Patterns and Controls of Light Use Efficiency in Four Contrasting Forest Ecosystems in Yunnan, Southwest China

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Abstract

Ecosystem light use efficiency (LUE) is a critical parameter in estimating CO2 uptake by vegetation from climatological and satellite data. However, the spatiotemporal dynamics and biophysical regulations of ecosystem-level LUE are not well understood, resulting in large uncertainties in the estimation of gross primary productivity (GPP) using LUE-based models. In this study, we used eddy covariance to explore spatiotemporal variations and controls of LUE in four contrasting forest ecosystems (savanna, tropical rainforest, subtropical evergreen forest, and subalpine coniferous forest). Based on 27 site years of data, we found that (1) the multiyear mean LUE was 0.063, 0.251, 0.247, and 0.140 g C mol photon−1 in the four contrasting ecosystems, respectively; (2) the LUE in the wet season (May–October) was higher than that in the dry season in all studied ecosystems; (3) the leaf area index controlled GPP and LUE significantly and explained 74%, 29%, 54%, and 36% of the variation in GPP and 51%, 19%, 41%, and 54% of the variation in LUE in the four contrasting ecosystems, respectively; (4) path analysis revealed the critical roles of GPP and vapor pressure deficit in controlling LUE in these four forest ecosystems; and (5) under warming scenarios, LUE may decrease in savanna but increase in the other three ecosystems, while decreasing precipitation (P) may reduce LUE in the ecosystems studied. This study improves our understanding of the influence of biophysical factors on LUE and demonstrates how LUE changes with variations in temperature, soil moisture, and leaf area index, thereby improving estimations of large-scale carbon exchange/cycling.

1. Introduction

Light use efficiency (LUE) was historically defined as the ratio of the total or aboveground net primary production (NPP or ANPP), or sometimes the gross primary production (GPP), to the incident photosynthetically active radiation (PAR; Austin et al., 1978; Nichol et al., 2000; Pangle et al., 2009), absorbed PAR (APAR; Monteith, 1972; Xiao, Hollinger, et al., 2004), or APAR for green leaves (Gitelson & Gamon, 2015; Hall et al., 1992). LUE is a characterization of the sensitivity of photosynthetic productivity to incoming solar irradiation, temperature, and water conditions (Gilmanov et al., 2007; Shi et al., 2014); thus, LUE is a critical trait of ecosystems and is the underlying basis for estimating carbon exchange in many existing scale-up models (e.g., CASA; Potter et al., 1993; GLO-PEM; Prince & Goward, 1995; MODIS GPP; Running et al., 2004; Zhao et al., 2005; VPM; He et al., 2014; Xiao, Hollinger, et al., 2004; and EC-LUE; Alton et al., 2007; Li et al., 2008; Mercado et al., 2009; Yuan et al., 2007; Zhou...
et al., 2016). All of these models rely on a priori estimates of LUE. Therefore, an understanding of LUE and its controls is usually necessary for studies on spatiotemporal variations in the global carbon cycle (Zhao et al., 2007).

Conceptually, there are two categories of LUE. The first is physiological LUE (LUEphys = GPP/APAR), which is widely applied in MODIS-based models to model regional/global GPP (Running et al., 2004; Tang et al., 2015; Zhao et al., 2007; Zhou et al., 2016), in studies at the leaf, individual, population, and community levels (especially at the canopy scale; Larcher, 2003) and in characterizations of physiological- biochemical parameters (Gilmanov et al., 2010). The second category is ecological LUE (LUEeco = GPP/PAR), which is used in studies at the ecosystem level and is mainly applied in EC-based models to scale GPP up to the biome/regional level (Austin et al., 1978; Cooper, 1970; Gilmanov et al., 2007, 2010; Odum & Barrett, 1971; Shi et al., 2014; Zhang, Cao, et al., 2015). In the present report, we focus on LUE at the ecosystem level. Therefore, the second definition of LUE (i.e., ecosystem light use efficiency, LUEeco) was employed in this study as LUEeco (hereafter LUE, with units in g C · mol photon−1), not only reflecting the ecophysiological properties of vegetation but also taking into account certain additional ecosystem-level characteristics (such as plant properties, aboveground biomass, and leaf area index [LAI]; Gilmanov et al., 2007).

Traditionally, the biomass inventory approach has been applied to study LUE, where the uptake of carbon is the increase in biomass, similar but not identical to the NPP (Cannell et al., 1987). New techniques, including the eddy covariance (EC)-based method (Li et al., 2008; Ruimy et al., 1995; Yuan et al., 2007) and model inversions based on EC or GIS (Garbulsky et al., 2010; Tang et al., 2015; Yebra et al., 2015), are currently applied in the study of LUE. EC-based LUE is broadly used because ecosystem-scale GPP can be estimated with good accuracy based on EC (Baldocchi, 2003) and because EC is widely used globally. In addition, at the ecosystem scale, EC-based LUE at well-instrumented sites provides important supplementary data for revealing the spatiotemporal characteristics and driving factors of LUE (Garbulsky et al., 2010; Gilmanov et al., 2016; Zhang, Cao, et al., 2015).

The combined effects of vegetation properties and climate (such as species composition, carboxylase activity/density, leaf nitrogen or phosphorus content, LAI, biomass, PAR, temperature [T], precipitation [P], and CO2 concentrations) result in obvious spatiotemporal variations in LUE (Green et al., 2003; Still et al., 2004; Tong et al., 2009). Previous studies have reported that LUE is mainly limited by temperature and soil moisture (Traore et al., 2014), as well as LAI through its modulation of canopy-scale photosynthesis Eamus et al. (2001). An analysis of a data set containing 21 ecosystems concluded that rainfall was the key factor affecting LUE (Kanniah et al., 2011). Therefore, studies on the spatial patterns and temporal dynamics of ecosystem LUE and the controlling factors thereof are necessary for understanding and predicting the carbon cycle and energy fixation (Gilmanov et al., 2007; Zhao et al., 2007; Zhang, Zhou, et al., 2015). However, the spatiotemporal variations in LUE and its controls remain poorly documented in many regions.

Yunnan Province, which is located in southwest China, is famous for its high biodiversity and has been called a biodiversity kingdom (Wu et al., 1987) due to its location and altitudinal variation (a difference of 6,664 m from south to north), which result in a climatic gradient. Additionally, almost all types of ecosystems (e.g., tropical/savanna/subtropical/temperate forest, alpine meadow, and tundra) can be found in Yunnan (Wu et al., 1987). Furthermore, southwest China (including Yunnan, Guizhou, and Sichuan) has the largest forest carbon storage (Tang et al., 2018) and highest carbon sink rate (Piao et al., 2009). However, to the best of our knowledge, there are no studies on LUE and its controlling factors at the ecosystem scale. Therefore, we conducted an EC-based assessment of LUE in four contrasting forest ecosystems (the Yuanjiang savanna ecosystem [YJ], Xishuangbanna tropical rainforest ecosystem [XSBN], Ailaoshan subtropical evergreen broad-leaved forest ecosystem [ALS], and Lijiang subalpine coniferous forest ecosystem [LJ]) in Yunnan with the following specific objectives: (1) to investigate LUE and its spatiotemporal dynamics between/within contrasting forest ecosystems, (2) to acquire the LUEmax value for calibrating and validating LUE-based models, and (3) to quantify the contributions of critical factors on LUE and its responses to LAI, T, and P. These objectives will contribute to a better understanding of the effects of critical controls on ecosystem LUE and validate LUE-based models for estimating biome/regional GPP and even global carbon cycling.

