1   **Comparison of four light use efficiency models for estimating**
2   **terrestrial gross primary production**

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Abstract:

Light use efficiency (LUE) models that with different structures (i.e., methods to address environmental stresses on LUE) have been widely used to estimate terrestrial gross primary production (GPP) because of their theoretical soundness and practical conveniences. However, a systematic validation of those models with field observations across diverse ecosystems is still lacking and whether the model can be further improved by structural optimization remains unclear. Using GPP estimates at global 51 eddy covariance flux towers that cover a wide climate range and diverse vegetation types, we evaluated the performances of the four major LUE models (i.e., Carnegie-Ames-Stanford approach (CASA), Global Production Efficiency Model (GLO-PEM), Vegetation Photosynthesis Model (VPM), and Eddy Covariance-Light Use Efficiency (EC-LUE)) and examined the possible further improvement of the better-performed model(s) via model structural optimization. Our results showed that the GLO-PEM, VPM, and EC-LUE exhibited the similar capabilities in simulating GPP (explained around 68% of the total variations) and overall performed better than CASA (58%). Nevertheless, the EC-LUE and VPM were the optimal ones because they required less model inputs than the GLO-PEM. For the two optimal models, we found that the minimum method is better than the multiplication approach to integrate multiple environmental stresses on LUE. Moreover, we found that the VPM can be further improved by incorporating the constraint of water vapor deficit (VPD_s). We suggested that a modified VPM by using minimum method and adding VPD_s may be the best model in estimating large-scale GPP if high-quality remote sensing data

34 available, otherwise, the modified models with the water stress reflected by VPD_s
35 only is optimal.
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1 Introduction

Gross Primary Production (GPP), the sum of photosynthetic carbon uptake by vegetation, is a critical indicator of ecosystem carbon cycle (Field et al., 1995; Goetz et al., 1999; Chapin et al., 2002). Because GPP cannot be directly observed at the regional or global scale, models have emerged as the major approaches for predicting terrestrial ecosystem GPP over large areas recently (Canadell et al., 2000). Among these, the light use efficiency (LUE) models have been widely used because of its theoretical soundness and practical convenience (Running et al., 2000).

The LUE models were usually developed based on two basic assumptions (Running et al., 2004): (a) the ecosystem GPP related directly to absorbed photosynthetically active radiation (APAR) through LUE, and (b) the actual LUE is lower than the potential value because of environmental stresses (e.g., low and high temperature and drought) (Landsberg, 1986). The GPP function of them takes the form of $GPP = PAR \times fPAR \times \varepsilon_{max} \times f$. Therein, PAR is the incident photosynthetically active radiation ($MJ\ m^{-2}$) per day or month, $fPAR$ is the fraction of PAR absorbed by the vegetation canopy, ε_{max} is the potential LUE ($g\ C\ m^{-2}\ MJ^{-1}\ APAR$) without environment stress, and f is a scalar varying from 0 to 1 that represents the reduction of LUE relative to ε_{max} due to environmental stresses (e.g., air temperature stress and water availability). The $\varepsilon_{max} \times f$ indicates the actual LUE. Note that the actual LUE can be also defined as the function of Photochemical Reflectance Index (PRI) (Drolet et al., 2005, 2008), which is out the scope of this study.

In practice, several LUE models, such as Carnegie-Ames-Stanford approach (CASA, Potter et al., 1993), Global Production Efficiency Model (GLO-PEM, Prince and Goward, 1995; Goetz et al., 1999), Moderate Resolution Imaging Spectroradiometer (MODIS) GPP algorithm (Running et al., 1999, 2000), Vegetation Photosynthesis Model (VPM, Xiao et al., 2004a, b), and Eddy Covariance-Light Use Efficiency (EC-LUE, Yuan et al., 2007), had been developed using different f scalars. Specifically, there were two major differences in the structure of f across LUE models. First, the strategies to integrate multiple environmental stresses into f were different. Models such as GLO-PEM, CASA, and VPM (Potter et al., 1993; Prince and Goward, 1995; Xiao et al., 2004a) used the multiplicative method, while the EC-LUE (Yuan et al., 2010) utilized the minimum method based on the theory of Liebig's law. Second, the water stress scalar (f_w), a key environmental constraint on the LUE, was quantified in different ways. It had been estimated by the water stress in the soil and (or) in the air (e.g., atmosphere water vapor deficit) in some models (e.g., GLO-PEM and CASA), and via land water index that can reflect the vegetation water stress in the other models (e.g., VPM and EC-LUE). For instance, f_w was calculated by the evaporative fraction in the EC-LUE model (Yuan et al., 2007), which was considered to be a good indicator of moisture conditions (Kurc and Small, 2004). However, the performances of those models are rarely validated with field observations across large areas (e.g., Yuan et al., 2010), and little is known about whether the better-performed LUE models can be further improved by model structural optimization (Medlyn, et al., 2011; Hashimoto et al., 2012; Yang et al., 2013). Specifically, most previous efforts

focused on only one of the LUE models and compared the model with other kinds of models at quite a few flux sites (Zhang et al., 2007; Coops et al., 2009; Wu et al., 2010). Yuan et al. (2014) might be the first to compare multiple LUE models via field observations over large areas, but they did not investigate the strength and weakness of the various model structures, as a result, the potential of model improvement by structural optimization.

