0 to 1 to downscale $\varepsilon_{\max}$ of the canopy to the
103 actual LUE value. They are calculated as:

$$104 \quad g(T_a) = \begin{cases} 0 & T_a \leq T_{\min} \\ \frac{T_a - T_{\min}}{T_{\max} - T_{\min}} & T_{\min} < T_a < T_{\max} \\ 1 & T_a \geq T_{\max} \end{cases} \quad (2)$$

$$f(VPD) = \begin{cases} 0 & VPD \geq VPD_{\max} \\ \frac{VPD_{\max} - VPD}{VPD_{\max} - VPD_{\min}} & VPD_{\min} < VPD < VPD_{\max} \\ 1 & VPD \leq VPD_{\min} \end{cases} \quad (3)$$

where $VPD_{\max}$, $VPD_{\min}$, $T_{\max}$, $T_{\min}$ are PFT-dependent parameters (Running et al. 2000; Heinsch et al., 2003; Liang et al., 2012; Cescatti, 2012; He et al. 2013) (Table 2).

2.2.2. Two-leaf light use efficiency model

The two-leaf LUE model (TL-LUE) is based on the SL-LUE and Dynamic Land Model (DLM, Chen et al., 2014). It calculates GPP by separately calculating the GPP of sunlit and shaded leaves as:

$$GPP = (\varepsilon_{msu} \times APAR_{su} + \varepsilon_{msh} \times APAR_{sh}) \times f(VPD) \times g(T_a) \quad (4)$$

where ε_{msu} and ε_{msh} are the maximum LUE for sunlit and shaded leaves, respectively; $APAR_{su}$ and $APAR_{sh}$ are the PAR absorbed by sunlit and shaded leaves. They are calculated as:

$$APAR_{sh} = (1 - \alpha) \times \left[(PAR_{dif} - PAR_{dif,u}) / (LAI + C) \right] \times LAI_{sh} \quad (5)$$

$$APAR_{su} = (1 - \alpha) \times (PAR_{dir} \times \cos(\beta) / \cos(\theta) + (PAR_{dif} - PAR_{dif,u}) / (LAI + C)) \times LAI_{su} \quad (6)$$

where α is the canopy albedo related to vegetation types (Table 2), PAR_{dif} and PAR_{dir} are the diffuse and direct components of incoming PAR , respectively. They are calculated using Eq. (7).

$PAR_{dif,u}$ is the diffuse PAR under the canopy and calculated following Chen et al., (1999);

$(PAR_{dif} - PAR_{dif,u}) / LAI$ represents the diffuse PAR on per unit leaf area within the canopy; C

quantifies the contribution of multiple scattering of the total PAR to the diffuse irradiance per unit

leaf area within the canopy (Norman, 1982); β is the mean leaf-sun angle and set as 60° for a

canopy with spherical leaf angle distribution (Chen et al., 1999); and θ is the solar zenith angle.

Diffuse and direct PAR were partitioned using the formula following Boland et al., 2008 with parameters (f and g in Eq. (7)) calibrated using half-hourly diffuse and total incoming radiation data measured at different PFTs.

$$PAR_{dif} = \frac{1}{\exp(f + g \times R)} \times PAR \quad (7)$$

$$PAR_{dir} = PAR - PAR_{dif} \quad (8)$$

where R is the sky clearness index and equals ($PAR/0.5S_0 \cos \theta$); S_0 is the solar constant (1367 W m⁻²). A constant 0.5 is used to convert incoming solar radiation into PAR (Weiss and Norman, 1985; Tsubo and Walker, 2005; Bosch et al., 2009).

The LAI_{su} and LAI_{sh} are the LAI of sunlit and shaded leaves. They are computed as (Chen et al., 1999; He et al., 2013):

$$LAI_{su} = 2 \times \cos \theta \times (1 - \exp(-0.5 \times \Omega \times LAI / \cos \theta)) \quad (9)$$

$$LAI_{sh} = \max(0, LAI - LAI_{su}) \quad (10)$$

where θ is the solar zenith angle; LAI is the leaf area index; Ω represents the vegetation clumping index according to Table 2.

2.3. Parameterization procedure

The LUE parameters (ε_{max} , ε_{msu} and ε_{msh}) were calibrated using the Bayesian method, which is based on Bayes' theorem combined with Markov Chain Monte Carlo (MCMC) estimator (Braswell et al., 2005). In this approach, the data assimilation scheme is based on Metropolis-Hasting (MH) algorithm (Chib et al., 1995). The lower and upper bounds of ε_{max} , ε_{msu} and ε_{msh} were determined from the range of these parameters used in LUE models (He et al., 2013; Yuan et al., 2014; Chen et al., 2014; Zhou et al., 2015). The procedure begins by the prior probability distribution as the uncertainty about parameter values. Then observations (e.g., GPP) were used to yield an updated posterior distribution of

the parameters. Next the MH algorithm generated a representative sample of parameter vectors from the posterior distribution by multiplying the prior with its corresponding data likelihood function, which usually assumes that the model error (the difference between the estimated and observed values) is independent and normally distributed with zero-mean (Van et al. 2005; Svensson et al. 2008). Logarithmic likelihood function is used to improve numerical stability and make L easier to work with:

$$\log L = \sum_{i=1}^n \left[-0.5 \left(\frac{obs_i - sim_i}{\delta_i} \right)^2 - 0.5 \log(2\pi) - \log(std_i) \right] \quad (11)$$

where n is the number of data points; obs_i is the observed GPP for measurement i ($i=1,2,\dots,n$), sim_i is the model estimation with the LUE parameters, and std_i is the standard deviation of the model error.

