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Beyond radiation use efficiency: A mechanistic biochemical photosynthesis model for crop growth simulation and agroecosystem modeling

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ABSTRACT

Agroecosystem models are widely used in digital agriculture for applications from forecasting crop yields to informing breeding. Most current models simulate crop growth by linearly scaling absorbed radiation to biomass via an empirical factor called radiation use efficiency (RUE). Such simplicity enables its widespread use but lacks a mechanistic representation of well-known biophysics and physiology, thus offering limited insights into how climates affect crops dynamically. To address this limitation and push for next-generation agroecosystem modeling, we first implemented a mechanistic crop growth module, named Radiation-Photosynthesis (RP) combining radiative transfer and photosynthesis processes, as an alternative to the RUE method; we then incorporated the RP method into a community-endorsed agroecosystem model–Environmental Policy Integrated Climate (EPIC)–to develop an enhanced version of EPIC, named as EPIC-RP. When evaluated in the standalone mode at flux tower sites in the US, the RP method improved accuracies of simulated gross primary production over the classical RUE method by 47 % ($R^2 = 0.85$, RMSE = 10.7 for RP vs $R^2 = 0.67$, RMSE = 15.7 g $CO_2/m^2/$day for RUE). When embedded in EPIC and tested in a Texas watershed, the new EPIC-RP model performs better than or comparable to the RUE-based EPIC model in simulating biomass and crop yields. Furthermore, the RP method captured biomass responses to elevated CO_2 more realistically and the RUE method gave unreasonable results for C4 crops. Overall, our RP method and EPIC-RP model are new attempts for next-generation agroecosystem modeling; as open-source tools, they promise to help understand crop growth responses to future climate conditions.

1. Introduction

Global food production is expected to be affected pronouncedly by increased climate variability and rising atmospheric CO_2 concentrations (Asseng et al., 2019, Leng and Hall 2019). Understanding how the changing climate conditions interact with crops is important for ensuring food security—a scientific task difficult to achieve without agroecosystem modeling. Agroecosystem models simulate crop growth dynamics and enable scientists and engineers to analyze complex processes, gain insights, and address factors influencing crop yields (Di Bene et al., 2022). However, many agroecosystem models lack explicit details of key crop growth processes such as photosynthesis (Rötter et al., 2011; Guan et al., 2022), making it difficult to understand how climates affect crop yields dynamically and mechanistically. For example, elevated CO_2 affects crop production interactively by co-regulating processes like photosynthesis and transpiration with leaf stomata (Yin and Laar 2005); high temperatures damage yields of staple crops sharply when going above 30 °C during flowering. However, most process-based models do not account for these mechanisms and thus may overestimate future yields under extreme weather (Rötter et al., 2011). Hence, there is an urgent need to improve agroecosystem models (Wang et al., 2019; Hu et al., 2023, 2024).

One key component of agroecosystem models is the simulation of crop growth and biomass accumulation. There are at least two schemes to calculate crop biomass: one is simple, and another is complex. A classical simple scheme uses radiation use efficiency (RUE) to linearly scale crop-intercepted photosynthetically active radiation (PAR) to biomass gain: Biomass=PAR*RUE. This method dates back to the 1970 s

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(Monteith et al., 1977) and, due to its simple form, has been widely used in current popular agroecosystem models, which include but are not limited to the Agricultural Production Systems sIMulator (APSIM; Keating et al., 2003), the Decision Support System for Agrotechnology Transfer (DSSAT; Jones et al., 1998), the Environmental Policy Integrated Climate model (EPIC; Wang et al., 2012), and the Crop Environment Resource Synthesis model (CERES; Basso et al., 2016). Another scheme is to explicitly calculate CO_2 flux between the air and canopies in the photosynthesis process. Examples of this type include the big-leaf model of Farquhar et al. (1980) or its variants. This biochemical photosynthesis method to simulate plant growth is often seen in earth system and geoscientific models such as the Community Land Model (Bonan et al., 2011; Lawrence et al., 2019) and STEMMUS-SCOPE (Wang et al., 2021), but has been rarely seen in agroecosystem models.

The classical RUE and biochemical photosynthesis methods differ in their complexity regarding how environmental factors (e.g., radiation, temperature, CO_2, vapor pressure) are involved in biomass calculation. The RUE method simplifies crop growth simulation significantly such that biomass accumulation is calculated at daily intervals by multiplying leaf-intercepted photosynthetic active radiation (PAR) with a RUE factor. RUE is an empirical parameter representing the conversion efficiency of solar energy to biomass. The RUE method requires daily total leaf intercepted radiation only, without explicitly accounting for other environmental factors (e.g., CO_2, temperature, and water vapor pressure). These additional effects on biomass accumulation are reflected in adjusting the RUE value itself. In contrast, the photosynthesis method describes a series of biochemical activities of chlorophyll, such as its reaction to light and CO_2. The calculation is often done at an hourly or sub-hourly step. The photosynthesis method requires instant inputs of multiple environmental factors (i.e., CO_2 concentrations, wind speed, temperature, and humidity) and calculates CO_2 assimilation under the given conditions.

Despite its simplicity and ease in use, the RUE method has important disadvantages. Foremost, the empirical nature of the RUE factor prevents us from gaining mechanistic insights into how climate factors affect biomass accumulation. The RUE factor is a ratio between radiation and biomass, and it represents the combined effects of multiple environmental factors (Zheng et al., 2022; Yuan et al., 2019; Zhang et al., 2023), such as leaf N content, water vapor pressure, and CO_2 concentration. Effects of these factors can be implicitly considered by adjusting the RUE values, but the adjustments are usually empirical and do not always hold for all crop species. In addition, determining the RUE value requires intensive fieldwork. To calculate RUE, absorbed PAR should be measured multiple times above and below the crop canopy from seedling emergence to harvest under non-stressed conditions for each plant plot (Molero et al., 2019). In addition, the RUE values are available only for some species under current environmental conditions, and they may even vary during the day (Rosati and Dejong, 2003). Plants need to be established in growth chambers to obtain those RUE values to obtain RUE values at elevated CO_2 levels or future climate conditions.

Biochemical photosynthesis models offer a mechanistic characterization of the complex crop-environment interactions and complement the RUE method. Though widely used in earth system models, mechanistic photosynthesis models are still rare in many existing agroecosystem models. One challenge is that such a model requires more input data and parameters. They also require the coupling with other ancillary models, such as those models about energy and water fluxes. For example, PAR absorbed by leaves—the energy source for photosynthesis—is often modelled by canopy radiative transfer theories; a common model is the two-stream approximation approach that has been widely used in earth system and terrestrial ecosystem models to describe the interception, reflection, transmission, and absorption in vegetation (Dai et al., 2004; Yin and Song, 2022; Bonan et al., 2011). Another potential drawback of mechanistic models is an intensive computation for large-scale simulations, but with advances in computer power, this could be less concerning. Ultimately, the photosynthesis method would advance agroecosystem models significantly by enabling mechanstic modeling of environmental impacts on crop growth, such as how elevated CO_2 concentrations and frequent extremely high temperatures–would affect crop yields. Although earlier studies attempted to integrate photosynthesis models into process-based models for simulating crop growth (Fleisher et al., 2010; Wang et al., 2021), a generic or easy-to-use photosynthesis module remains unavailable for integration with agroecosystem models.

This study seeks to leverage existing modeling capabilities from the earth science and geoscientific communities to address current limitations in agroecosystem modeling. We proposed a mechanistic photosynthesis approach, named the radiation-photosynthesis (RP) method, as an alternative to the widely used RUE method for simulating crop growth. To push for next-generation agroecosystem modeling, we also incorporated the RP method into EPIC—a community-endorsed agroecosystem model being widely used for agriculture research—to develop a new version of EPIC, named here as EPIC-RP. We compared the RP and RUE methods at three eddy-covariance sites in the US for maize and soybean. We further compared the new EPIC-RP model and the original RUE-based EPIC version for simulating biomass and crop yields at a watershed in Texas. We also examined biomass responses to elevated CO2 with both RP and RUE methods in the EPIC framework. Finally, we compared RP with two other photosynthesis-based crop models and illustrated their differences as a complementary validation. Our open-source RP model represents a new contribution to the existing suite of mechanistic crop growth models and serves as a robust alternative to the RUE method for simulating crop yields.

2. Methods

A schematic of the classical RUE and new RP methods is depicted in Fig. 1 to illustrate their conceptual differences. Technically, the RP method is a simple multiplicative equation “biomass=PAR*RUE” (Fig. 1a). Our newly proposed RP method is more complicated, consisting primarily of a canopy radiative transfer model and a Farquhar-based biochemical photosynthesis model (Fig. 1b). Below, we started with key equations of the two methods (Section 2.1 and 2.2) and then described the overall design of the EPIC-RP agroecosystem model (Section 2.3). The full details of the RP method are given in Supplementary. The Fortran source code of the RP method and EPIC-RP is publicly available at https://github.com/hutx2309/EPIC-RP.