In this study, we evaluated the performances of the four widely used LUE models (i.e., CASA, GLO-PEM, VPM, and EC-LUE) by *in-situ* GPP estimates at 51 global eddy covariance (EC) flux towers via using model-independent parameter values. Our objectives were to (1) identify the better-performed model(s) in estimating GPP over large areas and (2) investigate the optimal model structure, including the strategy to integrate multiple environmental stresses (i.e., multiplication or minimum) and the method to address water stress, for the further improvement of the LUE models. The performance of the well-known LUE-based MODIS-GPP algorithm was not assessed because the daily minimum temperature, an important parameter for the model, was not available in this study. However, the water stress expression used by it was evaluated when we discussed the optimal model structure.

2 Materials and Methods

2.1 Model Overview

2.1.1 The CASA model

Carnegie-Ames-Stanford approach (CASA) developed by Potter et al. (1993) can estimate monthly GPP and NPP with satellite data, monthly temperature and precipitation, and soil properties. The actual LUE (ϵ_g , g C m⁻² MJ⁻¹ APAR) in the model is defined as follows:

$$\epsilon_g = \epsilon_{\max} \times ft1 \times ft2 \times fw \quad (2.1a)$$

$$ft1 = 1.1814(1 + e^{(0.3(-T_{\text{opt}} - 10 + T))}) / (1 + e^{(0.2(T_{\text{opt}} - 10 - T))}) \quad (2.1b)$$

$$ft2 = 0.8 + 0.02T_{\text{opt}} - 0.0005T_{\text{opt}}^2 \quad (2.1c)$$

$$fw = W_s = 0.5 + EET / PET \quad (2.1d)$$

where $\epsilon_{\max}$ is the potential LUE (g C m⁻² MJ⁻¹ APAR), $ft1$ represents the effects of very high and very low temperatures on $\epsilon_{\max}$, $ft2$ indicates the effects of the temperature above or below the optimum temperature (T_{opt}) on $\epsilon_{\max}$, and fw represented by soil moisture condition (W_s) illustrates the water stress on $\epsilon_{\max}$. EET and PET are the estimated and potential evapotranspiration, respectively.

EET is calculated using the method proposed by Preisley and Taylor (1972) as follows:

$$EET = \min(PPT + (PET - PPT)RDR, (PPT + (SM - WPT))), \text{ when } PPT < PET \quad (2.1e)$$

$$EET = PET, \text{ when } PPT \geq PET \quad (2.1f)$$

$$RDR = (1 + a)(1 + aSM^b) \quad (2.1g)$$

where RDR is the relatively drying rate scalar for potential water extraction, SM is the soil moisture (volumetric moisture content, m/m), WPT , a , and b are the

texture-dependent empirical coefficients from Saxton et al. (1986).

Soil moisture is estimated using a one-layer bucket model (Malmstrom et al., 1997):

$$SM_t = SM_{t-1} - (PET_t - PPT_t)RDR_{t-1}, \text{ for } PPT < PET \quad (2.1h)$$

$$SM_t = SM_{t-1} - (PPT_t - PET_t), \text{ for } PPT \geq PET \quad (2.1i)$$

where SM_t and SM_{t-1} are the soil moisture at the t and $t-1$ days, respectively, in order to keep accordance with the temporal resolution of MODIS products that being used by us.

2.1.2 The GLO-PEM model

Global Production Efficiency Model (GLO-PEM) developed by Prince and Goward (1995) is driven by the variables derived almost entirely from satellite products. GLO-PEM has been successfully utilized to estimate global terrestrial GPP and NPP (Prince and Goward, 1995; Cao et al., 2004). The ε_g in the model is calculated as follows:

$$\varepsilon_g = \varepsilon_{\max} \times ft \times fw \quad (2.2a)$$

$$fw = W_s \times VPD_s \quad (2.2b)$$

where ft represents the effects of temperature on $\varepsilon_{\max}$, and fw is reflected by soil moisture condition (W_s) and atmosphere moisture condition (VPD_s).

$$ft = \frac{(T - T_{\min})(T - T_{\max})}{[(T - T_{\min})(T - T_{\max})] - (T - T_{opt})^2} \quad (2.2c)$$

$$VPD_s = 1 - 0.05\delta_q \quad (\text{when } 0 < \delta_q \leq 15), \text{ or } 0.25 \quad (\text{when } \delta_q > 15) \quad (2.2d)$$

$$\delta_q = Q_w(T) - q \quad (2.2e)$$

where $T_{\min}$ and $T_{\max}$ are the minimum and maximum temperature for photosynthetic activities, respectively, δ_q is the specific humidity deficit (g kg^{-1}), $Q_w(T)$ is the saturated specific humidity at the air temperature, and q is the specific air humidity. ft was set to be zero if the air temperature was lower than $T_{\min}$. Since the calculation of W_s in the original GLO-PEM needs the variable of equilibrium evapotranspiration, and the accuracy of which is poor at local scale (Jarvis & MacNaughton, 1986; Prentice et al., 1992, 1993; Cao et al., 2004), we thus adopted the W_s function in CASA (Eq. (2.1d)) for GLO-PEM in this study.