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2. Materials and Methods

2.1. Site information

Four representative forest ecosystems (YJ, XSBN, ALS, and LJ; Figure 1) were chosen several years ago and fully instrumented to enable state-of-the-art measurements of CO₂ fluxes. The work reported here is part of that larger investigation. The climate in this region is mainly influenced by the southwest monsoon and by the Tibetan Plateau in each of the four locations. The mean annual temperature (MAT) during the study period in YJ, XSBN, ALS, and LJ was 24.3, 21.4, 11.7, and 7.9 °C, and the mean annual precipitation (MAP) was 734, 1,415, 1,728, and 1,095 mm, respectively (Figure 1 and Table 1), with more than 77% of the MAP occurring during the wet season (May–October; Table 1). The geographical location, elevation, biophysical controls, dominant species, and soil physicochemical properties are listed in Table 1, and further information about the topography, climate, solar radiation, vegetation, and soil properties of this region can be found in previous studies (Cao et al., 2006; Fei et al., 2017, 2018; Huang et al., 2017; Song et al., 2017).

2.2. Eddy Covariance-Based LUE

2.2.1. Flux, Meteorological, and LAI Data

An open-path eddy covariance (OPEC) system, which directly provides a high time-resolution data set on energy/carbon/H₂O flux between the ecosystem and atmosphere (Aubinet et al., 2001; Baldocchi et al., 1996, 2001), and a routine meteorological observing system (RMOS) were applied to measure climatic variables simultaneously in all four of these ecosystems beginning in May 2013, October 2002, September 2008, and August 2014 in YJ, XSBN, ALS, and LJ, respectively. Details about the four sets of OPEC and RMOS used in the present research are provided in Table 2. The flux and meteorological data sampling frequencies were 10 and 0.5 Hz, respectively. All data were continuously collected using Campbell loggers (CR1000/CR3000/CR5000, Campbell Scientific Inc., Logan, UT, USA). A LAI-2200 plant canopy analyzer (Li-Cor Inc., USA) was used to measure the monthly LAI at the end of each month (8 plots × 4 repeats), and data were processed with FV2200 software (Li-Cor Inc., USA). Data from the following periods were used in the present study: May 2013 to 2016, 2003 to 2016, 2009 to 2014, and August 2014 to 2016 in YJ, XSBN, ALS, and LJ, respectively. All the data shown in tables/figures are multiday/month/year averaged values.

2.2.2. Flux Data Processing, Filling, and Partitioning

Quality assessment and control (QA/QC), including coordinate rotation (Tanner & Thurtell, 1969; Wilczak et al., 2001), WPL calibration (Lee & Massman, 2010; Webb et al., 1980), storage flux calculation (Baldocchi et al., 1996; Hollinger et al., 1994), outliers exclusion (Yu et al., 2006), and $u^*$ filtering.
(Reichstein et al., 2005), were applied to control and ensure the quality of flux data. In addition, the flux data gaps were filled, and the data were partitioned according to the FLUXNET/CarboEurope methodology (Falge et al., 2001; Reichstein et al., 2005) to obtain robust GPP data. The details of the flux data QA/QC and postprocessing procedures used in this study are described in Reichstein et al. (2005) and Yu et al. (2006).

### 2.2.3. Ecosystem LUE Calculation

Ecosystem LUE was defined as the ratio of GPP to total incident PAR (Austin et al., 1978; Gilmanov et al., 2007), as expressed in equation (1):

\[
\text{LUE} = \frac{\text{GPP}}{\text{PAR}}
\]  

(1)

where the units of GPP, PAR, and LUE are μg C m\(^{-2}\) s\(^{-1}\), μmol photon m\(^{-2}\) s\(^{-1}\), and g C \(\cdot\) mol photon\(^{-1}\), respectively. PAR was measured directly with the LQS70-10 sensor (Table 2), and GPP was derived from the eddy flux (Baldocchi et al., 2001; Gilmanov et al., 2007; Reichstein et al., 2005; Yu et al., 2006), as expressed in equations (2)-(4):

\[
\text{GPP} = R_{\text{eco}} + (-\text{NEE})
\]  

(2)

\[
\text{NEE} = F_c + F_s = \rho \frac{\Delta c}{\Delta t} z_f
\]  

(3)

\[
R_{\text{eco}} = R_{\text{eco,ref}} \times e^{-\left( \frac{E_{c}}{T_{\text{ref}}} + \frac{E_{s}}{T_{\text{ref}}} \right)}
\]  

(4)

Table 1

| Variables | YJ | XSBN | ALS | LJ |
|-----------|----|------|-----|----|
| Ecosystem type | Savanna ecosystem | Tropical rainforest ecosystem | Subtropical evergreen broad-leaved forest ecosystem | Subalpine coniferous forest ecosystem |
| Geographical location | 23°28′26″ N, 102°10′39″ E | 21°55′39″ N, 101°15′55″ E | 24°32′17″ N, 101°01′45″ E | 27°08′32″ N, 100°13′38″ E |
| Altitude (m) | 550 | 750 | 2,500 | 3,240 |
| MAT (°C) | 24.3 | 21.4 | 11.7 | 7.9 |
| MAP (mm) | 734 | 1,415 | 1,728 | 1,095 |
| Ratio of R/A | 77% | 80% | 79% | 80% |
| Soil type | Dry-red soil | Latosol | Yellow-brown soil | Dark-brown soil |
| Soil pH | 7.3 | 4.5–5.4 | 4.4–4.9 | 5.6–5.9 |
| Organic carbon (g kg\(^{-1}\)) | 12.1 | 27.8 | 138.4 | — |
| Total nitrogen (g kg\(^{-1}\)) | 1.0 | 2.8 | 8.8 | 4.0 |
| Total phosphorus (g kg\(^{-1}\)) | 0.30 | 0.26 | 0.82 | — |
| C/N ratio | 12.1 | 9.9 | 15.7 | — |
| Vegetation | Savanna | Tropical rainforest | Subtropical evergreen forest | Subalpine coniferous forest |
| Dominant species | Lannea coromandelica, Polyalthia suberosa, Heteropogon contortus. | Terminalia myricocarpa, Barringtonia pendula, Saprosma ternatum, Pteris cretica. | Lithocarpus xylocarpus, Schima noronhae, Fargesia nitida, Plagiogyria communis. | Picea likiangensis, Abies forrestii, Quercus guayavifolia, Acer pectinatum, Padus brachypoda. |
| Average canopy height (m) | 4–6 | 35 | 25–30 | 38–42 |
| LAI | 1.5 | 5 | — | — |
| Biomass (t ha\(^{-1}\)) | >500 | 465.7 | — | — |
| Litterfall (t ha\(^{-1}\)) | 4.3 | 9.9 | 8.62 | 5.11 |

Note: MAT: mean annual temperature, MAP: mean annual precipitation; Ratio of R/A: the ratio of precipitation in rainy season to annual precipitation. References include the following: a Liu et al. (2007); b Chan et al. (2006); c Qiao et al. (2014); d Qing (2004); e Yu, He, et al. (2013); f Fei et al. (2017); g Tan et al. (2010); h Nizami et al. (2017); i Tan et al. (2011).
where $\text{NEE}$ is the net ecosystem carbon exchange and consists of the turbulent eddy flux ($F_c$) and storage flux ($F_s$; (Aubinet et al., 2001; Baldocchi et al., 1996; Hollinger et al., 1994; Lee et al., 2006); $\rho$, $w$, and $c$ represent the air density, vertical wind velocity, and target scalar concentration (CO2 concentration in this case), respectively. The primes denote fluctuations from the average, and the overbar signifies a time average (30 min in this study). $\Delta c$ is the variation over a 30‐min period at height $z_r$, $z_r$ is the height of the EC system (13.9, 48.8, 34.0, and 60.0 m in YJ, XSBN, ALS, and LJ, respectively), and $\Delta t$ is the time interval (1,800 s in this case). $R_{\text{eco}}$ is the ecosystem respiration and is calculated according to Lloyd and Taylor (1994); $R_{\text{eco, ref}}$ is the reference ecosystem respiration at a reference temperature ($T_{\text{ref}}$; here 10 °C is used); $R_{\text{eco, ref}}$ and $E_0$ are the fitted parameters; $T_0$ is a constant and is set to 227.13 K (−46.02 °C); and $T$ is the measured 5-cm soil temperature in the present study. Note that $T_0$, $T_{\text{ref}}$, and $T$ in equation (4) are in Kelvin ($^\circ$K).