2.1. The radiation use efficiency (RUE) method

The RUE method (i.e., biomass=PAR*RUE) estimates biomass as a product of two inputs (Fig. 1a): photosynthetic active radiation (PAR) and a crop-specific RUE value. In most agroecosystem models, PAR is calculated using Beer’s law (Neitsch et al., 2011; Qin et al., 2018). The RUE value is often derived by fitting a linear regression between dried aboveground biomass accumulation under optimal growth conditions and leaf-absorbed radiation. Process-based crop models typically provide their own default RUE values for common crops. For example, in the EPIC model, RUE is 40.0 for maize and 35.0 kg/ha/(MJ/m^2) for winter wheat.

The RUE method is driven directly by PAR, with limited abilities to reflect direct impacts of environmental changes (e.g., temperature, water vapor, and wind) on biomass accumulation or to capture the interactions between these changes. These additional environmental effects can be implicitly taken into account by empirically modifying the RUE values. Practical strategies to adjust RUE vary with crop models (Asseng et al., 2015). For example, in the EPIC model, the CO_2-adjusted RUE is given by

$$RUE = \frac{100^*CO_2}{CO_2 + exp(a - b^*CO_2)} \tag{1}$$

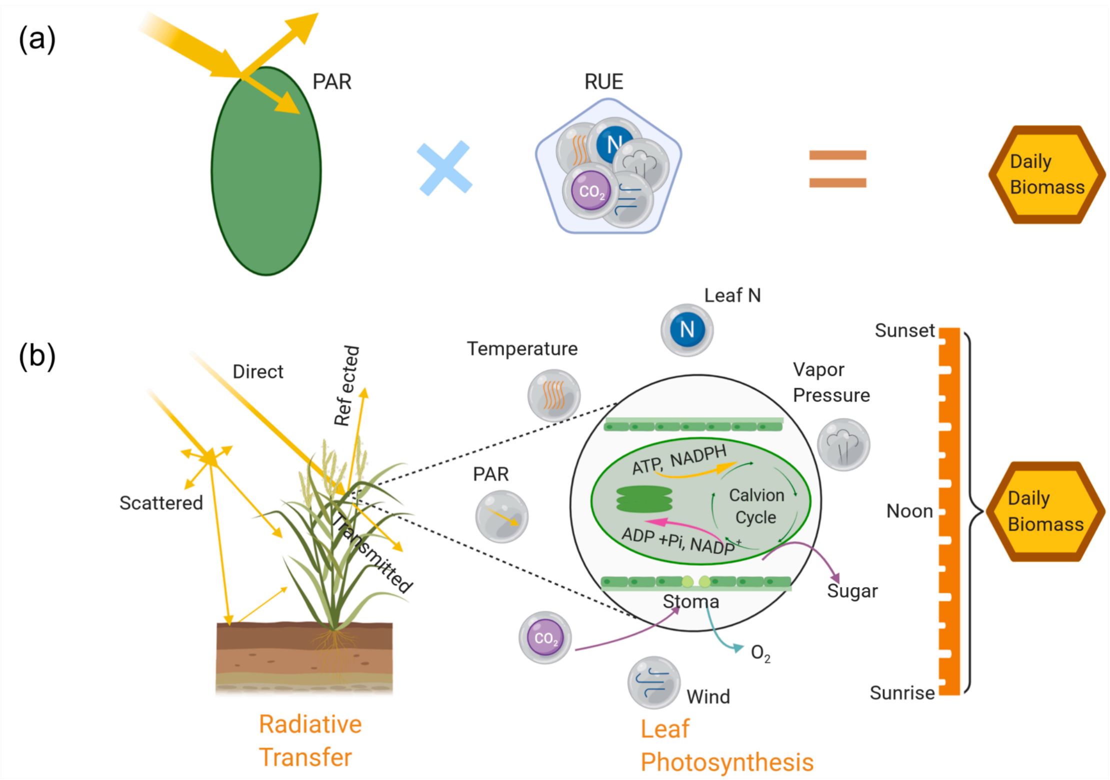

Fig. 1. Schematic of (a) the radiation use efficiency (RUE) method (biomass=PAR*RUE) and (b) the mechanistic Radiation-Photosynthesis (RP) method for calculating daily biomass accumulation.

where CO_2 is the atmospheric CO_2 concentration (ppm); a and b are empirical crop coefficients that vary with crops. It should be noted that this equation can only be used for CO_2 concentration below 660 ppm (Neitsch et al., 2011). EPIC also adjusts the VPD effects on RUE using

$$RUE = \begin{cases} RUE_1 - \Delta r^*(vpd - vpd_t) if vpd > vpd_r \\ RUE_1 if vpd \le vpd_r \end{cases} \tag{2}$$

where RUE_1 is the RUE value at a vapor pressure deficit of 1 kPa;vpd_t is the threshold vapor pressure deficit above which a plant will exhibit reduced leaf conductance (kPa); and Δr is the rate of decline in RUE due to a unit increase in VPD (kg/ha)/(MJ/m^2)/kPa).

The two examples of Eqs. (1) and (2) demonstrated that the RUE method requires additional empirical relationships, typically derived from greenhouse experiments, to account for environmental factors affecting plants' efficiency in using absorbed PAR to produce biomass. Obviously, there is a lack of systematic representation of the biophysical and biochemical mechanisms underlying crop growth responses to the interplay between multiple environmental factors.

2.2. The Radiation-Photosynthesis (RP) method

The RP method consists mainly of a biophysical model for radiative transfer within the canopy and a biochemical model for photosynthesis of C3 and C4 crops. The radiation transfer within the canopy is described with a two-stream approximation radiative transfer model (Dai et al., 2004; Zhao and Jackson, 2014), which provides the upward (I_{dir_up} and I_{dif_up}) and downward (I_{dir_down} and I_{dif_down}) fraction of radiation fluxes through canopy layers per unit incident flux (detailed equations given in supplementary materials Section 1). The actual radiation received by sunlit and shaded leaves is calculated based on the following assumption: Sunlit leaves are assumed to receive both direct (I_{dir_sun}) and diffuse (I_{dif_sun}) radiation on clear days, whereas shaded leaves receive only diffuse radiation (I_{dif_sha}). All leaves receive only diffuse radiation on cloudy or rainy days. The equations for the different radiation components are given below:

$$I_{dir\_sun} = (1-\tau)^*(1 - e^{-\{K_b{}^*LAI,50.0\}} + \frac{I_{dir\_up} + I_{dir\_down}}{\underline{\mu}}) \tag{3}$$

$$I_{dif\_sun} = (1-\tau)^*\frac{I_{dif\_up} + I_{dif\_down}}{\underline{\mu}} \tag{4}$$

$$I_{dif\_sha} = \left(1-\alpha_{plant}\right) - \sigma_{plant}{}^*\left(1-\alpha_{grnd}\right) - (1-\tau)^*\frac{I_{dif\_up} + I_{dif\_down}}{\underline{\mu}} \tag{5}$$

where $\tau, \alpha_{grnd}, \alpha_{plant}, \sigma_{plant}$ are ratios of scattering, reflection (i.e., albedo of ground and plants), and transmission, respectively; K_b is light extinction function coefficient; $\underline{\mu}$ is the average inverse diffuse optical depth per unit leaf, which is referenced in the CLM 5.0 documentation (http://www.cesm.ucar.edu/models/cesm2/land/).

The photosynthesis process for C3 and C4 crops is based on the biochemical models of Farquhar et al. (1980) and Collatz et al. (1992a), respectively (Table 1). The photosynthesis equations of Table 1 provide CO_2 assimilation rates per unit leaf area at the leaf level. The leaf-level rates need to be further scaled to the canopy level using the following equations:

$$V_{cmax\_canopy} = V_{cmax\_leaf}{}^*\frac{1 - e^{-(K_N+K_b)/LAI}}{K_N + K_b} \tag{6}$$

$$J_{max\_canopy} = J_{max\_leaf}{}^*\frac{1 - e^{-(K_d+K_b)/LAI}}{K_d + K_b} \tag{7}$$

$$R_{d\_canopy} = R_{d\_leaf}{}^*\frac{1 - e^{-K_b/LAI}}{K_b} \tag{8}$$

where K_N, K_b, and K_d are leaf N, diffuse, and direct radiation extinction coefficients through the canopy, respectively, and LAI is the leaf area

Table 1
Models and parameters for estimating photosynthesis rates for C3 and C4 plants.

