

Parameterization of Photoinhibition for Phytoplankton

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**This file contains the supplementary material for the manuscript titled
Parameterization of Photoinhibition for Phytoplankton.**

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Supplementary methods.

Introduction. A photosynthesis-irradiance (PI) curve describes the relationship between light availability and the photosynthetic rate in photoautotrophic organisms. It typically consists of three distinct regions: the light-limited region, where photosynthetic rate increases approximately linearly with irradiance; the light-saturated region, where photosynthesis reaches a plateau due to physiological constraints; and the photoinhibition region, where excessive light leads to a decline in photosynthetic rate due to photodamage. In some experiments the treatment irradiances used are not high enough to observe photoinhibition. The plateau of the curve represents the highest sustained photosynthetic rate. Since we focus on modeling the photoinhibition portion of the PI curve any reference to the *plateau* should be understood as the plateau in the presence of photoinhibition.

Identification of candidate models. We developed a list of photoinhibition models used in the literature (Table 1). One model that could not be reliably fit to data was excluded from our analysis¹. Two piecewise-defined models (Neale & Richerson 1987² with $I_T > 0$ and an alternate version of the extended Blackman 1905³ model with two independent photoinhibition parameters, β and I_β) were excluded as many of the PI curves with photoinhibition did not have sufficient data to reliably estimate the threshold irradiance where two pieces joined. We note that gathering enough data to resolve this transition is challenging as a practical matter as the experiment must be designed to sample photosynthetic rates at several irradiances near the transition, but the value of this irradiance is not known in advance, meaning a very large number of closely spaced irradiances must be used in the probable range where photoinhibition initiates. We included a piecewise photoinhibition model as an extension of Blackman 1905³ where the transition irradiance between the linear segments was defined by α , β , and $P_{\max}$. We created four new photoinhibition models based on light-saturating models in the literature⁴⁻⁷ by combining these models with the exponential model for photoinhibition (Eq. 2), by analogy with the Platt et al. 1980⁸ and Webb et al. 1974⁹ models. We have standardized and sometimes simplified the notation from published sources. We added six new photoinhibition models based on our use of a reciprocal function of irradiance and named them after the functional forms of the light-saturating and photoinhibition parts of the model (tanh-tanh, exp-tanh, tanh-exp, and exp-exp). When we used the hyperbolic tangent function for the photoinhibition formulation, we made two more versions with a fifth parameter for the shape factor noted by including a suffix γ on the model name. All equations are written using the notations I_α , I_β for the irradiance parameters associated with light saturation and photoinhibition. All models can be reformulated in terms of α , β , and $P_{\max}$ using the relations $I_\alpha = P_{\max}/\alpha$ and $I_\beta = P_{\max}/\beta$. In the literature P_s is often used instead of $P_{\max}$ and frequently the photosynthetic capacity is smaller than P_s ($P_{\max} < P_s$). For models with a unique optimum, a saturation irradiance, I_{sat} , is computed by setting $dP/dI = 0$. Formulae for interconversion of parameters are provided when available in Table S2.

Classification of PI curves as linear, saturating response, or exhibiting photoinhibition. We classified each PI curve by fitting the following three models to data for each PI curve:

$$P = \alpha I \quad (L)$$

$$P = P_{max} \frac{(I + I_\alpha - |I - I_\alpha|)}{2I_\alpha} = \begin{cases} \alpha I, & I < I_\alpha \\ P_{max}, & I_\alpha \leq I \end{cases} \quad (SR)$$

$$P = \begin{cases} \alpha I, & I < I_\alpha \\ P_{max}, & I_\alpha \leq I < I_\beta \\ P_{max} - \beta(I - I_\beta), & I_\beta \leq I \end{cases} \quad (P)$$

We used adjusted R^2 to score each model fit and for each PI curve selected the model with the smallest RMSE. Information criteria (e.g. AICc, BIC) tend to favour the L and SR models as many observations were made at sub-saturating irradiances and relatively few observations are made at irradiances that are photoinhibiting, even when photoinhibition is clearly present.

Model evaluation. The summary statistics used to assess model fits were computed as

$$R_{adj}^2 = 1 - (1 - R^2) \frac{n-1}{n-p-1},$$

where R^2 is the standard coefficient of determination representing the fraction of variability in the response variable explained by the model, n is the number of observations, and p is the number of parameters in the regression,

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - \hat{P}_i)^2}$$

where P_i and $\hat{P}_i$ are the i^{th} observation and corresponding model prediction of photosynthetic rate,

$$AICc = \ln L + 2p(p+1)/(n-p-1),$$

where L is the likelihood defined as

$$L = (2\pi\sigma^2)^{-n/2} \exp\left(-\frac{1}{2\sigma^2} \sum_{i=1}^n (P_i - \hat{P}_i)^2\right)$$

and $BIC = k \ln n - 2 \ln L$.