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151 **2.1.3 The VPM model**

The Vegetation Photosynthesis Model (VPM) (Xiao et al., 2004a, b) assumes that the leaf and forest canopies consist of photosynthetically active vegetation (mostly chloroplast) and non-photosynthetic vegetation (mostly senescent foliage, branches, and stems). The VPM has been successfully used to simulate GPP in different ecosystems, including tropical evergreen forest (Xiao et al., 2005b), temperate deciduous forest (Xiao et al., 2004a), evergreen needle leaf forest (Xiao et al., 2004b), cropland (Kalfas et al., 2011), and grassland (Liu et al., 2011). The ε_g in the model is

estimated as follows:

$$\varepsilon_g = \varepsilon_{\max} \times ft \times fw \quad (2.3a)$$

$$fw = WI = \frac{1 + LSWI}{1 + LSWI_{\max}} \times P_s \quad (2.3b)$$

where ft is the same as that in GLO-PEM (Eq. (2.2b)), and fw is reflected by land water index (WI) that was calculated by satellite-derived land surface water index ($LSWI$) (Xiao et al., 2002; Boles et al., 2004) with consideration of the phenology effect on $\varepsilon_{\max}(P_s)$ (Xiao et al., 2005b).

The P_s in the model is calculated as follow:

$$P_s = \frac{1 + LSWI}{2} \text{ (before leaf full expansion) or } 1 \text{ (after leaf full expansion)} \quad (2.3c)$$

where $LSWI_{\max}$ is the maximum $LSWI$ within the plant growing season. In this study, we took the maximum $LSWI$ value within the photosynthetically active period as the $LSWI_{\max}$ when multi-year $LSWI$ data are available and assumed that P_s equaled to 1 for evergreen forests (Xiao et al., 2004a). $LSWI$ is calculated via the NIR (841–875 nm) and $SWIR$ (1628–1652 nm) bands of MODIS images as follow:

$$LSWI = \frac{\rho_{nir} - \rho_{swir}}{\rho_{nir} + \rho_{swir}} \quad (2.3d)$$

2.1.4 The EC-LUE model

The Eddy Covariance-Light Use Efficiency model (EC-LUE, Yuan et al., 2007) assumes that the LUE is controlled by air temperature or ecosystem water stress,

whichever is most limiting. The EC-LUE has been successfully used to estimate the GPP in forest, grassland, savanna, cropland, and the global GPP (Yuan et al., 2007; Yuan et al., 2010). The ε_g in which is estimated as:

$$\varepsilon_g = \varepsilon_{\max} \times \min(ft, fw) \quad (2.4a)$$

$$fw = WI = EF = \frac{LE}{LE + H} \quad (2.4b)$$

where ft is the same as that in GLO-PEM (Eq. (2.2b)), and fw represented by WI is expressed by evaporative fraction (EF) and can be calculated by the EC-measured latent heat flux (LE) and sensible heat flux (H) (W m^{-2}). Unlike the VPM, GLO-PEM, and CASA models that assume the impacts of multiple environmental stresses on $\varepsilon_{\max}$ are multiplicative, the EC-LUE hypothesizes that the influences of temperature and water stress follow the Liebig's law of minimum.

2.2 Data

We used the *in-situ* observations at 51 global EC flux sites in the Fluxnet (ORNL DAAC, 2012) to assess the performances of the above-mentioned four models (Table 1). These sites cover a wide climate range and diverse plant functional types, including savanna (4 sites), grassland (7 sites), cropland (7 sites), shrubland (2 sites), mixed forest (MF, 4 sites), deciduous broadleaf forest (DBF, 7 sites), evergreen broadleaf forest (EBF, 2 sites), and evergreen needleleaf forest (ENF, 18 sites). For each site, EC flux data were extracted from the Level 4 product (download from <http://fluxnet.ornl.gov/>). In the dataset, the half-hourly GPP were calculated by the net

ecosystem exchange and ecosystem respiration. The data gaps associated with equipment failures and unsuitable micrometeorological conditions were filled using the Artificial Neural Network method (Papale and Valentini, 2003) and/or the Marginal Distribution Sampling method (Reichstein et al., 2005). The half-hourly GPP was summed to obtain daily GPP and then averaged to 8-day interval in order to keep accordance with the temporal resolution of MODIS data.

Two MODIS products including enhanced vegetation index (EVI) and surface reflectance data (i.e., NIR (841–875 nm) and SWIR (1628–1652 nm) bands) were used in this study. These data were provided by the Oak Ridge National Laboratory's Distributed Active Archive Center (DAAC) (ORNL DAAC, 2012). EVI time series (16-day composites with a spatial resolution of 250m) were obtained from the MODIS Vegetation Indices products (MOD13Q1), and the NIR and SWIR bands data (8-day composites with a spatial resolution of 500m) were acquired from the MODIS Surface Reflectance products (MOD09A1). Based on the geo-location information (latitude and longitude) of the 51 global EC flux sites, all data were extracted from 1.5 km×1.5 km area centered on the flux tower (Wu et al., 2010). Because there always remains some biases of EVI caused by cloud-contamination or other noises (Hill et al., 2006), these data were further smoothed over seasons by asymmetric Gaussian method which was proposed to be effective in obtaining high-quality NDVI/EVI time-series (Jönssonb and Eklundha, 2004).

The half-hourly meteorological observations (e.g., PAR, air temperature, precipitation, and relative humidity) (Level 4 product) were downloaded from the

Fluxnet website (ORNL DAAC, 2012) as well. The meteorological measurements were up-scaled to daily level and then to 8-day interval. Soil attributes were acquired from the global soil properties map provided by the FAO (<http://www.fao.org>).