	C3 (μ mol CO_2 /m^2/s)	C4 (μ mol CO_2 /m^2/s)
RuBP carboxylase limited (A_c)	$\frac{V_{cmax}(CO_{2i} - \Gamma)}{CO_{2i} + K_c(1 + O_{2i}/K_o)}$	V_{cmax}
Light limited (A_j)	$\frac{J(CO_{2i} - \Gamma)}{4CO_{2i} + 8\Gamma}$	0.05*4.6*I
Product/PEP limited (A_p)	0.5 V_{cmax}	pCO_{2i}/P
Net photosynthesis (A_n)	$A_n = \{A_c, A_j, A_p\} - R_d$	

V_{cmax}: the maximum rate of carboxylation (μ mol CO_2 /m^2/s)
J: the electron transport rate (μ mol CO_2 /m^2/s)
CO_{2i}, O_{2i}: the internal leaf CO_2 partial pressure (Pa) and O_2 partial pressure (Pa)
Γ: CO_2 compensation point (Pa)
K_c, K_o: the Michaelis-Menten constants for CO_2 and O_2 (Pa)
p: the initial slope of the C4 CO_2 response curve
P: the atmosphere pressure (Pa)
I: the absorbed photosynthetically active radiation (PAR, W/m^2)
R_d: the dark respiration (μ mol CO_2 /m^2/s)
Note: 0.05 is the quantum efficiency (mol CO_2 / mol photon); 4.6 is the conversion between PAR and photosynthetic photon, which is 4.6 μ mol photons per joule

index of the whole canopy (Zhao et al., 2019).

The biophysical radiation model and the biochemical photosynthesis model are fully coupled to maintain the balance of energy, water, and CO2, giving rise to a system of equations (Supplementary). A key state variable of the system equations is leaf temperature which is jointly influenced by transpiration, stomatal conductance, and photosynthesis. The temperatures of sunlit and shaded leaves are reported to differ by several degrees under sunny and dry conditions (Spayd et al., 2002, He et al., 2018). Neglecting such differences causes errors in the estimation of crop growth. In our implementation, sunlit and shaded leaves were treated separately; their respective leaf temperatures were solved numerically from the canopy energy and water balance equations using a Newton-like iterative method (Yin and Laar 2005).

Collectively, the RP model developed here directly links climate variables (e.g., radiation, temperature, CO_2 concentrations) to biomass accumulation (Fig. 1b): Radiation intercepted by leaves is determined by radiative transfer within the canopy. Air temperature and vapor pressure are jointly used to calculate leaf temperatures through transpiration and leaf energy balance. CO_2 concentrations influence biomass accumulation through photosynthesis.

To facilitate its further integration with existing agroecosystem models, the RP model was designed to run at both hourly and daily steps to simulate crop growth. The hourly step can make full use of hourly observations from weather stations. If no hourly data is available, a weather simulator will be activated to simulate the diurnal course of climate variables (Supplementary 4.2). The weather simulation allows both daily and hourly weather inputs (e.g., temperature, precipitation, radiation, and humidity), so that the RP method can be easily integrated into other crop models such as EPIC, DSSAT, and APSIM.

2.3. EPIC-RP: A new-generation of EPIC agroecosystem model

We integrated the RP module into the EPIC agroecosystem model as an alternative to the RUE method to simulate crop growth. The new EPIC version is named hereafter as EPIC-RP. EPIC is a comprehensive terrestrial ecosystem model capable of simulating key biophysical and biogeochemical processes, such as plant growth, soil erosion, water balances, and nutrient cycling (Zhang et al., 2015). It uses the RUE method for plant growth and has a RUE database for more than 120 plant species. We chose to update and improve the EPIC framework for two major reasons: (1) The EPIC model has been extensively tested in different cropping or management systems (Gassman et al., 2010; Wang et al., 2012); (2) the RUE method in the EPIC model has been used in other popular ecosystem models, such as the APEX (Agricultural Policy Environmental eXtender) model and the SWAT (Soil Water and Assessment Tool) model (Arnold et al., 1998).

EPIC is a daily model but RP is an hourly or sub-hourly method. Integration of the RP method into EPIC needs to convert hourly assimilated CO2 fluxes–A (μ mol CO_2 /m^2/h) to daily dry biomass (t/ha):

$$Bio = \sum_{sunrise}^{sunset} A * \frac{12}{44} * 2.5 * 60\% * 0.01 \tag{9}$$

where A is the hourly assimilated carbon fluxes, and 12/44 is the portion of carbon mass in CO_2. We used 40 % as the ratio (40 %-45 %) of respiration and photosynthesis (Atkin et al., 2007). The constant 2.5 (i.e., 1/[50%*80%]) is based on the assumption that carbon accounts for about 50 % of dry biomass and water content is 80 % in organic matter (Martin et al., 2021). The factor of 0.01 converts g C/m^2 to t/ha. More details on the integration for EPIC-RP are given in Supplementary 4.6.

EPIC-RP is not just an updated version of EPIC merely with the RP module added but also a restructured version of the original source code with modularized processes (Fig. 2). The restricting and re-writing of the original codebase are a major software engineering contribution of this study, given that the current codebase is a result from decades' continuous development. In the re-writing, many variable names were made more self-explained. The original Fortran source code was re-organized into 12 modules in EPIC-RP with eight for crop, soil, water, weather, gas, erosion, management, and nutrient cycling, respectively, and four for model controls (i.e., parameters, file I/O, initialization, procedure control). Modules communicate with other modules through certain global variables. Such a structure design would allow EPIC-RP to be easily extended when new functionalities are needed or to be reused if some modules are useful to other ecosystem models.

3. Experiments and model Assessment

The RP module is developed as an alternative to the RUE method for simulating crop growth, and it has functionality that could improve the power of crop models, for instance, quantifying climate impacts on yield with a mechanism. We evaluated the RP module and compared its performance against the RUE method using the following four experiments (Section 3.1-3.4). The emphasis of this work is not on tackling site-specific scientific questions; therefore, in the following experiments, we used default parameters for the RP method and the EPIC model without site-specific calibration.

3.1. Evaluation of RP vs RUE for simulating crop GPP

We evaluated the standalone versions of the RP and RUE methods for simulating GPP of maize or soybean crops at three AmeriFlux tower sites (i.e., US_Ne1, US_Ne2, and US_Ne3) in the U.S (Table 2). Flux datasets provided continuous measurements of ecosystem carbon, water, and energy flows between land and atmosphere. These measurements have been widely used for assessing terrestrial biosphere models across vegetation types and environmental conditions (Bonan et al., 2011; Zhang et al., 2013). For the three sites, we obtained site-level temperature, radiation, wind speed, air pressure, and leaf area index (LAI) data to drive the RP model for 14 years from 2001 to 2014. Observed GPP was also available for the same period. LAI data were available only from 2001 to 2007, as obtained from the North America Carbon Program (https://data.globalchange.gov/dataset/nasa-ornldaac-1183). For 2008–2014, we used multi-year average of the 2001–2007 LAI. The simulated GPP of the RP and RUE models was assessed in reference to the tower observed GPP.

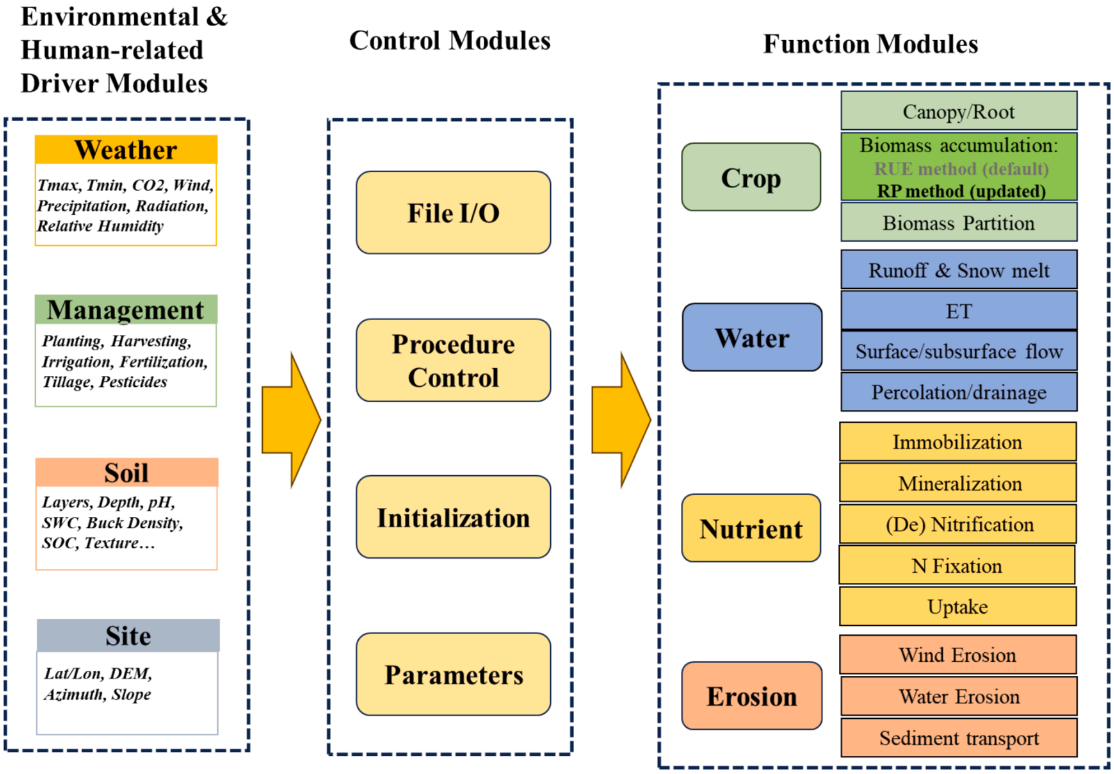

Fig. 2. Schematic representation of EPIC-RP modules and major processes. To build EPIC-RP, we are not just integrating the RP method for simulating crop growth, but rewrote the source code with self-explained variable names and restructured the EPIC framework through modularization. A total of 12 modules were included in the EPIC-RP framework with driving, control, and functional modules.