The prior distributions of the calibration parameters are chosen as normal distribution centered on values reported in the literature (Table 2) and non-correlated. The first step of MCMC is to run an initial simulation with parameter values from an arbitrary point $\varepsilon^{(0)}$, and to calculate the total data likelihood of that point with Eq. (11). The second step is to generate a candidate point $\varepsilon^{(new)}$ according to a proposal density $P(\varepsilon^{(new)} | \varepsilon^{(k-1)})$. The point $\varepsilon^{(new)}$ is accepted or rejected against the Metropolis criterion. Thus, a chain of accepted parameter values and corresponding simulation results are generated. We ran five parallel MCMC chains with 50,000 iterations each, evaluated the chains for convergence, and thinned the chains (every 30th iteration) when appropriate to reduce within-chain autocorrelation, thereby producing an independent sample of 5000 values for each parameter from the joint posterior distribution. The parameters of the LUE models were fitted to carbon exchange data. And the posterior mean and 95% confidence intervals (CIs: i.e., 2.5th and 97.5th percentiles) can be obtained from values of each parameter for each month.

168 2.4. Experiments

169 We performed the following simulations to document seasonal variations of maximum LUE
170 parameters applied to the one-leaf and two-leaf LUE algorithm:

171 LUE_{def}: A simulation with the one-leaf algorithm and the default biome-parameters supplied by
172 BPLUT (Table 2) (Zhao et al., 2010);

173 SL-LUE: A simulation with the one-leaf algorithm (Eq. (1)) and optimized monthly biome-
174 parameters ($\varepsilon_{\max}$), to investigate error introduced by the fixed maximum LUE values;

175 TL-LUE: A simulations with the two-leaf algorithm (Eq. (4)) and optimized monthly biome-
176 parameters (ε_{msu} and ε_{msh}), to investigate error introduced by the fixed maximum LUE values of
177 sunlit and shaded leaves.

178 2.5. Evaluation of model performance

179 The degree of seasonal variations of maximum LUE parameters were quantified by coefficient of
180 variation (CV) (Bonett et al., 2006), which is defined as:

$$181 \quad CV = \sqrt{\sum_{i=1}^n (\varepsilon_{\max_i} - \bar{\varepsilon}_{\max})^2 / (n-1)} / \bar{\varepsilon}_{\max} \times 100\% \quad (12)$$

182 The performance of model estimations was quantified by statistical analysis based on the half-
183 hourly GPP for each model-data pair. Estimation-Observation mismatch was evaluated using the bias,
184 coefficient of determination (R^2) and the root mean square error ($RMSE$) (Willmott et al., 1985, 2005).
185 The accuracy of model performance was characterized by Taylor diagram and Taylor skill (S) (Taylor
186 et al., 2001). Every point in the Taylor diagram indicates the linear correlation coefficient (R), the
187 normalized standard deviations and the root-mean-square (RMS) difference of the two patterns. A
188 single point in S is a single-value summary of a Taylor diagram, which is used to indicate perfect
189 agreement with observations. Each point for any arbitrary data group (Taylor et al., 2001; Schwalm et
190 al., 2010) can be expressed as

$$S=2(1+R)/(\sigma_{\text{norm}}+1/\sigma_{\text{norm}})^2 \quad (13)$$

3. Results

3.1. Posterior distribution of the LUE model parameters

We optimized the key parameters (ε_{max} , ε_{msu} and ε_{msh}) of the SL-LUE and TL-LUE models. Fig. 2 and Table 3 show plots and seasonal coefficient of variation (CV) of the posterior parameter distributions (PDFs) corresponding to the means after calibration with the different monthly dataset procedures. Such representation makes it possible to visualize monthly differences in the optimized parameters for different PDFs, while the shape of the plot reveals the dispersion and symmetry of the marginal distributions (Lehuger et al. 2009). For all PFTs, optimized ε_{max} values were always between ε_{msu} and ε_{msh} and the values of ε_{msu} were the lowest for all months. The main photosynthetic parameters (ε_{max} , ε_{msu} and ε_{msh}) varied substantially among the different plant functional types and were updated well by the MCMC procedure for most PFTs in all seasons, as demonstrated by seasonal variabilities and large CV for these parameters (Fig. 2; Table 3). The averaged CV ranged from 12.43% in summer to 34.28% in spring for ε_{max} , from 33.38% in summer to 51.50% in fall for ε_{msu} , and from 21.01% in summer to 35.97% in spring for ε_{msh} , respectively. However, this was not the case for needleleaf evergreen forest (NEF) in temperate and Mediterranean regions. That is, the posterior estimations of maximum LUE parameters were held relatively constant for different seasons with small CV throughout the seasons (Fig. 2b). In addition, we found that the posterior means of these parameters showed similar variation trends overall. For example, the average values of them for most PFTs showed a monopeak curve across four seasons with the peak appeared in winter for Tropical-BEF and Mediterranean-BEF or in summer for other PFTs, while showed a multiple extremums curve for C3 grass and C3/C4 grass.

213 3.2. Model-data agreement relative to climatic season

214 We simulated seasonal GPP using the one-leaf and two-leaf LUE models with default annual
215 parameters (LUE_{def}) and optimized monthly parameters. The simulation results were compared with
216 observed GPP values using Taylor skill (S) to explore the model's feedback to various weather
217 conditions in different seasons (Fig. 3). The site-level model-data agreement of SL-LUE and TL-LUE
218 exhibited an obvious low degree of scatter for all seasons, while LUE_{def} had a large range of Taylor
219 skill (ranged from zero to unity) especially in cold seasons. SL-LUE and TL-LUE produced higher R^2
220 and lower RMSE values than LUE_{def} for all seasons. The variations of GPP explained by SL-LUE and
221 TL-LUE were 64.1% and 68.6%, with averaged R^2 values increased by 2.3% and 6.8% than LUE_{def} .
222 And the corresponding averaged RMSE values reduced by 0.52 and 0.81 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively.
223 Although LUE_{def} had small biases in spring and fall (Table 4), its standard deviation was much greater
224 than the average bias of SL-LUE and TL-LUE. Thus, the small biases of LUE_{def} were most likely
225 caused by terms with opposite signs cancelling each other. In contrast, the biases of SL-LUE and TL-
226 LUE both had an obviously lower degree of scatter (mostly concentrated in 0.2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in all
227 seasons. These results imply that incorporating the seasonal fluctuations of LUE could improve the
228 robustness of GPP simulations and reduce the uncertainties for both the one-leaf and two-leaf LUE
229 models.