2.3 Analysis

As the major focus of this paper was to examine the impacts of model structure, rather than the parameters, on modelling accuracies, we used a universal set of parameters for all the models and all the vegetation types in this study. The expression of $fPAR$ was adopted from VPM (i.e., $fPAR = EVI$ (Xiao et al., 2005a)), $\varepsilon_{\max}$ was set to $2.25 \text{ g C m}^{-2} \text{ MJ}^{-1} \text{ APAR}$ (Yuan et al., 2010), $T_{\min}$, T_{opt} , and $T_{\max}$ were set to 0, 25, and 40 °C, respectively (Kotchenova et al., 2004; Xiao et al., 2004a). Then we conducted the analysis in following steps:

- 1) We identified the better-performed LUE model(s) by comparing the model accuracies of the four models at all the 51 EC sites.
- 2) We explored the optimal method to integrate environmental stresses into scalar f by comparing the performances of the better model(s) that being found in above step under the two different integration methods (i.e., multiplication and minimum).
- 3) We assessed the performances of the optimal LUE model(s) when the water stress was represented by land water stress index (WI) only, air moisture stress (VPD_s) only, or both to investigate the optimal method to define water stress. The methods to characterize VPD_s , included that of the GLO-PEM (Cao et al., 2004, Eq (2.2d)),

MODIS-GPP (Running et al., 2004), and SWH model (Hu et al., 2013). The VPD_s in MODIS-GPP (MOD_VPD_s) and SWH (SWH_VPD_s) are estimated as follows:

$$MOD\_VPD_s = \frac{VPD_{max} - VPD}{VPD_{max} - VPD_{min}} \quad (2.5)$$

where VPD_{max} is the daylight average vapor pressure deficit when the actual LUE (ϵ_g) equalled to the potential value (ϵ_{max}), VPD_{min} is the daylight average vapor pressure deficit when $\epsilon_g = 0$. VPD_{max} and VPD_{min} for each vegetation type were derived from Biome Parameter Look-Up Table (BPLUT) for MOD17 (Heinsch et al., 2003).

$$SWH\_VPD_s = \frac{VPD_{max} - VPD}{VPD_{max}} \quad (VPD > 0.5\text{kPa}) \text{ or } 1 \quad (VPD \leq 0.5\text{kPa}) \quad (2.6)$$

where VPD_{max} is 3kPa.

The correlation coefficients (R^2), root mean square error (RMSE), and bias (BIAS) between modeled results and field estimates were calculated using MATLAB (The MathWorks, Inc). A higher R^2 , lower RMSE and BIAS are believed to have a better model performance. The RMSE and BIAS are calculated as follows:

$$RMSE = \sqrt{\frac{\sum (O_i - M_i)^2}{N}} \quad (2.7)$$

$$BIAS = \frac{\sum (M_i - O_i)}{N} \quad (2.8)$$

where O_i and M_i represent the estimated and modeled GPP, respectively, and N indicates the total number of estimates at the study site.

3 Results and Discussion

3.1 Comparisons of the four LUE models in estimating GPP

Overall, the EC-LUE, GLO-PEM, and VPM explained the similar amounts of the GPP's variations, characterized by the R^2 of 0.69, 0.69, and 0.68, respectively, and performed better than the CASA model (0.58) (Table 2). Although the R^2 for the EC-LUE, GLO-PEM, and VPM were similar, the RMSE for GLO-PEM ($2.06 \text{ g C m}^{-2} \text{ day}^{-1}$) was lower than that for the VPM ($2.45 \text{ g C m}^{-2} \text{ day}^{-1}$) and EC-LUE ($2.41 \text{ g C m}^{-2} \text{ day}^{-1}$). Notably, all the four models underestimated the ecosystem GPP, with the least bias in the CASA model (i.e., $-0.43 \text{ g C m}^{-2} \text{ day}^{-1}$).

In addition, the model performances varied greatly across vegetation types (Figs. 1-2). At the non-forest sites (i.e., savanna, grassland, cropland, and shrubland), the mean R^2 for EC-LUE (i.e., 0.67) was higher than that for VPM, GLO-PEM, and CASA by 7.11%, 8.07%, and 36.79%, respectively. However, at the forest sites (i.e., MF, DBF, EBF and ENF), the mean R^2 for VPM and GLO-PEM were the same (i.e., 0.72), and higher than that for EC-LUE and CASA by 3.57% and 12.90%, respectively. Moreover, the VPM had the largest R^2 in DBF while the GLO-PEM had the greatest R^2 in MF, EBF, and ENF. CASA exhibited the poorest accuracy in all the vegetation types than the other three models.

The higher accuracies of EC-LUE, GLO-PEM, and VPM than CASA indicated that all these three models might be robust in estimating ecosystem GPP over large areas. However, it would be better if with briefer model structure and fewer input

variables without sacrificing of model accuracy (Goetz et al., 1999; Yang et al., 2013). Among those three models, the water stress expression (i.e., f_w) in GLO-PEM (Eq. (2.1d)) was more complicated than the other two models (EC-LUE and VPM). Specifically, the f_w for GLO-PEM needs soil moisture information which required more input variables including climate data (e.g., precipitation) and soil properties (e.g., soil texture) than the other two models. In contrast, the calculation of f_w for EC-LUE and VPM was much simple and the required data (e.g., MODIS surface reflectance products) was easy to obtain. Therefore, considering both the model performance and input variables, VPM and EC-LUE were the optimal LUE models for simulating GPP over large areas.

