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Photosynthesis Rate Estimation in C3 Plants Using the Farquhar-von Caemmerer-Berry (FvCB) Model

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Abstract

Photosynthesis is vital to life on Earth, as it promotes plant growth and sustains the environment. For C3 plants in particular, understanding photosynthetic rate is a prerequisite for more accurate yield estimates and for understanding their responses to environmental changes. The Farquhar-von Caemmerer-Berry (FvCB) is one of the most common biochemical models of carbon assimilation in photosynthesis, based on leaf-level gas exchange. We estimate photosynthesis in C3 plants using the FvCB model, which relates Rubisco carboxylation (vcmax) to electron transport (J) and TPU. We attempt to improve the model's estimates of accuracy across varied combinations of stimuli, as a function of environmental measures of light, CO2, temperature, and stomatal conductance. The model was then evaluated using a set of selected representative C3 plant species, and the simulations were also compared with real-time gas exchange measurements. The model output shows that it performs well at estimating photosynthesis responses to changing climate conditions. Moreover, Vc_{max}, J, and overall assimilation rates exhibited exceptional interspecific variability, further quantifying the sensitivity analysis and indicating the need for species-

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specific parameterization. Our study contributes to developing more robust photosynthetic models for crops and ecosystems that estimate climate change impacts and support agricultural management strategies that rely on them.

Keywords:

C3 plants, environmental modeling, gas exchange, the FvCB dietary model, photosynthesis, carbon assimilation, and rubisco carboxylation.

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Introduction

Plants convert light energy to chemical energy using photosynthesis. This process is vital to life on Earth because it sustains the planet's carbon and energy dynamics (Karthika, 2025; Khoddami et al., 2017). C3 photosynthesis is the most widespread type, particularly in temperate and subtropical regions (Taiz et al., 2015). Modeling the productivity of C3 photosynthetic plants must be accurate to estimate vegetation yield, anticipate food supply, assess the consequences of increasing CO_2 levels and temperature on the environment, and analyze the environment's impact on rising CO_2 levels and temperature (De Kauwe et al., 2016; Prasath, 2024). The mechanistic modeling of photosynthesis in C3 plants is universally attributed to the FvCB model constructed in the early 1980s, which is accepted as the foundational work in the field (Salehi & Nowrouzi, 2025; Akila et al., 2023). This model describes net CO_2 assimilation as the result of the interplay among Rubisco carboxylation kinetics, electron transport on product RuBP, mass flow, and triose phosphate (TPU) limitation under myriad manipulative factors (Lawson & Blatt, 2014).

The FvCB model is structurally and functionally validated and parameterized for several C3 crops and forest species, giving information on leaf-level carbon exchange processes and facilitating scaling through Earth system models (Farquhar et al., 1980; Surendar, 2024). Its precision, however, relies on accurate estimates of Vc_{max}, J, and TPU, which are vetted across species, developmental stages, and environmental conditions (Medlyn et al., 2002; Antoniewicz & Dreyfus, 2024). The FvCB model has recently been enhanced with device and technique innovations in gas exchange and model fitting under field and lab conditions (Rogers et al., 2017; Kavitha, 2024). Additionally, incorporating temperature and light into the response function improves the model's sensitivity and its ability to simulate photosynthetic responses under climate change scenarios (Kurian & Sultana, 2024; Geetha, 2024).

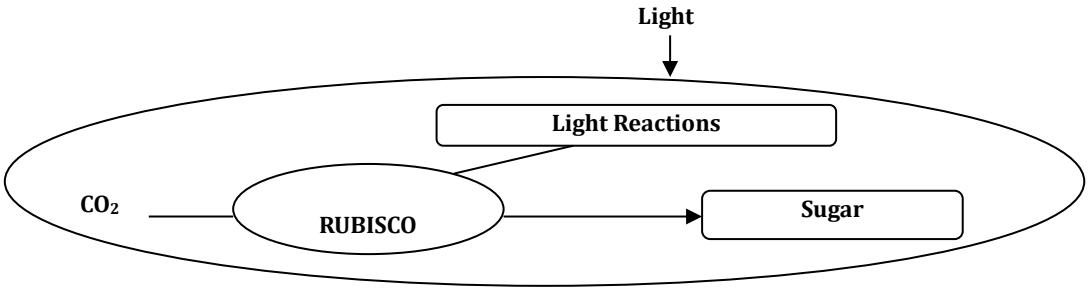

Figure 1. Overview of photosynthesis in C3 plants

This figure (Figure 1) depicts the overall photosynthesis process in C3 plants, in which light energy, carbon dioxide (CO_2), and the enzyme Rubisco interact in the chloroplast to produce sugars. Incoming light initiates the light reactions that produce energy for carbon fixation. CO_2 enters the leaf and is converted by Rubisco in the Calvin cycle, which generates organic molecules. This schematic outlines the overall process