2.3. Statistical Analysis

2.3.1. Path Analysis

In the present study, we applied path analysis (Wright, 1921) to explore which biophysical controls impact LUE significantly and to suggest the relative importance of these controls by parameterizing the standardized direct and total effects on LUE at a monthly timescale due to the effects of climatic factors on GPP (Baldocchi, 2008; Baldocchi et al., 2018; Reichstein et al., 2007; Yu, Zhu, et al., 2013). We designed the path structure for the correlations of global radiation ($R_g$), air temperature ($T_{\text{air}}$), vapor pressure deficit (VPD), relative humidity (RH), precipitation ($P$), soil volumetric water content (SVWC), GPP, and PAR as follows: (1) $R_g$ and SVWC influence GPP directly, while $T_{\text{air}}$ and $P$ determine GPP directly and indirectly; (2) $R_g$ influences PAR and $T_{\text{air}}$ directly, $P$ influences RH and SVWC directly, and $T_{\text{air}}$ and RH determine VPD jointly; and (3) $R_g$, $T_{\text{air}}$, VPD, RH, $P$, SVWC, GPP, and PAR determine LUE directly and indirectly.

Path analysis is based on the fundamental principles of multiple regression and correlation analysis but has a more interpretive structure (Grace & Bollen, 2005). It reveals not only the direct effects of independent factors on dependent variables but also the indirect and total effects (Li, 1975; Schemske & Horvitz, 1988; Wootton, 1994). The R package sem (Fox et al., 2016) was used to perform the path analysis, and the path coefficients (PCs) were standardized partial regression coefficients representing the relative strength of a given relationship and allowed us to quantitatively compare the relative influences of $R_g$, $T_{\text{air}}$, VPD, RH, $P$, SVWC, GPP, and PAR on LUE.

2.3.2. Regression Analysis

We used the following one-factor linear/quadratic regression model (equations (5) and (6)) to explore the responses of ecosystem LUE to $T_{\text{air}}$ and SVWC at daily timescales:

$$\text{LUE} = ax + b$$

$$\text{LUE} = ax^2 + bx + c$$

where $a$, $b$, and $c$ are fitted parameters; $x$ represents $T_{\text{air}}$ or SVWC in this research.

3. Results

3.1. Ecosystem LUE

3.1.1. Diurnal Patterns in GPP, PAR, and LUE

We analyzed the seasonally and yearly binned daytime (PAR > 50 $\mu$mol · m$^{-2}$ · s$^{-1}$) patterns of GPP, PAR, and LUE and found U patterns of daytime courses of GPP, PAR, and LUE in all four ecosystems (YJ, XSBN, ALS, and LJ; Figure 2). GPP increased with increasing PAR (after sunrise), peaked midday between 12:00 and 14:00, and then decreased with decreasing PAR values (after midday), whereas LUE showed the opposite diurnal trends and reached a minimum at midday, even though the maximum GPP remained stable during this period (Figure 2). LUE values were larger and ecosystems were more photosynthetically efficient at sunrise/sunset, while GPP values were lower for the lower PAR. Therefore, photosynthetic productivity (namely, GPP) was limited by lack of PAR in the early morning and at dusk.
LUE was very high at XSBN and ALS (>0.50 g C · mol photon−1) compared with YJ (<0.16 g C · mol photon−1), and the order of LUE diurnal amplitude was XSBN>ALS > LJ > YJ as a result of GPP showing the same general pattern. At the same time, the order of the diurnal amplitude of PAR was YJ > XSBN > LJ > ALS (Figure 2). These findings suggest that the broad-leaved forest ecosystems (e.g., XSBN and ALS) show higher photosynthetic efficiency than coniferous/savanna forest ecosystem (e.g., LJ and YJ, respectively) and the lower altitude is usually associated with a larger annual PAR.

**3.1.2. Ranges of Annual LUE and LUEmax Values**

Multiyear daily LUE values ranged from 0.008–0.316, 0.065–1.073, 0.060–1.129, and 0.052–0.881 g C · mol photon−1 in YJ, XSBN, ALS, and LJ, respectively (Figure 3). We analyzed the 8-day average LUEmax at an annual timescale to reduce the uncertainty caused by noise data, and many MODIS-based GPP estimations are produced at this timescale. The multiyear 8-day average LUEmax values were 0.171, 0.539, 0.708, and 0.480 g C · mol photon−1 in YJ, XSBN, ALS, and LJ, respectively (Table 3). These results suggest that ALS (evergreen broad-leaved forest) exhibits the highest photosynthetic capability, whereas the LUEmax in YJ (savanna) is the lowest and is severely constrained by biophysical factors compared to the other three ecosystems.
3.1.3. Intra-Annual Dynamics of the Controls and LUE

The variation in climatic factors and LUE showed the following: (1) $R_g$ and PAR peaked from April to May in each of the forest ecosystems. The dynamics of PAR were highly coincident with $R_g$ in the same ecosystems, whereas $R_g$ and PAR changed dramatically in the wet season in ALS and LJ compared with YJ (Figures 4a and 4e). (2) The lowest $T_{air}$ occurred from the end of December to the middle of January, and the highest $T_{air}$ was observed in May to June in YJ but in July in XSBN, ALS, and LJ (Figure 4b). Generally, VPD decreased with the onset of the rainy season in the four ecosystems. The multiyear mean VPD values were 13.7, 6.3, 3.4, and 3.6 hPa in YJ, XSBN, ALS, and LJ, respectively, and VPD was found to change dramatically in YJ, peaking from April to May (Figure 4b). (3) The SVWC at $-5$ cm changed consistently in the four ecosystems. The lowest SVWC occurred at the end of the dry season (April), and the SVWC was higher in the wet season (Figure 4d) because more than 77% of precipitation falls during the rainy season (Figure 4c and Table 1) and variations in SVWC are highly coupled with precipitation dynamics (Figure 4c). (4) According to the multiyear daily mean LUE results, the highest daily mean values of LUE (g C · mol photon$^{-1}$) were 0.196 (DOY 232), 0.448 (DOY 180), 0.630 (DOY 179), and 0.479 (DOY 199) in YJ, XSBN, ALS, and LJ, respectively. Additionally, the lowest GPP and the highest PAR resulted in the lowest LUE in YJ, and the daily LUE in this

Figure 2. Seasonally and yearly averaged daytime trends of gross primary productivity (GPP), photosynthetically active radiation (PAR), and ecosystem light use efficiency (LUE) in YJ (a1–a3), XSBN (b1–b3), ALS (c1–c3), and LJ (d1–d3). Figure (a3–1) shows dramatic changes in the diurnal trends in LUE in YJ, the identical figure is shown in (a3), but the scale of the y axis is different. The time of day is local time.
The range of daily LUE values during the study period in YJ, XSBN, ALS, and LJ. LUE values ranged from 0.008–0.316, 0.065–1.073, 0.060–1.129, and 0.052–0.881 g C · mol photon\(^{-1}\), and the median value was 0.056, 0.235, 0.219, and 0.134 g C · mol photon\(^{-1}\) in YJ, XSBN, ALS, and LJ, respectively.