The better performances of EC-LUE and VPM compared to CASA in all the vegetation types may be due to the more reasonable expression of f_w and/or temperature stress (i.e., f_t) in the two models than CASA. First, the CASA assumes little water stress on the GPP's variability (Potter et al., 1993), and used the value of 0.5 to 1 for f_w . However, the value of f_w estimated by us was much less than 0.5 at the water-limited non-forest sites (e.g., grassland, shrubland, and savanna). For example, the average values of f_w in EC-LUE and VPM were 0.24 and 0.39 at the non-forest sites, respectively. These suggested that the f_w of CASA might be not enough to reflect the drought stress on the GPP in non-forest sites. This can be further exemplified by the increased R^2 and decreased RMSE for CASA at the non-forest sites when we used f_w of EC-LUE and VPM (Eq. (2.4b) and (2.3b)) in the model (R^2 increased by 19.41% vs. 1.90%, and RMSE decreased by 51.30% vs. 54.83%).

Second, the CASA used the optimal temperature only to represent the f_t , while the VPM and EC-LUE utilized the minimum, maximum, and optimal temperature to reflect the effects of the f_t on the vegetation production. Our results demonstrated that the modeling accuracy of CASA improved significantly after using the similar f_t (Eq. (2.2c)) of the VPM and EC-LUE at all the sites. Specifically, the mean R^2 at the non-forest sites and forest sites increased by 8.91% and 10.09%, respectively. Notably, the expression of environmental stresses in the modified CASA (with f_t of the VPM and EC-LUE) was just short of the VPD_s (Eq. (2.2d)) compared to GLO-PEM (Eq. (2.2a)), but the mean R^2 (0.64) of the modified CASA in all the vegetation types was 7.81% lower than that of GLO-PEM (0.69), suggesting that the performances of the two optimal LUE models (VPM and EC-LUE) might be further improved by adding VPD_s , and we will discuss this in section 3.3.

The varying performances of the EC-LUE, GLO-PEM, and VPM across vegetation types can be mainly attributed to the different water stress scalars (f_w) used by them. Specifically, the EC-LUE performed best (compared to the GLO-PEM and VPM) in the non-forest sites (e.g., savanna and grassland that usually have semi-arid climates), since the f_w used by it (evaporative fraction, EF) related closely to the surface soil water content, which was documented as the major water stress on plant growth in those kinds of ecosystems (Sala et al., 1988; Kurc and Small, 2004). By contrast, the GLO-PEM and VPM performed better in the forest sites (characterized by the high annual precipitation and the deep roots system for accessing deep soil water in dry seasons), since the f_w utilized by them (soil water condition (W_s) and

atmosphere moisture condition (VPD_s), and the land surface water index (LSWI) , respectively) can reflect both the leaf and canopy water content, which were believed to mainly limit the light use efficiency of plants in those ecosystems (Nepstad et al., 1994; Xiao et al., 2005b). Moreover, the VPM had better performance than GLO-PEM in DBF because the f_w in it included the phenology scalar (P_s), which can account for the effects of leaf age on photosynthesis (Xiao et al., 2004b). Many studies suggested that the development of new leaves and senescence of old leaves (i.e., phenology) impacted the photosynthetic capacity significantly in DBF (Wilson et al., 2001; Barr et al. 2007, Richardson et al. 2007). Comparatively, the GLO-PEM showed higher modelling accuracy in MF, EBF, and ENF compared to the VPM, possibly due to the consideration of air water stress (i.e., VPD_s) in the f_w of the model (Cao et al., 2004). It was well-known that the stomata would progressively close to protect the leaf from desiccation as the air dries, which could decrease the photosynthetic capacity (Jarvis, 1976). The LSWI used in the VPM cannot reflect the air water condition because of the weak effects of atmospheric water vapor on *NIR* (841–875 nm) and *SWIR* (1628–1652 nm) bands that were used to calculate LSWI (Gao et al., 1996). These together highlight the possible further improvement of the LUE models by optimizing f_w scalar.

3.2 Comparisons of the methods to integrate multiple environmental stresses

For the two optimal LUE models (i.e., EC-LUE and VPM), the methods to

integrate environmental stresses were totally different (i.e., multiplication for VPM and minimum based on Liebig's law for EC-LUE). We thus exchanged their methods to check which method was better. Results indicated that the R^2 for the modified EC-LUE decreased by 4.82%, with an 11.03% increase in RMSE. By contrast, the R^2 for the modified VPM increased by 2.33%, with a reduction of RMSE by 8.16% (Table 3). These suggested that the minimum method was more robust in quantifying environmental effects on GPP than the multiplication method, which agreed well with the classical ecological theory of the Liebig's law of minimum (Liebig, 1842). Yuan et al. (2007) also indicated that the actual LUE was predominated by moisture conditions throughout the growing season, and by temperature only at the beginning and end of the growing season.

The underestimation of GPP by the VPM as mentioned in section 3.1 (Table 2), may be partly due to the multiplication method to integrate the environmental stresses. Since both the values of f_t and f_w ranged from 0 to 1, the value of $f_t \times f_w$ should be smaller than either f_t or f_w , therefore may overestimate the environmental stress on LUE and thus underestimate ecosystem GPP. For example, the underestimation of VPM would be greatly reduced (the BIAS decreased from $-1.33 \text{ g C m}^{-2} \text{ day}^{-1}$ to $-0.94 \text{ g C m}^{-2} \text{ day}^{-1}$) when we accounted for the environmental stresses following the minimum method (Table 3).

