

Multi-site evaluation of an improved SIF-based model for estimating canopy GPP

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Key Points:

(1) We developed a SIF-based q_L function to improve the simulation of q_L , and then to enhance the performance of a SIF-based GPP model.

(2) Tower-based datasets collected from 16 sites were used to evaluate model performance.

(3) Results showed that the improved SIF-based GPP model significantly reduced biases in GPP estimation.

Abstract: Sun-induced chlorophyll fluorescence (SIF) offers a promising path to quantify gross primary productivity (GPP) across spatiotemporal scales. Recent studies have demonstrated the applicability of the SIF-based mechanistic light response (qMLR-SIF) model for estimating canopy GPP. However, the inadequate simulation of the key parameter q_L (the fraction of open photosystem II reaction centers) restricts the applicability of the qMLR-SIF model. Therefore, we developed a SIF-based q_L function to improve the simulation of q_L , and thereby to enhance the performance of the qMLR-SIF model. Tower-based datasets collected from 16 sites were utilized to evaluate the improved qMLR-SIF model. Multi-site validation indicated that the improved qMLR-SIF model enhanced the accuracy of canopy GPP estimation for different plant functional types, photosynthetic pathways, and temporal scales. In particular, the improved qMLR-SIF model significantly reduced the underestimation and overestimation of GPP (y-slope = 0.94 to 1.05; y-intercept = -0.94 to 0.74 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Threshold analysis showed that environmental stresses decreased model performance, while even in this situation,

the improved qMLR-SIF model still outperformed the original model (except for the boreal evergreen needleleaf forests). The advantages of the SIF-based q_L function stem from the mechanistic link between SIF and q_L and several unique features of SIF. Our findings demonstrate the enhanced applicability of the improved qMLR-SIF model, highlighting its potential for estimating photosynthesis at regional and global scales.

Keywords: Sun-induced chlorophyll fluorescence (SIF); Gross primary productivity (GPP); Fraction of open photosystem II reaction centers (q_L); SIF-based mechanistic light response (MLR-SIF) model; Canopy photosynthesis

1. Introduction

Photosynthesis is a complex biophysical and biochemical process by which plants convert sunlight energy into stable chemical energy (Han et al., 2022b). This process covers three different stages of reactions: photophysical reactions, photochemical reactions, and biochemical reactions (Kamen, 1963; Sun et al., 2023a). Photophysical reactions involve sunlight harvesting and partitioning of excitation energy into photochemistry, thermal dissipation (including constitutive thermal dissipation and regulated thermal dissipation), and sun-induced chlorophyll fluorescence (SIF) emission (Porcar-Castell et al., 2014; Gu et al., 2019; Mohammed et al., 2019; Porcar-Castell et al., 2021). Photochemical reactions, as a bridge between the other two kinds of reactions, refer to electron transport from photosystem II (PSII) to photosystem I (PSI) as well as the generation of NADPH (nicotinamide adenine dinucleotide phosphate) and ATP (adenosine triphosphate), two key products subsequently used in biochemical reactions. Biochemical reactions, also known as dark reactions, relate to CO₂ fixation in the Calvin-Benson cycle (Sun et al., 2023a). These three stages, which are organically coordinated and give feedback to each other, form a remarkable and highly efficient energy conversion system.

SIF, produced in the photophysical reactions of photosynthesis, is an optical signal emitted from chlorophyll *a* molecules in plant leaves, with spectral range from 650 to 850 nm (Gu et al., 2019; Porcar-Castell et al., 2021). Since SIF emission competes for absorbed Photosynthetically Active Radiation (PAR) with photochemistry and thermal dissipation (Baker, 2008; Murchie and Lawson, 2013; Gu et al., 2019; Magney et al., 2019b; Porcar-Castell et al., 2021), the variation of SIF can reflect the dynamics of the other two processes (Murchie and Lawson, 2013; Sun et al., 2023a), and thus is deeply coupled with photosynthesis at the plant molecular level. The origin of SIF and its mechanistic link with photosynthesis endow SIF with several unique features: 1) SIF is an integrated indicator that contains rich information about

plant physiology status and responses of plants to environmental factors ([Gu et al., 2019](#); [Han et al., 2022a](#); [Sun et al., 2023a](#)); 2) SIF is a timely-response variable and can rapidly reflect changes in plant physiology status ([Baker, 2008](#)), which is quite different from traditional vegetation indices, such as the normalized difference vegetation index (NDVI), the near-infrared reflectance for vegetation (NIRv), and the photochemical reflectance index (PRI) ([Magney et al., 2019b](#); [Pierrat et al., 2022b](#)); 3) SIF is an internal variable of the leaf photosynthetic system and thus carries information about carbon fixation, which differs from environmental drivers (external variables), such as PAR, air temperature (T_a) and vapor pressure deficit (VPD) ([Liu et al., 2024a](#)). Owing to these unique features, SIF exhibits great potential in a wide range of applications ([Mohammed et al., 2019](#); [Porcar-Castell et al., 2021](#); [Sun et al., 2023b](#)), such as photosynthesis estimation ([Gu et al., 2019](#); [Han et al., 2022a](#); [Liu et al., 2022](#)), drought detection ([Qiu et al., 2022](#); [Wang et al., 2023](#); [Behera et al., 2025](#)), phenology evaluation ([Merrick et al., 2023](#); [Shi et al., 2025](#)), and transpiration simulation ([Shan et al., 2021](#); [Beauclaire et al., 2024](#)).

Rapid advances in remote sensing techniques and SIF retrieval methods have greatly promoted various SIF applications ([Meroni et al., 2009](#); [Frankenberg and Berry, 2018](#); [Cendrero-Mateo et al., 2019](#); [Mohammed et al., 2019](#); [Porcar-Castell et al., 2021](#); [Sun et al., 2023b](#)), especially the estimation of gross primary productivity (GPP) from SIF. This is because: 1) GPP, as a crucial indicator for understanding the global carbon cycle ([Pei et al., 2022](#)), cannot be directly measured at scales above the leaf level ([Welp et al., 2011](#)); 2) the accurate prediction of GPP across spatiotemporal scales is a long-standing challenge ([Gu et al., 2019](#)); 3) the mechanistic link between SIF and CO₂ fixation at the plant molecular level makes SIF extremely promising to accurately quantify GPP at multiple spatiotemporal scales ([Porcar-Castell et al., 2021](#)). Recent studies have demonstrated the strong correlation between SIF and GPP across biomes ([Yang et al., 2015](#); [Liu et al., 2017](#); [Magney et al., 2019b](#); [Dechant et al., 2020](#); [Pierrat et al., 2022b](#); [Wu et al., 2022a](#)) and spatiotemporal scales ([Yang et al., 2017](#); [Zhang et al., 2018](#); [He et al., 2020](#); [Yang et al., 2023](#)). Currently, SIF-based GPP models can be primarily classified into three classes: empirical models ([Damm et al., 2015](#); [Liu et al., 2019b](#); [Liu et al., 2021](#); [Pierrat et al., 2022b](#)), hybrid models ([Koffi et al., 2015](#); [Bacour et al., 2019](#)), and SIF-based mechanistic light response (MLR-SIF) models ([Gu et al., 2019](#); [Han et al., 2022a](#); [Liu et al., 2022](#); [Beauclaire et al., 2024](#); [Chen et al., 2024b](#); [Guo et al., 2024](#); [Liu et al., 2024a](#); [Liu et al., 2024b](#)). The empirical models rely on a strong linear or non-linear correlation between SIF and GPP, assuming that this correlation remains invariant across different conditions. This approach is simple but lacks wide applicability, because the assumption of

invariable SIF-GPP relationships may be invalid under some circumstances, such as across plant functional types (PFTs) (Liu et al., 2024a), photosynthetic pathways (Liu et al., 2017; He et al., 2020), temporal scales (Magney et al., 2019b; Li et al., 2020; Pierrat et al., 2022b), and even plant growth stages (Yang et al., 2018a; Li et al., 2020; Miao et al., 2020). The hybrid models combine data assimilation methods with terrestrial biosphere models (TBMs) to constrain the outputs and parameters of TBMs (Anav et al., 2015; Koffi et al., 2015; Norton et al., 2019). By assimilating SIF data into TBMs, hybrid models can improve the estimation of GPP (Norton et al., 2019). However, hybrid models contain numerous parameters and require a substantial amount of input data. Furthermore, large uncertainties and disagreements have been identified among different TBMs (Beer et al., 2010; Keenan et al., 2012; Anav et al., 2015), which may also be present in the hybrid models. The MLR-SIF models, as the state-of-the-art SIF-based GPP models, are based on the mechanistic link between SIF and photosynthesis (Gu et al., 2019; Han et al., 2022a). This type of model offers a novel way to infer GPP grounded in a rigorous theoretical basis of plant physiology and with fewer parameters than the hybrid models. The MLR-SIF models refer to two key chlorophyll fluorescence variables, i.e., the fraction of open PSII reaction centers based on the lake model (q_L) and the non-photochemical quenching (NPQ). q_L reflects the redox state of the primary quinone electron acceptor of PSII (Q_A). Higher q_L corresponds to more open (Q_A is oxidized) PSII reaction centers (Baker, 2008), and hence, means higher efficiency of photochemistry. NPQ indicates the degree of regulated thermal dissipation in PSII. Higher NPQ means that more excitation energy is dissipated as heat, and therefore, less energy is available for photochemistry and SIF emission due to energy conservation (Sun et al., 2023a). Compared to q_L , NPQ involves several complex photoprotective mechanisms (NPQ , not italic) operating at different timescales (e.g., energy-dependent type, state-transition type, and photoinhibition type) (Muller et al., 2001; Baker, 2008), which makes it rather difficult to be modeled (Zaks et al., 2012). Note that NPQ refers to several regulated thermal dissipation mechanisms, while NPQ is a fluorescence parameter to quantify the degree of NPQ (Porcar-Castell et al., 2014). Since either q_L or NPQ is required to calculate GPP (Han et al., 2022a), the MLR-SIF model containing q_L is referred to as the q_L -type (qMLR-SIF) model, and that containing NPQ as the NPQ -type (nMLR-SIF) model (Liu et al., 2024a). These two types of models are mechanistically equivalent, but the qMLR-SIF model has a simpler structure and requires fewer parameters, thereby having greater potential for large-scale applications (Han et al., 2022a; Liu et al., 2022).

In recent years, several studies have applied the qMLR-SIF model to quantify canopy GPP in a variety of terrestrial ecosystems, such as crops (CRO) (Beauclaire et al., 2024; Guo et al.,

2024), evergreen needleleaf forests (ENF) (Chen et al., 2024b) and deciduous broadleaf forests (DBF) (Liu et al., 2024a), demonstrating the wide applicability of the qMLR-SIF model in estimating GPP at the canopy scale. However, due to limited studies of q_L (Gu et al., 2019), the estimation of this key variable in the qMLR-SIF model only considers light effects (q_L is expressed as an exponential function of PAR, namely, q_{L_PAR} function) (Han et al., 2022a), which may lead to underestimation and/or overestimation of GPP (Liu et al., 2024a). Research has shown that PAR dominates q_L variations (Baker, 2008; Gu et al., 2019; Han et al., 2022a), but other factors (e.g., T_a , CO₂ concentration, and drought stress) may also affect q_L under specific scenarios (Kramer et al., 2004; Baker, 2008; Shin et al., 2021; Han et al., 2022a; Han et al., 2022b). For example, when light intensity is sufficient, decreased CO₂ supply may reduce NADPH and ATP demands in the dark reactions (Baker, 2008; Gu et al., 2019), thus leading to a decrease in the linear electron transport rate from PSII to PSI. This, in turn, causes a reduction in the amount of oxidized Q_A in PSII and eventually results in a decrease in q_L (see Fig. 2 in Kramer et al., 2004). Therefore, in order to improve the accuracy of the qMLR-SIF model, it is essential to consider other possible effects on q_L during the q_L simulation. Besides, existing relevant research primarily focuses on individual study sites with single PFTs, whereas comprehensive multi-site analysis is relatively sparse.

Given the fact that q_L decreases as SIF increases and the q_L -SIF curve pattern is similar to the q_L -PAR curve pattern across species (see q_L -SIF curves in Fig. S7c and q_L -PAR curves in Fig. S6a in Han et al., 2022a), we hypothesized that q_L could also be expressed as an exponential function of SIF, similar to that of PAR. Given the facts that 1) SIF is an integrated indicator and an internal variable of photosynthetic systems, which contains information not only about PAR effects on plants but also about plant physiology status and other effects (such as T_a , VPD) on plants (thus on q_L) (Sun et al., 2023a); 2) SIF is a timely-response variable which can rapidly reflect the changes of plant physiology (Baker, 2008), we further assumed that the SIF-based q_L function would more accurately estimate q_L , thereby improving the performance of the qMLR-SIF model. Based on the above hypothesis, this study aims to develop a SIF-based q_L (q_{L_SIF}) function to improve the simulation of q_L , and then to enhance the performance of the qMLR-SIF model in quantifying canopy GPP. To achieve this, we:

(1) established a dataset containing 16 study sites (mainly including far-red SIF, GPP, and key environmental variables) by collecting canopy-scale data from open sources and published articles;

(2) utilized this dataset to explore and develop a q_{L_SIF} function with the help of the qMLR-SIF model at the canopy scale;

(3) evaluated the performance of the improved qMLR-SIF model by comparing it with the original qMLR-SIF model across different PFTs (CRO, DBF, and ENF), photosynthetic pathways (C_3 and C_4), and temporal scales (half-hourly, daily, 4-day, and 8-day).

Note that, for convenience, we termed the qMLR-SIF model as q_{L_PAR} model when q_L was estimated by the conventional q_{L_PAR} function, and as q_{L_SIF} model when q_L was estimated by the novel q_{L_SIF} function developed in this study. These two names (q_{L_PAR} model and q_{L_SIF} model) are only meaningful in the context of this study.

2. Materials and Methods

2.1 Datasets establishment

2.1.1 Data collection

Canopy-level data containing tower-based top of canopy far-red SIF (SIF_{TOC_760}), GPP and other crucial variables (such as PAR, T_a and VPD), were collected from open data sources and published studies. These data came from 16 study sites and included three PFTs (10 CROs, 2 DBFs, and 4 ENFs), as well as two temporal resolutions (half-hourly at 8 sites and daily at the other 8 sites). Among the 16 study sites (**Table 1**), data from Butterfield et al. (2023) as well as Wu et al. (2023) lacked eddy-covariance (EC) fluxes and environmental variables; thus, they were downloaded from the AmeriFlux website (<https://ameriflux.lbl.gov/sites/site-search/>). Data from Tang (2017) were also lacking in EC fluxes and meteorological factors, which were downloaded from the Harvard Forest website (<https://harvardforest.fas.harvard.edu/data-archives>). Data from Magney and Frankenberg (2019) did not have T_a , hence we used T_a data downloaded from the National Centers for Environmental Information website (<https://www.ncei.noaa.gov/cdo-web/>). The remaining data from 11 sites contained all the key variables (SIF_{TOC_760} , GPP, PAR, T_a , and VPD). Basic information about all study sites and datasets is summarized in **Table 1**. Workflow of data collection and post-processing, data analysis, and GPP estimation conducted in this study is shown in **Fig. 1**. Tower-based observations and post-processing steps of the collected data are detailed in the following sections.

200 **Table 1** Basic information about the 16 study sites, datasets and SIF observations.

PFTs	Site ID	Latitude (°)	Longitude (°)	C ₃ /C ₄	MAT (°C)	MAP (mm)	Data years	Spectromet er	SIF retrieval method	NEE partition	Reference
Temperate DBF	US-Ha1	42.54	-72.17	C ₃	6.6	1071	2013*, 2014	HR2000+	FLD	NT	(Yang et al., 2015 ; Tang, 2017 ; Wu et al., 2022b)
	US-UMB	45.56	-84.71	C ₃	5.8	803	(2018, 2019)*	QE Pro	FLD	DT	(Butterfield et al., 2023)
Temperate ENF	US-Nr1	40.03	-105.55	C ₃	1.5	800	(2017, 2018)*	QE Pro	DOAS	NT	(Magney et al., 2019b ; Cheng et al., 2020b)
	TCK ^e	37.30	127.32	C ₃	11.5	1299	2018	QE Pro	SVD	NT	(Kim et al., 2021)
Boreal ENF	SOBS	53.98	-105.12	C ₃	1.4	406	(2019, 2020, 2021)*	QE Pro	FLD	DT	(Pierrat et al., 2022b ; Pierrat et al., 2022c)
	DEJU	63.88	-145.75	C ₃	-3.0	300	(2019, 2020, 2021)*	QE Pro	FLD	DT	(Pierrat et al., 2022c)
CRO	DaMan ^e	38.86	100.37	C ₄	8.0	300	2017, 2018	QE65 Pro	3FLD	NT	(Chen et al., 2020)
	UIUC ^e	40.06	-88.20	C ₄	11.3	928	2018	QE Pro	iFLD	DT	(Wu et al., 2022a)
	ZhaoXian ^e	37.77	114.82	C ₃	12.5	472	2018	QE Pro	3FLD	NT	(Ma et al., 2022)
	US-Br3	41.97	-93.69	C ₃	8.9	847	2017	QE Pro	DOAS	NT	(Magney and Frankenberg, 2019)
	INRA ^e	43.92	4.88	C ₃	—	—	2010	HR2000+	nFLD	DT	(Goulas et al., 2017)
	US-Ne3	41.18	-96.44	C ₄ / C ₃	10.1	784	(2017, 2018)*	QE Pro	SFM	NT	(Wu et al., 2023)
	US-Ne2	41.16	-96.47	C ₄ / C ₃	10.1	789	(2017, 2018)*	QE Pro	SFM	NT	(Wu et al., 2023)
	YangLing	34.28	108.07	C ₃	12.9	630	(2021, 2022)*	QE Pro	SVD	DT	(Liu et al., 2022 ; Liu et al., 2024b)
	ShangQiu	34.52	115.59	C ₄	13.9	708	2017, 2018, 2019	QE Pro	SFM	NT	(Wu et al., 2022b)
	JuRong	31.81	119.22	C ₃	15.2	1058.8	2016	QE Pro	SFM	NT	(Wu et al., 2022b)

201 PFT: plant functional type; MAT: mean annual temperature; MAP: mean annual precipitation; DOY: day of year; NEE: net ecosystem CO₂ exchange; NT: nighttime method; DT: daytime method
202 DBF: deciduous broadleaf forest; ENF: evergreen needleleaf forest; CRO: crop
203 e: means data of this study site was extracted from figures in the corresponding article. Study site without the mark 'e' means its data was downloaded from open sources in the corresponding
204 reference.

205 *: means the minimum temporal resolution of data is half-hourly, and the others are daily.

2.1.2 Ground-based SIF observations and retrievals

The ground-based SIF observation system, which is mostly mounted on towers above plant canopies, mainly consists of a narrowband spectrometer (such as the QE Pro) for SIF retrievals and a broadband spectrometer (such as the HR2000+ and Flame) for calculating vegetation indices (e.g., NDVI, NIRv and PRI) ([Grossmann et al., 2018](#); [Liu et al., 2022](#); [Wu et al., 2022b](#); [Tommervik et al., 2023](#); [Chen et al., 2024a](#)). The narrowband spectrometer has a high spectral resolution ($\sim 0.1 - 0.4$ nm) ([Liu et al., 2022](#); [Wu et al., 2022b](#); [Chen et al., 2024a](#)) and covers the spectral range of red and/or far-red regions ([Butterfield et al., 2023](#)). The broadband spectrometer, with a relatively low spectral resolution ($\sim 1 - 2$ nm) ([Grossmann et al., 2018](#); [Wu et al., 2022b](#); [Tommervik et al., 2023](#)), includes the full range of visible and near-infrared regions. Every spectrometer contains at least two channels. One channel collects the downwelling irradiance using an upward fiber which is equipped with a cosine corrector. The other channel is connected to a downward bare fiber with a specific field of view, e.g., 25° ([Yang et al., 2018b](#); [Liu et al., 2022](#)). To avoid dark current drifts and spectral shifts, both spectrometers are situated in a box where the temperature is controlled to an appropriate range, such as around 25°C ([Liu et al., 2022](#); [Beauclaire et al., 2024](#)). The high-resolution spectrometer for SIF retrievals is the central part of the SIF observation system. In this study, most of the 16 study sites were equipped with the advanced QE Pro spectrometer (**Table 1**).

The retrieval of SIF relies on the spectral properties of incoming sunlight and the additive contribution of SIF to the total reflected radiance at the top of canopy ([Mohammed et al., 2019](#); [Porcar-Castell et al., 2021](#)). SIF retrieval approaches involved in this study (**Table 1**) include the FLD-based (Fraunhofer line depth) method, spectral fitting method (SFM), singular vector decomposition (SVD), and differential optical absorption spectroscopy (DOAS). Detailed introductions to these approaches can be found in the previous reviews ([Meroni et al., 2009](#); [Cendrero-Mateo et al., 2019](#); [Chang et al., 2020](#)), along with the corresponding references in **Table 1**. To match the EC data, the retrieved SIF values are usually averaged to the half-hourly temporal resolution ([Yang et al., 2015](#); [Magney et al., 2019b](#); [Liu et al., 2022](#)).