From June to November, the monthly LUE values in ALS were higher than those in XSBN, whereas the rest of the monthly LUE values in ALS were lower than those in XSBN (Figure 5a). The lowest monthly LUE was observed in March (0.037 g C · mol photon\(^{-1}\)), February (0.162 g C · mol photon\(^{-1}\)), February (0.113 g C · mol photon\(^{-1}\)), and January (0.082 g C · mol photon\(^{-1}\)) in YJ, XSBN, ALS, and LJ, respectively. The highest monthly LUE occurred in August (0.119 g C · mol photon\(^{-1}\)) in YJ and in July (0.350, 0.495, and 0.294 g C · mol photon\(^{-1}\)) in XSBN, ALS, and LJ, although the highest monthly LAI values were observed in August (Figure 5b).

### 3.1.5. Seasonal and Annual Patterns in Meteorological Factors and LUE

The \(R_g\), PAR, \(P\), \(T_{air}\), RH, and SVWC were higher during the wet season than during the dry season except for the \(R_g\) and PAR in ALS and LJ (Table 4). The VPD in XSBN, ALS, and LJ was typically larger during the dry season than during the wet season because nearly 80% of the annual precipitation fell during the wet season. However, in YJ, VPD showed the opposite seasonal trend and was 15.2 hPa during the wet season and 12.1 hPa during the dry season (Table 4) due to abundance of \(g\) and higher temperature in the wet season (Figure 4).

Generally, the magnitude of LUE in these typical forest ecosystems in Yunnan exhibited the order XSBN > ALS > LJ > YJ regardless of whether it was examined only during the dry season, only during the wet season, or for the whole year, except the LUE in ALS in the wet season was greater than that in XSBN. The LUE in YJ was the lowest regardless of whether examining only the dry season, only the wet season, or the entire year was compared with XSBN, ALS, and LJ, and a lower LUE was observed in LJ than in XSBN and ALS. In addition, the seasonal and annual patterns of LUE in each of the four ecosystems showed a clear trend of wet season > annual > dry season. The LUE values were 0.044, 0.213, 0.160, and 0.098 g C · mol photon\(^{-1}\) in the dry season; 0.078, 0.290, 0.351, and 0.193 g C · mol photon\(^{-1}\) in the wet season; and 0.063, 0.251, 0.247 and 0.146 g C · mol photon\(^{-1}\) annually in YJ, XSBN, ALS, and LJ, respectively (Figure 6).

### 3.2. Quantifying the Contributions of Critical Factors to LUE

Results of the path analysis show a network of influences. To further quantify how critical controls influenced the LUE, we applied a path analysis to quantitatively compare the direct and total effects of \(R_g\), \(P\), and spatial/intersite variability (Figures 4d and 4e) that contributed to dramatic spatiotemporal variations in LUE. Though LUE showed large daily variability, we can clearly see that LUE during May–October (DOY121–305) was higher than that in the other periods (Figure 4f). Overall, the four forest ecosystems showed large fluctuations in the daily magnitude of LUE within the same ecosystem and clear spatial variations in LUE among YJ, XSBN, ALS, and LJ.

### Table 3

| Year | YJ  | XSBN | ALS  | LJ  |
|------|-----|------|------|-----|
| 2003 | —   | 0.650| —    | —   |
| 2004 | —   | 0.510| —    | —   |
| 2005 | —   | 0.560| —    | —   |
| 2006 | —   | 0.550| —    | —   |
| 2007 | —   | 0.650| —    | —   |
| 2008 | —   | 0.710| —    | —   |
| 2009 | —   | 0.520| 0.678| —   |
| 2010 | —   | 0.480| 0.690| —   |
| 2011 | —   | 0.380| 0.691| —   |
| 2012 | —   | 0.480| 0.735| —   |
| 2013 | 0.169| 0.430| 0.827| —   |
| 2014 | 0.187| 0.500| 0.628|0.417|
| 2015 | 0.172| 0.610| —    |0.491|
| 2016 | 0.155| 0.520| —    |0.534|
| Average | 0.171| 0.539| 0.708| 0.480|

**Figure 3.** The range of daily LUE values during the study period in YJ, XSBN, ALS, and LJ. LUE values ranged from 0.008–0.316, 0.065–1.073, 0.060–1.129, and 0.052–0.881 g C · mol photon\(^{-1}\), and the median value was 0.056, 0.235, 0.219, and 0.134 g C · mol photon\(^{-1}\) in YJ, XSBN, ALS, and LJ, respectively.
Figure 4. Intra-annual variations in controls and ecosystem light use efficiency (LUE) in Yuanjiang semiarid savanna ecosystem (YJ), Xishuangbanna tropical rainforest ecosystem (XSBN), Ailaoshan subtropical evergreen broad-leaved forest ecosystem (ALS), and Lijiang subalpine coniferous forest ecosystem (LJ), Yunnan Province, Southwest China. (a) Daily summed global radiation ($R_g$); (b) averaged daily air temperature ($T_{air}$, represented by gray-filled black circles) and saturation vapor pressure deficit (VPD, red lines); (c) soil volumetric water content (SVWC, black lines) at $-5$ cm depth and daily summed precipitation (precipitation, blue-filled rectangle); (d) daily summed gross primary productivity (GPP); (e) daily summed photosynthetically active radiation (PAR); and (f) daily ecosystem light use efficiency (LUE). Shaded area indicates the wet season (May–October), and the remainder represents the dry season (November–April). Data were available in YJ, XSBN, ALS, and LJ in May of 2013 to 2016, 2003 to 2016, and 2009 to 2014, and in August of 2014 to 2016, respectively. All the data shown in this figure are multiday averaged values.
Specifically, we found that the critical factors affecting LUE were as follows: (1) In YJ, the critical factors were GPP, P, RH, VPD, and PAR, and the standardized total effects (STE) were 0.96, 0.66, 0.60, −0.47, and −0.45, respectively. This finding suggests that higher VPD/PAR values have negative effects on LUE in YJ. (2) In XSBN, the critical factors were GPP, P, VPD, T\text{air}, and PAR with STEs of 0.93, 0.52, −0.33, 0.34, and −0.43, respectively. (3) In ALS, the critical factors were GPP, VPD, and T\text{air} with STEs of 0.81, −0.58, and 0.45, respectively. (4) In LJ, the critical factors were GPP, P, VPD, T\text{air}, and PAR with STEs of 0.77, 0.32, −0.70, 0.35, and −0.31, respectively. The results showed that LUE values in LJ and ALS were more sensitive to VPD than in YJ and XSBN. Overall, LUE showed a negative relationship with R\text{g}, VPD, and PAR and a positive relationship with other factors (P, T\text{air}, RH, SVWC, and GPP). Furthermore, LUE values were mainly controlled by GPP, which exhibited STEs of 0.96, 0.93, 0.81, and 0.77 on LUE in YJ, XSBN, ALS, and LJ, respectively (Figure 7). Therefore, the variations in LUE were mainly controlled by variations in GPP, P, T\text{air}, VPD, and PAR although with different path coefficients in different ecosystems. In summary, GPP and VPD play especially critical roles in controlling LUE in the four studied forest ecosystems.