3.3 Comparisons of the methods to define water stress

The water stress on LUE (i.e., f_w) had been characterized by air moisture condition (i.e., VPD_s) and/or soil water content (i.e., W_s), or via land water index (i.e., WI) that can reflect the vegetation water stress in different LUE models, yet there were controversies on which one was optimal (Medlyn, et al., 2011; Hashimoto et al., 2012; Yang et al., 2013). Coincidentally, both EC-LUE and VPM, the two better-performed LUE models, used WI. As discussed in section 3.1, the model accuracies might be improved by adding VPD_s , we thus tried to add three types of VPD_s , including the VPD_s of GLO-PEM (Eq. (2.2d)), MODIS-GPP (Eq. (2.5)), and SWH (Eq. (2.6)), to these two models to test whether the modeling accuracy can be further enhanced. Results indicated that the improvement for EC-LUE was minor despite how we defined water stress (i.e., $\min(WI, VPD_s)$, or $WI \times VPD_s$, or VPD_s) and integrated multiple environmental stresses (multiplication or minimum). More specifically, the mean R^2 elevated only if we defined the water stress as $\min(WI, VPD_s)$, addressed multiple environmental stresses (f) by minimum method (i.e., $f = \min(f_t, WI, VPD_s)$), and used the VPD_s from the GLO-PEM and SWH (increased by 1.45%, Fig.3a).

In contrast, the accuracy of VPM improved substantially when we added VPD_s , no matter how we defined the water stress, and how we integrated the water and temperature stress into f (Figs.3b-3g). The modeling accuracy reached to a maximum when f was defined as $\min(f_t, WI \times VPD_s)$ and the VPD_s was from GLO-PEM or SWH. The overall R^2 (i.e., 0.74) increased by 8.82%, accompanying by a decrease of RMSE (1.22%). The improvements varied with vegetation types, indicated by insignificant

changes in cropland and DBF, and evident improvements in the other vegetation types (i.e., the R^2 increases ranged from 5.28% for MF to 19.69% for grassland) (Fig.3f). Notably, the model performances of VPM can be improved even if we defined the water stress by VPD_s only, which implies that VPD_s was more important than WI in VPM. For example, the overall R^2 (i.e., 0.72, 0.71) enhanced by 5.88% and 4.41%, respectively, when we defined f as $f_t \times VPD_s$ and $\min(f_t, VPD_s)$ with the VPD_s from SWH (Figs.3d and 3g).

The weak improvement of EC-LUE and the significant improvement of VPM after adding VPD_s may be mainly due to the different f_w used by them originally. The f_w in EC-LUE was defined as the evaporative fraction (EF), which is a comprehensive indicator of ecosystem water stress at canopy level (balance between soil water availability and atmospheric demand). This indicator biophysically represents vegetation water stress using energy partitioning scheme (the more energy goes to latent heat, the less water stress for the vegetation) which already contained the effect of VPD (Yuan et al., 2007). By contrast, the f_w in VPM was defined as the function of LSWI, which is sensitive to leaf water content instead of canopy water content (Maki et al., 2004), and the regional GPP is limited more by the moisture condition at canopy level (Xiao et al., 2010). Moreover, the LSWI cannot reflect the atmospheric water stress because of the weak effects of atmospheric water vapor on NIR (841–875 nm) and $SWIR$ (1628–1652 nm) bands that were used to calculate LSWI (Gao et al., 1996). These two might mainly explain the significant improvement of VPM model after adding VPD information.

As illustrated above, the best expression of water stress was $WI \times VPD_s$ with the WI of VPM. The modified VPM may be the best LUE model in simulating large-scale terrestrial GPP provided with high-quality remote sensing data for the calculation of WI . However, there may be data acquisition problem when estimating the GPP before 1998, since the data of VGT-S10 (10-day composite Images from the VEGETATION sensor) and MODIS surface reflectance (MOD09A1) were not available for estimating the WI of the VPM in the time (Xiao et al., 2004a, 2005b). In this case, it was more appropriate to adopt the improved VPM with water stress being defined as VPD_s only.

3.4 The optimized LUE model structure and uncertainties

In summary, our results demonstrated that the better-performed LUE models (i.e., VPM and EC-LUE) can be further improved via model structural optimization. In particular, the modelling accuracy of VPM can be enhanced by changing the method to integrate multiple environmental stresses and/or adding VPD information in the water stress expression. Optimally, the actual LUE (ϵ_g) in LUE models can be defined as follow:

$$\begin{aligned} \epsilon_g &= \epsilon_{\max} \times \min(ft, fw) \\ fw &= WI \times VPD_s \end{aligned} \quad (3.1)$$

where ft is the same as that in GLO-PEM (Eq. (2.2c)), WI is the same as that in VPM (Eq. (2.3b)), and VPD_s is the same as that in GLO-PEM (Eq. (2.2d)) or SWH (Eq. (2.6)). If there were no high-quality remote sensing data for calculating WI , the ϵ_g can

alternatively be expressed as:

$$\begin{aligned}\varepsilon_g &= \varepsilon_{\max} \times ft \times fw \\ fw &= VPD_s\end{aligned}\tag{3.2}$$

where ft , WI , and VPD_s are the same as that in Eq. (3.1).