2.1.3 EC flux and meteorological measurements

The EC system, as a standard approach for measuring ecosystem CO_2 exchange, is commonly installed on towers above the top of the canopy. This system primarily contains an open-path or closed-path infrared gas analyzer for recording CO_2 and H_2O concentration and a three-dimensional sonic anemometer for monitoring wind speed and wind direction ([Miao et](#)

al., 2020; Kim et al., 2021; Ma et al., 2022; Pierrat et al., 2022b; Wu et al., 2022a). The raw flux data, collected at a frequency of 10 Hz, are converted into half-hourly net ecosystem exchange (NEE) of CO₂ using the EddyPro software (LI-COR Inc.). Then, the nighttime method (Reichstein et al., 2005) or the daytime method (Lasslop et al., 2010) is used to partition NEE into GPP and ecosystem respiration. Among the 16 study sites, ten of them utilized the nighttime method and the other six sites chose the daytime method (Table 1). Besides the flux measurements, the towers are also instrumented with meteorological sensors to observe environmental variables, such as PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), T_a ($^{\circ}\text{C}$) and relative humidity (RH, %) (Kim et al., 2021; Liu et al., 2022). More information about the EC flux systems and environmental observations can be found in the related references in Table 1.

2.1.4 Data post-processing

Post-processing of the collected data primarily includes three steps:

(1) Standardize the names of key variables. Since the same variable had different names in the original data files from different study sites, we firstly unified the names of key variables to facilitate subsequent analysis.

(2) Remove outliers. The performance of three commonly used methods for dropping outliers (including the interquartile range (IQR) method, the standard deviation (SD) method and the median absolute deviation (MAD) method) were pretested. We found that, sometimes, the SD and MAD methods either dropped normal values or could not identify abnormal values. In contrast, the IQR method demonstrated the best overall performance. Hence, we chose the IQR method combined with reasonable physical boundaries ($\text{SIF}_{\text{TOC}_{760}}$, GPP, PAR, VPD, $f\text{PAR}$ (the fraction of absorbed PAR), $\text{NIR}_v > 0$; $f\text{PAR}$, $\text{NIR}_v < 1$) to eliminate outliers.

(3) Gap filling, temporal resolution conversion and basic information addition. We utilized linear interpolation to fill gaps that were only surrounded by valid values and no more than two values apart (to avoid overinterpolation). Then, the half-hourly data were converted into data with daily, 4-day, and 8-day temporal resolution, respectively. Additionally, basic information for each study site was included in the data files.

Among the 16 study sites, data from 8 sites (US-Ha1, US-UMB, US-Nr1, SOBS, DEJU, US-Ne2, US-Ne3, and YangLing) were in half-hourly temporal resolution and the remaining data from 8 sites (TCK, DaMan, UIUC, ZhaoXian, US-Br3, INRA, ShangQiu, and JuRong) were in daily temporal resolution (Table 1). After the temporal resolution conversion, we finally obtained half-hourly data from 8 sites as well as daily/ 4-day/ 8-day data from all 16 study sites. Note that although possible inconsistencies across in-situ SIF datasets may decrease model

accuracy, they have limited influence on conclusions drawn in this study. On the one hand, this study aims to evaluate the degree of improvement in the q_{L_SIF} model by comparing it with the q_{L_PAR} model. Since the q_L function (q_{L_SIF} or q_{L_PAR}) is the only difference between the two models, the better overall performance of the q_{L_SIF} model (Fig. 4) suggests the superiority of the q_{L_SIF} function and the limited influence of the possible inconsistencies across in-situ SIF datasets. On the other hand, to minimize data inconsistencies, only canopy data containing far-red SIF were used; data with red SIF were excluded.

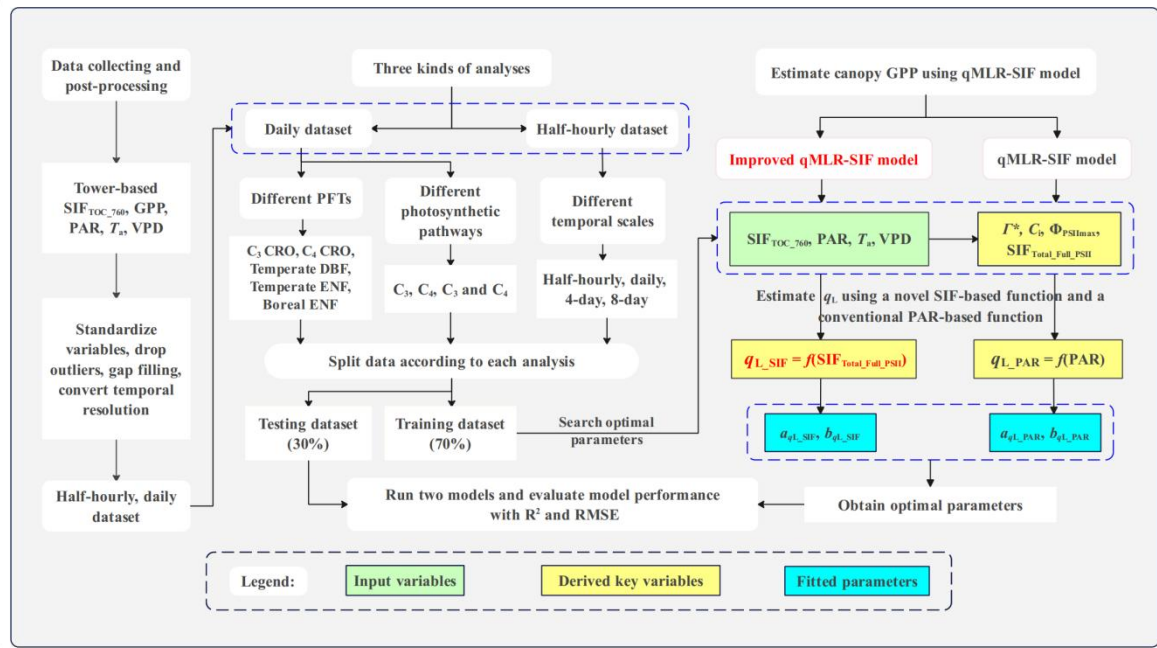


Fig. 1. Workflow diagram of data collection and post-processing, data analysis and GPP estimation in this study. SIF_{TOC_760}: top-of-canopy SIF at 760 nm; GPP: gross primary productivity; PAR: photosynthetically active radiation; T_a : air temperature; VPD: vapor pressure deficit; PFTs: plant functional types; CRO: crop; DBF: deciduous broadleaf forest; ENF: evergreen needleleaf forest; I^* : the CO₂ compensation point without dark respiration; C_i : the intercellular CO₂ partial pressure; $\Phi_{PSII_{max}}$: the maximum photochemical quantum yield of photosystem II; SIF_{Total_Full_PSII}: the total full band SIF emitted by photosystem II; q_L : the fraction of open photosystem II reaction centers; a_{qL_SIF} , b_{qL_SIF} : two fitted parameters in the q_{L_SIF} function; a_{qL_PAR} , b_{qL_PAR} : two fitted parameters in the q_{L_PAR} function.

2.2 qMLR-SIF model

Based on the following three assumptions: 1) nearly all electrons from PSII are used to either CO₂ fixation or photorespiration (Sun et al., 2023a); 2) the light-carbon reactions are

balanced perfectly (Gu et al., 2019; Han et al., 2022a); 3) the regeneration of RuBP (ribulose 1,5-biphosphate carboxylase-oxygenase) is primarily limited by insufficient NADPH supply (Gu and Sun, 2014), the fundamental equations, from the perspective of the light reactions, to estimate GPP for C₃ and C₄ species can be expressed as (Gu et al., 2019):

$$\text{GPP} = \begin{cases} \frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} \times J_a, & C_3 \\ \frac{1-\chi}{3} \times J_a, & C_4 \end{cases} \quad (1)$$

where C_c is the CO₂ partial pressure of chloroplast (μbar). Γ^* is the CO₂ compensation point without dark respiration (μbar) (Farquhar et al., 1980). χ is the fraction of total electron transport of bundle sheath and mesophyll cells allocated to mesophyll cells, which is commonly assumed to be 0.4 (von Caemmerer, 2000; von Caemmerer, 2021; Liu et al., 2022). J_a is the actual electron transport rate from PSII to PSI (μmol e⁻ m⁻² s⁻¹).

2.2.1 Estimation of C_c and Γ^*

C_c is approximately equal to the intercellular CO₂ partial pressure (C_i , μbar) by assuming infinite mesophyll conductance for CO₂. Based on the least-cost hypothesis that plants minimize the total unit costs of carboxylation and transpiration (Prentice et al., 2014), C_i can be estimated by the following equations:

$$C_i = \chi C_a \quad (2)$$

$$\chi = \frac{\Gamma^*}{C_a} + \left(1 - \frac{\Gamma^*}{C_a}\right) \times \frac{\xi}{\xi + \sqrt{\text{VPD}}}, \text{ with } \xi = \sqrt{\frac{\beta(K + \Gamma^*)}{1.6\eta^*}} \quad (3)$$

where C_a is the atmospheric CO₂ partial pressure (μbar) and 400 μbar is taken as the current C_a (Van Diepen et al., 2022). The constant β is 356.51 (Keenan et al., 2016; Yuan et al., 2019). The water viscosity (η^*) is a function of T_a (°C) (Korson et al., 1969). Γ^* can be calculated by the following function (Katul et al., 2010):

$$\Gamma^* = 36.9 + 1.18 \times (T_a - 25) + 0.036 \times (T_a - 25)^2 \quad (4)$$

K in Eq. (3) is the Michaelis-Menten coefficient of Rubisco and can be estimated (Yuan et al., 2019) by

$$K = K_c \left(1 + \frac{O}{K_o}\right) \quad (5)$$

$$K_c = 39.97 \times \exp^{\frac{79.43 \times (T_a - 25)}{298.15 \times 8.314 \times (T_a + 273.15)}} \quad (6)$$

$$K_o = 27480 \times \exp^{\frac{36.38 \times (T_a - 25)}{298.15 \times 8.314 \times (T_a + 273.15)}} \quad (7)$$

where K_o (mbar) and K_c (μbar) are Michaelis-Menten constants for RuBP oxygenation and RuBP carboxylation, respectively; O is the O₂ partial pressure of chloroplast and is assumed

to be 210 mbar (Farquhar et al., 1980).

2.2.2 Estimation of J_a

The power and simplicity of the qMLR-SIF model are due to the facts that 1) the qMLR-SIF model estimates GPP based on J_a rather than the potential electron transport; 2) J_a can be directly estimated from SIF and relevant fluorescence variables (Gu et al., 2019; Han et al., 2022a). Eq. (1) shows that GPP can be estimated immediately once J_a is known. In the qMLR-SIF model, J_a is calculated (Gu et al., 2019) by

$$J_a = q_L \times \frac{\Phi_{PSII_{\max}} (1+k_{DF})}{1-\Phi_{PSII_{\max}}} \times SIF_{\text{Total_Full_PSII}} \quad (8)$$

where $k_{DF} = k_D/k_F$, k_D and k_F are the rate constants of constitutive heat dissipation and fluorescence emission, respectively. Since k_D and k_F relate to intrinsic physical properties of chlorophyll molecules, they are often treated as constants (Zaks et al., 2012; Gu et al., 2019). Hence, k_{DF} is invariable and assumed to be 9 (Liu et al., 2022). $SIF_{\text{Total_Full_PSII}}$ is the total full band SIF emitted from PSII ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$).

$\Phi_{PSII_{\max}}$ is the maximum photochemical quantum yield of PSII, which is invariant across species under unstressed conditions (Baker, 2008; Gu et al., 2019) and is often assumed to be constant (~ 0.83) in estimating GPP (Liu et al., 2022; Guo et al., 2024; Liu et al., 2024b). However, environmental stresses (such as high light, high or low T_a) may cause a decrease in $\Phi_{PSII_{\max}}$ (Gu et al., 2019; Magney et al., 2019b; Chen et al., 2024b). The study of Chen et al. (2024b) suggested that T_a significantly affected seasonal variations of $\Phi_{PSII_{\max}}$ in the ENFs. By simulating $\Phi_{PSII_{\max}}$ with a quadratic function of T_a , their study effectively improved the accuracy of GPP estimation. Therefore, in this study, a piecewise function of T_a (Eq. (9)), which was derived from the results of Chen et al. (2024b) (see Fig. S2 in their study), was adopted to estimate $\Phi_{PSII_{\max}}$. Note that 0.73 (0.23) in Eq. (9) is approximately the upper (lower) bound of the $\Phi_{PSII_{\max}}$ in Chen et al. (2024b). We hypothesized that this temperature function of $\Phi_{PSII_{\max}}$ was suitable not only for ENF but also for CRO and DBF (the feasibility of this hypothesis was verified, see details in Section 3.2). Thus, $\Phi_{PSII_{\max}}$ is estimated by

$$\Phi_{PSII_{\max}} = \begin{cases} 0.23, & T_a \leq -5 \\ 0.44 + 0.036T_a - 0.0011T_a^2, & -5 < T_a < 15 \\ 0.73, & T_a \geq 15 \end{cases} \quad (9)$$

q_L represents the fraction of the open PSII reaction centers. As one of the key fluorescence variables in the qMLR-SIF model, it is often simulated using the q_{L_PAR} function developed by Han et al. (2022a), that is

$$q_{L_PAR} = a_{q_{L_PAR}} \times \exp^{-b_{q_{L_PAR}} \times PAR} \quad (10)$$

where $0 < a_{q_{L_PAR}} < 1$, $b_{q_{L_PAR}} > 0$. As mentioned in the Introduction, this q_{L_PAR} function only considers the effects of PAR on q_L , which may lead to biases in GPP estimation. Therefore, we developed a new function to predict q_L based on the hypothesis posed in the end of the Introduction. This new function is expressed as

$$q_{L_SIF} = a_{q_{L_SIF}} \times \exp^{-b_{q_{L_SIF}} \times \sqrt{SIF}} \quad (11)$$

where $0 < a_{q_{L_SIF}} < 1$, $b_{q_{L_SIF}} > 0$. $\sqrt{SIF}$ in Eq. (11) comes from prior tests. Initially, we used Eq. (10) with PAR replaced by SIF to simulate q_L . Results showed that biases in modeled GPP were significantly reduced, with linear fits of measured vs. modeled GPP yielding slopes closer to 1 and intercepts closer to 0. However, the estimated GPP was saturated at high-GPP levels due to excessively rapid decline in simulated q_L at high SIF. Hence, we used Eq. (10) with PAR replaced by $\sqrt[3]{SIF}$ to simulate q_L . $\sqrt[3]{SIF}$, where c is a fitted parameter, was also tested for simulating q_L . We found that both $\sqrt{SIF}$ and $\sqrt[3]{SIF}$ further improved GPP estimation, but their difference was minor. For simplicity, we finally adopted $\sqrt{SIF}$, thereby using Eq. (11) to simulate q_L .

2.2.3 Estimation of $SIF_{Total_Full_PSII}$

Three steps (canopy to PSII downscaling, PSII contribution separation and full band reconstruction) are required to convert SIF_{TOC_760} (the top of canopy far-red SIF, $\mu\text{mol photons m}^{-2} \text{ s}^{-1} \text{ nm}^{-1}$) to $SIF_{Total_Full_PSII}$ (the total full band SIF emitted by PSII, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) using the following equations (Liu et al., 2022):

$$SIF_{Total_760} = \frac{SIF_{TOC_760}}{f_{esc_P-C}} \quad (12)$$

$$SIF_{Total_760_PSII} = SIF_{Total_760} \times f_{PSII} \quad (13)$$

$$SIF_{Total_Full_PSII} = SIF_{Total_760_PSII} \times \sum_{\lambda=650}^{850} f_c(\lambda) \quad (14)$$

where SIF_{Total_760} is the total narrow band SIF at 760 nm emitted from PSI and PSII ($\mu\text{mol photons m}^{-2} \text{ s}^{-1} \text{ nm}^{-1}$). f_{PSII} (%) is the fraction of SIF_{Total_760} emitted by PSII, which is nearly constant for most of the growing season (Liu et al., 2022; Guo et al., 2024). According to Chen et al. (2024b), f_{PSII} can be assumed to be 0.6676 for SIF_{TOC_760} . $SIF_{Total_760_PSII}$ is the total single band SIF at 760 nm emitted from PSII ($\mu\text{mol photons m}^{-2} \text{ s}^{-1} \text{ nm}^{-1}$). $f_c(\lambda)$ is a conversion factor used to calculate SIF at λ nm by SIF at 760 nm, which

is invariable for the specific wavelength (Liu et al., 2022). Thus, $SIF_{Total_Full_PSII}$ is proportional to $SIF_{Total_760_PSII}$ according to Eq. (14). For simplicity, we assumed that $SIF_{Total_760_PSII}$ is sufficient to accurately infer canopy GPP. Therefore, $SIF_{Total_760_PSII}$ is utilized to calculate J_a in Eq. (8) (Feng et al., 2021).

f_{esc_P-C} is the fraction of SIF photons (at 760 nm) escaping from the photosystem level to the canopy level, which can be simulated (Liu et al., 2020; Liu et al., 2022) by

$$f_{esc_P-C} = f_{esc_P-L} \times f_{esc_L-C} \quad (15)$$

where f_{esc_P-L} and f_{esc_L-C} are the escape ratio of SIF photons from photosystems to leaf surface and that of SIF photons from leaf surface to canopy level, respectively. f_{esc_P-L} approximately equals the leaf albedo which is nearly invariant (~ 0.9) in the near-infrared (NIR) region (Liu et al., 2019a; Liu et al., 2020; Liu et al., 2022; Guo et al., 2024). f_{esc_L-C} in the NIR region can be estimated (Zeng et al., 2019) by

$$f_{esc_L-C} = \frac{NIRv}{f_{PAR}} \quad (16)$$

Yang and van der Tol (2018) showed that f_{esc_P-C} tends to be constant (~ 0.4) when the leaf area index is above 3. This is consistent with previous field studies (Dechant et al., 2020; Liu et al., 2022; Buareal et al., 2023) which indicated that f_{esc_P-C} was relatively stable during most of the growing season, particularly at the middle of the growing season (Liu et al., 2022). Besides, Liu et al. (2020) also found that canopy-level far-red SIF had similar performance to photosystem-level far-red SIF for GPP estimation. Hence, considering the data availability, f_{esc_P-C} was assumed to be 0.4 in this study. The feasibility of this simplification was demonstrated by comparing GPP estimated from two scenarios where f_{esc_P-C} is 0.4 and where f_{esc_P-C} is calculated by Eq. (15) and Eq. (16) (see details in Section 3.2).

Therefore, the final equation to estimate canopy GPP is

$$GPP = \begin{cases} \frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} \times q_L \times \frac{\Phi_{PSII_{max}} (1 + k_{DF})}{1 - \Phi_{PSII_{max}}} \times \frac{SIF_{TOC_760} \times f_{PSII}}{f_{esc_P-C}}, & C_3 \\ \frac{1-x}{3} \times q_L \times \frac{\Phi_{PSII_{max}} (1 + k_{DF})}{1 - \Phi_{PSII_{max}}} \times \frac{SIF_{TOC_760} \times f_{PSII}}{f_{esc_P-C}}, & C_4 \end{cases} \quad (17)$$

For convenience, GPP is referred to as $GPP_{q_L_SIF}$ when q_L is simulated by q_L_SIF function, and as $GPP_{q_L_PAR}$ when simulated by q_L_PAR function.

The observed top of canopy SIF has the unit of $mW\ m^{-2}\ nm^{-1}\ sr^{-1}$ and needs to be converted to $\mu mol\ photons\ m^{-2}\ s^{-1}\ nm^{-1}$ using the following equation (Han et al., 2022a):

$$SIF_{TOC_760} = \frac{SIF_{TOC_760}^* \times 10^{-3} \times \pi}{\frac{h \times c \times N_A}{\lambda}} \times 10^6 \quad (18)$$

where SIF_{TOC_760} and $SIF_{TOC_760}^*$ represent the observed top of canopy far-red SIF (760 nm) with the unit of $\mu\text{mol photons m}^{-2} \text{s}^{-1} \text{nm}^{-1}$ and $\text{mW m}^{-2} \text{nm}^{-1} \text{sr}^{-1}$, respectively. The Planck's constant, h , is equal to $6.626 \times 10^{-34} \text{ W s}^2$; The light speed (c) is $3 \times 10^8 \text{ m s}^{-1}$; The Avogadro's constant, N_A , is $6.022 \times 10^{23} \text{ mol}^{-1}$; The wavelength (λ) is $7.6 \times 10^{-7} \text{ m}$; π (sr) is used for converting SIF radiance to SIF irradiance; 10^{-3} is used for converting mW to W; 10^6 is used for converting mol to μmol .

2.3 Data analysis

Three kinds of analyses were conducted (different PFTs, photosynthetic pathways, and temporal scales) to compare the performance of the q_{L_SIF} model and the q_{L_PAR} model. For different PFTs, all daily data (16 sites) were grouped into five sub-datasets (C_3 CRO, C_4 CRO, temperate DBF, temperate ENF, boreal ENF). For different photosynthetic pathways, all daily data were grouped into two sub-datasets (C_3 and C_4 plants) and then three datasets (C_3 , C_4 , and all plants) were used for analysis. For different temporal scales, all half-hourly data (8 sites) were averaged to daily, 4-day, and 8-day temporal resolutions. Then, four sub-datasets (half-hourly, daily, 4-day, and 8-day) were produced.