Table 2
Flux site information used for assessing the RP method.

Site	Lat/Lon	Crop Type	GPP flux Record*	LAI Record*	Reference
US_Ne1	41.165, −96.477	Irrigated Maize	2001–2014	2001–2007	(Suyker et al., 2005, Chu et al., 2018)
US_Ne2	41.165, −96.470	Irrigated Maize/ Soybean	2001–2014	2001–2007	(Suyker et al., 2004, Matheny et al., 2014)
US_Ne3	41.178, −96.440	Rainfed Maize/ Soybean	2001–2014	2001–2007	(Verma et al., 2005, McCombs et al., 2018)

* 2001–2007: Flux sites have all necessary inputs for RP; 2007–2014: no LAI records but have all other inputs.

3.2. Evaluation of EPIC-RP vs EPIC-RUE for simulating biomass and crop yields

Within the EPIC agroecosystem modeling framework, we compared the RP and RUE methods (i.e., EPIC-RP vs EPIC v1102) for simulating crop biomass and grain yield at the Y8 site of the Riesel Watershed, Texas (38.47° N, 96.88° E) for 1998 to 2007. We chose the Y8 site because it provides all necessary input observations (e.g., meteorological data, management practices) for developing the EPIC model as well as observed biomass yield data for validating models (Allen et al., 2011). Daily meteorological data were from the USDA-ARS Grassland Soil and Water Research Laboratory (https://www.ars.usda.gov/plains-area/temple-tx/grassland-soil-and-water-research-laboratory/docs/hydrologic-data/). We compiled physical inputs including terrain and soil properties, and management practices data from 1998 to 2007 for the corn/winter wheat/sorghum rotation from Harmel et al. (2006) and Green et al. (2007). For comparison with EPIC-RP, we chose the version of EPIC v1102 that employs the RUE method for plant growth. For ease of presentation, EPIC v1102 is called EPIC-RUE in the latter presentation.

3.3. Evaluation of EPIC-RP vs EPIC-RUE for quantifying crop responses to elevated CO_2

Within the EPIC agroecosystem modeling framework, we also compared the RP and RUE methods (i.e., EPIC-RP vs EPIC-RUE/v1102) in quantifying responses of biomass (no stress conditions) to elevated CO_2. Three CO_2 scenarios were considered, including 370 ppm, 490 ppm, and 650 ppm. The level of 370 ppm is the default CO_2 concentration in EPIC as a benchmark; the values 490 and 650 ppm are around the levels in 2100 under RCP 2.5 and 4.5 scenarios. Because this experiment was hypothetical in nature, this simulation was intended to assess whether the results of EPIC-RP and EPIC-RUE are comparable when no stresses from other environmental factors such as water, temperature, and soil. We did not seek to validate the simulation against real observations; therefore, no observed biomass was involved. For this purpose, we chose to simulate daily potential biomass for winter wheat (C3) and maize (C4) at a site in Raleigh, North Carolina. The forcing inputs such as weather and LAI were internally generated by EPIC itself.

3.4. Comparison of the RP model with GECROS and DCaPS

We additionally conducted a complementary analysis of RP by comparing it with two other models with similar functionalities. The two models are the Genotype-by-Environment interaction on CROp growth Simulator (GECROS) and the Diurnal Canopy Photosynthesis Simulator (DCaPS). The GECROS is a comprehensive crop model with crop and soil components; for our purpose, we only extracted its radiation and photosynthesis components to show the results. The DCaPS is a web-based application (github.com/QAAFI/DCaPS) that can be integrated into other crop models. Documented parameterizations related to GECROS and DCaPS are referenced in Yin et al. (2005) and Wu et al. (2018), respectively. The differences between these three methods are summarized in Table S1. The comparisons of RP with GECROS and DCaPS help understand the potential uncertainties associated with using mechanistic crop growth models.

4. Results and Discussion

4.1. Performance of the standalone RP model for simulating GPP

Simulated GPP with the RP method showed high agreement with the measured GPP at the three Ameriflux tower sites with different crop rotations (Fig. 3). The R-squares for all the three sites were above 0.8 and the average RMSE was 10.50 g CO_2/m^2/day. In contrast, the accuracies of the RUE-based simulation were poorer, with an R-square around 0.65 and an averaged RMSE of 15.62 g CO_2/m^2/day. The RP method improved upon the RUE method with a 47 % reduction of error. Of particular note, when no LAI observations were available as input for the 2008–2014 period, the R-square across all three sites decreased to 0.7 and the averaged RMSE increased to 13.22 g CO_2/m^2/day when including the 2008–2014 period, during which no observed LAI available, but historical averaged daily LAI over 2001–2007 was used (Fig. 4).

4.2. Performance of the EPIC-RP model for simulating biomass

When tested at the Y8 site in the Riesel Watershed, EPIC-RP showed performances better than or comparable to the RUE-based version EPIC-RUE/v1102 for simulating crop biomass under real-world conditions (Fig. 5). When compared to the observed crop biomass and yield, the R^2 value of EPIC-RP was slightly better than that of EPIC-RUE (0.64 vs 0.63 for biomass, and 0.7 vs 0.68 for yield). Both methods slightly overestimated biomass, attributed possibly to a lack of model calibration. The result of grain yield showed the same pattern as that of biomass. This is because yield is the biomass multiplied by a crop-specific harvest index in EPIC. The simulations by EPIC-RP and EPIC-RUE/v1102 were highly correlated ($R^2 = 0.96$). Such results confirmed that the performance of RP and RUE methods are at least comparable in estimating biomass and yield accumulation under real conditions.

4.3. Crop responses to elevated CO_2 concentrations

The EPIC simulations at the Raleigh site under elevated CO_2 showed that the RP and RUE method differed greatly in the magnitudes of simulated biomass responses to elevated CO_2 for both C3 and C4 crops (Fig. 6). Relative to the baseline biomass of winter wheat (i.e., C3 crop) at 370 ppm, the average biomass increase was 1.38 at 490 ppm and 2.62 t/ha at 650 ppm for the RUE method, which were almost two times larger than the corresponding biomass increases for the RP method (i.e., 0.70 at 490 ppm and 1.30 t/ha at 650 ppm). Relative to the simulated baseline biomass of maize (i.e., C4) at 370 ppm, the RUE method showed that biomass increased by an average of 1.28 at 490 ppm and 1.85 t/ha at 650 ppm. However, the RP method showed no significant change in biomass (an average of 0.04 and 0.08 t/ha for 490 and 650 ppm, respectively) with elevated CO_2 concentrations. The biomass gains under elevated CO_2 for the C4 species, as simulated by RUE, were unreasonably large. The limited responses as obtained by the RP method were more consistent with the theoretical and experimental evidence in the literature for CO_2 effects under no stresses (Leakey et al. 2006). In their model formulation, the RP method considered C3 and C4 pathways for photosynthesis whereas RUE does not. The RUE method adjusted the RUE values using a C3 and C4 multiplier in Eq. (1) but did not consider the saturation effects of CO_2 for C4 crops. Overall, the RP method