230 In addition, the improvement of the SL-LUE and TL-LUE models than the LUE_{def} model was most
231 significant in spring, especially in April, with the RMSE decreased by 0.89 and 1.13 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,
232 respectively (Table 4). It is noteworthy that the LUE_{def} model tends to seriously underestimate or
233 overestimate GPP, especially in summer where the bias of $-1.19 (\pm 1.53)$ $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while the bias in
234 the SL-LUE and TL-LUE models in summer was reduced (0.40 and 0.68 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively).
235 These analyses suggest again that it would be important to incorporate the physiological changes in the
236 photosynthetic parameters for the LUE models.

237 3.3. Model and PFT-specific consistency with observations

238 The differences in modeling efficiency among the LUE_{def}, SL-LUE and TL-LUE models (both
239 across-PFT and across-model) were then quantified using Taylor diagrams (Fig. 5). The average model-
240 data agreement (σ_{norm}) values for LUE_{def} model ranged from 0.23 to 1.97, with R-values of 0.54-0.90.
241 The SL-LUE and TL-LUE models had the average values of σ_{norm} 0.91(± 0.04) and 0.91(± 0.02), in R
242 of 0.80(± 0.07) and 0.82(± 0.08), respectively. However, it is not the case for some PFTs. For instance,
243 the Mediterranean-NEF and temperate-NEF (number 11 and 15 in Fig. 5a-5c, number 6 and 8 in Fig.
244 5d), the averaged σ_{norm} of them only increased by 0.02(± 0.01)(see also Fig. 2 and Table 3). Fig. 6
245 further quantified the improvement of incorporating the seasonal variations of LUE values. The
246 increase of R^2 (ΔR^2) and the decrease of RMSE ($\Delta RMSE$, $\text{gC}\cdot\text{m}^{-2}\cdot\text{season}^{-1}$) were most significant in
247 summer and fall (red and blue bar in Fig. 6) for biomes in tropical and Mediterranean climate regions,
248 while most obvious in spring and winter (black and magenta bar in Fig. 6) for biomes in temperate and
249 boreal climate regions. Similar results can also be seen in Fig. 7 (orange box), which comparing the
250 simulations and observations of monthly composite diurnal variations for each PFT. The simulated GPP
251 overall captured the observed diurnal variations within or near the margin of ± 1 standard deviation for
252 most PFTs. The performance of the LUE_{def} model varied with seasons. For instance, it underestimated
253 GPP in summer and overestimated GPP in cold season for most PFTs and it overestimated GPP for
254 Mediterranean-BEF and C3 grass in Arctic in summer (Fig. 7-b2 and Fig. 7-c3). The modeled GPP by
255 the SL-LUE and TL-LUE models in contrast were consistent with measurements for most PFTs for all
256 seasons ($R^2 = 0.63 - 0.98$ and $0.73 - 0.99$, and $RMSE = 0.32 - 4.88$ and $0.22 - 4.45 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,
257 respectively). In the example shown, the LUE model using the default parameters already performs
258 very well for Mediterranean-NEF (Fig. 7-b3) and Temperate-NEF (Fig. 7-b4), so little improvement is
259 needed. However, though incorporating the seasonal fluctuations of the maximum LUE parameter, both
260 the SL-LUE and TL-LUE models showed poor performance for Tropical-BEF (Fig. 7-b5) and for C₃-

261 C₄ grass, similar to the results reported by [Chen et al., 2014](#).

262 4. Discussion

263 4.1. Seasonal variations of the LUE model parameters

264 The optimized $\epsilon_{\max}$ values were in between the values of ϵ_{msu} and ϵ_{msh} for all PFTs. The ϵ_{msh} values
265 were larger than ϵ_{msu} and $\epsilon_{\max}$ because the shaded leaves are only exposed to diffuse radiation, which
266 enters a canopy from all directions and distributes more evenly than direct radiation within the canopy
267 ([Sinclair et al., 1993](#), [Hammer&Wright, 1994](#)). The intensity of light absorbed by shaded leaves is
268 normally lower than light saturation point. Therefore, they have higher light use efficiency than the
269 sunlit leaves. The value of ϵ_{msh} is about four times as much as that of $\epsilon_{\max}$, while the value of ϵ_{msu}
270 is about 15% to 70% lower than the value of $\epsilon_{\max}$ ([Table 3](#)), both larger than that for 6 vegetation types
271 reported by [He et al. \(2013\)](#), in which the value of ϵ_{msh} is about two times as much as that of $\epsilon_{\max}$
272 and the value of ϵ_{msu} is about 45% to 59% lower than the value of $\epsilon_{\max}$. This can be explained by the
273 fact that 18 PFTs used in this study distributed across Europe, America, Asia and Africa while [He et al.](#)
274 ([2013](#)) only used 6 typical sites in China.