For each kind of analysis, each sub-dataset was first randomly shuffled and then divided into training data (70%) and testing data (30%). The training data were used to search for optimal parameters and the testing data were used to evaluate model performance. There were four parameters that required calibration: $a_{q_{L_SIF}}$ and $b_{q_{L_SIF}}$ for the q_{L_SIF} model, $a_{q_{L_PAR}}$ and $b_{q_{L_PAR}}$ for the q_{L_PAR} model. The bounds of these four parameters are: $0 < a_{q_{L_SIF}} < 1$, $0 < b_{q_{L_SIF}} < 1$; $0 < a_{q_{L_PAR}} < 1$, $0 < b_{q_{L_PAR}} < 0.1$. The `scipy.optimize.minimize()` function in Python 3.9.13 was utilized to find optimal parameters. Since the optimization method needs valid bounds for each parameter, the upper bounds of $b_{q_{L_SIF}}$ and $b_{q_{L_PAR}}$ were set to be greater than their possible values.

The coefficient of determination (R^2) and root mean square error (RMSE) were used to evaluate model performance. A model with higher R^2 and lower RMSE indicates better performance. Threshold analysis was performed to examine how key environmental factors (PAR, T_a , and VPD) affected the qMLR-SIF model performance for different PFTs. Specifically, for each factor, the data for each PFT were split into two groups using the PFT-specific mean value of that factor as the threshold. Then, the data of these two groups were used to run the models and evaluate model performance. The normalized RMSE (NRMSE, the ratio of RMSE to the standard deviation of observed GPP) was used to compare the model performance

between the two groups. Lower NRMSE indicates better model performance. Residual analysis was also conducted between GPP residuals and key environmental factors (PAR, T_a , and VPD) to identify potential deviations in GPP estimation. In addition, given the small differences among the evaluation results of training, testing, and all (both training and testing) data for the two models (**Table S1**), we used the results of all data to plot the figures. This provides more information about each analysis and the results from all data broadly reflect the comprehensive performance of each model.

3. Results

3.1 The effects of environmental factors on GPP and SIF_{TOC_760} across different PFTs

The relationships of GPP with SIF_{TOC_760} , PAR, T_a , and VPD (**Fig. 2**), as well as those of SIF_{TOC_760} with PAR, T_a , and VPD (**Fig. 3**) were drawn to analyze the responses of GPP and SIF_{TOC_760} to different environmental effects for different PFTs. GPP was significantly correlated with all four variables ($p < 0.001$, SIF_{TOC_760} , PAR, T_a and VPD) in different PFTs (**Fig. 2**). Except for the C₃ CRO, compared to PAR, T_a and VPD, SIF_{TOC_760} exhibited the highest correlation with GPP in different PFTs (**Fig. 2a-e**), with r values ranging from 0.70 (C₃ CRO) to 0.87 (Temperate ENF). With respect to environmental drivers, PAR dominated the variation of GPP in CRO (r values: PAR > T_a > VPD) (**Fig. 2f, g**), while T_a became the main driver in the temperate DBF (r values: T_a > PAR > VPD) (**Fig. 2m**), temperate ENF (r values: T_a > VPD > PAR) (**Fig. 2n**) and boreal ENF (r values: T_a > VPD > PAR) (**Fig. 2o**). Particularly, in the ENF, PAR had the lowest correlation with GPP compared to T_a and VPD (**Fig. 2i, j**). In the CRO, GPP was less affected by VPD (**Fig. 2p, q**), while the VPD influence was higher in the forests (**Fig. 2r-t**). Besides, GPP saturated at both high SIF_{TOC_760} and high PAR (**Fig. 2a-e, f-j**). However, the degree of saturation in the SIF_{TOC_760} -GPP relationship was stronger than that in the PAR-GPP relationship.

SIF_{TOC_760} showed a significant correlation ($p < 0.001$) with all three environmental variables (PAR, T_a and VPD) across different PFTs (**Fig. 3**), which was similar to GPP. Apart from the temperate ENF, PAR dominated the variation of SIF_{TOC_760} in different PFTs (**Fig. 3a-e**). In the CRO, SIF_{TOC_760} was primarily affected by PAR and T_a (**Fig. 3a-b, f-g**), while all three variables (PAR, T_a , and VPD) showed comparable influences on SIF_{TOC_760} in the forests (**Fig. 3c-e, h-j, m-o**). Across different PFTs, PAR exhibited stronger correlations with SIF_{TOC_760} (**Fig. 3a-e**) than with GPP (**Fig. 2f-j**). In contrast, T_a had higher correlations with GPP (**Fig. 2k-o**) than with SIF_{TOC_760} (**Fig. 3f-j**). Excluding the boreal ENF, VPD had similar correlations with GPP and SIF_{TOC_760} in different PFTs (**Fig. 2p-t; Fig. 3k-o**). In addition, the variation pattern of

SIF_{TOC_760} to PAR was significantly different from that of GPP to PAR. Specifically, as PAR increased, GPP tended to level off at high PAR (Fig. 2f-j) whereas SIF_{TOC_760} still increased and even increased faster at high PAR (except for the boreal ENF, in which SIF_{TOC_760} increased with PAR linearly) (Fig. 3a-e).

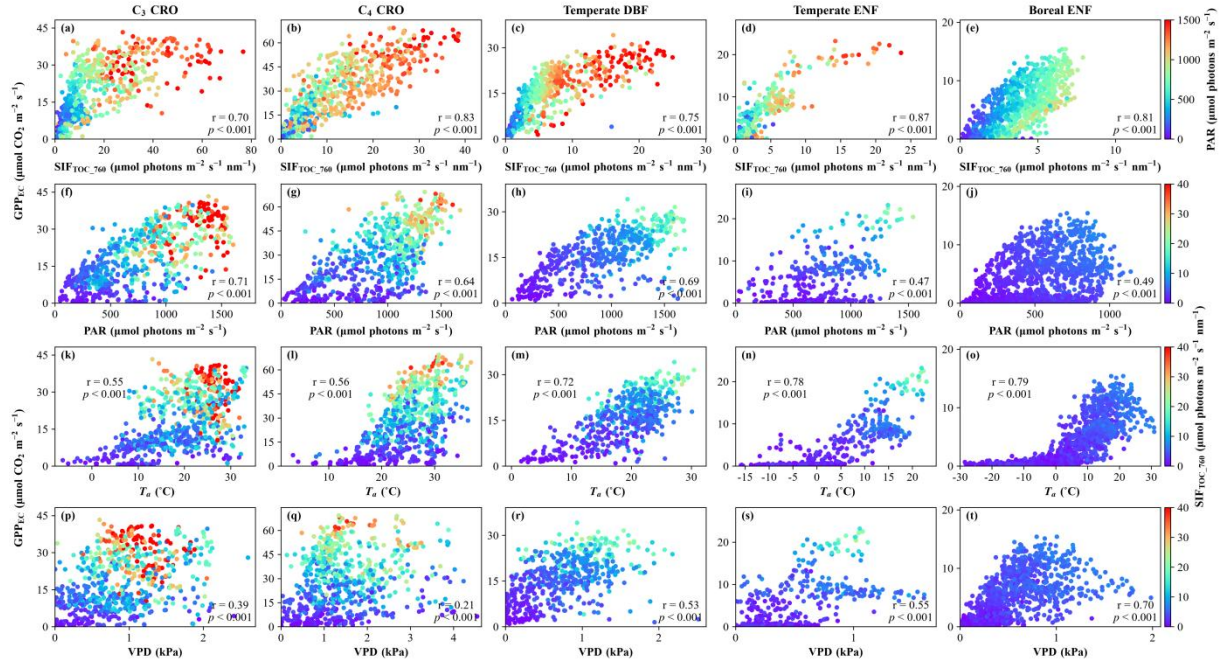


Fig. 2. The relationship of GPP with SIF_{TOC_760} (a-e), PAR (f-j), T_a (k-o), and VPD (p-t) for different PFTs. r is the Pearson correlation coefficient and p is the corresponding p -value.

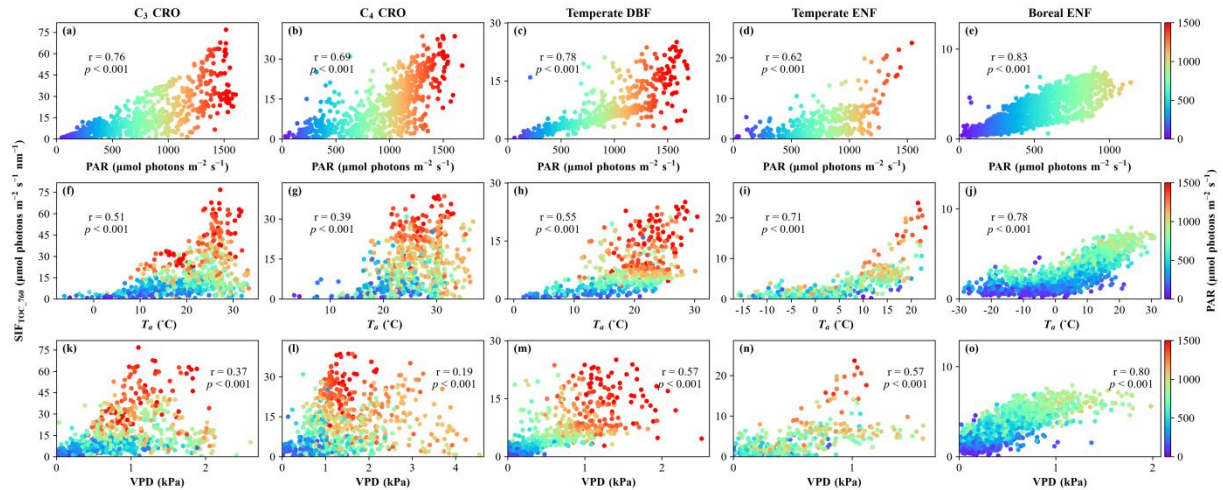


Fig. 3. The relationship of SIF_{TOC_760} with PAR (a-e), T_a (f-j), and VPD (k-o) for different PFTs. r is the Pearson correlation coefficient and p is the corresponding p -value.

3.2 Validating the feasibility of the qMLR-SIF model's parameter settings

In this study, we employed a piecewise function of T_a (Eq. (9)), derived from the study on ENFs (Chen et al., 2024b), to simulate $\Phi_{PSII_{max}}$. We hypothesized that this temperature function is suitable not only for ENF but also for CRO and DBF. To verify this hypothesis, we compared model performance under different parameter settings ($\Phi_{PSII_{max}} = 0.83$ and $\Phi_{PSII_{max}}$ estimated by the temperature function in Eq. (9), with all other conditions remaining the same) for different PFTs. Results showed that, in general, the temperature function of $\Phi_{PSII_{max}}$ enhanced the accuracy of the GPP estimation for both the q_{L_SIF} model and the q_{L_PAR} model across different PFTs, as indicated by increased R^2 and decreased RMSE (Table 2). Such improvement was particularly obvious in the boreal ENF, where R^2 increased from 0.67 to 0.76 (0.72 to 0.82) and RMSE decreased from 2.26 to 1.96 (2.10 to 1.69) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the q_{L_SIF} model (the q_{L_PAR} model) when considering the effects of T_a on $\Phi_{PSII_{max}}$. In addition, in the boreal ENF, the y-slope (y-intercept) of the linear relationship between modeled and observed GPP became closer to 1.00 (closer to 0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) after using the temperature function of $\Phi_{PSII_{max}}$, indicating less overestimation and/or underestimation of GPP. Therefore, the temperature function of $\Phi_{PSII_{max}}$ in Eq. (9) was not only suitable for different PFTs (CRO, DBF, and ENF), but also clearly improved the model performance of GPP estimation, especially in the boreal ENFs.

Due to data availability, f_{esc_P-C} was assumed to be invariable (0.4) in this study. To test the validity of this assumption, data from 6 study sites (JuRong, ShangQiu, US-Ne2, US-Ne3, US-Nr1, and YangLing), which contained key variables (f_{PAR} and NIR_v from ground-based observations) for calculating f_{esc_P-C} , were filtered to run models under two scenarios ($f_{esc_P-C} = 0.4$ and f_{esc_P-C} calculated by Eq. (15) and Eq. (16), with all other conditions being the same) for different PFTs. Data from these 6 sites included two PFTs (CRO and ENF). Results suggested that, overall, the scenario of constant f_{esc_P-C} had higher accuracy in GPP estimation for both the q_{L_SIF} and the q_{L_PAR} model, showing higher R^2 and lower RMSE (Table 3). The improvement of GPP estimation in the C₄ CRO was particularly notable. In detail, R^2 increased from 0.51 to 0.76 (0.50 to 0.69) and RMSE decreased from 13.52 to 9.45 (13.57 to 10.65) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the q_{L_SIF} model (q_{L_PAR} model) when assuming constant f_{esc_P-C} . In addition, the y-slope (y-intercept) of the linear relationship between modeled GPP and observed GPP was closer to 1.00 (closer to 0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the scenario of constant f_{esc_P-C} . We calculated statistics (mean $\pm$ standard deviation, relative standard deviation) of the f_{esc_P-C} estimated by Eq. (15) and Eq. (16) and found that large standard deviations existed in C₃ CRO (0.47 ± 0.15 , 31.97%), C₄ CRO (0.36 ± 0.14 , 39.23%) and temperate ENF (0.20 ± 0.08 , 38.96%). Thus, the decreased

accuracy of modeled GPP in the scenario with varied $f_{\text{esc_P-C}}$ may be due to the large uncertainties in the estimated $f_{\text{esc_P-C}}$.

Table 2 Comparison of model performance under different Φ_{PSIImax} settings for different PFTs.

PFTs		C ₃ CRO		C ₄ CRO		Temperate DBF		Temperate ENF		Boreal ENF	
Parameter settings		$\Phi_{\text{PSIImax}} = 0.83$	$\Phi_{\text{PSIImax}} = f(T_a)$	$\Phi_{\text{PSIImax}} = 0.83$	$\Phi_{\text{PSIImax}} = f(T_a)$	$\Phi_{\text{PSIImax}} = 0.83$	$\Phi_{\text{PSIImax}} = f(T_a)$	$\Phi_{\text{PSIImax}} = 0.83$	$\Phi_{\text{PSIImax}} = f(T_a)$	$\Phi_{\text{PSIImax}} = 0.83$	$\Phi_{\text{PSIImax}} = f(T_a)$
q_{L_SIF} model	R ²	0.60	0.61	0.73	0.73	0.63	0.65	0.79	0.82	0.67	0.76
	RMSE	7.15	7.07	9.54	9.51	4.56	4.43	2.60	2.43	2.26	1.96
	y-slope	1.00	0.97	0.99	0.99	0.98	0.96	1.05	0.94	1.21	0.98
	y-intercept	-0.07	0.74	0.67	0.65	0.23	0.70	-0.48	0.69	-1.19	0.16
q_{L_PAR} model	R ²	0.46	0.47	0.68	0.68	0.52	0.54	0.79	0.81	0.72	0.82
	RMSE	8.33	8.27	10.25	10.24	5.21	5.11	2.59	2.48	2.10	1.69
	y-slope	0.69	0.68	0.82	0.82	0.64	0.64	1.02	0.90	1.34	1.02
	y-intercept	7.25	7.58	7.13	7.13	6.93	7.04	-0.06	1.25	-1.89	-0.05

$f(T_a)$: the piecewise function of T_a , i.e., Eq. (9); y-slope (y-intercept) is the slope (intercept) of the linear relationship between modeled GPP and observed GPP_{EC}; The unit of RMSE is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Table 3 Comparison of model performance under different $f_{\text{esc_P-C}}$ settings for different PFTs.

PFTs		C ₃ CRO		C ₄ CRO		Temperate ENF	
Parameter settings		$f_{\text{esc_P-C}} = 0.40$	$f_{\text{esc_P-C}}$ is varied	$f_{\text{esc_P-C}} = 0.40$	$f_{\text{esc_P-C}}$ is varied	$f_{\text{esc_P-C}} = 0.40$	$f_{\text{esc_P-C}}$ is varied
q_{L_SIF} model	R ²	0.63	0.60	0.76	0.51	0.89	0.88
	RMSE	7.16	7.46	9.45	13.52	1.24	1.32
	y-slope	0.97	0.83	1.02	0.78	0.98	0.96
	y-intercept	0.03	3.43	-0.20	9.16	-0.12	0.00
q_{L_PAR} model	R ²	0.51	0.59	0.69	0.50	0.86	0.83
	RMSE	8.31	7.56	10.65	13.57	1.41	1.55
	y-slope	0.76	0.81	0.88	0.78	0.91	0.88
	y-intercept	5.44	3.84	5.49	9.45	0.48	0.75

$f_{\text{esc_P-C}}$ is varied means it was estimated by Eq. (15) and Eq. (16); y-slope (y-intercept) is the slope (intercept) of the linear relationship between modeled GPP and observed GPP_{EC}; The unit of RMSE is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

3.3 Performance of the improved qMLR-SIF model under different scenarios

In order to test the performance of the improved qMLR-SIF model (named q_{L_SIF} model for convenience), we compared the q_{L_SIF} model with the q_{L_PAR} model (qMLR-SIF model in which q_L is estimated using a conventional PAR-based function) under different scenarios (PFTs, photosynthetic pathways, and temporal scales). For different PFTs, results showed that the q_{L_SIF} model outperformed the q_{L_PAR} model across different PFTs (except for the boreal ENF), with higher R^2 and lower RMSE (**Fig. 4**). Specifically, R^2 increased from 0.47 to 0.61 (C₃ CRO), 0.68 to 0.73 (C₄ CRO), 0.54 to 0.65 (temperate DBF), and 0.81 to 0.82 (temperate ENF). RMSE decreased from 8.27 to 7.07 (C₃ CRO), 10.24 to 9.51 (C₄ CRO), 5.11 to 4.43 (temperate DBF), and 2.48 to 2.43 (temperate ENF) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Notably, the q_{L_SIF} model considerably reduced the underestimation and overestimation of GPP in the q_{L_PAR} model, as indicated by the y-slope and y-intercept of the linear relationship between observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}) being closer to 1.00 and 0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. Such improvements were particularly obvious in the C₃ CRO, temperate DBF, and C₄ CRO. In detail, the y-slope (y-intercept) improved from 0.68 to 0.97 (7.58 to 0.74 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for C₃ CRO, 0.64 to 0.96 (7.04 to 0.70 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for temperate DBF, and 0.82 to 0.99 (7.13 to 0.65 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for C₄ CRO. In the boreal ENF, neither model exhibited significant overestimation and underestimation of GPP. The linear fits of GPP_{EC} against GPP_{mod} yielded slopes and intercepts close to 1.00 and 0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (**Fig. 4e, j**). However, the q_{L_PAR} model exhibited better performance than the q_{L_SIF} model, with higher R^2 (0.82 vs 0.76) and lower RMSE (1.69 vs 1.96 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Residual analysis showed that GPP residuals had higher correlations with PAR for the q_{L_SIF} model than for the q_{L_PAR} model in the C₃ CRO, temperate ENF, and boreal ENF (**Fig. S1 f, i, j**). In the C₄ CRO and temperate DBF, T_a was positively correlated with GPP residuals for both models (**Fig. S1 l-m, q-r**). In the temperate ENF, VPD had negative correlations with GPP residuals for the two models (**Fig. S1 x, C**).

For different photosynthetic pathways, the q_{L_SIF} model surpassed the q_{L_PAR} model in C₃, C₄, and All (both C₃ and C₄) plants, showing higher R^2 and lower RMSE (**Fig. 5**). Specifically, R^2 increased from 0.64 to 0.77 (C₃ plants), 0.68 to 0.73 (C₄ plants), and 0.59 to 0.73 (All plants). RMSE decreased from 5.81 to 4.57 (C₃ plants), 10.24 to 9.51 (C₄ plants), and 8.83 to 7.21 (All plants) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Besides, the q_{L_SIF} model significantly improved the underestimation and overestimation of GPP compared to the q_{L_PAR} model. In detail, the y-slope (y-intercept) improved from 0.82 to 0.99 (3.26 to 0.11 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in C₃ plants, 0.82 to 0.99 (7.13 to 0.65 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in C₄ plants, and 0.87 to 1.05 (3.56 to -0.94 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in All plants. GPP residuals had positive correlations with PAR and T_a in C₄ plants (**Fig. S2 b, e; h, k**). VPD was correlated with GPP residuals in All plants (**Fig. S2 o, r**).

For different temporal scales, these two models had comparable performance in estimating GPP, as indicated by similar R^2 and RMSE (**Fig. 6**). However, the q_{L_SIF} model had fewer biases for GPP than the q_{L_PAR} model, as shown by the y-slope (y-intercept) being closer to 1.00 (0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). In addition, the accuracy of the two models increased as the temporal scale became larger. Specifically, R^2 increased from 0.76 (0.76) to 0.92 (0.92) and RMSE decreased from 5.64 (5.69) to 3.17 (3.18) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ as the temporal scale increased from half-hourly to 8-day for the q_{L_SIF} model (q_{L_PAR} model). GPP residuals had low correlations with PAR, T_a , and VPD for both models (**Fig. S3**).