3.3. Relationship Between GPP and PAR

We used a quadratic model to explore the light response of GPP and found that GPP increased first with increasing PAR and then decreased when PAR reached a certain threshold in YJ, XSBN, and ALS (the threshold was 1543, 1,440, and 1,113 μmol · m\textsuperscript{−}2 · s\textsuperscript{−}1, respectively; Figures 8a–8c), but a different pattern (the higher PAR, the larger the GPP) was observed in LJ (Figure 8d). Furthermore, GPP in ALS reached the maximum first with the increasing PAR and then in XSBN and in YJ. Thus, photoinhibition did not occur in LJ, while it did occur in the other three forest ecosystems. This finding revealed that the lack of PAR constrained GPP in LJ.

3.4. Responses of GPP and LUE to LAI

Based on the linear regression analysis, we found that the sensitivity of GPP to LAI was YJ > ALS > LJ > XSBN (R\textsuperscript{2} values were 0.74, 0.54, 0.36, and 0.29, respectively). LUE showed the highest sensitivity to LAI in LJ and YJ, whereas the lowest sensitivity was observed in XSBN (Figures 9a–9d). This result suggested that LAI exerts more influence on GPP and LUE in savanna ecosystems (e.g., YJ) than in tropical forest ecosystems (e.g., XSBN). Overall, LAI showed highly significant influences on GPP and LUE not only in each of the four forest ecosystems (Figures 9a–9d) but also in the studied forest ecosystems as a whole (Figure 9e).

3.5. Responses of LUE to Temperature and Soil Moisture

Generally, LUE increased with increasing temperatures in XSBN, ALS, and LJ, although the rate of increase in LUE was in the order XSBN < LJ < ALS according to the quadratic regression results (Figures 10b–10d). However, a different temperature response pattern was observed in YJ in which LUE increased first when temperature was lower than −26.5 °C and then decreased with increasing temperature (Figure 10a). Compared with the relationship between temperature and LUE, the relationship between SVWC and LUE was simple and coherent, exhibiting a trend in which LUE increased with increasing SVWC (Figure 11). Meanwhile, LUE increased dramatically in XSBN and ALS (Figures 11b and 11c). In summary, LUE showed positive relationships with temperature and soil moisture in all of the studied forest ecosystems except in YJ, where LUE decreased with temperatures >26.5 °C. These findings revealed that a decrease in precipitation will decrease the LUE of forest ecosystems, whereas warming might
increase the LUE in other ecosystems along with a decrease in the water-shortage area (e.g., arid/semi-arid/savanna ecosystem).

4. Discussion

4.1. The Spatiotemporal Variability/Dynamics of LUE

Understanding the spatial patterns and temporal dynamics of LUE is of great interest for estimating photosynthetic productivity and for studying the carbon cycle (Zhao et al., 2007; Zhang, Zhou, et al., 2015). In the present study, we found that with respect to the temporal dynamics of LUE, the multiyear mean daily maximum LUE (LUEmax) was 0.196 (DOY 232), 0.448 (DOY 180), 0.630 (DOY 179), and 0.479 (DOY 199) g C · mol photon$^{-1}$ in YJ, XSBN, ALS, and LJ, respectively (Figure 4f), which suggests that LUEmax occurred in the early-to-middle wet season and shows that favorable water and temperature conditions are helpful in increasing LUE. A general pattern was observed in which the LUE values in all four of the forest ecosystems studied here (Figure 1) increased consistently until the middle of the wet season (in July/August) and then decreased (Figure 5a). Consequently, the LUE values in the wet season were greater than those in the dry season in XSBN and ALS (i.e., evergreen broad-leaved forest (EBF)), in LJ (i.e., evergreen needle-leaved forest (ENF)), and in YJ (i.e., savanna) because nearly 80% of the precipitation falls during this period (Table 4 and Figure 4c) and higher GPP occurs in the wet season (Figure 4d). Previous studies found a similar trend in which the wet season had higher GPP and LUE values than the dry season (Gilmanov et al., 2007; Shi et al., 2014; Zhang, Cao, et al., 2015). Interestingly, the highest monthly LUE values in XSBN, ALS, and LJ were all observed in July, but there was a delay in YJ, where this highest value occurred in August (Figure 5a) although the monthly LAImax was reached in August in all four ecosystems (Figure 5b). However, YJ had the highest temperatures and VPD throughout the year compared with the other three ecosystems (Table 4 and Figure 4b). Therefore, we thought that variation in monthly VPD (Figure S1 in the supporting information) caused the highest monthly LUE value to delay to August in YJ.

With regard to the spatial variation of LUE, we observed that the multiyear mean annual LUE values were 0.063, 0.251, 0.247, and 0.140 g C · mol photon$^{-1}$ in YJ, XSBN, ALS, and LJ, respectively, which indicates that EBF ecosystems (e.g., XSBN and ALS) are more light efficient (i.e., exhibit higher LUEs) than coniferous forest ecosystems (e.g., LJ). Our
results reveal that the savanna ecosystem (e.g., YJ) shows the lowest LUE compared with the former two categories of forest ecosystems (Figures 5a and 6) regardless of whether examining only the dry/wet season or the annual value (Figure 6). Although our findings are contrary to those from a study in Canada, where LUE in grassland was found to be higher than in forest (Schwalm et al., 2006), our results agree well with most previous findings indicating that EBF has the highest LUE (Jia et al., 2016; Shi et al., 2014; Yuan et al., 2014), followed by ENF (Wei & Wang, 2010).

The multiyear mean 8-day binned $\text{LUE}_{\text{max}}$ ($0.480 \text{ g C} \cdot \text{mol photon}^{-1}$) in LJ (Table 3) was only slightly higher than 3-year mean 8-day binned $\text{LUE}_{\text{max}}$ ($0.476 \text{ g C} \cdot \text{mol photon}^{-1}$) in a broad-leaved Korean mixed pine forest (Zhang, Cao, et al., 2015), although the distance between these sites is greater than 3,500 km. This trend was also observed in XSBN and ALS (both of which are EBF, where the multiyear mean LUE was 0.251 and 0.247 g C · mol photon$^{-1}$, respectively; Figure 6). These findings indicate that ecosystems with a similar forest type may have similar LUEs. In summary, ecosystems with similar/same forest/vegetation type show nearly the same LUE despite considerable spatiotemporal variability, demonstrating that it is possible and reliable to upscale site-based LUE to predict regional/global GPP.