It should be noted that the main focus of the paper is to examine the impacts of structural differences in the LUE models, and the better performance of these models might be reached through use of model-dependent parameter values (this can be seen by comparing Figures 1 and 2 with the original publications of these models). For example, at the flux site US-MMS, the R^2 for the original EC-LUE reached up to 0.82 when T_{opt} and $\varepsilon_{\max}$ were set to 20.33°C and 2.14 g C m⁻² MJ⁻¹ APAR, respectively (Yuan et al., 2007). This value was 10.81% higher than the R^2 (i.e., 0.74) of the EC-LUE in this study (with T_{opt} of 25°C and $\varepsilon_{\max}$ of 2.25 g C m⁻² MJ⁻¹ APAR). Further studies are needed to address the parameter optimization for LUE models.

4. Conclusions

This study provides a comprehensive assessment on the four mostly used LUE models (i.e., CASA, GLO-PEM, VPM, and EC-LUE) in estimating ecosystem GPP, using eddy covariance (EC) flux data from 51 towers that cover a wide climate range and diverse vegetation types. Results showed that the EC-LUE, GLO-PEM, and VPM had the similar accuracies and were overall more robust in modeling GPP over large areas than the CASA. Considering the complexity of model structure, however, the EC-LUE and VPM were the two optimal LUE models. Then we explored the possible

further improvements of the two models by model structural optimization. Results indicated that the minimum approach based on Liebig's law was better than the multiplication method in addressing the multiple environmental stresses, and the water stress can be better reflected by the combination use of the original water stress scalar from VPM (WI) and the atmosphere water vapor deficit scalar (VPD_s). The accuracy of the VPM model could be enhanced even though we replaced the WI by VPD_s only. These suggested that the VPM model modified by using minimum method and adding VPD_s information was the best model in estimating terrestrial GPP over large areas, and that by replacing WI with VPD_s is optimal if there were no high-quality remote sensing data for the calculation of WI.

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Table 1. Descriptions of the eddy covariance (EC) flux sites in this study including vegetation type (Veg-Type), site identifier (Site ID), latitude (Lat), longitude (Lon), data period, country, and references.

Veg-Type	Site ID	Lat (°N)	Lon(°E)	Data period	Country	References
Savanna	AU-Fog	-12.542	131.307	2006-2007	Australia	Guerschman et al. (2009)
Savanna	AU-How	-12.494	131.152	2001-2006	Australia	Jamali et al. (2010)
Savanna	BW-Ma1	-19.916	23.560	2000-2001	Botswana	Veenendaal et al. (2004)
Savanna	US-Ton	38.432	-120.966	2001-2006	USA	Yuan et al. (2007)
Grassland	IT-Amp	41.904	13.605	2002-2006	Italy	Gilmanov et al. (2007)
Grassland	NL-Ca1	51.971	4.927	2003-2006	Netherlands	Gioli et al. (2004)
Grassland	NL-Hor	52.029	5.068	2005-2006	Netherlands	Smith et al. (2010)
Grassland	US-Aud	31.591	-110.510	2002-2006	USA	Meyers (2009a)
Grassland	US-Fpe	48.308	-105.102	2000-2006	USA	Meyers (2009b)
Grassland	US-Goo	34.255	-89.873	2002-2006	USA	Yuan et al. (2007)
Grassland	US-Var	38.413	-120.951	2001-2006	USA	Mu et al. (2007)
Cropland	NL-Lan	51.954	4.903	2005-2006	Netherlands	Moors et al. (2010)
Cropland	US-ARM	36.606	-97.489	2003-2006	USA	Hanan et al. (2002)
Cropland	US-Bkg	38.895	-120.633	2004-2006	USA	Goldstein et al. (2000)
Cropland	US-Bo1	44.345	-96.836	2000-2007	USA	Hollinger et al. (2005)
Cropland	US-Ne1	41.165	-96.477	2001-2005	USA	Verma et al. (2005)
Cropland	US-Ne2	41.165	-96.470	2001-2005	USA	Verma et al. (2005)
Cropland	US-Ne3	41.180	-96.440	2001-2005	USA	Gitelson et al. (2003)
Shrubland	CA-NS7	56.636	-99.948	2002-2005	Canada	Goulden et al. (2011)
Shrubland	RU-Cok	70.617	147.883	2003-2005	Russia	vanHuissteden. 2005
MF	CA-SF2	54.254	-105.878	2003-2005	Canada	Coursolle et al. (2006)
MF	US-Ho1	45.204	-68.740	2000-2004	USA	Hollinger et al. (2004)
MF	US-Pfa	45.946	-90.272	2000, 2003	USA	Gerbis (2003)
MF	US-Syv	46.242	-89.348	2002-2006	USA	Desai et al. (2005)
DBF	IT-Ro1	42.408	11.930	2000-2006	Italy	Reichstein (2003)
DBF	IT-Ro2	42.390	11.921	2002-2006	Italy	Reichstein (2003)
DBF	US-Bar	44.065	-71.288	2004-2005	USA	Saito et al. (2009)
DBF	US-Ha1	42.538	-72.172	2000-2006	USA	Saito et al. (2009)
DBF	US-MMS	39.323	-86.413	2000-2005	USA	Dragoni et al. (2007)
DBF	US-UMB	45.560	-84.714	2000-2003	USA	Curtis et al. (2002)
DBF	US-WCr	45.806	-90.080	2000-2006	USA	Cook et al. (2008)
EBF	AU-Tum	-35.656	148.152	2001-2006	Australia	Guerschman et al. (2009)
EBF	IT-Cpz	41.705	12.376	2000-2006	Italy	Hickler et al. (2006)
ENF	CA-Man	55.880	-98.481	2000-2003	Canada	Groenendijk et al. (2009)
ENF	CA-NS1	55.879	-98.484	2002-2005	Canada	Goulden et al. (2011)
ENF	CA-NS2	55.906	-98.525	2001-2005	Canada	Goulden et al. (2011)
ENF	CA-NS3	55.912	-98.382	2001-2005	Canada	Goulden et al. (2011)