To assess how the q_{L_SIF} model, compared to the q_{L_PAR} model, improved the performance in tracking GPP seasonal variations, we divided the daily dataset into several sub-datasets according to site years and used these sub-datasets to run the two models. Note that one specific study site (e.g., YangLing) and the corresponding specific year of data collection (e.g., 2021) together constitute one site year (i.e., YangLing 2021). All such site-year units for all study sites collectively constitute the site years. Then, for each PFT, the site year with the maximum difference in R^2 between the q_{L_SIF} and the q_{L_PAR} model (aiming to identify the improvements easily) was chosen to plot seasonal variations of GPP. Results showed that the q_{L_SIF} model effectively reduced underestimation and/or overestimation of GPP at the start (**Fig. 7b**), the middle (**Fig. 7b**) or the end (**Fig. 7d, h**) of the growing season for different PFTs. We further calculated the R^2 , RMSE, and mean absolute error (MAE) of GPP for each site year and grouped these metrics by PFT. Then, boxplots of these metrics for the two models were drawn across different PFTs (**Fig. S4-6**). We found that the results were consistent with those shown in **Fig. 7**.

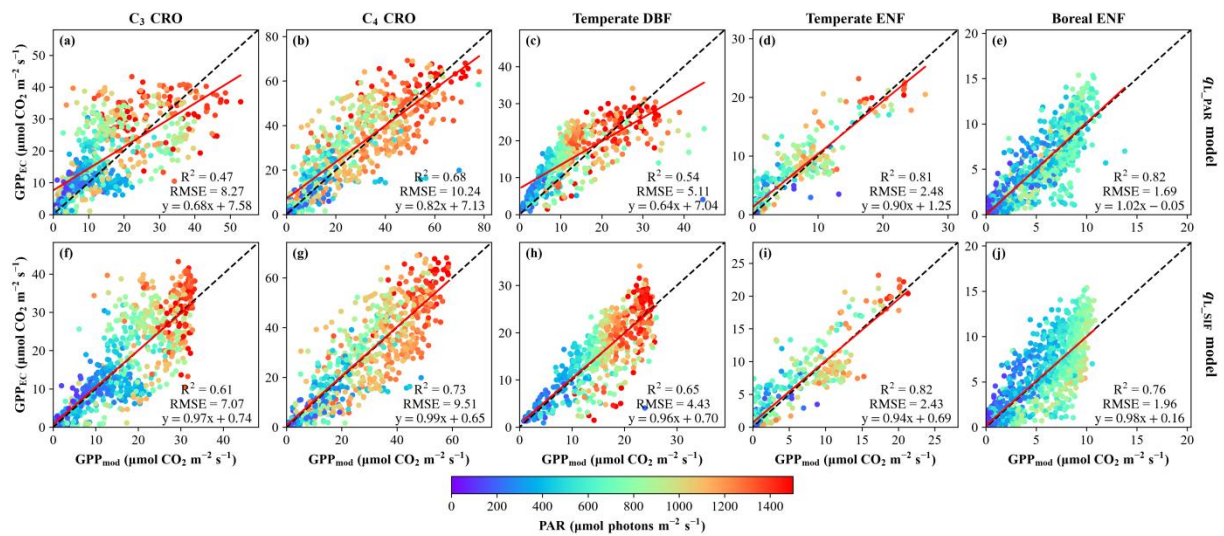


Fig. 4. Model performance of (a-e) the q_{L_PAR} model and (f-j) the q_{L_SIF} model for different PFTs. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line. The unit of RMSE is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

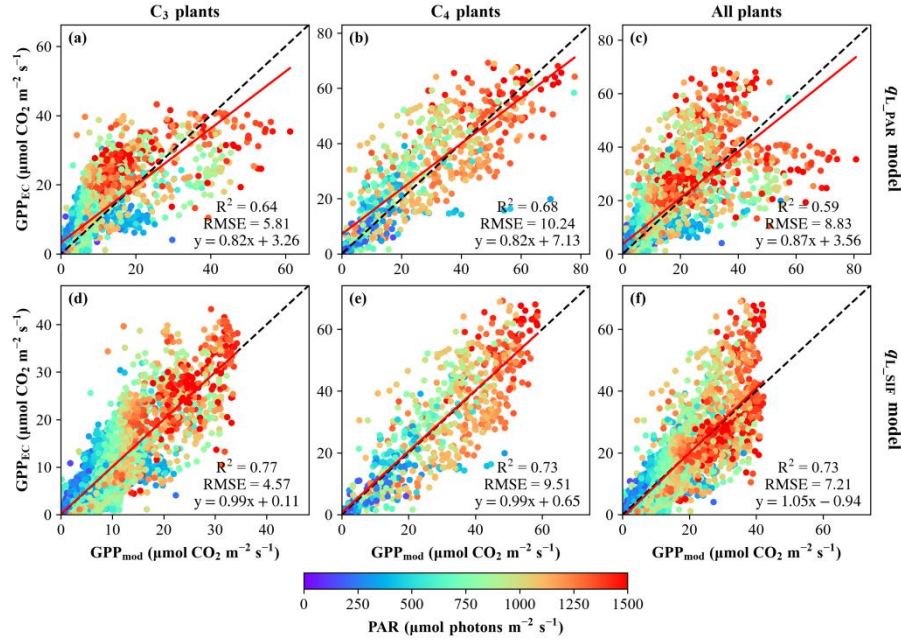


Fig. 5. Model performance of (a-c) the q_{L_PAR} model and (d-f) the q_{L_SIF} model for different photosynthetic pathways. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line. The unit of RMSE is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

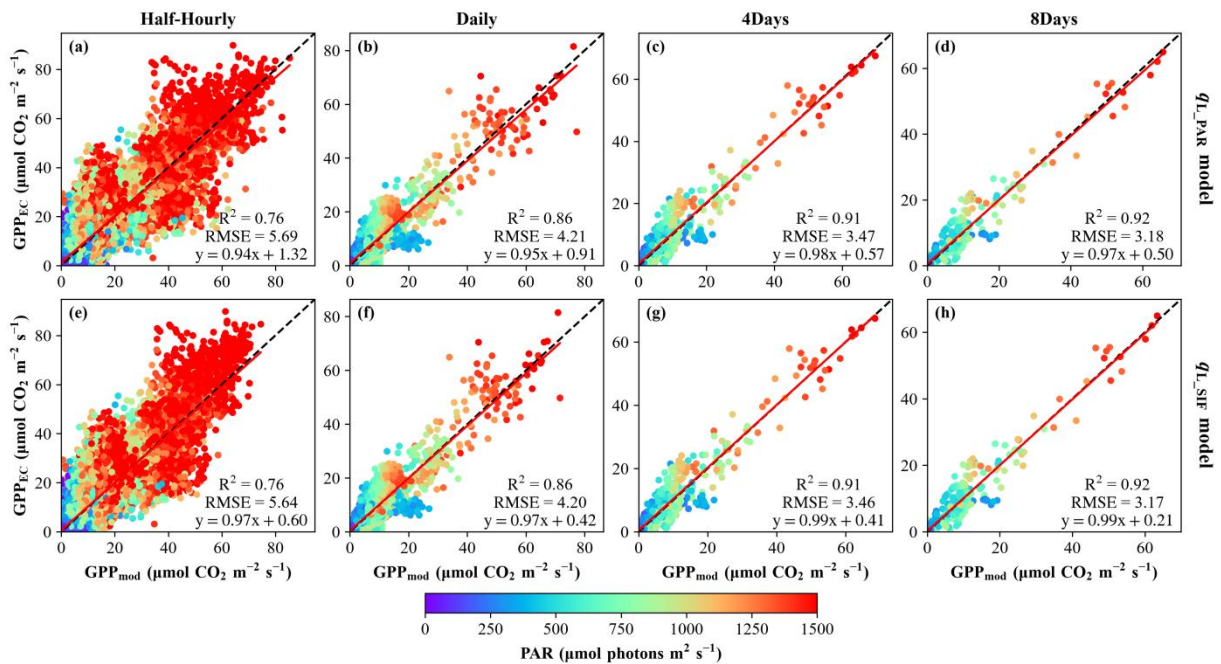


Fig. 6. Model performance of (a-d) the q_{L_PAR} model and (e-h) the q_{L_SIF} model for different temporal scales. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line. The unit of RMSE is $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

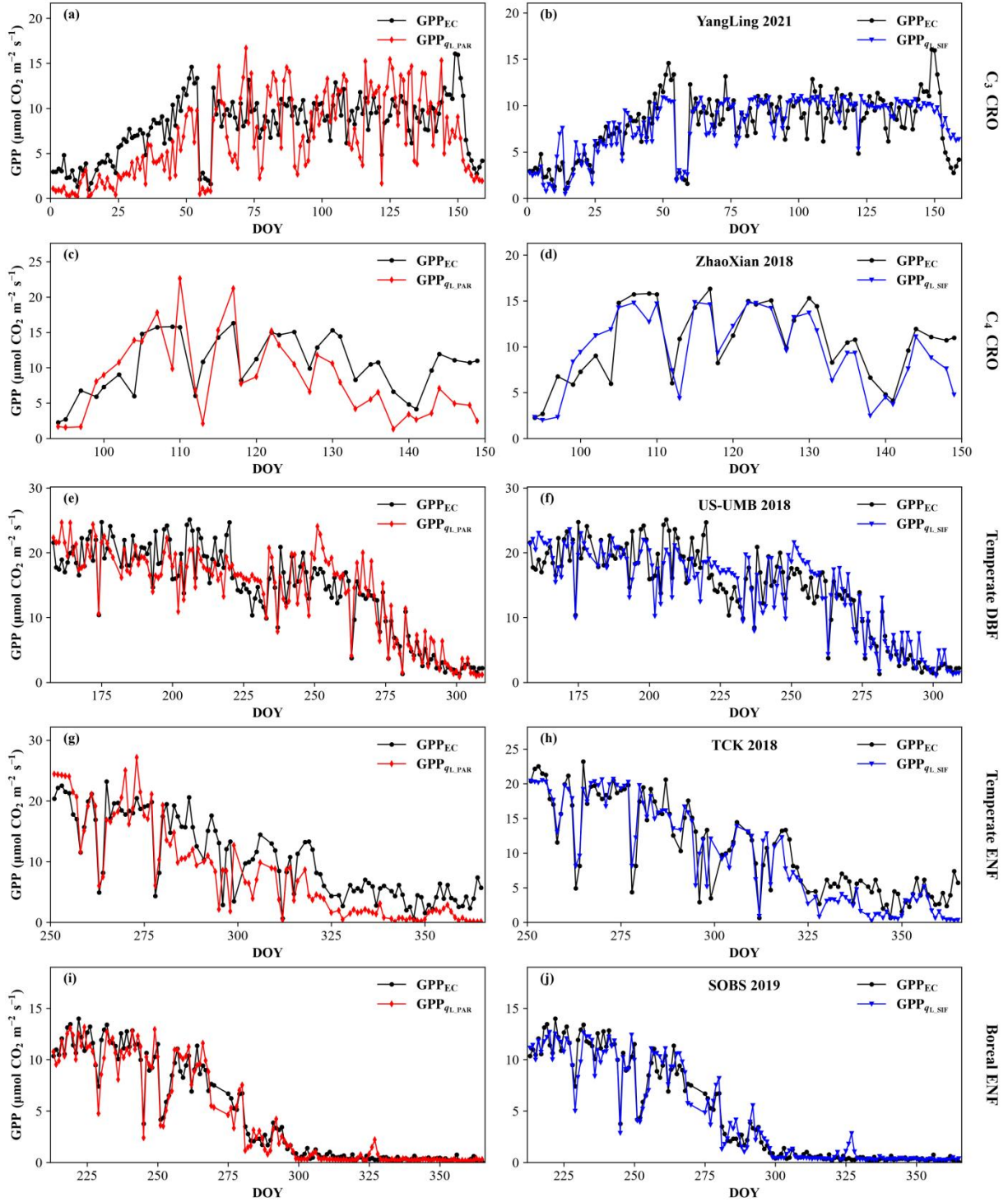


Fig. 7. Seasonal variations of GPP for the representative site years of different PFTs. DOY: day

of year.

3.4 The effects of environmental factors on the qMLR-SIF model performance

For the threshold analysis of PAR, results showed that, except for the temperate ENF, the q_{L_SIF} and q_{L_PAR} models had better performance when $PAR \leq PAR_{mean}$ (the mean value of PAR) than when $PAR > PAR_{mean}$ across different PFTs, with higher R^2 and lower NRMSE (**Fig. 8**). Apart from the boreal ENF, the q_{L_SIF} model outperformed the q_{L_PAR} model for both PAR conditions ($PAR \leq PAR_{mean}$ and $PAR > PAR_{mean}$) across different PFTs. The q_{L_SIF} model considerably reduced the underestimation and overestimation of GPP compared to the q_{L_PAR} model, with the y-slope closer to 1.00 and the y-intercept closer to 0.00 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. For the threshold analysis of T_a , both qMLR-SIF models exhibited better performance when $T_a \leq T_{a\ mean}$ than when $T_a > T_{a\ mean}$ in the C₃ CRO, C₄ CRO, and temperate DBF (**Fig. 9**). In contrast, in the temperate ENF and boreal ENF, the two models performed better when $T_a > T_{a\ mean}$ compared to when $T_a \leq T_{a\ mean}$. The q_{L_SIF} model had better performance and fewer biases for GPP than the q_{L_PAR} model for both T_a conditions ($T_a > T_{a\ mean}$ and $T_a \leq T_{a\ mean}$) in the C₃ CRO, C₄ CRO, and temperate DBF. In the temperate ENF and boreal ENF, the q_{L_PAR} model showed better performance than the q_{L_SIF} model, with relatively higher R^2 and lower NRMSE. For the threshold analysis of VPD, both qMLR-SIF models had better performance when $VPD \leq VPD_{mean}$ than when $VPD > VPD_{mean}$ across different PFTs (except for the temperate ENF) (**Fig. 10**). Apart from the boreal ENF, the q_{L_SIF} model demonstrated superior performance compared to the q_{L_PAR} model across both conditions ($VPD \leq VPD_{mean}$ and $VPD > VPD_{mean}$). It achieved higher R^2 , lower NRMSE, and exhibited reduced biases in GPP estimations.

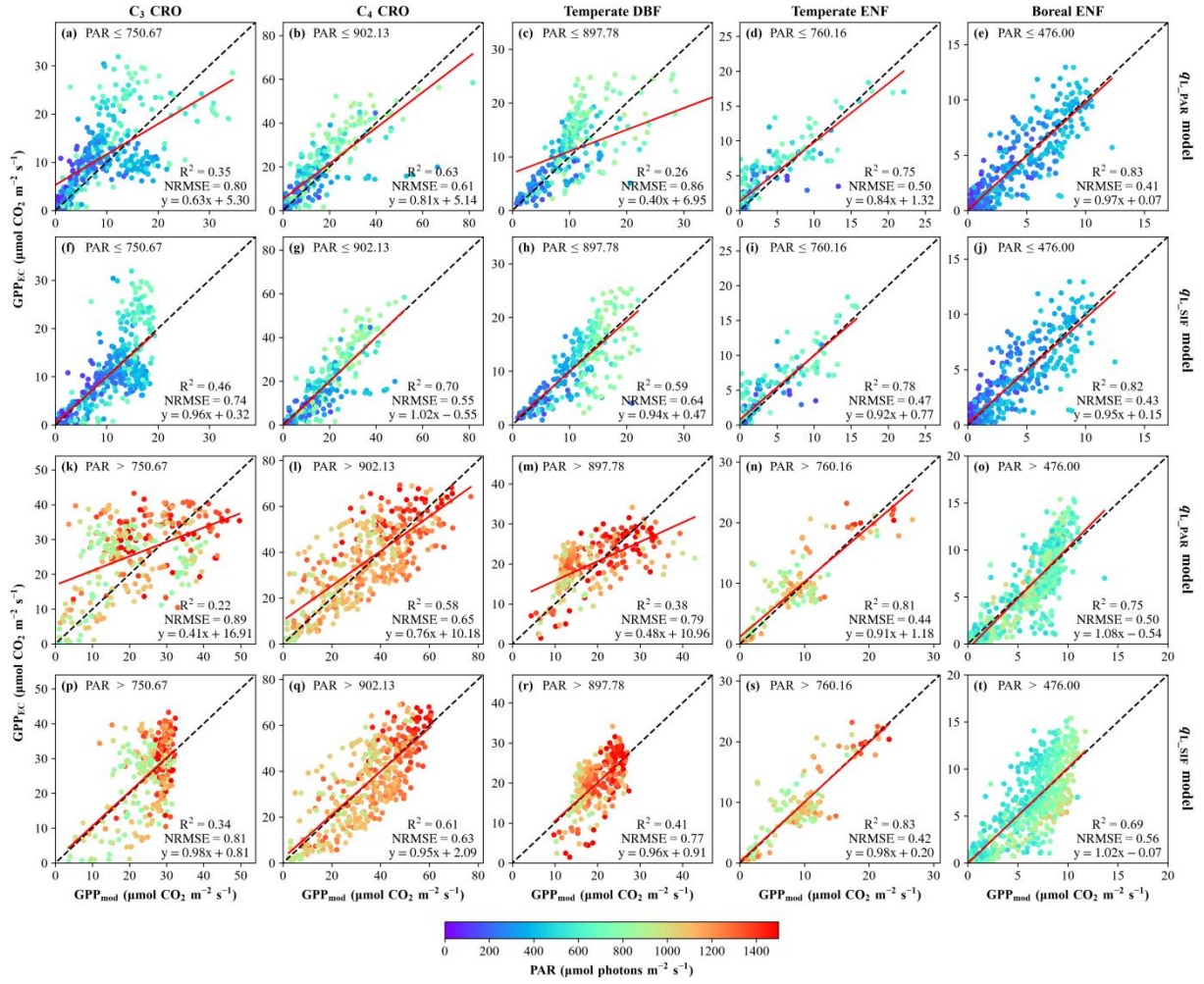


Fig. 8. Model performance of the q_{L_PAR} model and the q_{L_SIF} model for data below (a-e; f-j) and above (k-o; p-t) the mean value of PAR for different PFTs. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line.

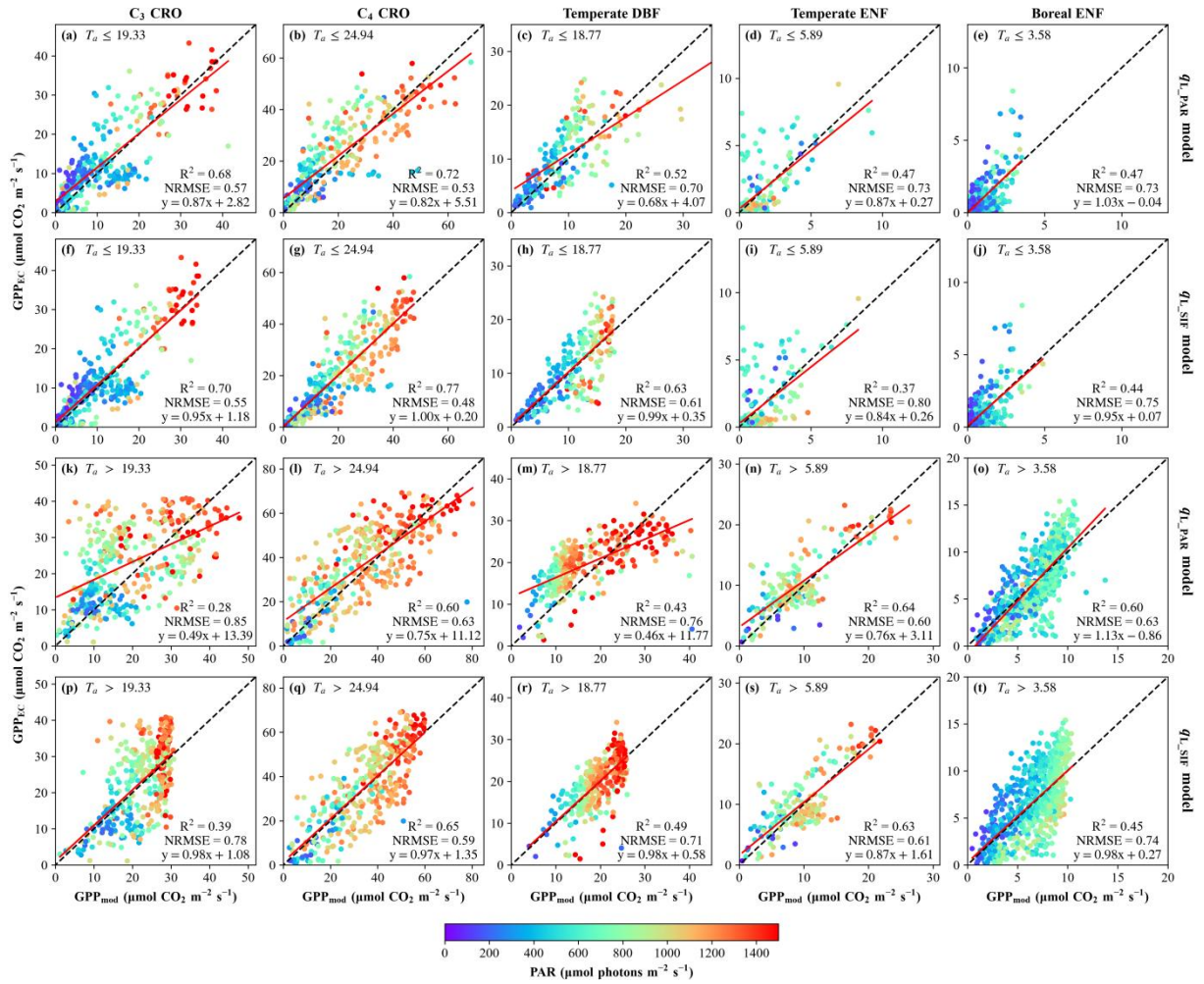


Fig. 9. Model performance of the qL_PAR model and the qL_SIF model for data below (a-e; f-j) and above (k-o; p-t) the mean value of T_a for different PFTs. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line.