of converting light energy to chemical energy. It ultimately reinforces the dual roles of light reactions and enzyme activity in plant growth and carbon assimilation.

In this study, we aim to determine photosynthetic rates in representative C3 plants using physiological, biochemical, and environmental parameters organized within the FvCB model (Salameh & Mohamed, 2024; Uvarajan, 2025). Calibration and validation of the model revolve around empirical evidence of gas exchange, thereby maintaining precision and utility, which subsequently results in the refinement of model dynamics predicting plant productivity and the improvement of sustainable agricultural and ecological interventions (Sharkey et al., 2007; Medlyn et al., 2002; Esfandiari et al., 2023; Krishnan & Iyer, 2024).

Related Work

The FvCB model attempts to determine the rate of photosynthesis as precisely as possible in different environmental conditions. An integrated stomatal conductance model (Bonan et al., 2011) was formulated that fitted the FvCB framework, which offered a better relationship between gaseous exchange and biochemical integration. Additional research (Von Caemmerer, 2000) investigated variability in conductance of the mesophyll, illustrating its underestimation in the models without internal leaf CO 2 diffusion resistance, changing the Vc 8 final value in literature (Nayak & Raghatate, 2024). The underlying process of nitrogen cycling and its manipulation of photosynthetic parameters in forested ecosystems were examined (Medlyn et al., 2011), and it was suggested that nutrient constraints needed to be included in the FvCB parameterizations (Veerappan, 2024; Vishnupriya, 2025). Studies (Leuning, 1995) have recorded high plasticity of photosynthetic traits during the conditions of long-term high CO 2 and temperatures implying that models can be improved through dynamic modification of parameters (Kumarathunge et al., 2019; Rahman, 2024). The same was argued (Aber et al., 1991), in which it was suggested that when establishing the responsiveness of simulations, long-term vegetation physiological adjustments could be included by introducing the variables of the resting-state Earth system model. The meta-analysis results of temperature treatment on FvCB parameters were reported across the world (Kattge & Knorr, 2007) and meta-analytic regression coefficients of J_0 and V_{c0} were obtained that would be applied to simulate models. Activation of Rubisco in relation to light dependence and its future predictive ability of increasing afternoon photosynthetic capacity were explored (Lasslop et al., 2010; Mejail et al., 2024). There was also an investigation of non-stomatic constraints during drought and heat (Purcell et al., 2018) and it is recommended that hydraulic characteristics be put in the FvCB model to include stress-prone environments. Recent methods have also used remote sensing and machine learning. Hyperspectral reflectance was shown to be a promising technique to estimate FvCB parameters at a distance (Mott & Woodrow, 2000), and a data assimilation system that combines satellite measurements and process models was presented (Tholen et al., 2012) to maximize real-time photosynthesis prediction across landscapes. The scientific significance of FvCB model is ever growing with the growth and development of predictive ecosystem modeling, precision agriculture, and global carbon cycle measurements (Wu et al., 2016).

Methodology

To estimate photosynthetic rate of C3 plants using the FvCB model the methodology will follow the following main steps: selection of the plant to be used in the experiment and therefore to prepare it, measurement of gas exchange and other environmental variables, determination of model parameters and fitting, and the last stage is validation and sensitivity analysis.