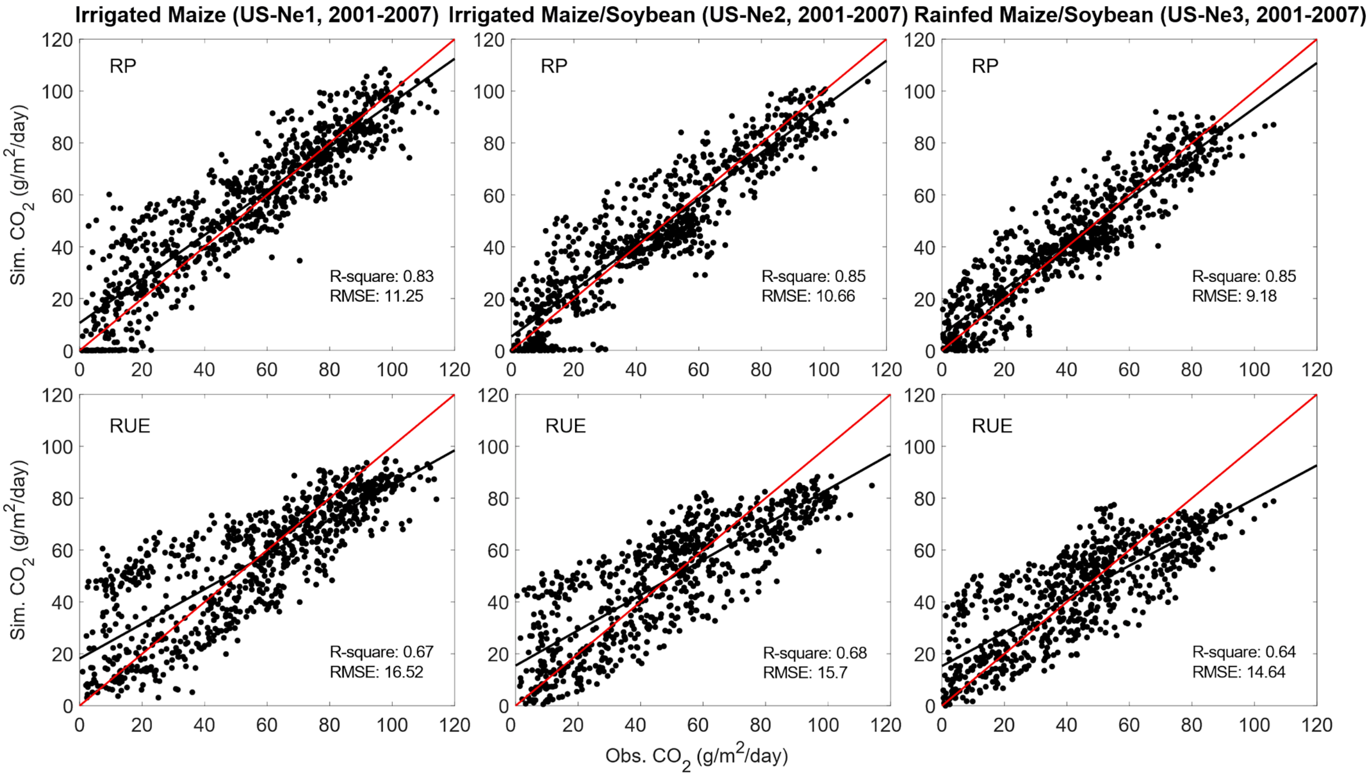

Fig. 3. Comparisons of RP (top panel) and RUE (bottom panel) methods for simulating G PP at three AmerFlux sites from 2001 to 2007 with measured inputs (for RP: temperature, radiation, wind speed, air pressure, leaf area index (LAI), date, and latitude/longitude; for RUE: radiation). The RUE values (i.e., 40.0 kg/ha/(MJ/m^2) for maize and 25.0 kg/ha/(MJ/m^2) for soybean) are obtained from the EPIC input files. The red line is a 1:1 line and the black one is a least square fitting line.

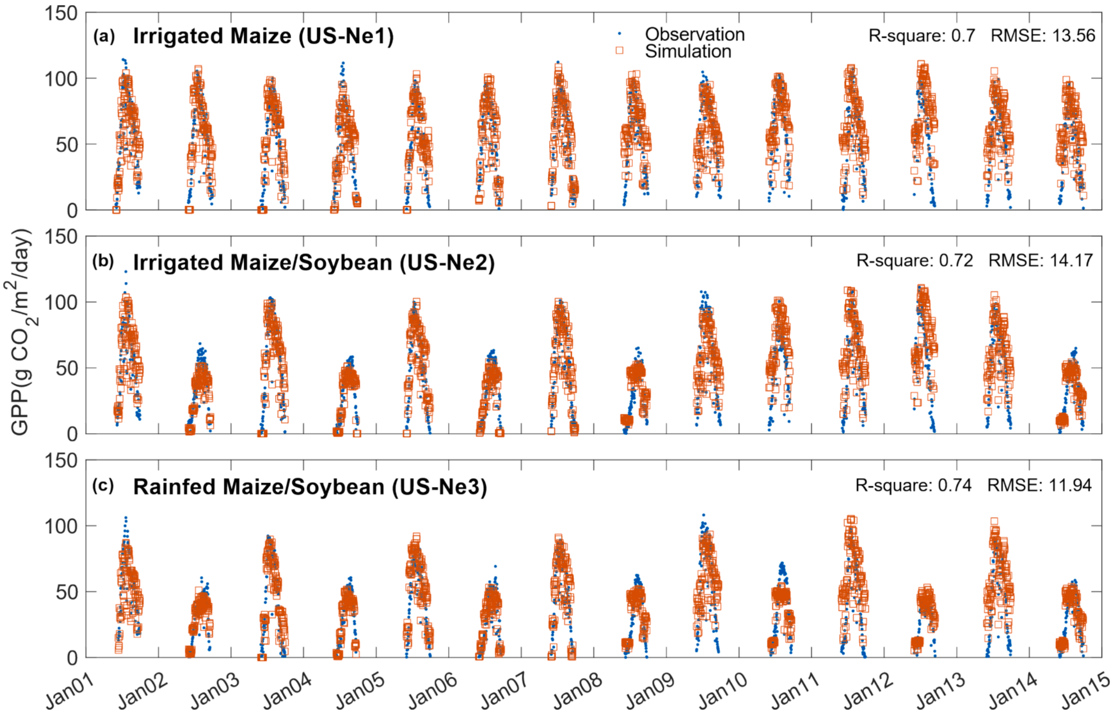

Fig. 4. Comparisons of simulated (orange squares) and observed CO_2 flux (GPP, blue dots) using both observed LAI (2001–2007) and averaged historical LAI data (2008–2014) over three crop types. (a) Maize for all years; (b) Soybean for 2002, 2004, 2006, 2008, and 2014; Maize for other years. (c) Maize for odd years and soybean for even years.

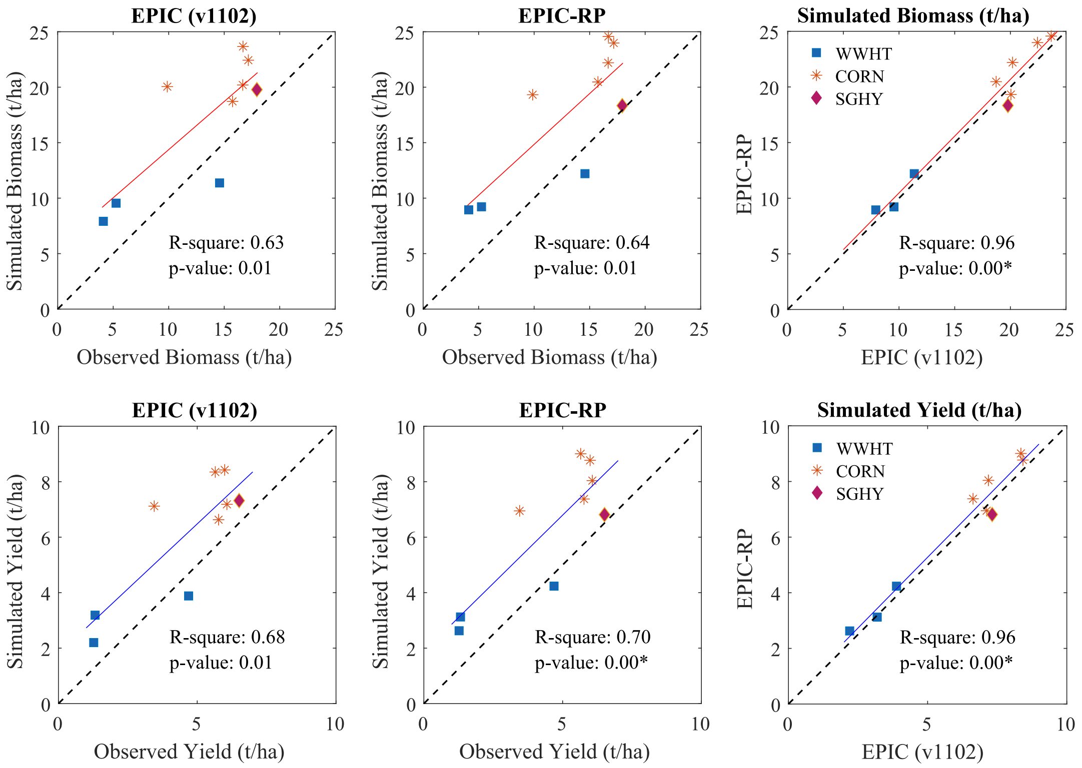

Fig. 5. Comparisons of simulated crop biomass and yield by uncalibrated EPIC (EPIC v1102) with the RUE method and EPIC-RP using observed data in the Riesel Experimental Watershed, TX. Note that the correlation between EPIC-RUE and EPIC-RP was high with significant P values (rounded to 0.00). MAZE: Maize; SGHY: Sorghum; WWHT: Winter Wheat.

showed more realistic crop responses to elevated CO_2 concentrations than the RUE method.