Figure 7. Schematic illustrating the effects of biophysical controls on monthly variations in LUE in typical forest ecosystems in Yunnan (YJ, XSBN, ALS, and LJ). Solid arrows are direct effects (standardized partial regression coefficients), and dashed arrows indicate total effects (total effects = direct effects + indirect effects). The values adjacent to the solid arrows and dashed arrows represent the direct effect and the total effect, respectively. $R_g$, $T_{\text{air}}$, VPD, RH, P, SVWC, GPP, and PAR indicate global radiation, air temperature, saturation vapor pressure deficit, relative humidity, precipitation, soil volumetric water content, gross primary productivity, and photosynthetically active radiation, respectively.
4.2. Responses of GPP to PAR and LAI

The critical factors driving GPP should be explored as GPP and LUE are closely related (Figure 7). We mainly focus on PAR and LAI in this study because both factors not only influence GPP but also influence LUE directly and significantly (Shi et al., 2014; Zhao et al., 2007). We found that with increasing PAR, GPP first increases and then decreases when PAR exceeds a certain threshold in YJ, XSBN, and ALS (Figure 8). This finding is consistent with previously published results (Gilmanov et al., 2007; Mercado et al., 2009; Turner et al., 2003). Similar to other results reported for a mixed forest (Zhang, Cao, et al., 2015), GPP was linearly correlated with PAR in LJ, meaning that a higher PAR did not saturate photosynthesis (Figure 8d) and that a decreased PAR in the wet season may inhibit photosynthesis (Figure 4e). These findings indicate that slightly increasing PAR (i.e., a little less rainy/cloudy days) in the wet season might enhance the GPP in LJ. Compared with the responses of GPP to PAR, there is clear evidence that GPP increases continuously with increasing LAI (Gilmanov et al., 2010; Li et al., 2008; Wang et al., 2008). Our results show that LAI plays a key positive role in forest photosynthesis (Figure 9a), although LAI shows less of an influence on GPP in XSBN (tropical forest), where LAI explained nearly 30% of the variation in GPP (Figure 9b1). However, LAI explained 74% of the variation in GPP in YJ (savanna; Figure 9a1). This finding indicates that the higher the LAI is, the higher the GPP. Therefore, LAI should be considered seriously when estimating/upscaling regional GPP based on the LUE model.

4.3. Influences of Biophysical Factors on LUE

Theoretically, and under ideal conditions, the assimilation of 1 mol of CO$_2$ requires 8 moles of photons (Xiao, 2006) at the leaf scale, which means that the leaf-scale theoretical maximum LUE$_\text{max}$ is 1.5 g C · mol photon$^{-1}$. Thus, the ecosystem-scale LUE$_\text{max}$ should be higher than 1.5 g C · mol photon$^{-1}$. However, the measured LUE values were much lower than the theoretical LUE$_\text{max}$ because LUE is constrained by many biophysical factors, such as the community structure, biomass, carboxylase density, nutrition content in soil/leaf, LAI, PAR, T, water, CO$_2$ concentration, VPD, spectral composition, and stomatal conductance (Green et al., 2003; Still et al., 2004; Zhao et al., 2007). In this study, the daily LUE values ranged from 0.008–0.316, 0.065–1.073, 0.060–1.129, and 0.052–0.881 g C · mol photon$^{-1}$ in YJ, XSBN, ALS, and LJ, respectively (Figure 3). The highest 8-day binned LUE$_\text{max}$ was 0.827 g C · mol photon$^{-1}$ in ALS (Table 3), and the values in the middle of the wet season were much lower than the theoretical LUE$_\text{max}$ (1.5 g C · mol photon$^{-1}$). Therefore, it is necessary to explore the critical factors that determine the variations in LUE. Increasing P/SVWC leads to decreased VPD (Zhao et al., 2007), which increases GPP by enhancing canopy stomatal conductance (Beer et al., 2009) and results in increased CO$_2$ and H$_2$O exchanges. As a result, LUE is enhanced when P/SVWC increases and when VPD decreases.
Figure 9. Influences of leaf area index (LAI) on gross primary productivity (GPP) and ecosystem light use efficiency (LUE) at a monthly scale. (a–d) Represent YJ, XSBN, ALS, and LJ, respectively; (e) integrates all the studied forest ecosystems’ GPP, LAI, and LUE values together correspondingly to explore how GPP and LUE respond to the variations in LAI in these forest ecosystems. The results indicated that LAI had a highly significant influence on the GPP and LUE in the studied forest ecosystems. In addition, Figure S2 in supporting information reveals that the variation in yearly LAI dominated the dramatic change in LUE.
In the present study, the path analysis results revealed that LUE has a positive relationship with \( P \), \( T_{\text{air}} \), RH, SVWC, and GPP and a negative relationship with \( R_g \), VPD, and PAR (Figures 7, 10, and 11). These results agree well with those of previously published studies (Beer et al., 2009; Shi et al., 2014; Zhao et al., 2007; Zhang, Cao, et al., 2015). Specifically, \( P \) is a strong determinant of GPP and, hence, LUE in the savanna ecosystem (YJ; Figure 7), and this finding is consistent with previous studies (Li et al., 2008; Shi et al., 2014), while \( T \) shows more influence on GPP and LUE in the subtropical evergreen broad-leaved forest ecosystem (ALS; Figure 7), which has a high MAP and a lower MAT (Tables 1 and 4). In addition, \( P \) plays a key role in LUE in YJ and XSBN, which have a higher MAT than that found in ALS and LJ (Table 4). This dynamic indicates that water availability constrains LUE in hot and dry areas. In contrast, \( T \) is more important in determining LUE than \( P \) in ALS and LJ (Figure 7), where the MAT is lower (Table 4), suggesting that \( T \) is the determinant in cold/high elevation areas. LUE shows a strong positive relationship with LAI in which LUE increases strongly with increasing LAI (Figures 9 and S2). This trend of a strong control of LUE by LAI has also been found in other studies (Eamus et al., 2001; Shi et al., 2014; Zhang, Cao, et al., 2015).

Figure 10. Linear/quadratic responses of ecosystem light use efficiency (LUE) to air temperature at daily timescales (\( n = 365 \)) in Yunnan, Southwest China. (a) Yuanjiang semiarid savanna ecosystem, (b) Xishuangbanna tropical rainforest ecosystem, (c) Ailaoshan subtropical evergreen broad-leaved forest ecosystem, and (d) Lijiang subalpine coniferous forest ecosystem. The quadratic regression equation for YJ was \( Y = -0.0003X^2 + 0.0159X - 0.131 \) (\( R^2 = 0.12, P < 0.001 \)), which suggested that warming will decrease LUE in the savanna ecosystem.

Figure 11. Linear/quadratic responses of ecosystem light use efficiency (LUE) to soil volumetric water content (SVWC) at daily timescales (\( n = 365 \)) in Yunnan, Southwest China. (a) Yuanjiang semiarid savanna ecosystem, (b) Xishuangbanna tropical rainforest ecosystem, (c) Ailaoshan subtropical evergreen broad-leaved forest ecosystem, and (d) Lijiang subalpine coniferous forest ecosystem.
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Some studies have shown that LUE is mainly controlled by 7 and soil moisture (Tao et al., 2014; Xiao, Zhang, et al., 2004) or P (Kanniah et al., 2011; Li et al., 2008). In summary, T, P, VPD, LAI, PAR, and GPP are the primary determinants (especially GPP, VPD, and LAI) of LUE, although the magnitudes of each influence are not exactly the same among the four studied forest ecosystems (YJ, XSBN, ALS, and LJ) on a monthly timescale (Figures 7 and 9). The regression analysis revealed that LUE increased with increasing $T_{air}$ and SVWC in all of the forest ecosystems except for YJ (savanna), where LUE decreased when $T_{air}$ exceeded approximately 26.5 °C, which indicated that LUE will decrease in YJ but may increase in XSBN, ALS, and LJ under warming scenarios. Therefore, the changing climate (warming/decreasing precipi-

5. Implications and Conclusions

Based on the 27 site-years of LUE results and the above discussion, LUE shows considerable spatiotemporal variability, and the evergreen broad-leaved forest (EBF) ecosystem has the highest LUE, while the savanna ecosystem has the lowest. Therefore, it is maybe an alternative way to plant the EBF plantation to uptake CO$_2$ where water and temperature are favorable under the circumstance of global increasing CO$_2$ concentra-

Radon, T. (2019). The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Global Change Biology, 13(4), 776–787. https://doi.org/10.1111/gcb.12646.00136

References

Alton, P. B., North, P. R., & Los, S. O. (2007). The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Global Change Biology, 13(4), 776–787. https://doi.org/10.1111/gcb.12646.00136

Baldocchi, D., Chu, H. S., & Reichstein, M. (2018). Inter

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., et al. (2001). Gap filling strategies for defensible annual sums of net ecosystem exchange. Agricultural and Forest Meteorology, 107(1), 43–69. https://doi.org/10.1016/S0168-1923(00)00225-2

Fei, X.-H., Jin, Y., Zhang, Y., Sha, L., Liu, Y., Song, Q., et al. (2017). Eddy covariance and biometric measurements show that a savanna ecosystem in Southwest China is a carbon sink. Scientific Reports, 7(1), 41025. https://doi.org/10.1038/srep41025

Eamus, D., Hutley, L. B., & O’Grady, A. P. (2001). Tree Physiology. 21(1), 1–13.