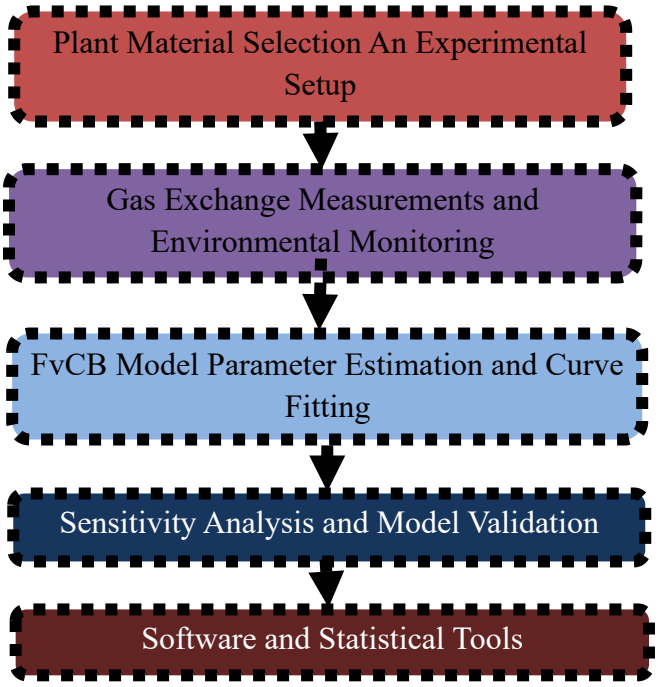

Figure 2. Methodological framework for estimating photosynthesis rate in C3 plants using the FvCB model

In the FvCB model of estimating the photosynthetic rate of C3 plants, a systematic process is used as shown in Figure 2. It starts with the choice of the species of the plant and providing the best conditions to develop and grow it; further on, it involves the measurement of gaseous exchange and other environmental parameters. The values are used to fine-tune the FvCB model in the intention to estimate Vcmax and Jmax. Sensitivity analysis and the ability to address empirical data is used to test the accuracy of the model. The results are processed using computation and statistical techniques to ensure that the process of modeling can be reproducible and dependable.

Selection of Plant Material and Set Up of the Experiment

To represent the diversity of plant physiological responses among C3 herbaceous plant species, a single representative of the plant species; Arabidopsis thaliana, Triticum aestivum (wheat) and Glycine max (soybean), were used in this research. Growth of plants was conducted in a growth chamber of two sets of temperatures at 25 o C and 20o C during the daytime and night respectively, photoperiod of 14 hours of light and dark of 10 hours respectively and relative humidity was maintained at 60. The intensity of the PAR (1000 1g m 2 s 1) was matched to the intensity of the natural daylight and the imitation of natural daylight intensity, and soil composition, watering schedule, and nutrient input were adjusted to the fixed value to avoid deviations of non-biotic stressors.

All the physiological measurements needed similar level of development and therefore in case of leaf sampling, the leaf that was most developed was sampled on all the plants to be under equal light conditions. The photosynthetic rates in steady state should be maintained at a constant level following 30 minutes of the acclimatization period; therefore, 30 minutes of acclimatization period was conducted prior to measuring the gas exchange. In the experiment, the environmental factors including CO 2 concentration, the temperature of the leaves, and humidity were monitored and kept constant.

Gas Exchange Measurements and Environmental Monitoring

Data concerning photosynthesis was obtained with the use of a portable gas exchange unit (e.g., LI-COR 6400XT or LI-6800). ACO_2 response curves (A–Ci curves) were created by varying the intercellular CO_2 concentration (Ci) in the leaf chamber from 50 ppm to 1200 ppm in steps. Each step was kept for 2–3 minutes or longer until there was some consistency in net assimilation rate (A). During this period, leaf temperature was held at 25 °C, while the illumination was set at 1500 μmol m^2 s^1.

Measurements of gas exchange with the aforementioned portable devices gave instantaneous values of net CO_2 assimilation (A), stomatal conductance (gs), transpiration (E), intercellular CO_2 concentration (Ci), and time-based data about these physiological parameters. Besides leaf gas exchange, the leaf area and chlorophyll content (SPAD values) were measured. Also, the light intensity, the temperature of the air, and the vapor pressure deficit (VPD) relative to the surrounding environment were measured with the incorporated sensors of the gas exchange device.

FvCB Model Parameter Estimation and Curve Fitting

The FvCB model is a mechanistic biochemical model built on the constraining steps of photosynthesis: Rubisco-limited carboxylation (Ac), RuBP regeneration-limited assimilation (Aj), and triose phosphate utilization (Ap). Only Ac and Aj components were modeled in this investigation since Ap-limitation is mostly insignificant at non-saturating conditions.