Although EPIC has been widely used to study the CO_2 fertilization effect on crop yields, there is a concern that EPIC overestimates that effect (Beach et al., 2015). EPIC calculates RUE for a given CO_2 concentration by interpolating the RUE values measured through chamber

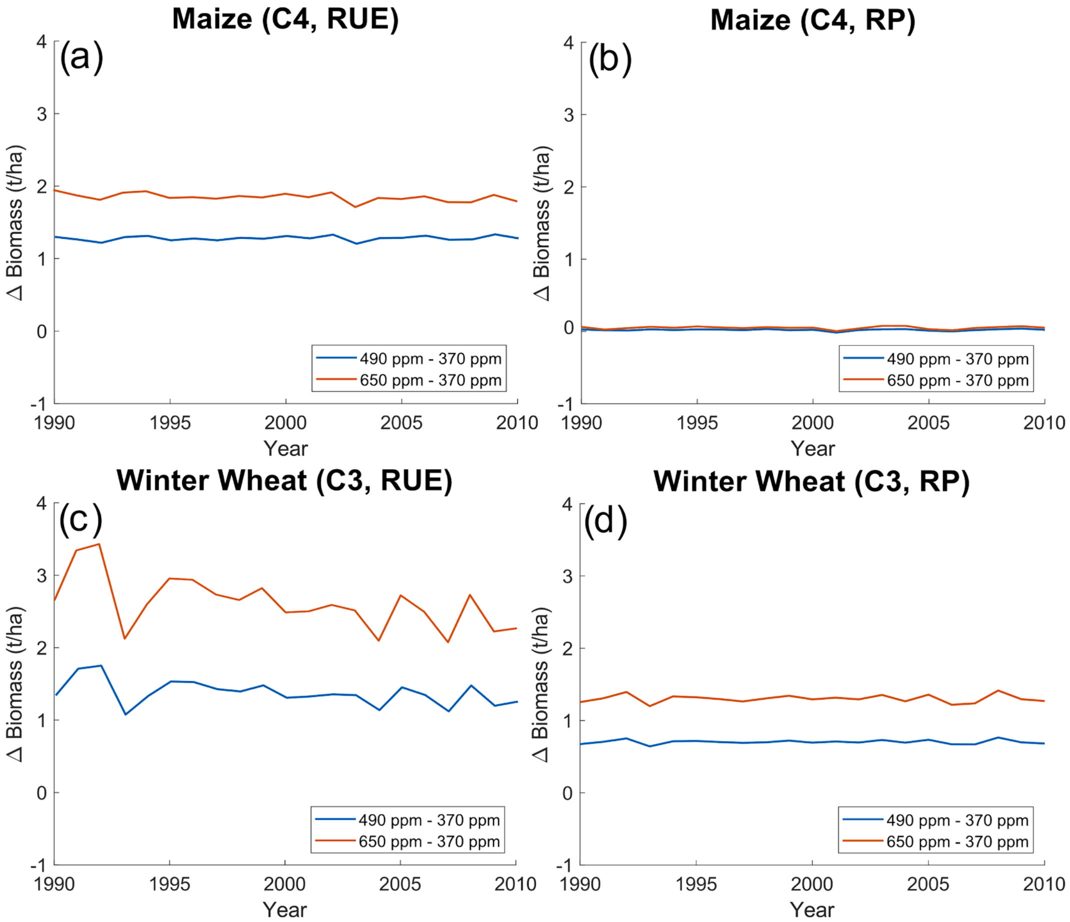

Fig. 6. Responses of biomass to elevated CO_2 concentrations for C3 and C4 crops by the RP and RUE methods in Raleigh, North Carolina. The RP responds significantly differently to increasing CO_2 for C3 and C4 crops, while the RUE method in EPIC responds similarly for C3 and C4 crops.

experiments at different CO_2 concentration levels (i.e., 330 vs. 660 ppm) (Stockle et al., 1992). This approach has multiple drawbacks. First, the Free Air CO_2 Experiments (FACE) have shown the crop response to increases in CO_2 concentrations is much lower than that observed in chamber studies (Ainsworth and Long, 2021). Second, chamber measurements are limited to measured crop species, and extrapolation is needed to estimate CO_2 fertilization effects on RUE for other crops. Third, the RUE-CO_2 concentration relationship derived from the chamber experiments may not apply to CO_2 concentrations beyond the range of experiments (i.e., 660 ppm). Fourth, when using the RUE method to represent CO_2 fertilization effects, additional empirical relationships are needed to estimate CO_2 concentration effects on stomatal conductance. Those empirical relationships describing CO_2 impacts on RUE and stomatal conductance may not be consistent with each other. Hatfield et al. (2011) reviewed field studies that examined responses of C3 and C4 crops to a doubling of CO_2 concentrations and found that biomass of C3 crops increased 30 % or more, but C4 crops only showed 3–4 % increases. Collectively, the RUE method used in EPIC likely substantially overestimates the positive influence of CO_2, particularly for C4 crops, while the RP method provides more reasonable estimates of the responses of C3 and C4 crops to elevated CO_2 concentrations.

4.4. Comparisons with DcaPS and GECROS

We further compared the RP method with DcaPS and GECROS with respect to simulated absorbed PAR by the canopy, sensitivity of photosynthesis environmental variables (e.g., PAR, CO_2, and leaf temperature), and estimated Vmax (i.e., Rubisco-limited carbon assimilation rate) and Jmax (i.e., light-limited carbon assimilation rate).

Simulated absorbed PAR by sunlit and shaded leaves varies differently during the diurnal course (Fig. 7). The PAR varied dramatically and reached the maximum around noon (when the solar zenith angle is 0) for sunlit leaves. But for shaded leaves, the changes of PAR from sunrise to sunset are small (Fig. 7a) because they only receive diffuse radiation. The absorbed PAR is also slightly different from RP, GECROS, and DcaPS. GECROS and DcaPS use the same algorithm (i.e., Beer's Law) to calculate absorbed PAR, except for a different extinction coefficient (Kd) for diffused PAR. The three models used different approaches to calculated Kd: (1) empirical—Kd is determined by a nonlinear combination of extinction coefficients for direct PAR at three different solar zenith angles (i.e., 15, 45, and 75 degrees) in GECROS, (2) constant—a value of 0.78 is used in DcaPS; (3) mechanical—Kd is calculated considering light transmission, scattering, and reflection processes through the canopy profile (details of calculation in the two-stream model). The different ways to deal with diffused PAR probably led to the difference of total absorbed PAR.

RP also calculates fractions of PAR received by sunlit/shaded leaves explicitly, but GECROS and DcaPS do not. The PAR received by plants increases sharply with an increase in LAI when LAI is low ($< 4\ m^2/m^2$), and that pace slows down and stabilizes when LAI reaches around 6 m^2/m^2 (Fig. 7b). In general, the majority of PAR (direct and diffuse) is absorbed by sunlit leaves. For example, about 80 % of the radiation is absorbed by sunlit leaves when LAI is around 6 m^2/m^2, and approximately 17 % is received by shaded leaves. Particularly, shaded leaves receive very low portion (<8%) of the beam. The result is consistent with that from Dai et al. (2004).

Sensitivity analysis of photosynthesis rate to changes in PAR, CO_2, and leaf temperature shows that DcaPS and GECROS have similar

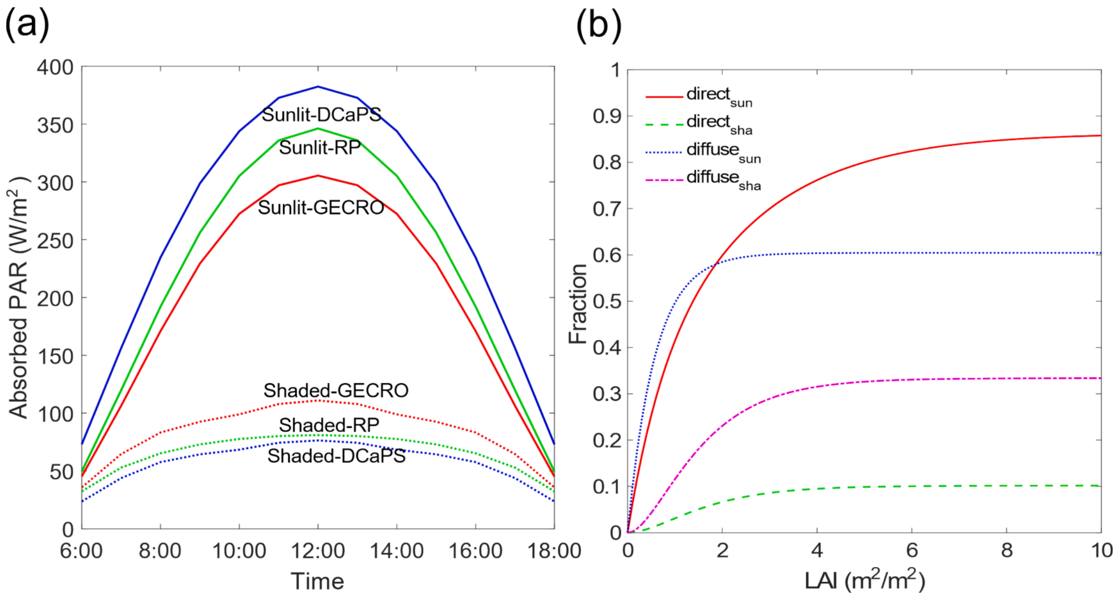

Fig. 7. (a) Diurnal course of simulated PAR and (b) fractions of radiation absorbed by sunlit/shaded leaves for a virtual site at 31.5 °N and for the day of the year is 198. The atmospheric transmission ratio is taken as 0.75. Other reference values for (a) are leaf angle = 60 degrees; soil albedo = 0.3; reflectance of diffuse PAR = 0.057 (used only by DcaPS and GECROS); scattering coefficient for PAR = 0.2 (used only by DcaPS and GECROS); reflection coefficient of leaf = 0.15; transmissivity = 0.05; LAI = 6 m^2/m^2. (b) is simulated by RP with the same leaf parameters as above at local noon (solar zenith angle = 0 degrees).

response curves with slight differences regarding responses to PAR and CO_2 (blue and green dashed lines in Fig. 8 a, b, c, d), which is mainly because they share a similar variation of Farquhar's photosynthesis model (Farquhar et al., 1980). But their responses to leaf temperature (i.e., photosynthesis rate vs. leaf temperature) are quite different, since DcaPS uses air temperature to approximate sunlit/shaded leaf temperature (Wu et al., 2018) while GECROS distinguishes leaf temperatures and air temperatures (Yin and Laar 2005).