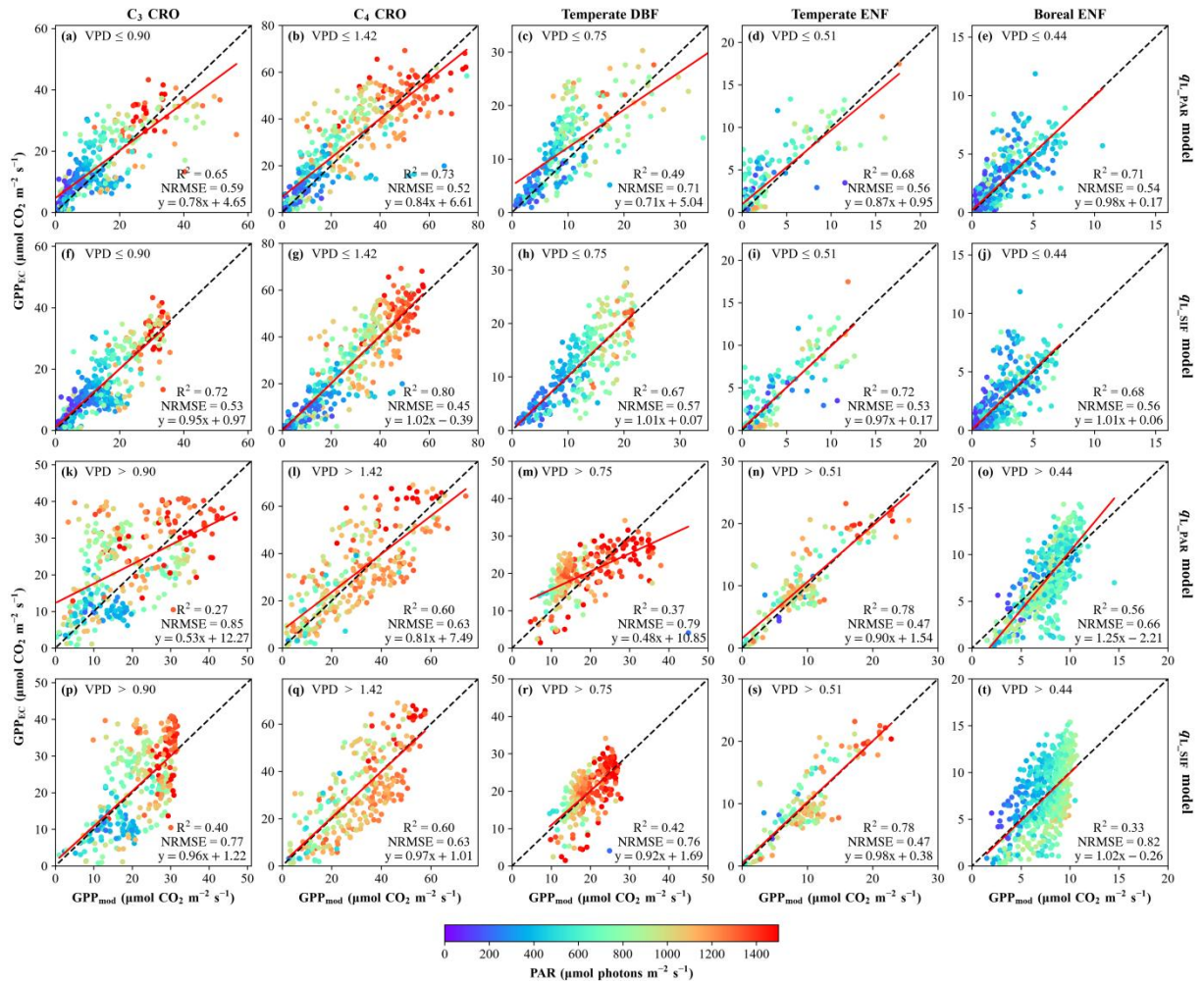


Fig. 10. Model performance of the q_{L_PAR} model and the q_{L_SIF} model for data below (a-e; f-j) and above (k-o; p-t) the mean value of VPD for different PFTs. The red solid line is the linear regression curve of observed GPP (GPP_{EC}) and modeled GPP (GPP_{mod}). The black dashed line is the 1:1 line.

4. Discussion

4.1 Why did environmental factors have different effects on GPP and SIF_{TOC_760} ?

Both GPP and SIF_{TOC_760} were significantly affected by PAR, T_a , and VPD across the different PFTs examined (Fig. 2, Fig. 3). The degree of environmental effects on GPP and SIF_{TOC_760} , however, differed. Specifically, across the different PFTs, PAR had a stronger influence on SIF_{TOC_760} than on GPP (Fig. 3a-e, Fig. 2f-j), while T_a had a higher effect on GPP compared to SIF_{TOC_760} (Fig. 2k-o, Fig. 3f-j). These differences may be primarily due to the distinct processes involved in SIF emission and carbon fixation. In detail, photosynthesis comprises three crucial reaction stages: photophysical reactions, photochemical reactions, and biochemical reactions (also known as dark reactions) (Kamen, 1963; Gu et al., 2023; Sun et al.,

[2023a](#)). The emission of SIF takes place as part of the photophysical reactions, which include light harvesting and excitation energy partitioning ([Gu et al., 2023](#); [Sun et al., 2023a](#)). In contrast, the fixation of CO₂ occurs within the biochemical reaction stage, which involves numerous crucial enzymatic reactions ([Blankenship, 2014](#); [Gu et al., 2023](#)). Temperature is known to influence enzymatic activities and thus affects the rate of CO₂ assimilation, thereby explaining the clear and direct impact of T_a on GPP. In contrast, SIF emission is controlled by physical principles ([Gu et al., 2023](#)) and does not involve enzymatic reactions. Consequently, T_a has a limited impact on SIF. SIF originates from the partitioning of absorbed PAR; therefore the variation of PAR can directly affect the variation of SIF. Conversely, PAR indirectly influences the rate of CO₂ fixation (GPP) by affecting the production of NADPH and ATP synthesis in the photochemical reactions.

The different ways (direct or indirect) in which PAR influences SIF and GPP, along with the forward and backward feedbacks among the three reaction stages, may jointly result in the distinct variation patterns of GPP-PAR (increased and leveled off, **Fig. 2f-j**) and SIF_{TOC_760}-PAR (increased and even increased faster at high PAR, **Fig. 3a-e**) observed in this study. From the perspective of energy supply and demand, photophysical, photochemical, and biochemical reactions can be regarded as the supply side, the supply chain and the demand side, respectively. Energy input to the supply side is the PAR absorbed by antenna pigments. When PAR is low, the energy supply falls short of the energy demand in biochemical reactions. Thus, carbon fixation is mainly limited by the energy supply in photophysical reactions (corresponding to the limitation of RuBP regeneration ([Van Diepen et al., 2022](#))). Therefore, GPP approximately linearly increases with PAR in this situation. As PAR exceeds the level where the energy supply and demand are equal, the rate of carbon fixation becomes primarily limited by the dark reaction processes (e.g., the Rubisco limitation ([Van Diepen et al., 2022](#)) or the insufficient supply of CO₂ due to decrease in stomatal aperture ([Gu et al., 2019](#))). In this case, the increase rate of GPP slows down and GPP levels off at high PAR once light saturation occurs. In contrast, the emission of SIF is a photophysical process and is directly related to the absorption of PAR. The dynamics of SIF are largely attributed to the variations of energy consumption in the carbon fixation and heat dissipation, because the input energy is conserved among these three processes ([Sun et al., 2023a](#)). When PAR is not high, the regulated thermal dissipation mechanisms (NPQ) can effectively dissipate excess excitation energy beyond the energy demand for carbon fixation (i.e., NPQ is not saturated), which in turn makes the quantum yield of SIF relatively stable ([Kramer et al., 2004](#); [Gu et al., 2019](#); [Chang et al., 2021](#); [Liu et al., 2022](#)). Therefore, SIF increases nearly linearly with PAR. However, if the excess excitation energy exceeds the

amount of energy that NPQ can dissipate as heat (i.e., NPQ is saturated ([Kramer et al., 2004](#))), the energy partitioned to SIF emission will increase. This leads to an increase in the quantum yield of SIF ([Kramer et al., 2004](#)) and eventually results in a higher-than-linear increase of SIF with increasing PAR. This situation may occur when NPQ is saturated whereas the excitation energy still increases via some processes (e.g., PAR continues to increase to higher levels ([Kramer et al., 2004](#); [Baker, 2008](#); [Gu et al., 2019](#)) and/or energy consumption by carbon fixation decreases due to environmental stresses or reduced supply of CO₂ ([Kramer et al., 2004](#))). Hence, the faster increase of SIF_{TOC_760} at higher PAR (~ above 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) observed in this study (**Fig. 3a-d**) may be largely due to the saturation of NPQ. The exception in the boreal ENF where SIF_{TOC_760} increased linearly with PAR throughout (**Fig. 3e**) may be due to the relatively low maximum PAR and higher capacity of NPQ in evergreen conifers ([Demmig-Adams and Adams, 2006](#); [Verhoeven, 2014](#)), and thus NPQ is not saturated in this situation. In addition, it is the increased quantum yield of SIF_{TOC_760} at high PAR that causes the saturation of GPP to SIF_{TOC_760} being more pronounced than that to PAR across different PFTs (**Fig. 2a-e, f-g**). Furthermore, the significant correlations of SIF_{TOC_760} with environmental factors (PAR, T_a and VPD, **Fig. 3**) and GPP (**Fig. 2a-e**) demonstrated that SIF is an integrated indicator containing information about various environmental effects and plant physiology status ([Gu et al., 2019](#); [Han et al., 2022a](#); [Sun et al., 2023a](#)).

4.2 The improved qMLR-SIF model significantly reduced biases in GPP estimation

To evaluate the performance of the improved qMLR-SIF model (q_{L_SIF} model) in quantifying canopy GPP, we first validated the feasibility of key parameter settings of the qMLR-SIF model; then compared the q_{L_SIF} model with the original qMLR-SIF model (q_{L_PAR} model) under various scenarios (PFTs, photosynthetic pathways, and temporal scales); and finally analyzed the impacts of key environmental factors on model performance. Our results demonstrated the feasibility of using a piecewise function of T_a (Eq. (9)) to simulate $\Phi_{PSII_{max}}$ for different PFTs (CRO, DBF, and ENF) (**Table 2**). Although this piecewise function is derived from a study performed with ENF ([Chen et al., 2024b](#)), it is also suitable for the CRO and DBF. This is because the piecewise function takes into account both situations where $\Phi_{PSII_{max}}$ is affected and unaffected by T_a . For the ENF, most of the data fell in the middle part of the piecewise function ($-5\text{ }^{\circ}\text{C} < T_a < 15\text{ }^{\circ}\text{C}$) (**Fig. 2n-o**); thus, the estimated $\Phi_{PSII_{max}}$ considered the effects of T_a . In contrast, the data from CRO and DBF primarily fell in the upper part of the piecewise function ($T_a \geq 15\text{ }^{\circ}\text{C}$) (**Fig. 2k-m**); therefore, the estimated $\Phi_{PSII_{max}}$ was constant and less affected by T_a during most of the time. Such simulation is consistent with the facts that 1)

$\Phi_{\text{PSII}_{\text{max}}}$ is a capacity parameter of photochemical quantum yield of PSII and is invariant across species under normal conditions (Baker, 2008; Gu et al., 2019); 2) compared to the ENF, low temperature stresses occur rarely or are even absent in the CRO and DBF (this is shown in Fig. 2k-o, where the minimum T_a is above zero in the CRO and DBF). Thus, $\Phi_{\text{PSII}_{\text{max}}}$ is nearly unaffected by T_a and invariable in these PFTs. This is also the reason why using the piecewise function (vs. fixed $\Phi_{\text{PSII}_{\text{max}}}$) led to more significant improvements in model performance in the ENF compared to the CRO and DBF (Table 2). We also verified the feasibility of the constancy assumption for $f_{\text{esc_P-C}}$. Results showed that the scenario of constant $f_{\text{esc_P-C}}$ had better performance in estimating GPP than that of the varied $f_{\text{esc_P-C}}$ (Table 3). This is primarily attributed to the following reasons: 1) $f_{\text{esc_P-C}}$ is approximately constant when LAI exceeds 3 (Yang and van der Tol, 2018), such as during most of the growing season (Dechant et al., 2020; Liu et al., 2022; Buareal et al., 2023); 2) the constancy assumption may avoid uncertainties introduced in the estimated $f_{\text{esc_P-C}}$ by Eq. (15) and Eq. (16) and therefore enhanced the accuracy of GPP estimation. In addition, it should be noted that the specific value of the constant $f_{\text{esc_P-C}}$ (within its physical boundaries, i.e., 0~1) has limited effects on the model performance. Because the difference between the default (0.4) and true values of $f_{\text{esc_P-C}}$ will be compensated for in the fitted parameters during parameterization. This also explains why, in the ENF, although the default value of $f_{\text{esc_P-C}}$ differed from the mean value of estimated $f_{\text{esc_P-C}}$ (0.4 vs. 0.2), the qMLR-SIF models still performed well (Table 3).

Recent studies have demonstrated the wide applicability of the qMLR-SIF model in estimating canopy GPP for different PFTs (Beauclaire et al., 2024; Chen et al., 2024b; Liu et al., 2024a). However, the inadequate simulation of the key variable q_L may diminish the accuracy of GPP estimation (Liu et al., 2024a), thereby limiting the applicability of the qMLR-SIF model in complex contexts. Therefore, this study developed a new SIF-based function to improve the simulation of q_L , and then to enhance the accuracy of the qMLR-SIF model in estimating GPP. In general, compared to the original qMLR-SIF model (q_{L_PAR} model), the improved qMLR-SIF model (q_{L_SIF} model) enhanced the model performance in quantifying canopy GPP for different PFTs (Fig. 4), photosynthetic pathways (Fig. 5) and temporal scales (Fig. 6), with higher R^2 and lower RMSE. In particular, the q_{L_SIF} model could significantly improve the underestimation and/or overestimation of GPP compared to the q_{L_PAR} model. Besides, the q_{L_SIF} model exhibited better performance in tracking the seasonal variation of GPP (Fig. 7). Moreover, although environmental factors can influence model accuracy, the q_{L_SIF} model still outperformed the q_{L_PAR} model overall (Fig. 8 - 10). Since the q_L function is the only difference between the q_{L_PAR} model and q_{L_SIF} model (Eq. (17)), the enhancements of the q_{L_SIF}

model in estimating GPP demonstrated the effectiveness of our new SIF-based q_L function, and thus further illustrated the rationality of the hypothesis that we posed in the development of the novel q_L function. The superior performance of the SIF-based q_L function (Eq. (11)) in comparison to the PAR-based q_L function (Eq. (10)) is primarily attributed to the mechanistic link between SIF and q_L at the molecular level. Specifically, photosynthesis involves a series of photophysical, photochemical and biochemical reactions ([Kamen, 1963](#); [Gu et al., 2023](#); [Sun et al., 2023a](#)), which are organically coordinated and give feedback to each other. Photophysical, photochemical and biochemical reactions can be regarded as the upstream, midstream, and downstream parts, respectively, of photosynthesis in which solar energy is converted into stable chemical energy. The key to photosynthesis is the upstream partitioning of absorbed sunlight energy, the midstream production of NADPH and ATP via linear and cyclic electron transports using the partitioned energy, and the downstream fixation of CO₂ using the reducing power (NADPH) and chemical energy (ATP) ([Gu et al., 2023](#); [Sun et al., 2023a](#)). The absorbed sunlight energy in the upstream part is mainly partitioned into photochemistry, SIF emission, and heat dissipation ([Porcar-Castell et al., 2014](#); [Gu et al., 2019](#)). The midstream linear electron transport (LET) from PSII to PSI tightly links the upstream energy partition to the downstream carbon fixation, while q_L reflects the degree of ‘traffic jam’ of LET from PSII to PSI ([Gu et al., 2019](#)) (lower q_L corresponds to higher degree of ‘traffic jam’) and to some extent, represents the efficiency of photochemistry in PSII ([Kramer et al., 2004](#)). Since the absorbed energy is conserved, the variation of energy allocated to photochemistry and heat dissipation will inevitably lead to the variation of energy allocated to SIF emission. Therefore, the variation in q_L is closely associated with the variation in SIF. Moreover, due to mechanistic links and feedbacks among the three parts (the upstream, midstream, and downstream parts of photosynthesis) ([Gu et al., 2023](#); [Sun et al., 2023a](#)), biotic and abiotic factors that may influence any of the three parts will directly or indirectly affect the others as well. This implies that factors influencing q_L also directly or indirectly impact SIF, and vice versa. For example, when PAR is high, decreased CO₂ supply in the downstream reactions will lead to decreased rate of electron consumption, thereby intensifying the ‘traffic jam’ of LET (thus decreasing q_L) in the midstream part ([Kramer et al., 2004](#); [Baker, 2008](#)). The decreased q_L indicates a reduced quantum yield of photochemistry of PSII, resulting in less energy being utilized for photochemistry. Consequently, more energy is allocated to SIF emission, especially when NPQ is saturated. This situation is illustrated in Fig. 2 of Kramer et al. (2004). In contrast, PAR only represents the external effect of light on q_L and cannot reflect the influences of other factors, such as T_a and CO₂ concentration. Therefore, compared to the SIF-based q_L function, the PAR-based q_L

function is assumed to be less effective in accurately simulating q_L under stressed conditions. This point was partly confirmed by our threshold analysis, in which the q_{L_PAR} model showed an overall worse performance than the q_{L_SIF} model under stressed conditions (**Fig. 8-10**).

In our analyses, the q_{L_SIF} model was unexpectedly outperformed by the q_{L_PAR} model in the boreal ENF (**Fig. 4e, j**), with both lower R^2 and higher RMSE indicating the inferior performance of the SIF-based q_L function. This may be primarily attributed to the particular environments in the boreal ENF and various mechanisms that trees have evolved to adapt to corresponding stresses. Specifically, the boreal ENF experiences strong seasonal variations and faces severe stresses from low T_a and high PAR during winter months ([Verhoeven, 2014](#); [Magney et al., 2019b](#)), which is significantly different from other PFTs. Low T_a does not preclude light absorption in photophysical reactions, but it substantially inhibits the energy consumption of biochemical reactions ([Verhoeven, 2014](#)), thereby leading to a serious light energy excess. To avoid excess light damage, species in the boreal ENF evolved a variety of photoprotective mechanisms, such as suppression of xanthophyll cycle dynamics, sustained engagement of xanthophyll as well as rearrangement or degradation of PSII core proteins ([Adams et al., 2004](#); [Demmig-Adams and Adams, 2006](#); [Verhoeven, 2014](#)). These adaptive mechanisms can impact the partitioning of absorbed sunlight energy (e.g., decreasing the quantum yield of SIF) by enhancing sustained NPQ ([Verhoeven, 2014](#); [Magney et al., 2019b](#)). This, in turn, may alter the relationship between SIF and q_L , causing the SIF- q_L relationship modeled with Eq. (11) to deviate from reality. Such deviation may eventually introduce biases in GPP estimation. In contrast, PAR is an external variable that is not affected by adaptive mechanisms; therefore, the influence of sustained NPQ on the PAR-based q_L function may be smaller. Threshold analysis for PAR, to some extent, indicated the existence of such effects in the boreal ENF. We found that the performance difference between the q_{L_SIF} model and the q_{L_PAR} model was larger under high PAR (**Fig. 8o, t**) than under low PAR (**Fig. 8e, j**). That means high PAR reduces the performance of the q_{L_SIF} model more prominently. Since the q_L function is the only difference between these two models, we can infer that high PAR reduces the capability of the SIF-based q_L function more significantly than it does for the PAR-based q_L function. Considering that high PAR corresponds to high sustained NPQ, the worse performance of the q_{L_SIF} model may be partly due to larger effects of high sustained NPQ on the SIF-based q_L function in the boreal ENF.