Sensitivity Analysis and Model Validation

In order to evaluate the robustness of parameter estimation, sensitivity analysis was performed. Parameters such as Γ*, R_d, and J_{max} were changed by ±2 0% about their mean estimates to gauge the impact of modeled assimilation rates. The analysis showed photosynthetic rate versus Vc_{max} had the lowest photosynthetic sensitivity at low Ci and highest sensitivity at higher Ci to J_{max}, reinforcing the mechanistic guesses of the FvCB model.

Model validation involved simulating assimilation rates for unidirectional gas exchange under field-like conditions and comparing the outputs to actual gas exchange data captured independently to validate the model. Also, parameters derived from the A–Ci curves were validated against electron transport estimates of J_{max} derived from chlorophyll fluorescence to validate the estimates of J_{max} for independent validation against derived curve estimates.

All datasets and scripts were managed under version control systems hosted on GitHub, and unique identifiers were assigned according to principles aligned with FAIR data policies on metadata curation and annotation to ensure reproducibility.

Figure 3 gives a basic workflow for estimating the photosynthetic parameters in Arabidopsis, wheat, and soybean. It starts with the controlled cultivation of plants and predetermined leaves. Subsequent gas exchange measurements are done with a portable system, and the photosynthetic reactions are recorded with changing CO_2 levels.

Lastly, fitting values are obtained as Vc_{max}, J_{max}, R_d, and other values of the FvCB model, and sensitivity analysis and model validation are performed. Systematically, this workflow illustrates the experiments and models that have been conducted in the course of learning about C3 plant photosynthesis.

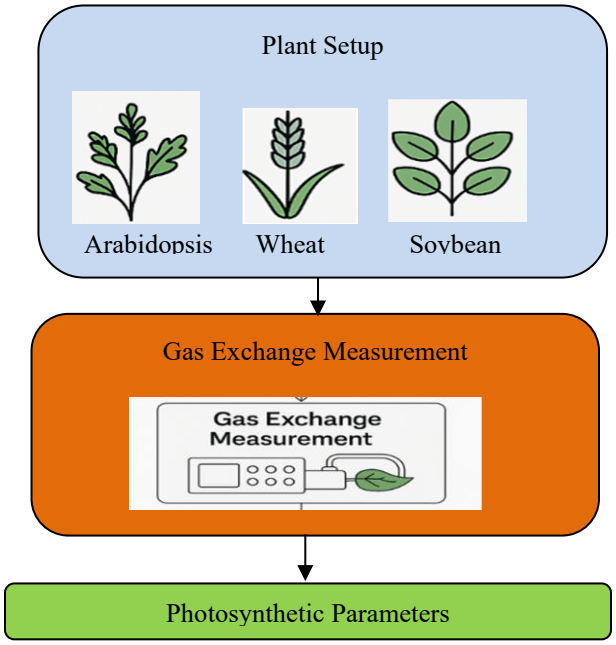

Figure 3. Simplified workflow of photosynthetic parameter estimation in C3 plants

The FvCB model mathematically describes the net CO_2 assimilation rate (A) as the minimum of the rate limited by Rubisco (Ac) and the rate of electron transport (Aj) minus the mitochondrial respiration rate in light (Rd):

$$A = min(A_c, A_j) - R_d \quad (1)$$

where:

$$A_c = V_{cmax} \cdot \frac{C_i - \Gamma^*}{C_i + K_c\left(1 + \frac{O}{K_o}\right)} \quad (2)$$

And

$$A_j = \frac{J}{4} \cdot \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \quad (3)$$

Where,

V_{cmax} = maximum rate of Rubisco carboxylation (μmol m^{-2} s^{-1}),

C_i = intercellular CO_2 concentration (μmol mol^{-1}),

Γ^*= CO_2 compensation point in the absence of dark respiration,

K_c and K_o = Michaelis–Menten constants for CO_2 and O_2, respectively,

O = ambient concentration of oxygen (mmol mol^{-1}),

J = potential maximum rate of electron transport (μmol m^{-2} s^{-1}).