275 [Houborg et al. \(2009; 2011\)](#) demonstrated the importance of allowing the maximum LUE to vary
276 seasonally, responding realistically to changes in leaf biochemistry as well as short-term variations in
277 environmental conditions. In this study, For Temperate-NEF and Mediterranean-NEF, the maximum
278 LUE parameters almost keep constant throughout the four seasons. It may be explained by the fact that
279 coniferous forests are noted for the ability to fix carbon throughout the year at the expense of low
280 physiological activity and slow growth rates ([Monk, 1966](#); [Chapin, 1980](#); [Monk & Day, 1985](#);
281 [Baldocchi et al., 2010](#)), thus the LUE parameters failed to show obvious seasonality ([Huang et al.,](#)
282 [2014](#)). For other PFTs, the posterior means of $\epsilon_{\max}$, ϵ_{msu} and ϵ_{msh} were observed to vary significantly

283 over the seasons, especially in mid- and high-latitude areas (Fig. 2; Table 3). Seasonal variability of
284 these parameters has been shown to occur in the deciduous forests (Muramatsu et al., 2014; Biudes et
285 al., 2014), coniferous forests and mixed forests (Huang et al., 2014), shrubs (Stagakis et al., 2014;
286 Huang et al., 2014), and grassland (Chen et al., 2010; Huang et al., 2014). Canopy structure is a key
287 factor influencing light interception by a forest stand with a given LAI (Teh et al., 2000) and may
288 influence branching strategies that optimize light capture (Whitney, 1976; Kempf & Pickett, 1981;
289 Brantley & Young, 2009). Large seasonal variations in maximum LUE parameters could also be
290 explained by changes in ambient temperatures (Wilson et al., 2000; Medlyn et al. 2002; Xu and
291 Baldocchi 2014; Zhu et al., 2011). Similar results were obtained in this study. The R^2 between the
292 maximum LUE parameters and LAI ranged from 0.32 to 0.84. The corresponding R^2 values between
293 the maximum LUE parameters and ambient temperature ranged from 0.11 to 0.40 (Fig. 8).

294 The posterior of $\varepsilon_{\max}$, ε_{msu} and ε_{msh} had lower CV value in summer compared with other seasons
295 and ε_{msu} had relatively higher CV compared with $\varepsilon_{\max}$ and ε_{msh} (Table 3). Evidence has showed that there
296 were no pronounced differences in LUE values from June to September (summer and early fall) and the
297 seasonal variation in LUE (coefficient of variation) was lower on cloudy days (ε_{msh}) than on partly
298 cloudy or sunny days (ε_{msu}) (Chen et al., 2010). In addition, the three parameters mostly have similar
299 variations trends and mostly showed a monopeak or single valley curve across four seasons, with peak
300 or valley values during the mid-growing season (Fig. 2). To understand further how the parameters
301 correlated, we consider the 2-D representation in Fig. 8. The regression analysis shows that both
302 ε_{msu} and ε_{msh} increased linearly with $\varepsilon_{\max}$, with an increase as much as by a half and three times,
303 respectively. Similar findings were also reported by Zhou et al. (2015). This result provides another
304 feasible constraint condition to estimating the maximum LUE values of sunlit and shaded leaves with
305 an unique determination solution by taking the relationship here as a sine qua non. Further validations

306 were needed with more flux sites.

307 4.2. Responses of GPP to seasonal variations in LUE parameters

308 Imposing a seasonal variability of the maximum LUE significantly improved the accuracy of
309 carbon flux estimates in all seasons for both the one-leaf and two-leaf LUE models. The comparison of
310 biases and RMSE indicates that the improvement is more significant in spring and fall seasons (Fig 4
311 and Table 4), which is consistent with the seasonal fluctuations (CV) of the maximum LUE in Table 3,
312 with the highest CV of 34.28% for $\varepsilon_{\max}$ in spring, 51.50% for ε_{msu} in fall, and 35.97% for ε_{msh}
313 in spring, respectively. For a given climate region, the outperformance of both the one-leaf and two-leaf
314 models incorporating the seasonal variations of LUE parameter were most significant in summer in
315 tropical and Mediterranean climate regions, while most obvious in spring and winter in temperate and
316 boreal climate regions (Fig. 6 and Fig. 7). These results probably resulted from the determination mode
317 of the maximum LUE in previous studies, which was parameterized with observations in the growing
318 peak season (e.g., Potter et al., 1993; Prince and Goward, 1995; Landsberg and Waring, 1981; Running
319 et al., 2000; Xiao et al., 2004; Yuan et al., 2007; He et al., 2013). For example, the combination of
320 warm-season datasets had a comparatively larger number of observations in temperate and boreal
321 climate regions, and subsequently gained more weight in the likelihood function when using multi-
322 dataset to parameterize the maximum LUE parameters in the optimized process. And subsequently
323 using monthly-dataset to parameterize the maximum LUE parameters would have a pronounced effect
324 on GPP simulation in cold seasons. However, whether or not to incorporate the seasonal variations of
325 the maximum LUE parameters, both the one-leaf and two-leaf LUE models performed similarly for
326 needleleaf evergreen forests in temperate and Mediterranean regions. Therefore, in order to reduce the
327 number of parameters, previous investigators used fixed values of $\varepsilon_{\max}$, ε_{msu} and ε_{msh} for these PFTs
328 (Potter et al., 1993; Yuan et al., 2007; He et al., 2013; Chen et al., 2014). We thought it was acceptable
329 because the CV of them was relatively lower (Table 3) and the simulated GPP showed a little

330 improvement (Fig. 5, Fig. 6, Fig. 7).

331 4.3. Recommendations for long-term and large-scale applications

332 The study has two major implications for modeling long term carbon cycle. First, it seems to be
333 more reasonable to take the seasonal variations of these three main photosynthetic parameters into
334 account for long-term modeling applications for most PFTs. In contrast, the low variations of posterior
335 distributions of the maximum LUE parameters for NEF in mid- and low-latitude climate areas in all
336 seasons and for all other PFTs in the temperate and boreal regions in summer, which indicated that
337 these parameters could be constant for modeling purposes.