The RP method used a variation of Farquhar's photosynthesis model, akin to what is used in DcaPS and GECROS for C3 crops, but with distinct parameterizations; for C4 crops, it utilized an entirely different model than those found in either GECROS or DcaPS. So the response curves (i.e., photosynthesis rate to changes in PAR, CO_2, and leaf temperature) of RP are different from that derived by GECROS or DcaPS for both C3 and C4 crops. For example, the RP-simulated net photosynthesis rates increase faster than those simulated by DcaPS and GECROS in response to increases in PAR for C4 crops; while for C3 crops DcaPS and GECROS simulated responses of net photosynthesis rate increase to PAR outpace that estimated by the RP method. The differences between RP, DcaPS and GECROS arise from the use of different algorithms to describe radiative transfer and photosynthesis processes, as well as different parameterization strategies as presented in Table S1.

Vmax and Jmax are two critical intermediate variables to calculate net photosynthesis rates in all three methods. DcaPS and GECROS have the same response curves of $V_{max} - LAI$ and $J_{max} - LAI$, as they share the same method and parameters for calculating Vmax and Jmax (Fig. 9, top panel). Both DcaPS and GECROS calculate two types of photosynthesis rates: RuPB-limited rates by Vmax and light-limited rates by Jmax. The biggest difference between DcaPS/GECROS and RP is that: Vmax and Jmax for shaded leaves increase to infinite in DcaPS/GECROS, while they will get saturated in RP. Another difference is that the magnitudes for both Vmax and Jmax in RP are smaller than those by DcaPS/GECROS because of different model structures (Table S1). DcaPS and GECROS calculated net photosynthesis rates with two components (i.e., RuPB- and light-limited), while RP has three components (with an additional component of PEP carboxylase-limited).

4.5. RUE vs. RP, which is better for simulating crop growth?

Which one to choose for agroecosystem modeling? A common argument for favoring the RUE method goes like this: The RUE value is typically calculated by conducting ideal field experiments; therefore, the RUE method is expected to achieve more realistic biomass predictions under no-stress conditions than the RP method (Kiniry et al., 1999). Whether this argument is truly defensible is a question. Regardless, due to its model simplicity and fewer constraints on input data, the RUE method is an appealing choice for its ease of scaling up to the continental and global levels. Meanwhile, there are at least three reasons why the RP method can be a better option:

(1) RUE values are empirical and likely location-specific. A RUE value is a lumping factor encompassing the overall growing conditions at experiment sites; the experiment-derived RUE at one location might not be suitable for other locations. In the simulation of Section 3.1, the default RUE value in EPIC was unlikely the true value for the three flux tower sites, explaining why the RP method performed better. Moreover, the RUE values are only available for some species examined in previous experiments.

(2) The RUE method represents only aggregated results of various changes in environmental factors (Sadras and Calderini, 2014), making it difficult to apply it beyond the experiment conditions under which to measure RUE. In contrast, the RP method can explicitly quantify the individual or interactive effects of multiple environmental factors because their factors are directly linked to photosynthesis in the model formulation. Such a linkage makes the RP more suitable for quantifying the impacts of extreme weathers. For example, the RP method could clearly show a sharp decline in photosynthesis rates when the temperature goes beyond 35 °C (Fig. 9e and f). Thus, RP could account for the impacts of short-term (several hours) exposure in extremely high temperatures, which is impossible for the RUE method.

(3) The RP method provides more realistic simulations than the RUE method under elevated CO_2 concentrations. Although the RUE values could be modified through some coefficients to include the effects of elevated CO_2 concentrations (Neitsch et al., 2011),

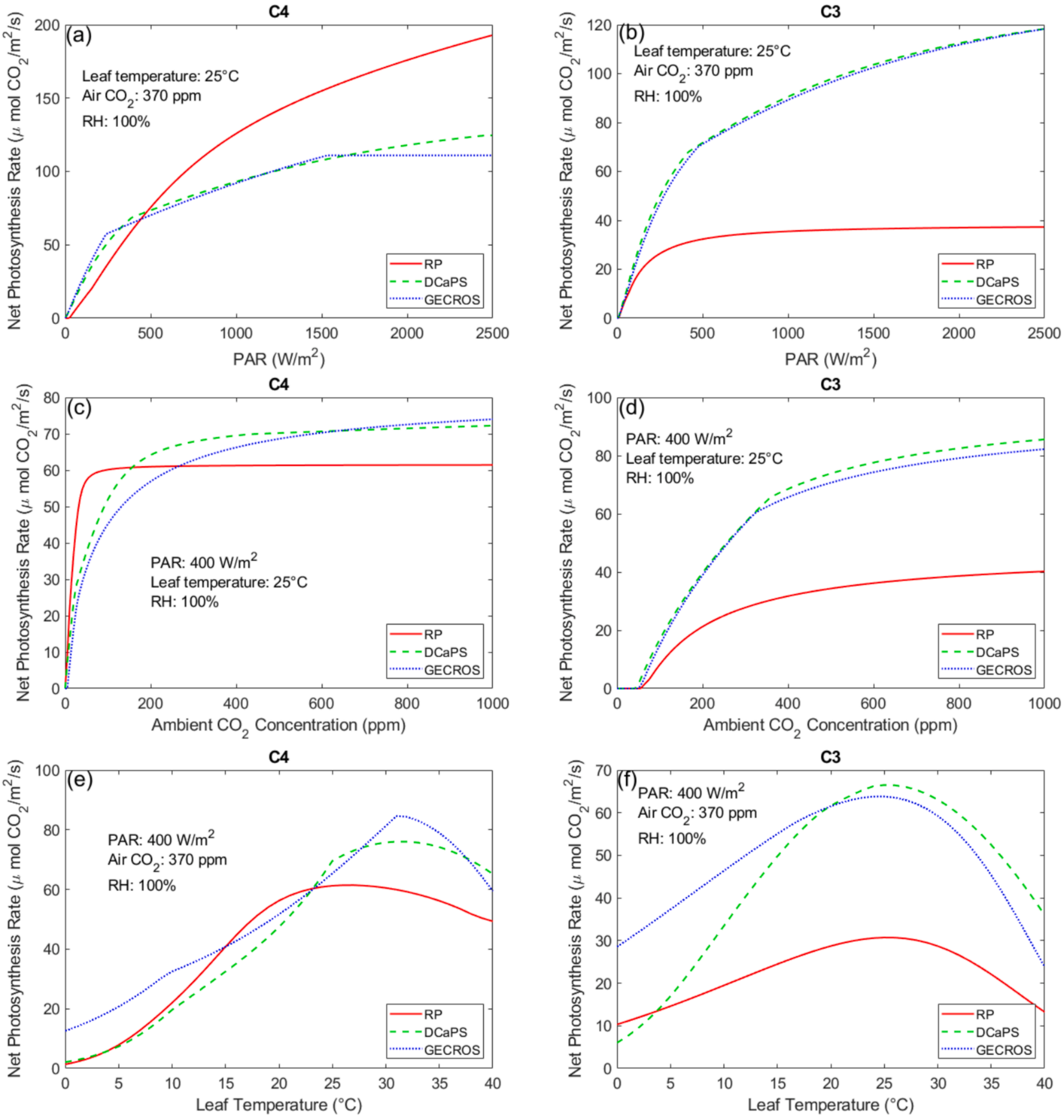

Fig. 8. Sensitivity analysis of photosynthesis rate to PAR, CO$_2$, and leaf temperature for three methods: RP, DcaPS, and GECROS. DcaPS and GECROS shared the same version of Farquhar's photosynthesis model (Farquhar et al 1980) for C3 crops, but GECROS distinguished sunlit/shaded leaf temperature from air temperature while DcaPS did not. RP used a modified variation of Farquhar's photosynthesis model for C3 and it also calculated the sunlit/shaded leaf temperatures. All methods used different models for C4 crops.

there are no known ways to account for the interactive impacts of all the climate and CO2 factors; it is also hard to distinguish the responses between C3 and C4 crops. In Fig. 6 for the simulation with the RP method, elevated CO$_2$ significantly increased biomass for C3 crops but not for C4 crops (Fig. 6) because photosynthesis gets saturated at a low level of CO$_2$ concentrations for C4. Such results are confirmed by the field experiment—Free Air-CO$_2$ Enrichment (Leakey et al., 2009). However, the RUE method estimated that both C3 and C4 crops significantly benefited from CO$_2$ fertilization effects, which is contrary to field data.