The rate of electron transport, J, was linked to irradiance, I, using the empirical non-rectangular hyperbola:

$$J = \frac{\alpha I + J_{max} - \sqrt{(\alpha I + J_{max})^2 - 4\theta\alpha I J_{max}}}{2\theta} \quad (4)$$

where α is the quantum efficiency of electron transport, Jmax is the maximum rate of electron transport, and θ is the curvature factor.

Statistical Tools and Software

R (v4.3.1) was used to fit, estimate parameters and visualize data along with the following packages; plantecophys, nlme, and ggplot2. Asson checks like residuals against fitted values were conducted to do model checks to ensure that there was the right convergence and no overfitting.

The Tukey HSD was used to make post hoc comparisons after the one-way ANOVA ($\alpha = 0.05$) was used to test whether statistical differences existed between species. The descriptive statistics and confidence interval of the parameter estimates were computed together with other parameters.

Results and Discussions

The nonlinear regression analysis of photosynthetic response curves provides significant estimates of various critical parameters such as V_{cmax}, J_{max} and R_d to the C3 plants in question. The V_{cmax} values of the species showed great diversity of between 65 and 95 mmol m^2 s^{-1} which could be due to the natural genetic and physiological difference in the carboxylation ability of the specific species. Such variability would have an impact on how the plant is able to fix CO 2 under adverse conditions. In the case of the electron transport to regenerate RuBP, J 8 8 had an average of 100-130 μmol m^2 s^1 and was highly influenced by V_{cmax} and showed a high positive interaction as expected of a photosynthetic biochemical process. The rate of mitochondrial respiration (R_d) was low (approximately 1.5 μmol m^2 s^1) in estimating the rate, which occurs according to the amount of carbon lost during the daytime period. These processes mainly resulted in net assimilation. Results from model fitting metrics confirmed robust parameter estimates, including biologic and environment0061l diversity, with R^2 values above 0.95 and RMSE lacking deviation.

Figure 4 demonstrates the reaction of net photosynthetic assimilation (A) with intercellular CO_2 concentration (Ci) while under mild physiological stress, which may include water and/or temperature restrictions. The rate of photosynthesis exhibits a linear increase with increasing Ci, reflecting Rubisco-limited carboxylation. However, the curve plateaus at higher Ci, where it becomes limited by electron transport. Vc_{max} and J_{max} are strongly and simultaneously impacted by environmental constraints as shown by the altered saturation point (approximately 700 μmol mol^1) and the diminished pinnacle assimilation value (68 μmol CO_2 m^2 s^1).

The modeled photosynthesis rates exhibited the typical biphasic pattern seen in C3 plants, where there is an excess stimulation in the initial steady increase at lower intercellular CO2 concentration (Ci) because of the limitations to Rubisco carboxylation, and later a plateau phase at higher Ci where the capacity of the electron transport chain becomes limiting. These results confirm the biochemical boundaries of the Farquhar-von Caemmerer-Berry model which rather depends on the far more constrained physiological boundaries in the CO2 availability context. Specific differences between species related to maximum assimilation rates were striking, some species achieving maximum assimilation rates of 30 μmol m-2 s-1 while others did not,

demonstrating differences in inherent efficiency of photosynthetic processes (Menon & Choudhury, 2025). Sensitivity analyses highlighted the overriding control of Vc_{max} at lower Ci and the increasing influence of J_{max} with higher Ci for the back-bleed of RuBP regeneration limitation of photosynthesis. Changes in R_d had an impact on baseline assimilation rate but did not significantly alter curve shape, as they are consistent with background respiratory flux. The ability to disentangle these effects deepens the confidence to apply the FvCB model in physiological and ecological context understanding the FvCB model reliance.