338 In addition to LAI and ambient temperature, the variations of $\varepsilon_{\max}$, ε_{msu} and ε_{msh} across different
339 PFTs might also be caused by several other factors, including forest age, nitrogen content of leaves, and
340 fraction of diffuse radiation. These factors have not been included yet in the SL-LUE and TL-LUE
341 models, suggesting the necessity of further improving their parameterization for a better simulation of
342 GPP. The inclusion of the changes in LUE with the factors mentioned above will further improve the
343 ability of LUE models to simulate GPP. Thus, a function of them should be used to describe the
344 seasonal variations of the photosynthetic capacity parameters. Secondly, our study indicated that
345 parameters estimated by the Bayesian method based on half-hourly gas-exchange data have a strong
346 linear relationship for most PFTs. This relationship could be used for estimating maximum LUE of
347 sunlit and shaded leaves with unique determination solution by taking the relationship here as a
348 constraint condition.

349 As the canopy-scale CO₂ fluxes are the integral representation of the individual leaf-scale
350 photosynthesis process, the eddy covariance measurements can be used to obtain the biological
351 parameters for the terrestrial ecosystem models. However, there is still much to learn about the
352 differences in parameters determined by data at different scales (e.g., leaf-scale and canopy-scale)
353 using more flux data, and the mechanistic correlation between them.

354 **5. Conclusions**

355 By comparing the performances of the LUE models with and without consideration of seasonal
356 parameterization adjustment for 18 PFTs, the main findings can be as follows:

357 (1) Consideration of the seasonal variations of the maximum LUE parameters ($\varepsilon_{\max}$, ε_{msu} and
358 ε_{msh}) was more satisfactory in GPP simulation than with default annual parameters (especially in
359 spring and winter). For most PFTs, namely in temperate and boreal climate regions in the cold seasons
360 and in the tropical and Mediterranean climate regions in the warm seasons, the seasonal fluctuations of
361 photosynthetic parameters should be incorporated in estimating GPP; while for the needleleaf
362 evergreen forests in mid- and low- latitude, it is acceptable to estimate GPP for all seasons with annual
363 parameters.

364 (2) Even with seasonal parameters, both the one-leaf and two-leaf LUE models cannot correctly
365 capture the seasonal GPP dynamics for some PFTs in Mediterranean and tropical regions (e.g.,
366 Tropical-BEF, C3-C4 grass). Further improvement in the LUE models is required based on more and
367 better cold-season observations and incorporate the seasonal variations of the other key parameters and
368 variables for these PFTs.

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784

Figures and Tables

Table 1.

ID, climate type, vegetation type and other characteristics of the study sites used for model calibration and validation.

Site ID ^a	Lat(°N)	Lon(°E)	Elev(m)	PFTs (Biomes Types ^b and Climate Zones)	Average annual Temperature (°C)	Precipitation (mm.yr ⁻¹)	References
CA-Ca1	49.867	-125.334	313	Temperate-NEF	9.93	1456	<i>Schwalm et al., 2007</i>
CA-Ca3	49.534	-124.900	120	Temperate-NEF	9.94	1683	<i>Jassal et al., 2008</i>
DE-Tha	50.964	13.567	380	Temperate-NEF	7.70	804	<i>Grünwald et al., 2007</i>
CN-Qia	26.741	115.058	64	Temperate-NEF	18.95	1467	<i>Zhang et al., 2010</i>
ES-ES1	39.346	-0.319	1	Mediterranean-NEF	17.69	457	<i>Berbigier et al., 2001</i>
CA-Obs	53.987	-105.118	629	Boreal-NEF	0.79	406	<i>Brümmer et al., 2012</i>
CA-Qfo	49.693	-74.342	382	Boreal-NEF	-0.36	962	<i>Raczka et al., 2013</i>
CA-Ojp	53.916	-104.692	579	Boreal-NEF	0.12	431	<i>Barr et al., 2013</i>
CA-NS1	55.879	-98.484	253	Boreal-NDF	-2.89	500	<i>COURSOLLE et al., 2012</i>
FI-Hyy	61.847	24.295	185	Boreal-NDF	3.80	709	<i>Sulkava et al., 2012</i>
RU-Ylr	62.255	129.241	214	Boreal-NDF	-10.37	241	<i>Eugster et al., 2000</i>
FR-Pue	43.741	3.596	270	Mediterranean-BEF	13.50	883	<i>Misson et al., 2010</i>
IT-Cpz	41.705	12.376	9	Mediterranean-BEF	15.99	778	<i>Garbulsky et al., 2008</i>
BR-Sa1	-2.857	-54.959	90	Tropical-BEF	26.13	2075	<i>Hutyra et al., 2008</i>
BR-Sa3	-3.018	-54.971	100	Tropical-BEF	26.12	2044	<i>Fisher et al., 2009</i>
TH-Sak	14.492	101.916	470	Tropical-BEF	24.37	1027	<i>Fisher et al., 2009</i>
US-Los	46.083	-89.979	485	Temperate-BDF	4.08	828	<i>Bakwin et al., 2004</i>
CH-Lae	47.478	8.365	645	Temperate-BDF	7.80	1222	<i>Smith et al., 2010</i>
JP-Tak	36.146	137.423	1355	Temperate-BDF	6.54	1024	<i>Saitoh et al., 2015</i>
IT-Co1	41.849	13.588	1645	Mediterranean-BDF	7.32	971	<i>Valentini et al., 1996</i>
US-MOz	38.744	-92.200	212	Mediterranean-BDF	12.11	986	<i>Gu et al., 2006</i>
DE-Gri	50.949	13.513	385	Boreal-BDF	7.20	853	<i>Gilmanov et al., 2010</i>
DE-Hai	51.079	10.452	430	Boreal-BDF	8.30	720	<i>Gioli et al., 2004</i>
DK-Sor	55.487	11.646	40	Boreal-BDF	8.20	660	<i>Pilegaard et al., 2003</i>
CA-Oas	53.629	-106.198	580	Boreal-BDF	0.34	429	<i>Barr et al., 2007</i>
Th-Mae	14.576	98.844	231	Tropical-BDF	26.02	2266	<i>Huete et al., 2006</i>
ZM-Mon	-15.438	23.253	1094	Tropical-BDF	25.00	945	<i>Merbold et al., 2011</i>
CA-Mer	45.409	-75.519	65	Temperate-BDS	6.07	891	<i>Lafleur et al., 2003</i>
CA-NS6	55.917	-98.964	244	Boreal-BDS	-3.08	495	<i>Goulden et al., 2006</i>
BW-Ma1	-19.916	23.561	13.5	Tropical-SAV	22.00	493	<i>Veenendaal et al., 2004</i>
CG-Tch	-4.289	11.656	1	Tropical-SAV	25.70	1150	<i>Ciais et al., 2011</i>
ZA-Kru	-25.020	31.497	357	Tropical-SAV	21.90	547	<i>Archibald et al., 2009</i>
JP-Tom	42.737	141.521	115	Temperate-MF	6.72	1156	<i>Hirano et al., 2003</i>
CN-Cha	42.403	128.096	745	Temperate-MF	2.16	664	<i>Zhang et al., 2010</i>
BE-Vie	50.306	5.997	450	Boreal-MF	7.80	1062	<i>Sulkava et al., 2011</i>
CA-Gro	48.217	-82.156	340	Boreal-MF	1.30	831	<i>Bernier et al., 2006</i>
AT-Neu	47.116	11.320	970	C ₃ grass	6.30	852	<i>Wohlfahrt et al., 2008</i>
CN-Nmg	43.500	117.450	1720	C ₃ grass	0.70	343	<i>Lei et al., 2012</i>
IE-Dri	51.987	-8.752	187	C ₃ grass	9.18	1084	<i>Montaldo et al., 2007</i>
US-Ton	38.432	-120.966	177	C ₃ and C ₄ grass	15.80	559	<i>Fisher et al., 2008</i>
US-FPe	48.308	-74.434	638	C ₃ and C ₄ grass	5.48	335	<i>Gilmanov et al., 2010</i>
US-Wkg	31.736	109.942	1531	C ₃ and C ₄ grass	15.64	407	<i>Scott, 2010</i>
FI-Kaa	69.141	27.295	155	C ₃ grass, arctic	-1.40	454	<i>Aurela et al., 2001</i>
CN-Hab	37.613	101.305	3183	C ₃ grass, arctic	1.43	351	<i>Yi et al., 2006</i>