4.3 Limits and uncertainties

Although our SIF-based q_L simulation significantly enhanced the accuracy of the qMLR-

SIF model in quantifying canopy GPP in most PFTs, some limitations and uncertainties still exist. Firstly, the SIF-based q_L function needs to be further improved to accurately simulate q_L under stressed conditions. Threshold analysis indicated that environmental stresses (high PAR, high/low T_a , high VPD) could reduce model accuracy (**Fig. 8-10**). Although the q_{L_SIF} model generally outperformed the q_{L_PAR} model under stressed conditions, the decreased model accuracy implies that environmental factors still need to be considered in estimating q_L . The existence of positive or negative correlations between GPP residuals and environmental variables (PAR, T_a , and VPD) also suggested, to some extent, the necessity of considering other effects on q_L (**Fig. S1-3**). A recent study developed a semi-empirical model to simulate q_L , incorporating both SIF and T_a ([Liu et al., 2024b](#)). Their results showed that the semi-empirical q_L model could significantly improve the accuracy of the qMLR-SIF model in estimating canopy GPP of winter wheat. However, whether this semi-empirical q_L model is applicable to other PFTs remains unclear and needs further testing. Nevertheless, their study demonstrated the effectiveness of considering the impacts of both SIF and T_a for simulating q_L . Secondly, the piecewise function for estimating $\Phi_{PSII_{max}}$ (Eq. (9)) may introduce some uncertainties. The applicability of the piecewise function for different PFTs (CRO, DBF, and ENF) indicated that it captured major effects of T_a on $\Phi_{PSII_{max}}$. However, the exact influences of T_a on $\Phi_{PSII_{max}}$ may vary across different PFTs and may not be fully captured by this function. Hence, some biases may be introduced in the estimated GPP. In addition, our study only includes three PFTs; therefore, whether this piecewise function is applicable to other PFTs still needs to be verified. Moreover, since the decrease in $\Phi_{PSII_{max}}$ reflects the downregulation of plant's photosynthetic capacity via various NPQ mechanisms under stressed conditions ([Demmig-Adams and Adams, 2006](#); [Verhoeven, 2014](#)), other biotic or abiotic stresses (such as severe droughts and heatwave events) may also lead to a decrease in $\Phi_{PSII_{max}}$. Considering these effects on $\Phi_{PSII_{max}}$ in the piecewise function or even directly estimating $\Phi_{PSII_{max}}$ from a mechanistic perspective may enhance the capability of the qMLR-SIF model in quantifying GPP under complex conditions, especially in the context of global climate change. Thirdly, due to data availability, f_{esc_P-C} was assumed to be constant in this study, which may introduce some biases in the modeled GPP. Although we verified the feasibility of fixing f_{esc_P-C} for GPP estimation, this assumption may fail under some special situations, such as at the start and end of the growing seasons ([Dechant et al., 2020](#); [Lu et al., 2020](#); [Liu et al., 2022](#); [Liu et al., 2024b](#)). These particular situations do not affect the general conclusions drawn in this study, but may decrease the accuracy of the qMLR-SIF model. Finally, this study only includes three PFTs. Therefore, to what extent the improved qMLR-SIF model could enhance the accuracy of quantifying GPP for other PFTs

(e.g., evergreen broadleaf forest, grassland, and shrubland) needs further research.

5. Conclusions

In summary, this study developed a SIF-based q_L function that improves the simulation of q_L and consequently enhances the accuracy of the qMLR-SIF model for estimating canopy GPP. We compared the improved qMLR-SIF model with the original model for different PFTs (CRO, DBF, and ENF), photosynthetic pathways (C_3 and C_4), and temporal scales (half-hourly, daily, 4-day, and 8-day). Multi-site evaluation results showed that the improved qMLR-SIF model significantly reduced biases in GPP estimation. Although environmental stresses decreased the accuracy of the two models, the improved qMLR-SIF model still surpassed the original model (except for the boreal ENF), demonstrating the effectiveness of our improvement for the q_L simulation. In addition, we found that PAR exerted a stronger influence on SIF_{TOC_760} , whereas T_a had a stronger effect on GPP across different PFTs. Such differences may be primarily attributed to the different processes involved in SIF emission (photophysical reactions related to light absorption and energy partition) and carbon fixation (biochemical reactions related to numerous crucial enzymes). We also found that the saturation of GPP to SIF_{TOC_760} was more pronounced than that to PAR across different PFTs, which is probably attributed to the saturation of NPQ at high PAR. Moreover, the high correlations of SIF_{TOC_760} with GPP and environmental variables (PAR, T_a , and VPD) observed in this study demonstrated that SIF is an integrated indicator containing rich information about plant physiology status and environmental effects on plants. Our research expands the applicability of the qMLR-SIF model for accurate canopy GPP estimation, an essential step toward its large-scale applications. Further studies are required to elucidate and quantify the mechanisms underlying the variation of q_L , particularly under stressed conditions.

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Data availability

The data that support the findings of this study are collected from open sources. Specifically, data for ShangQiu and JuRong sites are available from ([Wu, 2022](#)). For US-Ha1 site, SIF data are available from ([Tang, 2017](#); [Wu, 2022](#)); EC and meteorological data are available from ([Munger and Wofsy, 2022](#)). For US-Nr1 site, SIF data are available from ([Magney et al., 2019a](#)); EC and meteorological data are available from ([Cheng et al., 2020a](#)). For SOBS site, SIF data are available from ([Pierrat and Stutz, 2022](#)); EC and meteorological data are available from ([Pierrat et al., 2022a](#)). Data for DEJU site are available from ([Pierrat et al., 2022d](#)). Data for YangLing site are available at <https://github.com/luxiaoliangnwafu/SIF2GPP> and https://github.com/luxiaoliangnwafu/qL_SIF_GPP. For US-UMB site, SIF data are available from ([Butterfield et al., 2022](#)); EC and meteorological data are available from ([Gough et al., 2024](#)). Data for US-Br3 are available at ([Magney and Frankenberg, 2019](#)). SIF data for US-Ne2 and US-Ne3 sites are available from ([Wu et al., 2023](#)). EC and meteorological data for US-Ne2 and US-Ne3 are available from ([Suyker, 2024a](#)) and ([Suyker, 2024b](#)), respectively. Data for TCK, DaMan, UIUC, ZhaoXian, and INRA sites can be found in Kim et al. (2021), Chen et al. (2020), Wu et al. (2022a), Ma et al. (2022), and Goulas et al. (2017), respectively.

Conflict of interest disclosure

The authors declare there are no conflicts of interest for this manuscript.

References

- Adams, W.W., Zarter, C.R., Ebbert, V. and Demmig-Adams, B. (2004). Photoprotective strategies of overwintering evergreens. *Bioscience* 54, 41–49. [https://doi.org/10.1641/0006-3568\(2004\)054\[0041:PSOOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0041:PSOOE]2.0.CO;2).
- Anav, A., Friedlingstein, P., Beer, C., Ciais, P., Harper, A., Jones, C., Murray-Tortarolo, G., Papale, D., Parazoo, N.C., Peylin, P., Piao, S., Sitch, S., Viovy, N., Wiltshire, A. and Zhao, M. (2015). Spatiotemporal patterns of terrestrial gross primary production: A review. *Rev. Geophys.* 53, 785–818. <https://doi.org/10.1002/2015rg000483>.
- Bacour, C., Maignan, F., MacBean, N., Porcar-Castell, A., Flexas, J., Frankenberg, C., Peylin, P., Chevallier, F., Vuichard, N. and Bastrikov, V. (2019). Improving Estimates of Gross Primary Productivity by Assimilating Solar-Induced Fluorescence Satellite Retrievals in a Terrestrial Biosphere Model Using a Process-Based SIF Model. *J. Geophys. Res.: Biogeosci.* 124, 3281–3306. <https://doi.org/10.1029/2019JG005040>.
- Baker, N.R. (2008). Chlorophyll fluorescence: a probe of photosynthesis in vivo. *Annu. Rev. Plant Biol.* 59, 89–113. <https://doi.org/10.1146/annurev.arplant.59.032607.092759>.
- Beauclaire, Q., De Cannière, S., Jonard, F., Pezzetti, N., Delhez, L. and Longdoz, B. (2024). Modeling gross primary production and transpiration from sun-induced chlorophyll fluorescence using a mechanistic light-response approach. *Remote Sens. Environ.* 307, 114150. <https://doi.org/10.1016/j.rse.2024.114150>.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I. and Papale, D. (2010). Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329, 834–838. <https://doi.org/10.1126/science.1184984>.
- Behera, S., T L, E., Sarkar, A. and Dutta, D. (2025). Solar-Induced Chlorophyll Fluorescence Yield Holds the Potential for Drought Early Warning. *Geophys. Res. Lett.* 52, e2024GL113419. <https://doi.org/10.1029/2024GL113419>.
- Blankenship, R.E. (2014). *Molecular mechanisms of photosynthesis*. John Wiley & Sons.
- Buareal, K., Kato, T., Morozumi, T., Ono, K. and Nakashima, N. (2023). Red solar-induced chlorophyll fluorescence as a robust proxy for ecosystem-level photosynthesis in a rice field. *Agric. For. Meteorol.* 336, 109473. <https://doi.org/10.1016/j.agrformet.2023.109473>.

- Butterfield, Z., Magney, T., Grossmann, K., Bohrer, G., Vogel, C., Barr, S. and Keppel-Aleks, G. (2023). Accounting for changes in radiation improves the ability of SIF to track water stress-induced losses in summer GPP in a temperate deciduous forest. *J. Geophys. Res.: Biogeosci.* 128, e2022JG007352. <https://doi.org/10.1029/2022JG007352>.
- Butterfield, Z., Muccio, D. and Keppel-Aleks, G. (2022). Tower observations of solar-induced chlorophyll fluorescence at the University of Michigan Biological Station [Dataset]. University of Michigan - Deep Blue Data. <https://doi.org/10.7302/SX8C-Y281>.
- Cendrero-Mateo, M.P., Wieneke, S., Damm, A., Alonso, L., Pinto, F., Moreno, J., Guanter, L., Celesti, M., Rossini, M., Sabater, N., Cogliati, S., Julitta, T., Rascher, U., Goulas, Y., Aasen, H., Pacheco-Labrador, J. and Mac Arthur, A. (2019). Sun-induced chlorophyll fluorescence III: Benchmarking retrieval methods and sensor characteristics for proximal sensing. *Remote Sens.* 11, 962. <https://doi.org/doi:10.3390/rs11080962>.
- Chang, C.Y., Guanter, L., Frankenberg, C., Köhler, P., Gu, L., Magney, T.S., Grossmann, K. and Sun, Y. (2020). Systematic assessment of retrieval methods for canopy far-red solar-induced chlorophyll fluorescence using high-frequency automated field spectroscopy. *J. Geophys. Res.: Biogeosci.* 125, e2019JG005533. <https://doi.org/10.1029/2019jg005533>.
- Chang, C.Y., Wen, J., Han, J., Kira, O., LeVonne, J., Melkonian, J., Riha, S.J., Skovira, J., Ng, S., Gu, L., Wood, J.D., Nätke, P. and Sun, Y. (2021). Unpacking the drivers of diurnal dynamics of sun-induced chlorophyll fluorescence (SIF): Canopy structure, plant physiology, instrument configuration and retrieval methods. *Remote Sens. Environ.* 265, 112672. <https://doi.org/10.1016/j.rse.2021.112672>.
- Chen, J., Huang, L., Zuo, Q. and Shi, J. (2024a). Assessing the potential for photochemical reflectance index to improve the relationship between solar-induced chlorophyll fluorescence and gross primary productivity in crop and soybean. *Atmosphere* 15, 463. <https://doi.org/10.3390/atmos15040463>.
- Chen, J., Liu, X., Du, S., Ma, Y. and Liu, L. (2020). Integrating SIF and clearness index to improve maize GPP estimation using continuous tower-based observations. *Sensors (Basel)* 20, 2493. <https://doi.org/10.3390/s20092493>.
- Chen, R., Liu, L., Liu, Z., Liu, X., Kim, J., Kim, H.S., Lee, H., Wu, G., Guo, C. and Gu, L. (2024b). SIF-based GPP modeling for evergreen forests considering the seasonal variation in maximum photochemical efficiency. *Agric. For. Meteorol.* 344, 109814. <https://doi.org/10.1016/j.agrformet.2023.109814>.

- Cheng, R., Frankenberg, C., Magney, T., Grossmann, K., Bowling, D., Burns, S., Stutz, J. and Blanken, P. (2020a). Hyperspectral reflectance at Niwot Ridge, Colorado 2017-2018 (Version 1.0) [Dataset]. CaltechDATA. <https://doi.org/10.22002/D1.1597>.
- Cheng, R., Magney, T.S., Dutta, D., Bowling, D.R., Logan, B.A., Burns, S.P., Blanken, P.D., Grossmann, K., Lopez, S., Richardson, A.D., Stutz, J. and Frankenberg, C. (2020b). Decomposing reflectance spectra to track gross primary production in a subalpine evergreen forest. *Biogeosciences* 17, 4523–4544. <https://doi.org/10.5194/bg-17-4523-2020>.
- Damm, A., Guanter, L., Paul-Limoges, E., Van der Tol, C., Hueni, A., Buchmann, N., Eugster, W., Ammann, C. and Schaepman, M.E. (2015). Far-red sun-induced chlorophyll fluorescence shows ecosystem-specific relationships to gross primary production: An assessment based on observational and modeling approaches. *Remote Sens. Environ.* 166, 91–105. <https://doi.org/10.1016/j.rse.2015.06.004>.
- Dechant, B., Ryu, Y., Badgley, G., Zeng, Y., Berry, J.A., Zhang, Y., Goulas, Y., Li, Z., Zhang, Q., Kang, M., Li, J. and Moya, I. (2020). Canopy structure explains the relationship between photosynthesis and sun-induced chlorophyll fluorescence in crops. *Remote Sens. Environ.* 241, 111733. <https://doi.org/10.1016/j.rse.2020.111733>.
- Demmig-Adams, B. and Adams, W.W. (2006). Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytol.* 172, 11–21. <https://doi.org/10.1111/j.1469-8137.2006.01835.x>.
- Farquhar, G.D., von Caemmerer, S.v. and Berry, J.A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149, 78–90. <https://doi.org/10.1007/BF00386231>.
- Feng, H., Xu, T., Liu, L., Zhou, S., Zhao, J., Liu, S., Xu, Z., Mao, K., He, X. and Zhu, Z. (2021). Modeling transpiration with sun-induced chlorophyll fluorescence observations via carbon-water coupling methods. *Remote Sens.* 13, 804. <https://doi.org/10.3390/rs13040804>.
- Frankenberg, C. and Berry, J. (2018). 3.10 Solar Induced Chlorophyll Fluorescence: Origins, Relation to Photosynthesis and Retrieval. *Compr. Remote Sens* 3, 143–162. <https://doi.org/10.1016/b978-0-12-409548-9.10632-3>.
- Gough, C., Bohrer, G. and Curtis, P. (2024). AmeriFlux BASE US-UMB Univ. of Mich. Biological Station (Version 21-5) [Dataset]. AmeriFlux AMP. <https://doi.org/10.17190/AMF/1246107>.

- Goulas, Y., Fournier, A., Daumard, F., Champagne, S., Ounis, A., Marloie, O. and Moya, I. (2017). Gross primary production of a wheat canopy relates stronger to far red than to red solar-induced chlorophyll fluorescence. *Remote Sens.* 9, 97. <https://doi.org/10.3390/rs9010097>.
- Grossmann, K., Frankenberg, C., Magney, T.S., Hurlock, S.C., Seibt, U. and Stutz, J. (2018). PhotoSpec: A new instrument to measure spatially distributed red and far-red solar-induced chlorophyll fluorescence. *Remote Sens. Environ.* 216, 311–327. <https://doi.org/10.1016/j.rse.2018.07.002>.
- Gu, L., Grodzinski, B., Han, J., Marie, T., Zhang, Y.J., Song, Y.C. and Sun, Y. (2023). An exploratory steady-state redox model of photosynthetic linear electron transport for use in complete modelling of photosynthesis for broad applications. *Plant, Cell Environ.* 46, 1540–1561. <https://doi.org/10.1111/pce.14563>.
- Gu, L., Han, J., Wood, J.D., Chang, C.Y.Y. and Sun, Y. (2019). Sun-induced Chl fluorescence and its importance for biophysical modeling of photosynthesis based on light reactions. *New Phytol.* 233, 1179–1191. <https://doi.org/10.1111/nph.15796>.
- Gu, L. and Sun, Y. (2014). Artefactual responses of mesophyll conductance to CO₂ and irradiance estimated with the variable *J* and online isotope discrimination methods. *Plant, Cell Environ.* 37, 1231–1249. <https://doi.org/10.1111/pce.12232>.
- Guo, C., Liu, Z., Jin, X. and Lu, X. (2024). Improved estimation of gross primary productivity (GPP) using solar-induced chlorophyll fluorescence (SIF) from photosystem II. *Agric. For. Meteorol.* 354, 110090. <https://doi.org/10.1016/j.agrformet.2024.110090>.
- Han, J., Chang, C.Y.-Y., Gu, L., Zhang, Y., Meeker, E.W., Magney, T.S., Walker, A.P., Wen, J., Kira, O., McNaull, S. and Sun, Y. (2022a). The physiological basis for estimating photosynthesis from chlorophyll *a* fluorescence. *New Phytol.* 234, 1206–1219. <https://doi.org/10.1111/nph.18045>.
- Han, J., Gu, L., Warren, J.M., Guha, A., McLennan, D.A., Zhang, W. and Zhang, Y. (2022b). The roles of photochemical and non-photochemical quenching in regulating photosynthesis depend on the phases of fluctuating light conditions. *Tree Physiol.* 42, 848–861. <https://doi.org/10.1093/treephys/tpab133>.
- He, L., Magney, T., Dutta, D., Yin, Y., Köhler, P., Grossmann, K., Stutz, J., Dold, C., Hatfield, J., Guan, K., Peng, B. and Frankenberg, C. (2020). From the ground to space: Using solar-induced chlorophyll fluorescence to estimate crop productivity. *Geophys. Res. Lett.* 47, e2020GL087474. <https://doi.org/10.1029/2020GL087474>.
- Kamen, M.D. (1963). *Primary processes in photosynthesis*, 1. New York: Academic Press.

- Katul, G., Manzoni, S., Palmroth, S. and Oren, R. (2010). A stomatal optimization theory to describe the effects of atmospheric CO₂ on leaf photosynthesis and transpiration. *Ann. Bot.* 105, 431–442. <https://doi.org/10.1093/aob/mcp292>.
- Keenan, T.F., Baker, I., Barr, A., Ciais, P., Davis, K., Dietze, M., Dragoni, D., Gough, C.M., Grant, R., Hollinger, D., Hufkens, K., Poulter, B., McCaughey, H., Raczka, B., Ryu, Y., Schaefer, K., Tian, H., Verbeeck, H., Zhao, M. and Richardson, A.D. (2012). Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO₂ exchange. *Global Change Biol.* 18, 1971–1987. <https://doi.org/10.1111/j.1365-2486.2012.02678.x>.
- Keenan, T.F., Prentice, I.C., Canadell, J.G., Williams, C.A., Wang, H., Raupach, M. and Collatz, G.J. (2016). Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake. *Nat. Commun.* 7, 13428. <https://doi.org/10.1038/ncomms13428>.
- Kim, J., Ryu, Y., Dechant, B., Lee, H., Kim, H.S., Kornfeld, A. and Berry, J.A. (2021). Solar-induced chlorophyll fluorescence is non-linearly related to canopy photosynthesis in a temperate evergreen needleleaf forest during the fall transition. *Remote Sens. Environ.* 258, 112362. <https://doi.org/10.1016/j.rse.2021.112362>.
- Koffi, E., Rayner, P., Norton, A., Frankenberg, C. and Scholze, M. (2015). Investigating the usefulness of satellite-derived fluorescence data in inferring gross primary productivity within the carbon cycle data assimilation system. *Biogeosciences* 12, 4067–4084. <https://doi.org/10.5194/bg-12-4067-2015>.
- Korson, L., Drost-Hansen, W. and Millero, F.J. (1969). Viscosity of water at various temperatures. *The Journal of Physical Chemistry* 73, 34–39. <https://doi.org/10.1021/j100721a006>.
- Kramer, D.M., Johnson, G., Kiirats, O. and Edwards, G.E. (2004). New Fluorescence Parameters for the Determination of Q_A Redox State and Excitation Energy Fluxes. *Photosynth. Res.* 79, 209–218. <https://doi.org/10.1023/B:PRES.0000015391.99477.0d>.
- Lasslop, G., Reichstein, M., Papale, D., Richardson, A.D., Arneth, A., Barr, A., Stoy, P. and Wohlfahrt, G. (2010). Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biol.* 16, 187–208. <https://doi.org/10.1111/j.1365-2486.2009.02041.x>.

- Li, Z., Zhang, Q., Li, J., Yang, X., Wu, Y., Zhang, Z., Wang, S., Wang, H. and Zhang, Y. (2020). Solar-induced chlorophyll fluorescence and its link to canopy photosynthesis in maize from continuous ground measurements. *Remote Sens. Environ.* 236, 111420. <https://doi.org/10.1016/j.rse.2019.111420>.
- Liu, L., Guan, L. and Liu, X. (2017). Directly estimating diurnal changes in GPP for C₃ and C₄ crops using far-red sun-induced chlorophyll fluorescence. *Agric. For. Meteorol.* 232, 1–9. <https://doi.org/10.1016/j.agrformet.2016.06.014>.
- Liu, X., Guanter, L., Liu, L., Damm, A., Malenovsky, Z., Rascher, U., Peng, D., Du, S. and Gastellu-Etchegorry, J.-P. (2019a). Downscaling of solar-induced chlorophyll fluorescence from canopy level to photosystem level using a random forest model. *Remote Sens. Environ.* 231, 110772. <https://doi.org/https://doi.org/10.1016/j.rse.2018.05.035>.
- Liu, X., Liu, L., Hu, J., Guo, J. and Du, S. (2020). Improving the potential of red SIF for estimating GPP by downscaling from the canopy level to the photosystem level. *Agric. For. Meteorol.* 281, 107846. <https://doi.org/10.1016/j.agrformet.2019.107846>.
- Liu, X., Liu, Z., Liu, L., Lu, X., Chen, J., Du, S. and Zou, C. (2021). Modelling the influence of incident radiation on the SIF-based GPP estimation for maize. *Agric. For. Meteorol.* 307, 108522. <https://doi.org/10.1016/j.agrformet.2021.108522>.
- Liu, Y. (2026). Data from: Multi-site evaluation of an improved SIF-based model for estimating canopy GPP (Version 1.0.0) [Dataset]. Zenodo. <https://doi.org/https://doi.org/10.5281/zenodo.23004914>.
- Liu, Y., Hu, Z., Wang, G., Gessler, A. and Sun, S. (2024a). The applicability of a SIF-based mechanistic model for estimating GPP at the canopy scale. *Agric. For. Meteorol.* 356, 110192. <https://doi.org/10.1016/j.agrformet.2024.110192>.
- Liu, Z., Guo, C., Yu, Q., Zhu, P., Peng, X., Dong, M., Cai, H. and Lu, X. (2024b). A SIF-based approach for quantifying canopy photosynthesis by simulating the fraction of open PSII reaction centers (q_L). *Remote Sens. Environ.* 305, 114111. <https://doi.org/10.1016/j.rse.2024.114111>.
- Liu, Z., Lu, X., An, S., Heskel, M., Yang, H. and Tang, J. (2019b). Advantage of multi-band solar-induced chlorophyll fluorescence to derive canopy photosynthesis in a temperate forest. *Agric. For. Meteorol.* 279, 107691. <https://doi.org/10.1016/j.agrformet.2019.107691>.
- Liu, Z., Zhao, F., Liu, X., Yu, Q., Wang, Y., Peng, X., Cai, H. and Lu, X. (2022). Direct estimation of photosynthetic CO₂ assimilation from solar-induced chlorophyll

fluorescence (SIF). *Remote Sens. Environ.* 271, 112893.
<https://doi.org/10.1016/j.rse.2022.112893>.