ENF	CA-NS4	55.912	-98.382	2002-2004	Canada	Bond-Lamberty et al. (2004)
ENF	CA-NS5	55.863	-98.485	2001-2005	Canada	Bond-Lamberty et al. (2004)
ENF	CA-NS6	55.917	-98.964	2001-2005	Canada	Bond-Lamberty et al. (2004)
ENF	CA-Qcu	49.267	-74.036	2001-2006	Canada	Coursolle et al. (2006)
ENF	CA-Qfo	49.693	-74.342	2003-2006	Canada	Bonan et al. (2011)
ENF	CA-SF1	54.485	-105.818	2003-2005	Canada	Coursolle et al. (2006)
ENF	CA-SF3	54.092	-106.005	2003-2005	Canada	Coursolle et al. (2006)
ENF	DE-Tha	50.964	13.567	2000-2006	Germany	Kramer et al. (2002)
ENF	FI-Hyy	61.847	24.295	2000-2006	Finland	Kramer et al. (2002)
ENF	IL-Yat	31.345	35.051	2001-2006	Israel	Reichstein et al. (2005)
ENF	SE-Faj	64.113	19.457	2005-2006	Sweden	Gamon et al. (2010)
ENF	SE-Fla	60.086	17.480	2000-2002	Sweden	Verstraeten et al. (2006)
ENF	US-Blo	40.006	-88.290	2000-2006	USA	Goldstein et al. (2000)
ENF	US-Me4	44.499	-121.622	2000-2000	USA	Law et al. (2000)

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Table 2. Accuracies of EC-LUE, VPM, GLO-PEM, and CASA in estimating GPP across the eight vegetation types as reflected by R^2 , RMSE, and BIAS.

Vegetation Type	R^2				RMSE (g C m ⁻² day ⁻¹)				BIAS (g C m ⁻² day ⁻¹)			
	EC-LUE	VPM	GLO-PEM	CASA	EC-LUE	VPM	GLO-PEM	CASA	EC-LUE	VPM	GLO-PEM	CASA
Savanna	0.66	0.59	0.63	0.40	1.77	1.37	1.50	3.16	-0.17	-0.41	0.62	2.50
Grassland	0.64	0.57	0.58	0.45	1.96	2.36	1.91	2.61	-0.94	-1.47	-0.24	-0.02
Cropland	0.73	0.70	0.67	0.59	2.95	4.65	3.77	3.51	-1.29	-2.88	-1.17	-0.38
Shrubland	0.63	0.65	0.60	0.51	1.27	1.41	1.07	1.60	-0.85	-1.07	0.18	-0.14
MF	0.74	0.78	0.80	0.72	3.36	3.21	2.29	2.54	-2.78	-2.65	-1.76	-1.95
DBF	0.76	0.82	0.76	0.76	2.88	2.50	2.13	2.32	-1.83	-1.46	-0.50	-0.27
EBF	0.51	0.58	0.61	0.50	4.02	3.56	2.77	3.27	-3.80	-1.41	-2.27	-2.26
ENF	0.69	0.68	0.71	0.60	2.08	1.67	1.52	1.82	-1.71	-0.56	-0.80	-0.81
Average	0.69	0.68	0.69	0.58	2.41	2.45	2.06	2.44	-1.57	-1.33	-0.72	-0.43

739 **Table 3.** Comparisons of modeling accuracies (as reflected by R^2 , RMSE, and BIAS) of the
 740 EC-LUE and VPM when we assumed the environmental impacts as multiplication with that as
 741 minimum based on Liebig's law.

	$f_t \times f_w$			$\min(f_t, f_w)$		
	R^2	RMSE(g C m ⁻² day ⁻¹)	BIAS(g C m ⁻² day ⁻¹)	R^2	RMSE(g C m ⁻² day ⁻¹)	BIAS(g C m ⁻² day ⁻¹)
EC-LUE	0.66	2.68	-1.94	0.69	2.41	-1.57
VPM	0.68	2.45	-1.33	0.69	2.25	-0.94

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Figure legends

Figure 1. Comparisons between the observed GPP and the simulated GPP by the EC-LUE, VPM, GLO-PEM, and CASA models in non-forest sites. Dashed line is the 1:1 line and solid line indicates the best linear fit curve.

Figure 2. Comparisons between the observed GPP and the simulated GPP by the EC-LUE, VPM, GLO-PEM, and CASA models in forest sites. Dashed line is the 1:1 line and solid line indicates the best linear fit curve.

Figure 3. R^2 changes for all the vegetation types of EC-LUE (panel a) and VPM (panels b-g) after adding the VPD_s .