^a The site ID are taken from FLUXNET.

^b Biome types: needleleaf evergreen forest (NEF), needleleaf deciduous forest (NDF), broadleaf evergreen forest (BEF), broadleaf deciduous forest (BDF), broadleaf deciduous shrub (BDS), grassland (C₃ grass, C₃ and C₄ grass, C₃ grass, arctic), Mixed forest (MF), savanna (SAV).

794 **Table 2.**

795 Plant Functional Types, Climate Rules and Dependent parameters used in light use efficiency models

796 for GPP estimation, including $\varepsilon_{\max}$, $VPD_{\max}$, $VPD_{\min}$, $T_{\max}$, $T_{\min}$, albedo (α) and clumping index (Ω) of

797 different plant functional types (PFTs).

PFTs (Biomes Types and Climate Zones)	clumping index ^a	Stem area index ^a	$VPD_{\min}$ ^b [K Pa]	$VPD_{\max}$ ^b [K Pa]	$T_{\min}$ ^b [°C]	$T_{\max}$ ^b [°C]	Albedo ^b [-]	$\varepsilon_{\max}$ ^b [g C M J ⁻¹]	Climate Rules ^c
NEF, temperate	0.55	0.90	0.65	2.50	-8.00	8.31	0.12	1.008	$T_c > -19^{\circ}\text{C}$ and $\text{GDD} > 1200$
NEF, boreal	0.55	0.90	0.65	2.50	-8.00	8.31	0.12	1.008	$T_c \leq -19^{\circ}\text{C}$ or $\text{GDD} \leq 1200$
NEF, Mediterranean	0.55	0.90	0.65	2.50	-8.00	8.31	0.12	1.008	-
NDF, boreal	0.68	0.90	0.65	3.10	-8.00	10.4	0.12	1.103	-
BEF, tropical	0.63	0.90	1.10	3.90	-8.00	9.09	0.18	1.159	$T_c > 15.5^{\circ}\text{C}$
BEF, Mediterranean	0.63	0.90	1.10	3.90	-8.00	9.09	0.18	1.159	$T_c \leq 15.5^{\circ}\text{C}$
BDF, tropical	0.70	0.90	0.65	2.50	-8.00	7.94	0.18	1.044	$T_c > 15.5^{\circ}\text{C}$
BDF, temperate	0.70	0.90	0.65	2.50	-8.00	7.94	0.18	1.044	$-15^{\circ}\text{C} < T_c \leq 15.5^{\circ}\text{C}$ and $\text{GDD} > 1200$
BDF, boreal	0.70	0.90	0.65	2.50	-8.00	7.94	0.18	1.044	$T_c \leq -15^{\circ}\text{C}$ or $\text{GDD} \leq 1200$
BDF, Mediterranean	0.70	0.90	0.65	2.50	-8.00	7.94	0.18	1.044	-
BDS, temperate	0.70	0.66	0.65	3.60	-8.00	8.80	0.17	0.774	$T_c > -19^{\circ}\text{C}$ and $\text{GDD} > 1200$ and ($P_{\text{ann}} \leq 520\text{mm}$ or $P_{\text{win}} \leq 2/3 P_{\text{ann}}$)
BDS, boreal	0.70	0.66	0.65	3.60	-8.00	8.80	0.17	0.774	$T_c \leq -19^{\circ}\text{C}$ or $\text{GDD} \leq 1200$
SAV, tropical	0.70	0.90	0.65	3.10	-8.00	11.39	0.17	0.800	-
MF, temperate	0.70	0.90	0.65	2.50	-8.00	8.50	0.17	1.116	-
MF, boreal	0.70	0.90	0.65	2.50	-8.00	8.50	0.17	1.116	-
C ₃ grass, arctic	0.80	0.90	0.65	3.50	-8.00	12.02	0.21	0.604	$\text{GDD} < 1000$
C ₃ grass	0.80	0.90	0.65	3.50	-8.00	12.02	0.21	0.604	$\text{GDD} > 1000$ and ($T_w \leq 22^{\circ}\text{C}$ or $P_{\text{mon}} \leq 25\text{mm}$ and for months with $T > 22^{\circ}\text{C}$)
C ₃ and C ₄ grass	0.73	0.90	0.65	3.50	-8.00	12.02	0.21	0.604	50% C ₃ and C ₄ if $\text{GDD} > 1000$ and neither the C ₃ nor C ₄ criteria are met