Lu, X., Liu, Z., Zhao, F. and Tang, J. (2020). Comparison of total emitted solar-induced chlorophyll fluorescence (SIF) and top-of-canopy (TOC) SIF in estimating photosynthesis. *Remote Sens. Environ.* 251, 112083.
<https://doi.org/10.1016/j.rse.2020.112083>.

Ma, L., Sun, L., Wang, S., Chen, J., Chen, B., Zhu, K., Amir, M., Wang, X., Liu, Y., Wang, P., Wang, J., Huang, M. and Wang, Z. (2022). Analysis on the relationship between sun-induced chlorophyll fluorescence and gross primary productivity of winter wheat in northern China. *Ecol. Indic.* 139, 108905.
<https://doi.org/10.1016/j.ecolind.2022.108905>.

Magney, T. and Frankenberg, C. (2019). Chlorophyll fluorescence spectra for a wide range of species and conditions (Version 0.1) [Dataset]. <https://doi.org/10.22002/D1.1226>.

Magney, T., Frankenberg, C., Grossmann, K., Bowling, D., Logan, B., Burns, S. and Stutz, J. (2019a). Canopy and needle scale fluorescence data from Niwot Ridge, Colorado 2017-2018 (Version 1.2) [Dataset]. CaltechDATA. <https://doi.org/10.22002/D1.1231>.

Magney, T.S., Bowling, D.R., Logan, B.A., Grossmann, K., Stutz, J., Blanken, P.D., Burns, S.P., Cheng, R., Garcia, M.A., Köhler, P., Lopez, S., Parazoo, N.C., Raczka, B., Schimel, D. and Frankenberg, C. (2019b). Mechanistic evidence for tracking the seasonality of photosynthesis with solar-induced fluorescence. *Proc. Natl. Acad. Sci. U. S. A.* 116, 11640–11645. <https://doi.org/10.1073/pnas.1900278116>.

Meroni, M., Rossini, M., Guanter, L., Alonso, L., Rascher, U., Colombo, R. and Moreno, J. (2009). Remote sensing of solar-induced chlorophyll fluorescence: Review of methods and applications. *Remote Sens. Environ.* 113, 2037–2051.
<https://doi.org/10.1016/j.rse.2009.05.003>.

Merrick, T., Bennartz, R., Jorge, M.L.S., Merrick, C., Bohlman, S.A., Silva, C.A. and Pau, S. (2023). Comparing phenology of a temperate deciduous forest captured by solar-induced fluorescence and vegetation indices. *Remote Sens.* 15, 5101.
<https://doi.org/10.3390/rs15215101>.

Miao, G., Guan, K., Suyker, A.E., Yang, X., Arkebauer, T.J., Walter-Shea, E.A., Kimm, H., Hmimina, G.Y., Gamon, J.A., Franz, T.E., Frankenberg, C., Berry, J.A. and Wu, G. (2020). Varying contributions of drivers to the relationship between canopy photosynthesis and far-red sun-induced fluorescence for two maize sites at different

temporal scales. *J. Geophys. Res.: Biogeosci.* 125, e2019JG005051.
<https://doi.org/10.1029/2019jg005051>.

Mohammed, G.H., Colombo, R., Middleton, E.M., Rascher, U., van der Tol, C., Nedbal, L., Goulas, Y., Pérez-Priego, O., Damm, A., Meroni, M., Joiner, J., Cogliati, S., Verhoef, W., Malenovsky, Z., Gastellu-Etchegorry, J.-P., Miller, J.R., Guanter, L., Moreno, J., Moya, I., Berry, J.A., Frankenberg, C. and Zarco-Tejada, P.J. (2019). Remote sensing of solar-induced chlorophyll fluorescence (SIF) in vegetation: 50 years of progress. *Remote Sens. Environ.* 231, 111177. <https://doi.org/10.1016/j.rse.2019.04.030>.

Muller, P., Li, X.-P. and Niyogi, K.K. (2001). Non-photochemical quenching. A response to excess light energy. *Plant Physiol.* 125, 1558–1566.
<https://doi.org/10.1104/pp.125.4.1558>.

Munger, W. and Wofsy, S. (2022). Canopy-Atmosphere Exchange of Carbon, Water and Energy at Harvard Forest EMS Tower since 1991 [Dataset]. Environmental Data Initiative.
<https://doi.org/10.6073/PASTA/87DE3421E155B05FD166B17D17C73C6D>.

Murchie, E.H. and Lawson, T. (2013). Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. *J. Exp. Bot.* 64, 3983–3998.
<https://doi.org/10.1093/jxb/ert208>.

Norton, A.J., Rayner, P.J., Koffi, E.N., Scholze, M., Silver, J.D. and Wang, Y.-P. (2019). Estimating global gross primary productivity using chlorophyll fluorescence and a data assimilation system with the BETHY-SCOPE model. *Biogeosciences* 16, 3069–3093. <https://doi.org/10.5194/bg-16-3069-2019>.

Pei, Y., Dong, J., Zhang, Y., Yuan, W., Doughty, R., Yang, J., Zhou, D., Zhang, L. and Xiao, X. (2022). Evolution of light use efficiency models: Improvement, uncertainties, and implications. *Agric. For. Meteorol.* 317, 108905.
<https://doi.org/10.1016/j.agrformet.2022.108905>.

Pierrat, Z., Johnson, B., Helgason, W., Barr, A. and Stutz, J. (2022a). Gross primary production and environmental observations for a mature black spruce site located in central Saskatchewan, Canada, for the period Sep-2018 to Dec-2020 [Dataset]. Federated Research Data Repository. <https://doi.org/10.20383/102.0550>.

Pierrat, Z., Magney, T., Parazoo, N.C., Grossmann, K., Bowling, D.R., Seibt, U., Johnson, B., Helgason, W., Barr, A., Bortnik, J., Norton, A., Maguire, A., Frankenberg, C. and Stutz, J. (2022b). Diurnal and seasonal dynamics of solar-induced chlorophyll fluorescence, vegetation indices, and gross primary productivity in the boreal forest. *J. Geophys. Res.: Biogeosci.* 127, e2021JG006588. <https://doi.org/10.1029/2021jg006588>.

- Pierrat, Z. and Stutz, J. (2022). Tower-based solar-induced fluorescence and vegetation index data for Southern Old Black Spruce forest [Dataset]. Zenodo. <https://doi.org/10.5281/ZENODO.5884643>.
- Pierrat, Z.A., Bortnik, J., Johnson, B., Barr, A., Magney, T., Bowling, D.R., Parazoo, N., Frankenberg, C., Seibt, U. and Stutz, J. (2022c). Forests for forests: combining vegetation indices with solar-induced chlorophyll fluorescence in random forest models improves gross primary productivity prediction in the boreal forest. *Environ. Res. Lett.* 17, 125006. <https://doi.org/10.1088/1748-9326/aca5a0>.
- Pierrat, Z.A., Magney, T., Bowling, D.R., Johnson, B., Barr, A. and Stutz, J. (2022d). Boreal forest tower-based remote sensing data (solar-induced fluorescence and reflectance-based vegetation indices) [Dataset]. Zenodo. <https://doi.org/10.5281/ZENODO.7231157>.
- Porcar-Castell, A., Malenovský, Z., Magney, T., Van Wittenberghe, S., Fernández-Marín, B., Maignan, F., Zhang, Y., Maseyk, K., Atherton, J., Albert, L.P., Robson, T.M., Zhao, F., Garcia-Plazaola, J.-I., Ensminger, I., Rajewicz, P.A., Grebe, S., Tikkanen, M., Kellner, J.R., Ihalainen, J.A., Rascher, U. and Logan, B. (2021). Chlorophyll *a* fluorescence illuminates a path connecting plant molecular biology to Earth-system science. *Nat. Plants* 7, 988–1009. <https://doi.org/10.1038/s41477-021-00980-4>.
- Porcar-Castell, A., Tyystjärvi, E., Atherton, J., Van der Tol, C., Flexas, J., Pfündel, E.E., Moreno, J., Frankenberg, C. and Berry, J.A. (2014). Linking chlorophyll *a* fluorescence to photosynthesis for remote sensing applications: mechanisms and challenges. *J. Exp. Bot.* 65, 4065–4095. <https://doi.org/10.1093/jxb/eru191>.
- Prentice, I.C., Dong, N., Gleason, S.M., Maire, V. and Wright, I.J. (2014). Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. *Ecol. Lett.* 17, 82–91. <https://doi.org/10.1111/ele.12211>.
- Qiu, R., Li, X., Han, G., Xiao, J., Ma, X. and Gong, W. (2022). Monitoring drought impacts on crop productivity of the US Midwest with solar-induced fluorescence: GOSIF outperforms GOME-2 SIF and MODIS NDVI, EVI, and NIRv. *Agric. For. Meteorol.* 323, 109038. <https://doi.org/10.1016/j.agrformet.2022.109038>.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.-M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. and Valentini, R. (2005). On

the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biol.* 11, 1424–1439. <https://doi.org/10.1111/j.1365-2486.2005.001002.x>.

Shan, N., Zhang, Y., Chen, J.M., Ju, W., Migliavacca, M., Peñuelas, J., Yang, X., Zhang, Z., Nelson, J.A. and Goulas, Y. (2021). A model for estimating transpiration from remotely sensed solar-induced chlorophyll fluorescence. *Remote Sens. Environ.* 252, 112134. <https://doi.org/10.1016/j.rse.2020.112134>.

Shi, D., Jiang, Y., Cui, M., Guan, M., Xu, X. and Kang, M. (2025). Comparison of Spring Phenology from Solar-Induced Chlorophyll Fluorescence, Vegetation Index, and Ground Observations in Boreal Forests. *Remote Sens.* 17, 627. <https://doi.org/10.3390/rs17040627>.

Shin, Y.K., Bhandari, S.R., Jo, J.S., Song, J.W. and Lee, J.G. (2021). Effect of drought stress on chlorophyll fluorescence parameters, phytochemical contents, and antioxidant activities in lettuce seedlings. *Horticulturae* 7, 238. <https://doi.org/10.3390/horticulturae7080238>.

Sun, Y., Gu, L., Wen, J., van der Tol, C., Porcar-Castell, A., Joiner, J., Chang, C.Y., Magney, T., Wang, L., Hu, L., Rascher, U., Zarco-Tejada, P., Barrett, C.B., Lai, J., Han, J. and Luo, Z. (2023a). From remotely sensed solar-induced chlorophyll fluorescence to ecosystem structure, function, and service: Part I-Harnessing theory. *Glob Chang Biol* 29, 2926–2952. <https://doi.org/10.1111/gcb.16634>.

Sun, Y., Wen, J., Gu, L., Joiner, J., Chang, C.Y., van der Tol, C., Porcar-Castell, A., Magney, T., Wang, L., Hu, L., Rascher, U., Zarco-Tejada, P., Barrett, C.B., Lai, J., Han, J. and Luo, Z. (2023b). From remotely-sensed solar-induced chlorophyll fluorescence to ecosystem structure, function, and service: Part II-Harnessing data. *Glob Chang Biol* 29, 2893–2925. <https://doi.org/10.1111/gcb.16646>.

Suyker, A. (2024a). AmeriFlux BASE US-Ne2 Mead - irrigated maize-soybean rotation site (Version 18-5) [Dataset]. AmeriFlux AMP. <https://doi.org/10.17190/AMF/1246085>.

Suyker, A. (2024b). AmeriFlux BASE US-Ne3 Mead - rainfed maize-soybean rotation site (Version 18-5) [Dataset]. AmeriFlux AMP. <https://doi.org/10.17190/AMF/1246086>.

Tang, J. (2017). Continuous measurement of canopy fluorescence at harvard forest 2013-2014 (Version 4.0) [Dataset]. Harvard Forest Data Archive: HF283 <https://doi.org/10.6073/pasta/99c883ee28987ac32a98d621c7ec3bb6>.

Tommervik, H., Julitta, T., Nilsen, L., Park, T., Burkart, A., Ostapowicz, K., Karlsen, S.R., Parmentier, F.-J., Pirk, N. and Bjerke, J.W. (2023). The northernmost hyperspectral

FLoX sensor dataset for monitoring of high-arctic tundra vegetation phenology and sun-induced fluorescence (SIF) [Dataset]. <https://doi.org/10.1016/j.dib.2023.109581>.

Van Diepen, K., Goudriaan, J., Vilà-Guerau de Arellano, J. and De Boer, H. (2022). Comparison of C₃ photosynthetic responses to light and CO₂ predicted by the leaf photosynthesis models of Farquhar et al. (1980) and Goudriaan et al. (1985). *J. Adv. Model. Earth Syst.* 14, e2021MS002976. <https://doi.org/10.1029/2021ms002976>.

Verhoeven, A. (2014). Sustained energy dissipation in winter evergreens. *New Phytol.* 201, 57–65. <https://doi.org/10.1111/nph.12466>.

von Caemmerer, S. (2000). Biochemical models of leaf photosynthesis. CSIRO, 176 pp.

von Caemmerer, S. (2021). Updating the steady-state model of C₄ photosynthesis. *J. Exp. Bot.* 72, 6003–6017. <https://doi.org/10.1093/jxb/erab266>.

Wang, X., Blanken, P.D., Wood, J.D., Nouvellon, Y., Thaler, P., Kasemsap, P., Chidthaisong, A., Petchprayoon, P., Chayawat, C. and Xiao, J. (2023). Solar-induced chlorophyll fluorescence detects photosynthesis variations and drought effects in tropical rubber plantation and natural deciduous forests. *Agric. For. Meteorol.* 339, 109591. <https://doi.org/10.1016/j.agrformet.2023.109591>.

Welp, L.R., Keeling, R.F., Meijer, H.A.J., Bollenbacher, A.F., Piper, S.C., Yoshimura, K., Francey, R.J., Allison, C.E. and Wahlen, M. (2011). Interannual variability in the oxygen isotopes of atmospheric CO₂ driven by El Niño. *Nature* 477, 579–582. <https://doi.org/10.1038/nature10421>.

Wu, G., Guan, K., Jiang, C., Kimm, H., Miao, G., Bernacchi, C.J., Moore, C.E., Ainsworth, E.A., Yang, X., Berry, J.A., Frankenberg, C. and Chen, M. (2022a). Attributing differences of solar-induced chlorophyll fluorescence (SIF)-gross primary production (GPP) relationships between two C₄ crops: corn and miscanthus. *Agric. For. Meteorol.* 323, 109046. <https://doi.org/10.1016/j.agrformet.2022.109046>.

Wu, G., Guan, K., Kimm, H., Miao, G. and Jiang, C. (2023). SIF and Vegetation Indices in the US Midwestern Agroecosystems, 2016-2021 (Version 1.0) [Dataset]. ORNL Distributed Active Archive Center. <https://doi.org/10.3334/ORNLDAAAC/2136>.

Wu, Y. (2022). SIF-GPP sky conditions [Dataset]. figshare. <https://doi.org/10.6084/M9.FIGSHARE.19295009>.

Wu, Y., Zhang, Z., Zhang, X., Wu, L. and Zhang, Y. (2022b). How do sky conditions affect the relationships between ground-based solar-induced chlorophyll fluorescence and gross primary productivity across different plant types? *J. Geophys. Res.: Biogeosci.* 127, e2022JG006865. <https://doi.org/10.1029/2022JG006865>.

- Yang, H.L., Yang, X., Zhang, Y.G., Heskell, M.A., Lu, X.L., Munger, J.W., Sun, S.C. and Tang, J.W. (2017). Chlorophyll fluorescence tracks seasonal variations of photosynthesis from leaf to canopy in a temperate forest. *Global Change Biol.* 23, 2874–2886. <https://doi.org/10.1111/gcb.13590>.
- Yang, K., Ryu, Y., Dechant, B., Berry, J.A., Hwang, Y., Jiang, C., Kang, M., Kim, J., Kimm, H. and Kornfeld, A. (2018a). Sun-induced chlorophyll fluorescence is more strongly related to absorbed light than to photosynthesis at half-hourly resolution in a rice paddy. *Remote Sens. Environ.* 216, 658–673. <https://doi.org/10.1016/j.rse.2018.07.008>.
- Yang, P., Liu, X., Liu, Z., van der Tol, C. and Liu, L. (2023). The roles of radiative, structural and physiological information of sun-induced chlorophyll fluorescence in predicting gross primary production of a corn crop at various temporal scales. *Agric. For. Meteorol.* 342, 109720. <https://doi.org/10.1016/j.agrformet.2023.109720>.
- Yang, P. and van der Tol, C. (2018). Linking canopy scattering of far-red sun-induced chlorophyll fluorescence with reflectance. *Remote Sens. Environ.* 209, 456–467. <https://doi.org/10.1016/j.rse.2018.02.029>.
- Yang, X., Shi, H., Stovall, A., Guan, K., Miao, G., Zhang, Y., Zhang, Y., Xiao, X., Ryu, Y. and Lee, J.-E. (2018b). FluoSpec 2 — an automated field spectroscopy system to monitor canopy solar-induced fluorescence. *Sensors* 18, 2063. <https://doi.org/10.3390/s18072063>.
- Yang, X., Tang, J., Mustard, J.F., Lee, J.-E., Rossini, M., Joiner, J., Munger, J.W., Kornfeld, A. and Richardson, A.D. (2015). Solar-induced chlorophyll fluorescence that correlates with canopy photosynthesis on diurnal and seasonal scales in a temperate deciduous forest. *Geophys. Res. Lett.* 42, 2977–2987. <https://doi.org/10.1002/2015gl063201>.
- Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E.M.S., Qin, Z., Quine, T., Sitch, S., Smith, W.K., Wang, F., Wu, C., Xiao, Z. and Yang, S. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Sci. Adv.* 5, eaax1396. <https://doi.org/10.1126/sciadv.aax1396>.
- Zaks, J., Amarnath, K., Kramer, D.M., Niyogi, K.K. and Fleming, G.R. (2012). A kinetic model of rapidly reversible nonphotochemical quenching. *Proc. Natl. Acad. Sci. U. S. A.* 109, 15757–15762. <https://doi.org/10.1073/pnas.1211017109>.
- Zeng, Y., Badgley, G., Dechant, B., Ryu, Y., Chen, M. and Berry, J.A. (2019). A practical approach for estimating the escape ratio of near-infrared solar-induced chlorophyll

fluorescence. Remote Sens. Environ. 232, 111209.
<https://doi.org/10.1016/j.rse.2019.05.028>.

Zhang, Y., Xiao, X., Zhang, Y., Wolf, S., Zhou, S., Joiner, J., Guanter, L., Verma, M., Sun, Y.,
Yang, X., Paul-Limoges, E., Gough, C.M., Wohlfahrt, G., Gioli, B., van der Tol, C.,
Yann, N., Lund, M. and de Grandcourt, A. (2018). On the relationship between sub-
daily instantaneous and daily total gross primary production: Implications for
interpreting satellite-based SIF retrievals. Remote Sens. Environ. 205, 276–289.
<https://doi.org/10.1016/j.rse.2017.12.009>.

Supporting Information

Table S1 The determination coefficient (R^2) and root mean square error (RMSE) between
modeled GPP and observed GPP for different plant functional types (PFTs), photosynthetic
pathways and temporal scales for the two models.

Fig. S1. Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-e; f-j), T_a (k-o; p-t), and
VPD (u-y; z-D) for the q_{L_PAR} model and q_{L_SIF} model for different PFTs. r is the correlation
coefficient and p is the corresponding p -value.

Fig. S2. Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-c; d-f), T_a (g-i; j-l), and
VPD (m-o; p-r) for the q_{L_PAR} model and q_{L_SIF} model for different photosynthetic pathways. r
is the correlation coefficient and p is the corresponding p -value.

Fig. S3. Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-d; e-h), T_a (i-l; m-p),
and VPD (q-t; u-x) for the q_{L_PAR} model and q_{L_SIF} model for different temporal scales. r is the
correlation coefficient and p is the corresponding p -value.

Fig. S4. Boxplot of the determination coefficient (R^2) of estimated GPP for the q_{L_PAR} model
and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.