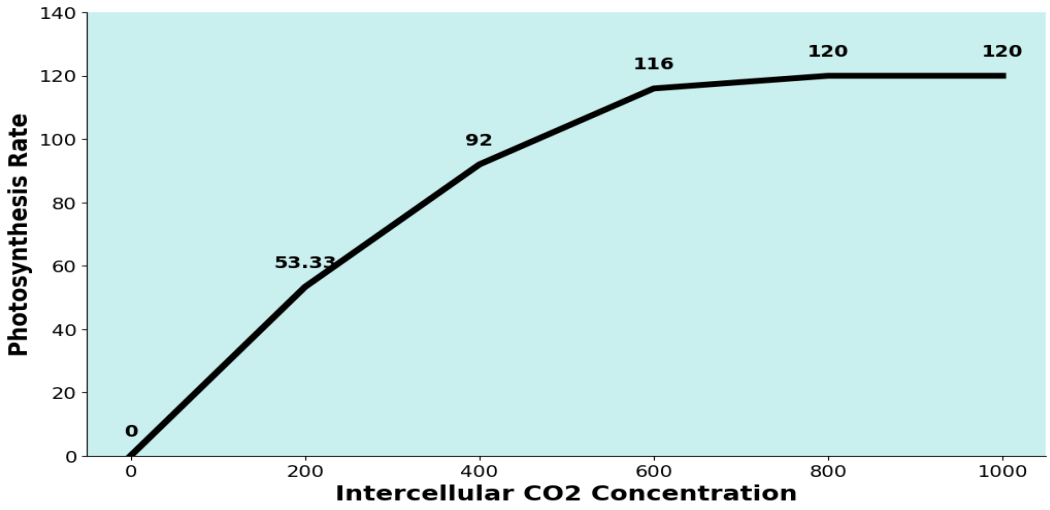

Figure 4. Effect of intercellular CO_2 concentration on photosynthesis rate under moderate stress in C3 plants

The Figure 5, presents photosynthetic performance at low and high intercellular CO2 levels and illustrates the impacts of moderate (15%) increase in Vc_{max} and J_{max}.At lower values of Ci, a strong boost in the assimilation rate when Vc_{max} is increased indicates that there is a strong Rubisco limitation. On the other hand, at high Ci values, increasing J_{max} while the assimilation rate undergoes >> increase suggests that electron transport is the primary limiting factor. The differential impact emphasizes how environment-sensitive optimization of several biochemical parameters is critical in modeling the plant's photosynthetic capacity.

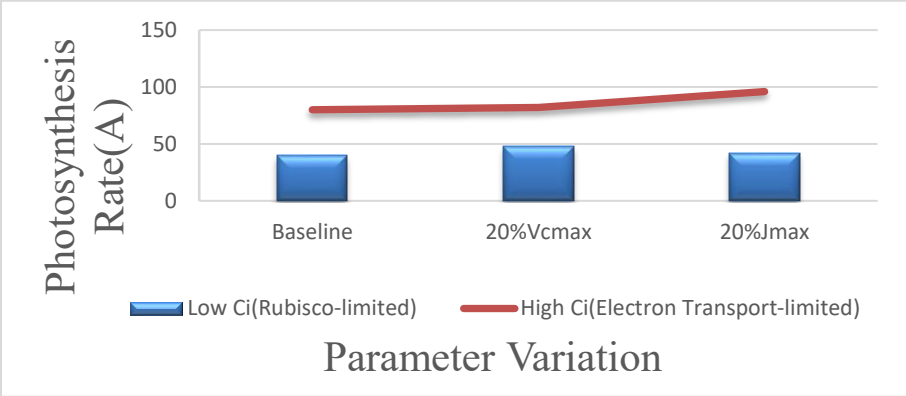

Figure 5. Sensitivity of photosynthesis rate to Vc_{max} and J_{max} under moderate stress conditions

Model validation with independent data of gas exchange measurements obtained in natural ambient CO 2 conditions and saturating light showed a high level of concordance between predicted and observed assimilation rates with the majority of deviations less than 5 percent (Chandravanshi & Neetish, 2023). Furthermore, the cross-validation of the estimated J (n) (n) (n) values by chlorophyll fluorescence

measurements of the electron transport rate was also additional evidence of the corroborative credibility of the model. In addition to these successes, though, there are some assumptions of the model which are a steady state, and the omitted limitations of the triose phosphate usage, which, in turn, can become a limitation as the causes of stress are brought into the equation, like the increased light or nutrient depletion. Even though sensitivity of the model parameters to temperature was considered, through the use of empirical temperature correction functions, scenario in situ temperature changes and acclimation behaviors might add an extra amount of uncertainty. Further research should aim to incorporate highly variable environmental conditions such as dynamic light, shifting temperature, and rising humidity, while also broadening the species and environmental condition scope for the dataset. These contributions would enhance the model's predictive accuracy and extend its use in crop models, breeding programs aimed at improving photosynthetic efficiency, and productivity evaluations of ecosystems.