798 ^a Data were extracted from [Tang et al., 2007](#); [He et al., 2013](#).

799 ^b Data were extracted from [zhao et al., 2010](#); [Cescatti et al., 2012](#); [Liang et al., 2012](#); [He et al., 2013](#).

800 ^c Rules referred to [Bonan et al., 2002](#).

802 **Table 3.**
 803 The coefficients of variation (CV= standard deviations/mean×100%) of the optimized posterior
 804 probability distribution of the maximum LUE ($\varepsilon_{\max}$), maximum LUE of sunlit and shaded leaves
 805 (ε_{msu} and ε_{msh}) for different PFTs in four seasons.

Plant Funtional Types (PFTs)	Coefficients of variation (CV, %)											
	$\varepsilon_{\max}$ (gC·MJ ⁻¹)				ε_{msu} (gC·MJ ⁻¹)				ε_{msh} (gC·MJ ⁻¹)			
	Spr.	Sum.	Fall	Win.	Spr.	Sum.	Fall	Win.	Spr.	Sum.	Fall	Win.
Boreal-BDF	43.22	9.18	45.23	- ^a	75.38	7.08	97.43	-	24.34	11.14	37.58	-
Boreal-NDF	28.32	4.06	0.02	-	2.65	34.16	30.18	-	2.03	28.67	51.37	-
Mediterranean-BDF	30.73	8.22	24.41	-	50.41	26.3	23.81	-	21.28	47.48	17.23	-
Temperate-BDF	18.01	13.74	57.49	-	34.24	10.22	128.9	-	21.98	12.05	10.80	-
Tropical-BDF	23.53	6.39	16.3	-	22.6	8.98	38.51	-	44.88	11.87	2.49	-
Boreal-BDS	102.5	7.26	41.39	-	74.01	23.62	26.28	-	58.97	11.30	40.58	-
Temperate-BDS	53.87	5.58	20.67	-	74.19	30.35	31.92	-	46.39	25.74	27.47	-
Boreal-NEF	87.75	6.59	53.51	29.85	62.76	44.26	44.65	26.34	90.40	23.04	50.30	26.95
Mediterranean-BEF	8.31	24.17	20.19	3.82	6.140	43.45	51.35	23.30	13.20	16.08	38.38	21.16
Mediterranean-NEF	5.39	20.04	5.87	11.17	21.37	27.83	16.20	66.19	11.41	12.57	18.28	23.83
Temperate-NEF	4.54	6.08	4.28	22.68	26.08	35.96	56.80	139.5	9.45	2.92	13.03	7.12
Tropical-BEF	22.58	7.64	5.23	16.35	67.57	66.13	56.95	33.01	9.49	3.57	7.08	17.79
Boreal-MF	6.93	12.64	12.74	53.04	61.26	61.36	75.19	51.45	28.82	6.40	9.12	30.10
Temperate-MF	96.97	13.94	60.83	23.66	100.9	39.68	62.74	31.45	68.09	9.81	29.72	54.63
C3-C4-grass	17.6	23.74	45.28	90.81	55.84	19.44	54.24	74.95	23.98	41.74	28.52	75.44
C3-grass	10.64	20.67	13.94	14.03	9.66	55.47	35.48	15.87	18.35	9.48	24.66	15.92
C3-grassArctic	10.73	33.33	71.82	48.54	16.78	22.29	58.38	69.33	121.0	18.57	115.4	48.25
Tropical-SAV	45.43	0.47	26	22.39	82.10	44.20	37.96	16.39	33.39	85.81	10.42	73.85

806 Note: ^a parameterization from March to November for deciduous vegetations, from January to December for other vegetations.
 807

808 **Table 4.**

809 Bias and root-mean-square error (RMSE) of half-hourly GPP (in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with respect to
810 individual months and seasons.