RUE-based agroecosystem models, including de Wit school models, DSSAT, and APSIM, contribute substantially to achieving sustainable agriculture. Earlier studies showed that the empirical RUE-based method performed well under high radiation and low water stress conditions (Kiniry et al., 1999) but the mechanistic photosynthesis-based method is more accurate under low radiation and high water stress conditions (Zhu et al., 2010). However, more evidence from recent studies suggests that the photosynthesis method could predict photosynthetic responses to multiple environmental factors more accurately than the RUE method (Sun et al., 2022). The RUE-based models are generally weak in accurately predicting performance under

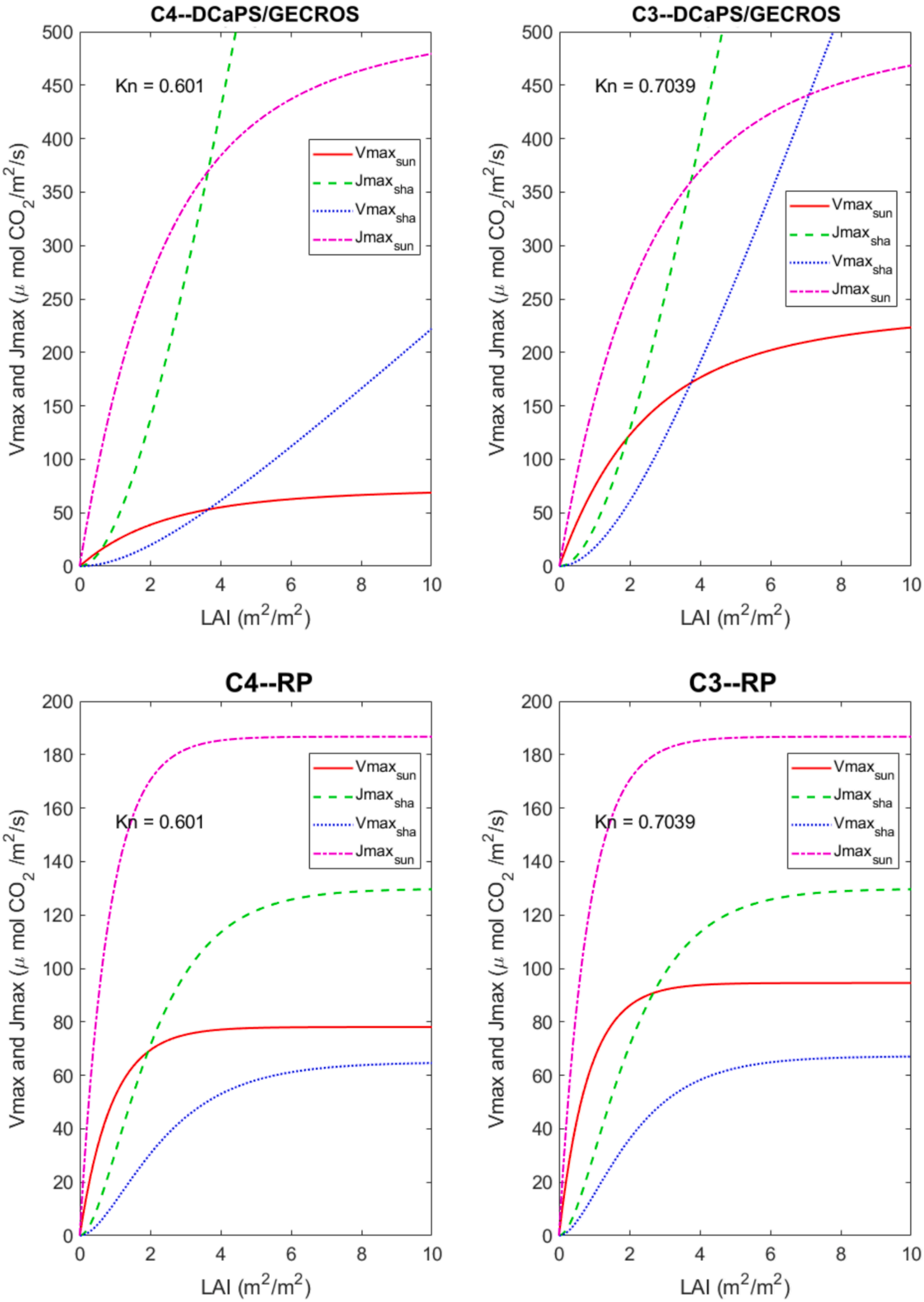

Fig. 9. Responses of Vmax and Jmax to LAI for three methods: RP, DcaPS, and GECROS. DcaPS and GECROS share a similar method for calculating Vmax and Jmax for C3 and C4 crops but are different from that used by RP, so the response curves of DcaPS and GECROS are the same. In DcaPS and GECROS, net photosynthesis rate $A_n = (A_c, A_j)$ where A_c and A_j determined by Vmax and Jmax, respectively. In RP, $A_n = (A_c, A_j, A_p)$ where A_c is determined by Vmax and A_j by Jmax, but with A_p by Vmax (C3) or CO_2 (C4) concentrations (Table 1).

environmental perturbations (Zhu et al., 2011). To better forecast crop growth under extreme weather, model evolution with a high level of mechanistic basis is needed (Antle et al., 2017).

From a model selection perspective, evidence was strong that the RP method outperformed the classical RUE method. For instance, when considering both model errors and model complexity for the simulation results of Section 3.1, the Akaike Information Criterion (AIC) differences between the RP and RUE models were consistently negative across the three Ameriflux sites (e.g., 6219.2 for RP versus 6799.8 for RUE at the US-Ne1 site Table S2): A lower AIC value indicates a better model (Burnham and Anderson, 2004; Li et al., 2024; Zhao et al., 2019). However, it is important to note that our calculation of AIC was loosely defined because AIC is applicable only for statistical models but both the RP and RUE models in this study are physical models rather than statistical models. Additionally, we used the default parameter values for both models without performing parameter estimation or statistical inference. Despite these limitations, the AIC-based "statistical" evidence supporting the superiority of the RP model is likely conservative. If a proper statistical framework and likelihood-based inference procedure were imposed, the RP model would likely give even smaller errors. Overall, the evidence overwhelmingly supports the RP method as being closer to the true model—an outcome that aligns with its theoretical foundation that the RP model captures the biophysical and biochemical processes more realistically.

4.6. The RP method is a step closer to next-generation agroecosystem modeling

As urged by Rötter et al. (2011), crop-climate models need an overhaul. One important reason is that many current models are badly out of date. For example, only a limited number of agroecosystem models include the photosynthetic process explicitly (Guan et al., 2022). Photosynthesis is critical for the interaction between water use and production; without it, crop models may overemphasize the effects of droughts. Incorporating both radiative transfer and photosynthetic processes, the RP method is open-source and well-structured, making it easy to integrate into other holistic biophysical, biogeochemical, and economic models to simulate crop growth (e.g., EPIC-RP in Fig. 2). Such modular models are needed to ensure efficient scientific progress as well as model longevity and maintainability (Jones et al., 2017). In addition, well-structured processes such as RP could easily allow intercomparison of different methods (e.g., RP vs. RUE) in the same model framework (e.g., EPIC). The RP model also has been incorporated into the Soil and Water Assessment tool – Carbon (SWAT-Carbon; Zhang et al., 2013). Stand-alone versions of the RP model are available in MATLAB and FORTRAN (https://github.com/hutx2309/RP_model.git). In addition, RP in EPIC and SWAT-Carbon are also shared (https://sites.google.com/view/swat-carbon/).

5. Conclusions

The empirical RUE method and the mechanistic RP methods represent two types of approaches to simulating crop growth. The RUE method is widely used in agroecosystem modeling for crop growth responses to elevated CO_2 concentrations and extremely high temperatures, due to the lack of mechanistic representation of some key processes such as photosynthesis. Our study integrated radiative transfer and photosynthesis algorithms into the mechanistic RP model to serve as an alternative to the RUE method for simulating crop growth. Through multiple case studies, we demonstrated that the RP model can (1) capture well crop GPP at three flux-tower sites, (2) perform comparably to the RUE method for simulating crop yields, and (3) more reasonably estimate responses of crop growth to elevated CO_2 concentrations. As such, the RP model represents a new contribution to the suite of crop growth models that directly link climate variables with crop growth. It is well-structured, so can be easily plugged into current RUE-based agroecosystem models to quantify the impacts of environmental changes on yield and support sustainable agricultural management strategies.

CRediT authorship contribution statement

Tongxi Hu: Writing – original draft, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Xuesong Zhang:** Writing – review & editing, Software, Methodology. **Sami Khanal:** Writing – review & editing, Methodology. **Kaiguang Zhao:** Writing – original draft, Software, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.compag.2025.110199.

Data availability

Data will be made available on request.

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