Eamus, D., Hutley, L. B., & O’Grady, A. P. (2001). Tree Physiology. 21(1), 1–13.

Fei, X.-H., Jin, Y., Zhang, Y., Sha, L., Liu, Y., Song, Q., et al. (2017). Eddy covariance and biometric measurements show that a savanna ecosystem in Southwest China is a carbon sink. Scientific Reports, 7(1), 41025. https://doi.org/10.1038/srep41025

References

Alton, P. B., North, P. R., & Los, S. O. (2007). The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. Global Change Biology, 13(4), 776–787. https://doi.org/10.1111/gcb.12646.00136

Aubinet, M., Chermenane, B., Vandenhaute, M., Longdoz, B., Yernaux, M., & Laitet, E. (2001). Long term carbon dioxide exchange above a forest stand in the Belgian Ardennes. Agric. and Forest Meteorology, 108(4), 293–315. https://doi.org/10.1016/S0168-1923(01)00244-1

Austin, R. S., Kingston, G., Longden, P. C., & Donovan, P. A. (1978). Gross energy yields and the support energy requirements for the production of sugar from beet and cane: A study of four production areas. Journal of Agricultural Science, 91(03), 667–675. https://doi.org/10.1017/S0021859600006068

Baldocchi, D. (2008). Breathing of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems. Australian Journal of Botany, 56(1), 1–26. https://doi.org/10.1071/BO07151

Baldocchi, D., Chu, H. S., & Reichstein, M. (2018). Inter-annual variability of net and gross ecosystem carbon fluxes: A review. Agricultural and Forest Meteorology, 249, 520–533. https://doi.org/10.1016/j.agrformet.2017.05.015

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., et al. (2001). FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society, 82(11), 2415–2434. https://doi.org/10.1175/1520-0477(2001)082(2415:ATOTST)2.0.CO;2

Baldocchi, D., Valentini, R., Running, S., Oechel, W., & Dahlman, R. (1996). Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. Global Change Biology, 2(3), 159–168. https://doi.org/10.1006/gcfg.1996.0006

Baldocchi, D. D. (2003). Assessing the eddy covariance procedure for evaluating carbon dioxide exchange rates of ecosystems: Past, present and future. Global Change Biology, 9(4), 479–492. https://doi.org/10.1046/j.1365-2486.2003.06029.x

Beer, C., Ciais, P., Reichstein, M., Baldocchi, D., Law, B. E., Papale, D., et al. (2009). Temporal and among-site variability of inherent water use efficiency at the ecosystem level. Global Biogeochemical Cycles, 23, GB2018. https://doi.org/10.1029/2008GB003233

Cannell, M. G. R., Milne, R., Sheppard, L. J., & Usworth, M. H. (1987). Radiation interception and productivity of willow. Journal of Applied Ecology, 24(1), 261–278. https://doi.org/10.2307/2403803

Cao, M., Zou, X., Warren, M., & Zhu, H. (2006). Tropical forests of Xishuangbanna, China. Biotropica, 38(3), 306–309. https://doi.org/10.1111/j.1744-7296.2006.00146.x

Chan, O. C., Yang, X., Fu, Y., Feng, Z., Sha, L., Casper, P., & Zou, X. (2006). 16 S rRNA gene analyses of bacterial community structures in the soils of evergreen broad-leaved forests in south-west China. FEMS Microbiology Ecology, 59(2), 247–259. https://doi.org/10.1111/j.1574-6941.2006.00156.x

Cooper, J. P. (1970). Potential production and energy conversion in temperate and tropical grasses. Herbage Abstracts, 40(1), 1–13.

Eamus, D., Hutley, L. B., & O’Grady, A. P. (2001). Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. Tree Physiology, 21(12–13), 977–988. https://doi.org/10.1093/treephys/21.12.977

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., et al. (2001). Gap filling strategies for defensible annual sums of net ecosystem exchange. Agricultural and Forest Meteorology, 107(1), 43–69. https://doi.org/10.1016/S0168-1923(00)00225-2
Fei, X.-H., Song, Q., Zhang, Y., Liu, Y., Sha, L., Yu, G., et al. (2018). Carbon exchanges and their responses to temperature and precipitation in forest ecosystems in Yunnan, Southwest China. *Science of the Total Environment, 616–617*, 824–840. https://doi.org/10.1016/j.scitotenv.2017.10.239

Fox, J., Z. Nie, J. Byrnes, M. Cullbertson, D. Roy, S., Friendly, M., et al. (2016). Sem: Structural equation models. R package version3.1-8. Retrieved from https://CRAN.R-project.org/package=sem

Garbulsky, M. F., Penuelas, J., Papale, D., Ardo, J., Goulden, M. L., Kiely, G., et al. (2010). Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. *Global Ecology and Biogeography, 19*(2), 253–267. https://doi.org/10.1111/j.1466-8238.2009.00304.x

Gilmannow, T. G., Aires, L., Barca, Z., Baron, V. S., Beilelli, L., Beringer, J., et al. (2010). Productivity, respiration, and light parameters of world grassland and agroecosystems derived from flux-tower measurements. *Rangeland Ecology & Management, 63*(1), 16–39. https://doi.org/10.2111/Rem-D-09-0072.1

Gilmannow, T. G., Soussana, J. F., Aires, L., Allard, V., Ammann, C., Balzarolo, M., et al. (2007). Partitioning European grassland net ecosystem CO2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agriculture Ecosystems & Environment, 121*(1–2), 93–120. https://doi.org/10.1016/j.agee.2006.12.008

Gilteon, A. A., & Gamon, J. A. (2015). The need for a common basis for defining light-use efficiency: Implications for productivity estimation. *Remote Sensing of Environment, 156*, 196–201. https://doi.org/10.1016/j.rse.2014.09.017

Grace, J. B., & Bollen, K. A. (2005). Interpreting the results from multiple regression and structural equation models. *The Bulletin of the Ecological Society of America, 86*(4), 283–295. https://doi.org/10.1890/0112-6696(2005)086[0283:ITRTRM]2.0.CO;2

Green, D. S., Erickson, J. E., & Kruger, E. L. (2003). Foliar morphology and canopy nitrogen as predictors of light-use efficiency in terrestrial vegetation. *Agricultural and Forest Meteorology, 115*(3–4), 163–171. https://doi.org/10.1016/S0168-1923(02)00210-1

Hall, F. G., Huemmrich, K. F., Goetz, S. J., Sellers, P. I., & Nickeson, J. E. (1992). Satellite remote-sensing of surface-energy balance—success, failures, and Unresolved Issues in Fife. *Journal of Geophysical Research, 97*(D17), 19,061–19,089. https://doi.org/10.1029/92JD02189