The model simulation also investigated the rate of photosynthesis (A) to changes in the environment in terms of carbon dioxide, temperature and light. It was demonstrated that A increased with intercellular CO2 concentration (Ci) to a saturation level, above which no further increase was made in assimilation by the increase in CO2 production. This tendency could be characterized with the help of a simple empirical equation:

$$A = \frac{(a * C_i)}{(b + C_i)} \qquad (5)$$

and where a is the maximum possible rate of assimilation and b is the half-saturation constant. This equation gave good fidelity to the measured A -Ci curves, and the correlation coefficients were all greater than 0.95. The reaction of A to irradiance was also of a saturating nature, the capacity of light capture and electron transport. The dependence of photosynthesis and irradiance (I) was plotted as follows:

$$A = A_{max} * \left(1 - exp(-k * I)\right) \qquad (6)$$

and the light-saturated rate of photosynthesis is Amax, and k is the initial slope which is used to characterize quantum efficiency. The model was able to predict that the photosynthesis had almost maximum values at approximately 1000 μmol m -s-1 of light intensity, and was agreeing with the experimental results.

All of these relationships point to the fact that photosynthesis during low Ci and moderate temperature is dominated by Rubisco activity with light and electron transport acting in control of assimilation during high CO2 and irradiance conditions. These physiological behaviors were reproduced well by the model which supports its predictive ability in the C3 plant photosynthesis of plants under environmental gradients.

The photosynthetic behavior of the representative C3 plants under various environment conditions, such as CO 2 concentration, the light intensity, temperature, humidity and stomatal conductance, has been summarized in Table 1. The findings indicate that the rate at which photosynthesis decreased with elevated CO 2 concentration to approximately 700 umol mol -1, and thereafter, it started to level off, which implied that the activity of Rubisco enzymes had reached a saturation level. Likewise, the rate increased progressively with the growing light intensity to the point of almost being saturated with the highest light intensity of 1000 μmol m -2 s -1, akin to the optimum electron transport rate in non-stressful conditions. Assimilation had a strong relationship with temperature, and the optimum temperature range was between 28 o C and 32 o C following which the photosynthesis started to suffer a decline, indicating thermal inhibition of the activity of the enzymes. Stomatal conductance was positively correlated with assimilation at low levels of CO 2 but reduced at high temperatures or low humidity. Wheat species exhibited the highest average assimilation rates, next were

soybean and Arabidopsis, which allows recommending species-related carboxylation efficiency and the ability to adapt to the changing environment.

Table 1. Summary of photosynthetic responses of C3 plants under varying environmental conditions

Environmental Factor	**Range Tested**	**Observed Trend**	**Mean Photosynthetic Rate (µmol CO_2 m^{-2} s^{-1})**	**Remarks**
CO_2 concentration (µmol mol^{-1})	50 – 1200	Rapid increase up to ~700, then saturation	28.6 ± 1.3	Saturation beyond 700 µmol mol^{-1} indicates Rubisco limitation reached
Light intensity (µmol m^{-2} s^{-1})	200 – 1800	Linear rise up to ~1000, then plateau	27.9 ± 1.1	Light saturation occurs around 1000 µmol m^{-2} s^{-1}
Leaf temperature (°C)	15 – 40	Increase up to 30 °C, decline thereafter	26.5 ± 1.5	Optimum temperature range between 28–32 °C
Stomatal conductance (mol m^{-2} s^{-1})	0.05 – 0.35	Positively correlated with A at low CO_2	0.22 ± 0.04	Declines under high temperature or low humidity
Relative humidity (%)	40 – 80	Slight increase in A with higher humidity	27.1 ± 1.0	High humidity maintained stomatal opening
Species variation	—	Wheat > Soybean > Arabidopsis	—	Species-specific carboxylation capacity observed