Fig. S5. Boxplot of the root mean square error (RMSE) of estimated GPP for the q_{L_PAR} model
and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.

Fig. S6. Boxplot of the mean absolute error (MAE) of estimated GPP for the q_{L_PAR} model and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.

Multi-site evaluation of an improved SIF-based model for estimating canopy GPP

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Table S1

Figures S1 - S6

Table S1 The determination coefficient (R^2) and root mean square error (RMSE) between modeled GPP and observed GPP for different plant functional types (PFTs), photosynthetic pathways and temporal scales for the two models.

Different Scenarios	Classification	q_{L_SIF} model			q_{L_PAR} model		
		Training	Testing	All	Training	Testing	All
PFTs	C ₃ CRO	(0.60, 7.18)	(0.62, 6.82)	(0.61, 7.07)	(0.45, 8.42)	(0.50, 7.88)	(0.47, 8.27)
	C ₄ CRO	(0.73, 9.46)	(0.72, 9.57)	(0.73, 9.51)	(0.69, 10.19)	(0.67, 10.32)	(0.68, 10.24)
	Temperate DBF	(0.66, 4.37)	(0.64, 4.55)	(0.65, 4.43)	(0.53, 5.10)	(0.54, 5.12)	(0.54, 5.11)
	Temperate ENF	(0.81, 2.53)	(0.85, 2.18)	(0.82, 2.43)	(0.80, 2.57)	(0.84, 2.24)	(0.81, 2.48)
	Boreal ENF	(0.75, 1.98)	(0.76, 1.90)	(0.76, 1.96)	(0.81, 1.74)	(0.84, 1.56)	(0.82, 1.69)
Photosynthetic pathways	C ₃	(0.77, 4.59)	(0.78, 4.53)	(0.77, 4.57)	(0.64, 5.79)	(0.64, 5.85)	(0.64, 5.81)
	C ₄	(0.73, 9.46)	(0.72, 9.57)	(0.73, 9.51)	(0.69, 10.19)	(0.67, 10.32)	(0.68, 10.24)
	All	(0.73, 7.13)	(0.74, 7.39)	(0.73, 7.21)	(0.58, 8.78)	(0.62, 8.89)	(0.59, 8.83)
Temporal scales	Half-hourly	(0.76, 5.63)	(0.77, 5.67)	(0.76, 5.64)	(0.75, 5.69)	(0.77, 5.69)	(0.76, 5.69)
	Daily	(0.86, 4.22)	(0.86, 4.13)	(0.86, 4.20)	(0.86, 4.23)	(0.86, 4.17)	(0.86, 4.21)
	4-Day	(0.90, 3.40)	(0.92, 3.58)	(0.91, 3.46)	(0.90, 3.40)	(0.92, 3.61)	(0.91, 3.47)
	8-Day	(0.90, 3.16)	(0.95, 3.19)	(0.92, 3.17)	(0.90, 3.17)	(0.95, 3.19)	(0.92, 3.18)

Training, Testing and All represent evaluating results of training, testing and all data, respectively.

Statistical results are presented as (R^2 , RMSE), RMSE with unit of $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

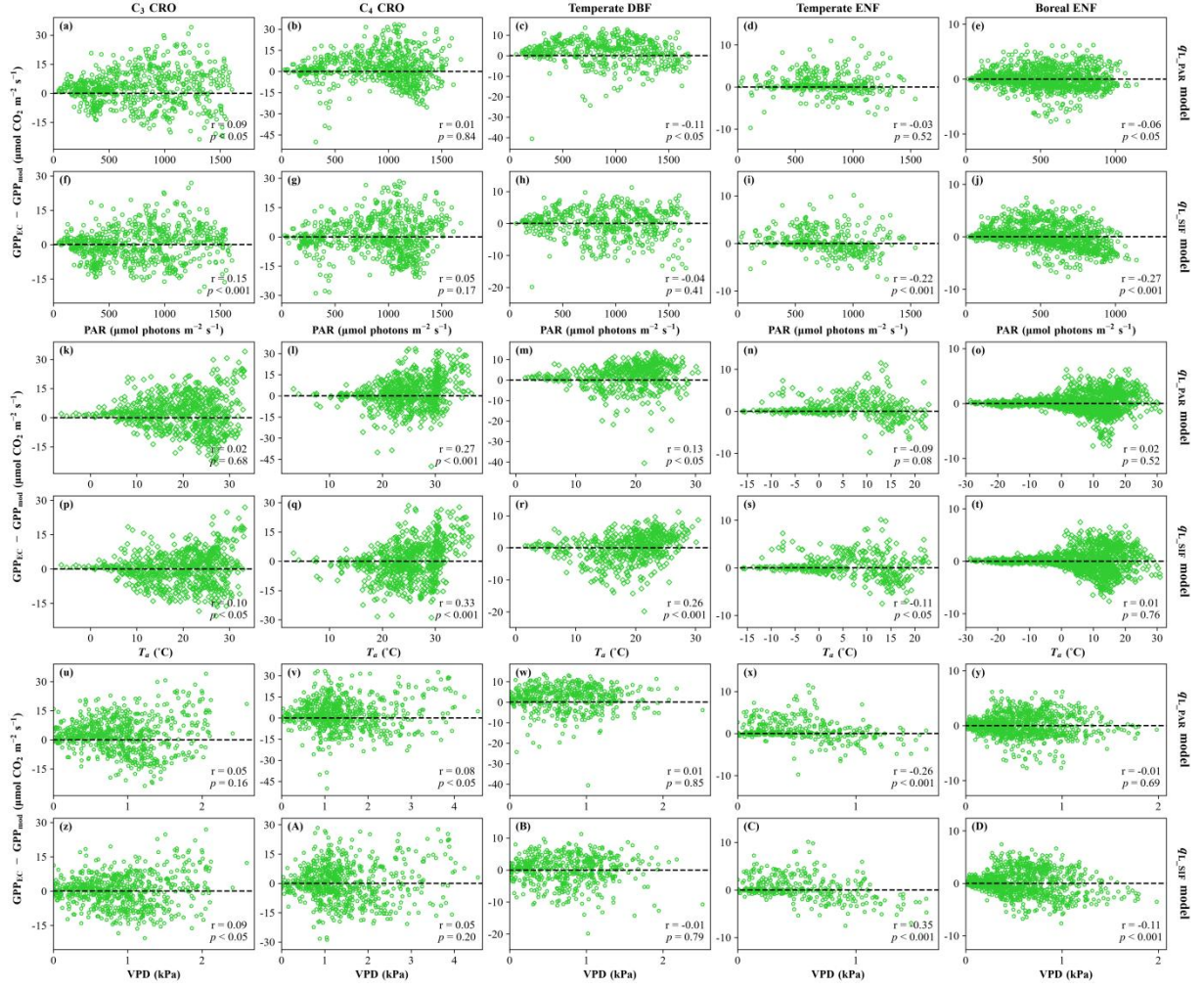
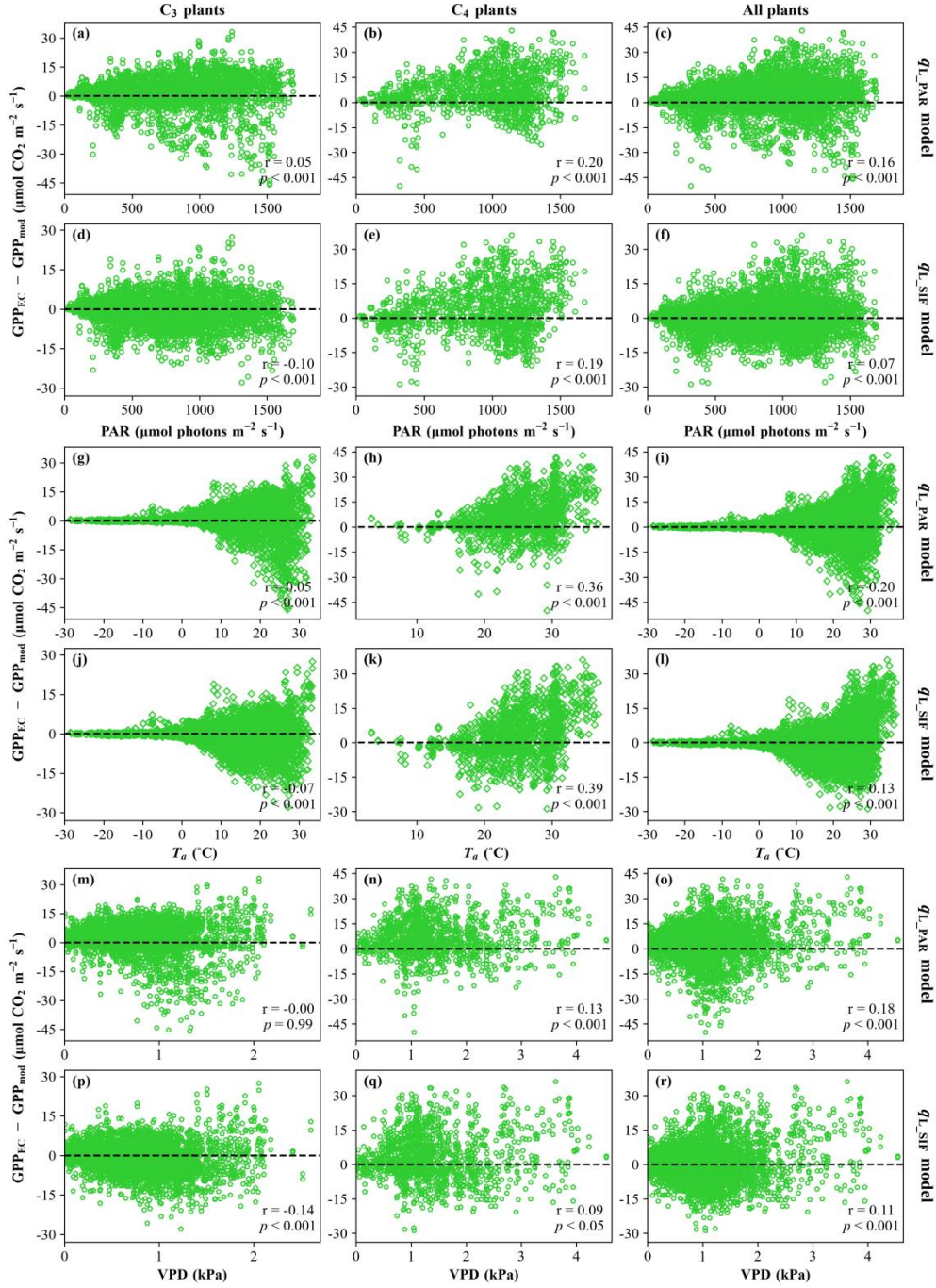


Fig. S1. Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-e; f-j), T_a (k-o; p-t), and VPD (u-y; z-D) for the qL_{PAR} model and qL_{SIF} model for different PFTs. r is the correlation coefficient and p is the corresponding p -value.



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30 **Fig. S2.** Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-c; d-f), T_a (g-i; j-l),
 31 and VPD (m-o; p-r) for the q_{L_PAR} model and q_{L_SIF} model for different photosynthetic
 32 pathways. r is the correlation coefficient and p is the corresponding p -value.

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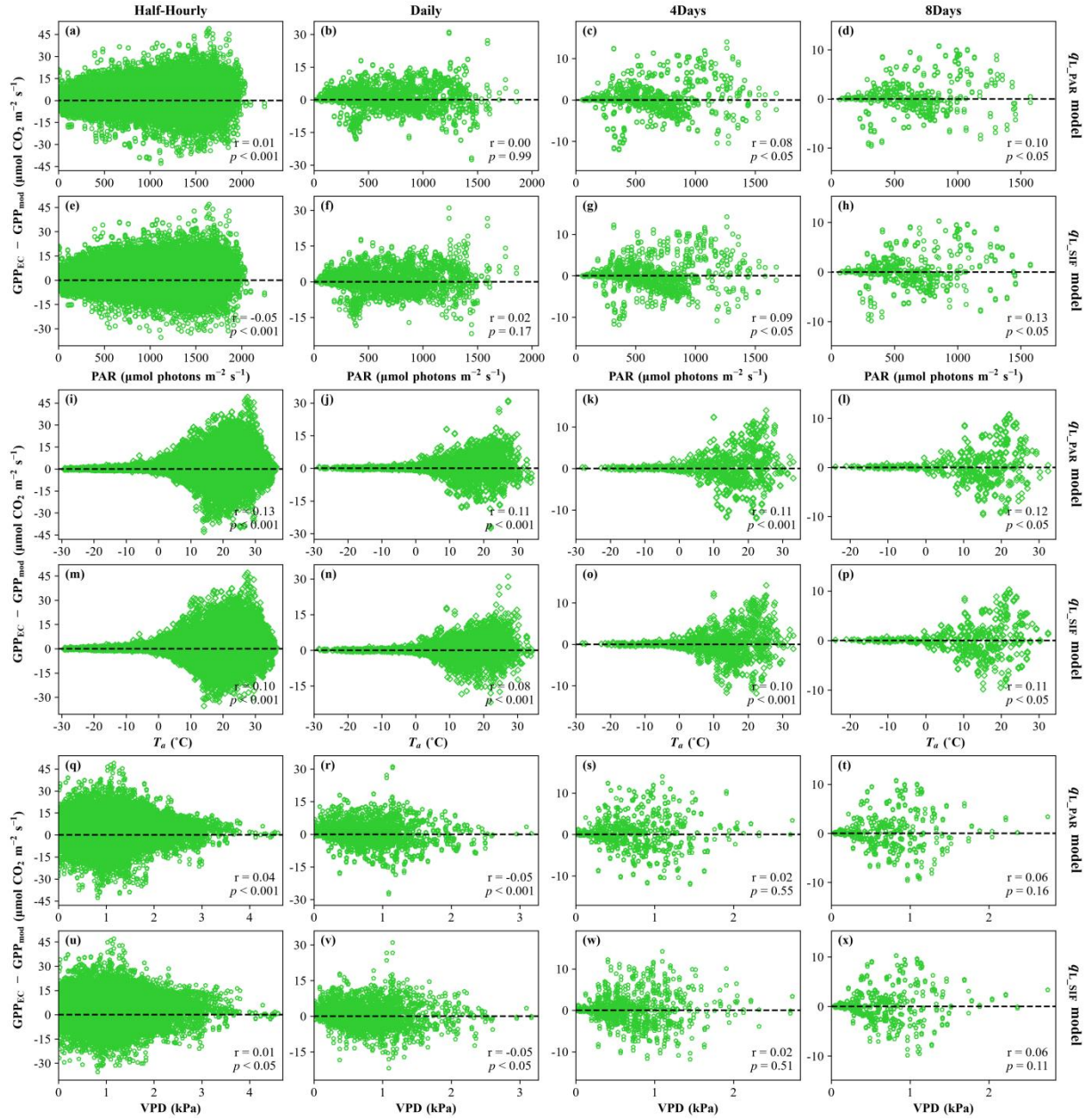


Fig. S3. Scatterplot of GPP residuals ($GPP_{EC} - GPP_{mod}$) against PAR (a-d; e-h), T_a (i-l; m-p), and VPD (q-t; u-x) for the qL_{PAR} model and qL_{SIF} model for different temporal scales. r is the correlation coefficient and p is the corresponding p -value.

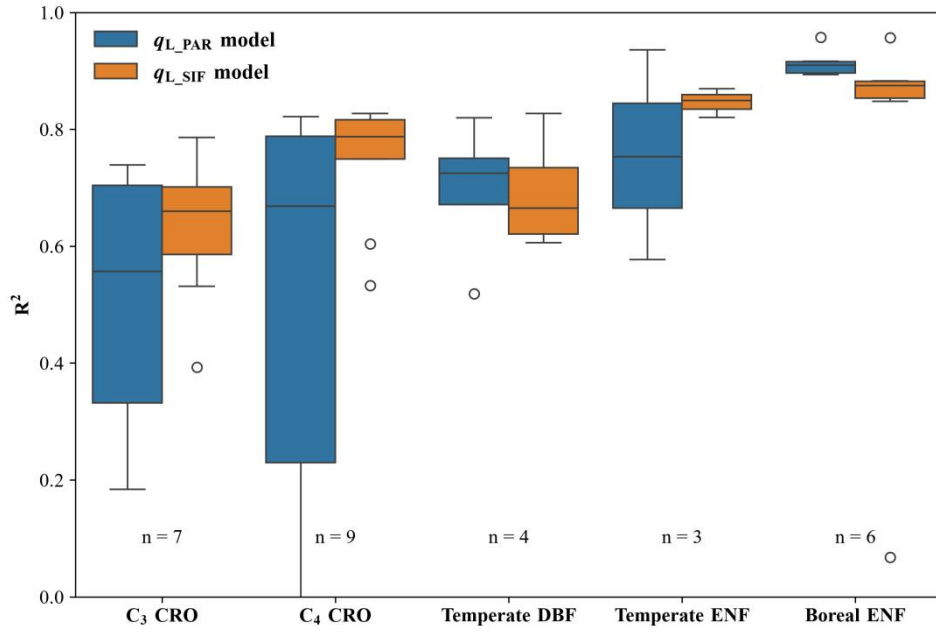


Fig. S4. Boxplot of the determination coefficient (R^2) of estimated GPP for the q_{L_PAR} model and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.

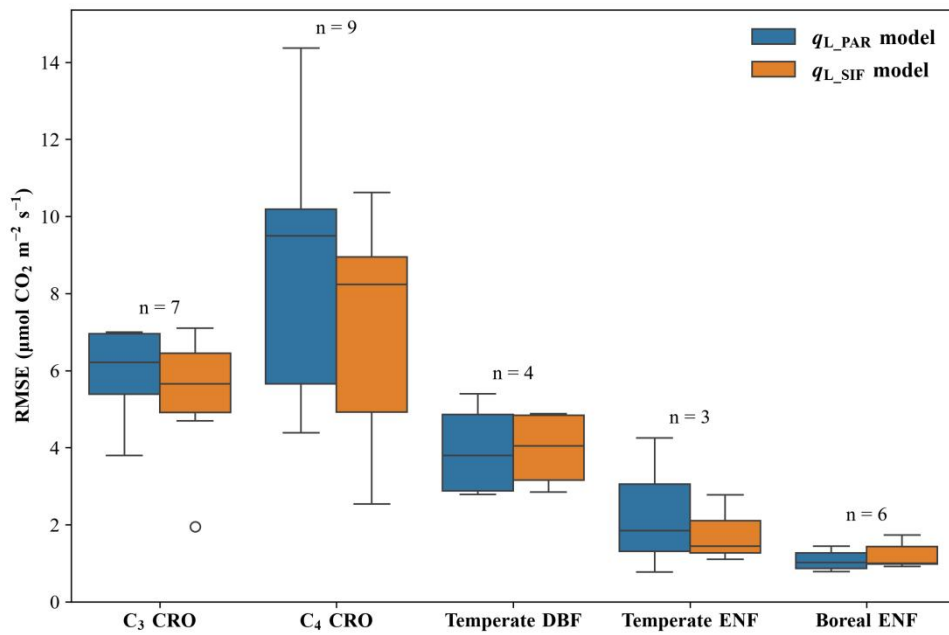


Fig. S5. Boxplot of the root mean square error (RMSE) of estimated GPP for the q_{L_PAR} model and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.

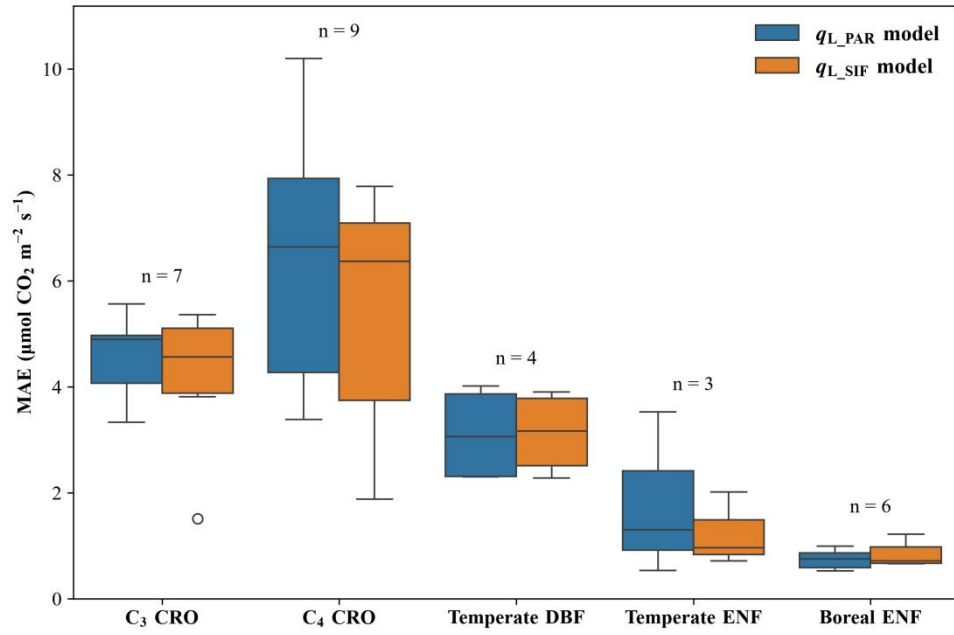


Fig. S6. Boxplot of the mean absolute error (MAE) of estimated GPP for the q_{L_PAR} model and q_{L_SIF} model across different PFTs. n is the number of site-year datasets for each PFT.