He, H. L., Liu, M., Xiao, X., Ren, X., Zhang, L., Sun, X., et al. (2014). Large-scale estimation and uncertainty analysis of gross primary production in Tibetan alpine grasslands. *Journal of Geophysical Research: Biogeosciences, 119*, 466–486. https://doi.org/10.1002/2013JG002449

Hollinger, D. Y., Kellner, F. M., Byers, J. N., Hunt, J. E., Mceveney, T. M., & Weil, P. L. (1994). Carbon-dioxide exchange between an undisturbed old-growth temperate Forest and the atmosphere. *Ecology, 75*(1), 134–150. https://doi.org/10.2307/1939390

Huang, H., Chen, Z., Liu, D., He, G., He, R., Li, D., & Xu, K. (2017). Species composition and community structure of the Yulongxueshan (jade dragon Snow Mountains) forest dynamics plot in the cold temperate spruce-fir forest, Southwest China. *Biodiversity Science, 25*(3), 255–264. https://doi.org/10.17522/biods.2016274

Jia, W., Liu, M., She, Q., Yin, C., Zhu, X., & Xiang, W. (2016). Optimization and evaluation of key photosynthesis parameters in forest ecosystems based on FLUXNET data and VPM model. *Chinese Journal of Applied Ecology, 27*(4), 1095–1102.

Kanniah, K. D., Beringer, J., & Hutley, L. B. (2011). Environmental controls on the spatial variability of savanna productivity in the Northern Territory, Australia. *Agricultural and Forest Meteorology, 151*(11), 1429–1439. https://doi.org/10.1016/j.agrformet.2011.06.009

Larcher, W. (2003). *Physiological plant ecology: ecophysiology and stress physiology of functional groups* (4th ed., p. 513). Berlin, Germany: Springer Science & Business Media.

Lee, X., Massman, W., & Law, B. (2006). *Handbook of Micrometeorology—a Guide for Surface Flux Measurement and Analysis*. New York: Springer Science Business Media.

Lee, X., & Massman, W. J. (2010). A perspective on thirty years of the Webb, Pearman and Leuning density corrections. *Boundary-Layer Meteorology, 139*(1), 37–59. https://doi.org/10.1007/s10546-010-9575-z

Li, C. C. (1975). *Path Analysis—a Primer*. Pacific Grove, CA: Boxwood Press.

Li, S. G., Eugster, W., Asanuma, J., Kotani, A., Davaa, G., Oyumbaatar, D., & Sugita, M. (2008). Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. *Journal of Geophysical Research, 113*, G01019. https://doi.org/10.1029/2007JG000349

Liu, F. Y., Zhu, H., Shi, J. P., & Chen, X. M. (2007). Characteristics of plant communities and their soil fertilities in dry-hot valley of Yunnan County, Yunnan, China. *Chinese Journal of Applied & Environmental Biology, 13*(6), 782–787.

Lloyd, J., & Taylor, J. A. (1994). On the temperature-dependence of soil respiration. *Functional Ecology, 8*(3), 315–323. https://doi.org/10.2307/2389824

Mercado, L. M., Bellouin, N., Sitch, S., Boucher, O., Huntingford, C., Wild, M., & Cox, P. M. (2009). Impact of changes in diffuse radiation on the global land carbon sink. *Nature, 458*(7241), 1014–1017. https://doi.org/10.1038/nature07949

Monteith, J. L. (1972). Solar-radiation and productivity in tropical ecosystems. *Journal of Applied Ecology, 9*(3), 747–766. https://doi.org/10.2307/2401901

Nichol, C. J., Huemmrich, K. F., Black, T. A., Jarvis, P. G., Walthall, C. L., Grace, J., & Hall, F. G. (2000). Remote sensing of photosynthetic-light-use efficiency of boreal forest. *Agricultural and Forest Meteorology, 101*(2–3), 131–142. https://doi.org/10.1016/S0168-1923(99)00167-7

Nizami, S. M., Yiping, Z., Zheng, Z., Zhiyuan, L., Guoping, Y., & Liqing, S. (2017). Evaluation of forest structure, biomass and carbon sequestration in subtropical pine forests of SW China. *Environmental Science and Pollution Research International, 24*(9), 8137–8146. https://doi.org/10.1007/s11356-017-8506-7

Oдум, E. P., & Barrett, G. W. (1971). *Fundamentals of ecology* (p. 574). Philadelphia, PA: Saunders.

Pangle, L., Vose, J. M., & Teskey, R. O. (2009). Radiation use efficiency in adjacent hardwood and pine forests in the southern Appalachians. *Forest Ecology and Management, 257*(3), 1034–1042. https://doi.org/10.1016/j.foreco.2008.11.004

Piao, S., Fang, J., Ciais, P., Peißen, P., Huang, Y., Sitch, S., & Wang, T. (2009). The carbon balance of terrestrial ecosystems in China. *Nature, 458*(7241), 1009–1013. https://doi.org/10.1038/nature07844

Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A., & Kloster, S. A. (1993). Terrestrial ecosystem production - a process model-based on global satellite and surface data. *Global Biogeochemical Cycles, 7*(4), 811–841. https://doi.org/10.1029/92GB02725

Prince, S. D., & Goward, S. N. (1995). Global primary production: A remote sensing approach. *Journal of Biogeography, 22*(4/5), 815–835. https://doi.org/10.2307/2845983

Qiao, N., Schaefli, D., Blagodatskaya, E., Zou, X., Xu, X., & Kuyasov, Y. (2014). Labile carbon retention compensates for CO2 released by priming in forest soils. *Global Change Biology, 20*(6), 1943–1954. https://doi.org/10.1111/gcb.12458
Yuan, W., Cai, W., Xia, J., Chen, J., Liu, S., Dong, W., et al. (2014). Global comparison of light use efficiency models for simulating terrestrial vegetation gross primary production based on the LaThuile database. *Agricultural and Forest Meteorology, 192-193*, 108–120. https://doi.org/10.1016/j.agrformet.2014.03.007

Yuan, W. P., Liu, S., Zhou, G., Zhou, G., Tieszen, L. L., Baldocchi, D., et al. (2007). Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. *Agricultural and Forest Meteorology, 143*(3–4), 189–207. https://doi.org/10.1016/j.agrformet.2006.12.001

Zhang, L., Cao, P., Zhu, Y., Li, Q., Zhang, J., Wang, X., et al. (2015). Dynamics and regulations of ecosystem light use efficiency in a broad-leaved Korean pine mixed forest, Changbai Mountain. *Chinese Journal of Plant Ecology, 39*(12), 1156–1165.

Zhang, L. X., Zhou, D. C., Fan, J. W., & Hu, Z. M. (2015). Comparison of four light use efficiency models for estimating terrestrial gross primary production. *Ecological Modelling*, 300, 30–39. https://doi.org/10.1016/j.ecolmodel.2015.01.001

Zhao, M. S., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment, 93*(2), 164–176. https://doi.org/10.1016/j.rse.2004.12.011

Zhao, Y., Niu, S., Wang, J., Li, H., & Li, g. (2007). Light use efficiency of vegetation: A review. *Chinese Journal of Ecology, 26*(9), 1471–1477.

Zhou, Y. L., Wu, X., Ju, W., Chen, J. M., Wang, S., Wang, H., et al. (2016). Global parameterization and validation of a two-leaf light use efficiency model for predicting gross primary production across FLUXNET sites. *Journal of Geophysical Research: Biogeosciences, 121*, 1045–1072. https://doi.org/10.1002/2014JG002876