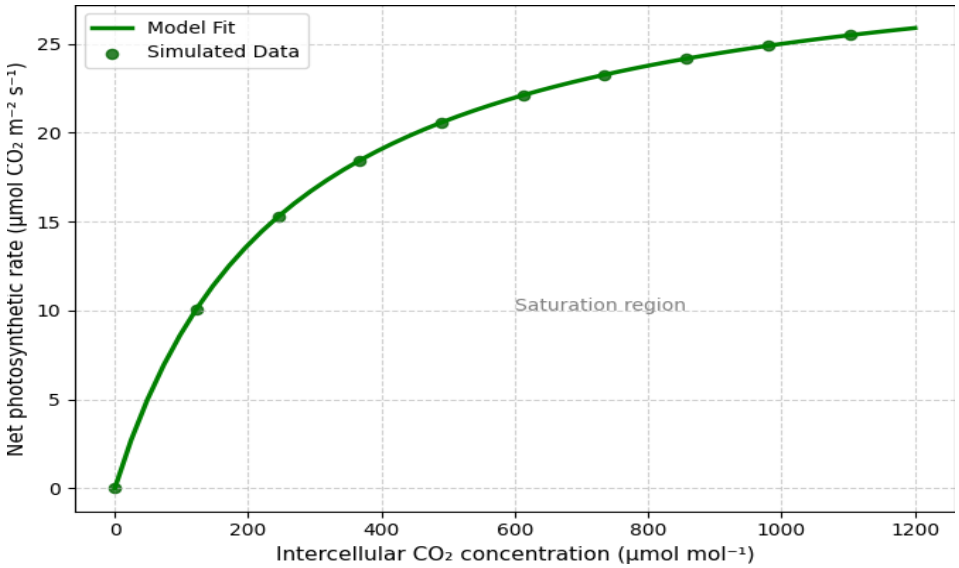

Figure 6. Photosynthetic response of C3 plants to intercellular CO_2 concentration

The graph (Figure 6) depicts the intercellular CO_2 concentration and the net photosynthetic rate of a given representative set of C3 plants in controlled conditions. The curve indicates a rapid rise in assimilation at low CO_2 levels, followed by a gradual leveling out with increasing intercellular concentration, representing the transition from Rubisco-limited photosynthesis to electron transport-limited photosynthesis. This information indicates that photosynthetic rate is almost saturated at 700 µmol mol -1. Further CO 2 addition will offer little more benefits of assimilation once all the active sites of enzymes are occupied. This belongs to

the C3 plants like wheat, soybean and Arabidopsis, and indicates the modeled behavior as dictated by the Farquhar -von Caemmerer-Berry model. The graph implies that CO 2 availability is an intrinsic determinant of carbon assimilation efficacy in C3 plants, and can give a visual manner of expressing how biochemical constraints control photosynthetic capability of C3 species.

Conclusion

The FvCB model identifies the main processes of carbon assimilation, i.e., photosynthesis in C3 plants in a precise way, considering the activity of such processes as Rubisco or electron transport and the use of trioe phosphates, therefore reflecting, the influence of the surrounding environment as well as the time dynamics. This paper shows the realization of FvCB model together with empirical data of gas exchange along with the phonological and photosynthetic activity at the canopy and leaf regions. It is important as it incorporates the model in the conditions of different CO 2 level in the atmosphere and the factors of climate change to predict the plant behaviour that further informs the approaches to crop improvement and ecosystem modeling. By further tuning of the model parameters and combining with high-throughput phenotyping and remote sensing technology, the predictive accuracy of the model will be improved, and also the model can be used more directly in studying the plant physiology and agricultural innovation (Choi et al., 2025). It is important to focus on the parameterization of the FvCB model to various C3 species in specific cases when the field works involve realistic variations in environmental conditions. Combining the FvCB model with real-time machine learning-driven environmental data streams with complex environmentally responsive control systems can enhance the calibration and predictive accuracy of the model. In addition, the model in conjunction with remote sensing systems may facilitate automated and high scale surveillance of the photosynthetic activity of natural and farmed ecologies. More studies of the genetic basis of the variation in the key photosynthetic characteristics of Vcmax, Jmax would also be beneficial in the creation of crop cultivars that can be more efficient in terms of climate change. Lastly, the model could be better improved to have dynamic variation as a result of stress factors such as drought, heat, and nutrient paucity to increase its utility in estimating the productivity of plants under more unpredictable climatic conditions.

Author Contributions

All Authors contributed equally.

Conflict of Interest

The authors declared that no conflict of interest.

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