Months /Seasons	LUE _{def}		SL-LUE		TL-LUE	
	Bias	RMSE	Bias	RMSE	Bias	RMSE
Jan.	-0.38(±0.81) ^a	1.79(±1.45)	-0.29(±0.39)	1.57(±1.33)	-0.21(±0.22)	1.39(±0.96)
Feb.	-0.59(±1.14)	2.31(±1.79)	-0.38(±0.48)	1.85(±1.65)	-0.25(±0.35)	1.61(±1.42)
Mar.	-0.21(±1.01)	2.41(±1.51)	-0.35(±0.44)	1.82(±1.47)	-0.30(±0.38)	1.69(±1.23)
Apr.	0.24 (±1.17)	3.10 (±1.34)	-0.43 (±0.38)	2.21 (±1.31)	-0.29 (±0.26)	1.97 (±1.07)
May.	-0.46(±1.57)	3.95(±1.71)	-0.64(±0.43)	3.20(±1.65)	-0.41(±0.40)	2.81(±1.50)
Jun.	-1.53(±1.74)	4.42(±2.20)	-0.96(±0.62)	3.90(±1.88)	-0.59(±0.43)	3.40(±1.55)
Jul.	-1.42(±1.72)	4.22(±2.30)	-0.89(±0.61)	3.60(±1.92)	-0.53(±0.37)	3.12(±1.60)
Aug.	-1.05(±1.54)	3.98(±2.05)	-0.79(±0.53)	3.35(±1.69)	-0.47(±0.33)	2.86(±1.40)
Sep.	-0.73(±1.32)	3.57(±1.98)	-0.61(±0.42)	2.98(±1.70)	-0.37(±0.28)	2.60(±1.50)
Oct	-0.23(±0.78)	2.68(±1.48)	-0.41(±0.35)	2.30(±1.31)	-0.25(±0.26)	2.04(±1.14)
Nov.	-0.19(±0.16)	1.94(±1.33)	-0.30(±0.32)	1.61(±1.26)	-0.23(±0.22)	1.47(±1.05)
Dec.	-0.25(±0.67)	1.75(±1.31)	-0.19(±0.41)	1.49(±1.29)	-0.10(±0.27)	1.40(±1.12)
Winter ^b	-0.32(±0.73)	1.78(±1.38)	-0.23(±0.38)	1.48(±1.30)	-0.15(±0.23)	1.35(±1.06)
Spring	-0.16(±1.05)	3.06 (±1.42)	-0.43(±0.37)	2.38 (±1.32)	-0.30(±0.28)	2.10 (±1.13)
Summer	-1.19(±1.53)	3.88 (±2.08)	-0.79(±0.54)	3.29 (±1.67)	-0.51(±0.33)	2.89 (±1.36)
Fall	-0.35(±0.70)	2.67(±1.43)	-0.39(±0.32)	2.25(±1.24)	-0.25(±0.20)	1.97(±1.03)
All year	-0.51(±0.30)	2.95(±1.37)	-0.52(±0.33)	2.73(±1.25)	-0.33(±0.23)	2.40(±1.05)

811 Note: ^a Values in parentheses are standard deviations. ^b Winter is composed of December, January and February with one year divided
812 into four seasons.

813

814 **Fig. 1.**

815 Spatial distribution of the 46 sites (for details see [Table 1](#)) at which measured GPP was used for

816 calibrating and validating the LUE models. The background is the synergetic global land cover map

817 (synGLC) based on Bayes theorem ([Xu et al., 2014](#)).

818

819 **Fig. 2.**

820 Posterior mean estimates for seasonal variation of the LUE parameters ($\epsilon_{\max}$, ϵ_{msu} and ϵ_{msh} from left to
 821 right) given by the Bayesian approach based on in situ data for (a) deciduous forests and shrubs; (b)
 822 evergreen forests; (c) mixed forests; (d) grassland; (e) savanna. Among them, from March to November
 823 for deciduous vegetations, from January to December for other vegetations.

Fig. 3.

Boxplots of Taylor skill (S) for GPP by models and seasons (from Spring to Winter) across eighteen plant functional types. Panels show the interquartile range (box), mean (square), median (solid line), range (whiskers), and outliers (cross). The models and seasons are sorted by the median Taylor skill.

831 **Fig. 4.**

832 R^2 , root-mean-square error (RMSE) and Bias (observations minus simulations) of half-hourly GPP (in

833 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with respect to individual season for one-leaf and two-leaf LUE models, respectively.

834 Panels show the interquartile range (box), mean (square), median (solid line), range (whiskers), and

835 outliers (cross). The models and seasons are sorted by the median.

836 **Fig. 5.**

837 Comparing the models' performance for eighteen PFTs from spring to fall and ten PFTs in winter

838 (Table 2). The statistics in the Taylor diagram were calculated from the simulated (SL-LUE, TL-LUE,

839 and LUE_{def}) and observed GPP values of the selected year for each plant functional type: (a) average

840

841 values in spring, (b) average values in summer, (c) average values in fall and (d) average values in
 842 winter. An ideal model has a standard deviation ratio (σ_{norm}) of 1.0 and a correlation coefficient of 1.0
 843 (REF, the reference point).

844

845 **Fig. 6.**

846 The improvement of GPP simulations after considering the seasonal variations of the maximum LUE
 847 parameters for different PFTs. Pannels (a)-(b) represent the improvement of R^2 with respect to
 848 individual seasons for the one-leaf and two-leaf LUE models, respectively. Pannels (c)-(d) show the

849 decrease of RMSE ($\text{gC} \cdot \text{m}^{-2} \cdot \text{season}^{-1}$) with respect to individual seasons for the one-leaf and two-leaf
850 LUE models, respectively.

Fig. 7.

Monthly averaged diurnal composites of observed GPP (dark lines) and simulated GPP. The monthly-averaged diurnal composites were calculated by accumulating the data of the same half-hourly point over each month and then averaging.

859

860 **Fig. 8.**

861 The seasonally averaged LAI (LAI, LAI_{su} and LAI_{sh}, m²/m²) and ambient temperature (T_{air-avg}, °C)

862 versus the optimized seasonal maximum LUE (ε_{max}, ε_{msu} and ε_{msh}, gC·MJ⁻¹) parameters for 18 PFTs,

863 respectively.

864
865 **Fig. 9.**

866 The optimized monthly maximum LUE ($\epsilon_{\max}$, $\text{gC} \cdot \text{MJ}^{-1}$) *versus* maximum LUE for sunlit and shaded
867 leaves (ϵ_{msu} and ϵ_{msh} , $\text{gC} \cdot \text{MJ}^{-1}$) for 18 different vegetation types.