PI data are typically imbalanced, with many data points concentrated at low irradiances, so typical performance metrics will be weakly sensitive to photoinhibition that occurs predominantly at high irradiances. To assess model performance emphasizing the plateau

and photoinhibition regions, we computed RMSE and adjusted R^2 after omitting the light-limited portion of each PI curve ($I < I_\alpha$), with I_α estimated from the Blackman 1905 model (Table 1). This approach ensures that the imbalance in data distribution does not bias the model comparison toward better performance at low irradiances, where most models already perform well.

Simulation study to compare parameter values. We developed a simulation procedure to compare parameters estimated from a suite of models with known true values that span the distribution values in our database. The parameters for Eq. (3) with $\gamma = \cosh^2(1)$ were fit to a multivariate normal distribution of log alpha, log Pmax, log beta, and R. We drew 10,000 random samples of PI parameters, used them to generate simulated PI curves with Eq. (3) with $\gamma = \cosh^2(1)$ and estimated parameters for all PI models with photoinhibition. We compared the estimated parameter values across models to the known reference parameter value for the simulated data by computing the relative difference; e.g., for maximum photosynthesis rate in equation i ,

$$\frac{P_{max,i} - P_{max, best Eq}}{P_{max, best Eq}}.$$

Does a PI curve with photoinhibition exhibit a plateau? For each PI curve judged to exhibit photoinhibition, we determined if there was a plateau present using RMSE, BIC, and AICc statistics for the set of photoinhibition models with and without plateaus. We determined that a plateau was present if the lowest score for each PI curve was found among models with a plateau (Fasham & Platt, extended Blackman, and our six new models) compared to models without a plateau (all the remaining models in Table 1).

Interpretation of photoinhibition parameter β . In published photoinhibition models, the photoinhibition parameter indicates if photoinhibition is present ($\beta > 0$) or absent ($\beta = 0$) and larger values indicate more rapid decreases in photosynthetic rate with increases in irradiance at high irradiances. There is no further easy and consistent interpretation of the β parameter across the various models.

In our tanh-tanh- γ model (Eq. (3)) the derivative of photosynthetic rate as a function of irradiance is

$$\frac{dP}{dI} = \alpha \operatorname{sech}^2(I/I_\alpha) \tanh((I_\beta/I)^\gamma) - \beta \gamma (I_\beta/I)^{\gamma+1} \tanh(I/I_\alpha) \operatorname{sech}^2((I_\beta/I)^\gamma) \quad (S1)$$

The first term approaches zero rapidly as I/I_α increases and $\operatorname{sech}^2(I/I_\alpha) < 10^{-4}$ for $I/I_\alpha > 5.3$. Since we are focused on the derivative at $I = I_\beta$ and $I_\beta/I_\alpha > 5.5$ for 95% of our PI curves (Fig. S4), we make the approximation to neglect this first term of the derivative. In the second term, the factor $\tanh(I/I_\alpha)$ differs from 1 by less than 10^{-4} for $I_\beta/I_\alpha > 5.5$, so we neglect this factor as well. The simplified derivative evaluated at I_β is

$$\left. \frac{dP}{dI} \right|_{I=I_\beta} = -\beta\gamma \operatorname{sech}^2(1).$$

This result and the estimated value of $\gamma = 2.30 \pm 0.09$ from the tanh-tanh- γ model motivated us to select a value for the shape parameter of $\gamma = \cosh^2(1) \approx 2.38$ for the Amiran model (Table 1) which makes this derivative equal to $-\beta$. In these common cases, the photoinhibition parameter then has an easy interpretation: the slope of the decrease in photosynthetic rate near the onset of photoinhibition (Fig S2).

Re-analysis of light-saturating PI curves. We revisited the analysis of Jassby & Platt (1976)¹⁰ using the methods described here and a set of PI models without photoinhibition (Table S2).

Supplementary Results.

Re-analysis of light-saturating PI models on our database. An analysis of 1807 PI curves not exhibiting photoinhibition were consistent with the results of Jassby & Platt (1976)¹⁰ that the model with the best statistical fit to data is the hyperbolic tangent model (Eq. 1a, Table S5). The evidence we obtained in support of the Jassby & Platt (1976)¹⁰ model was not strong. There were three 3-parameter models with very similar median and mean RMSE^{5,9,10}. The Jassby & Platt (1976)¹⁰ had the nominally smallest mean RMSE, but this difference from the other two models was not statistically significant. Models with an extra shape parameter^{6,7} had smaller RMSE as expected than models without the shape parameter, but the three parameter Jassby & Platt (1976)¹⁰ model had smaller BIC and AICc for more than half of all PI curves tested.

Table S1.

Established PI curve models formulated with the parameters P_{max} , I_α , and a shape parameter γ with $0 < \gamma < 1$ for the model marked with a ‡. Models are identified by reference. All models are fit with an intercept, R , which was omitted from the table.

Name	Equation
Blackman (1905) ³	$\begin{cases} P_{max}(I/I_\alpha), & \text{if } I < I_\alpha \\ P_{max}, & \text{if } I_\alpha \leq I \end{cases}$
Baly (1935) ⁴	$P_{max} \left(\frac{I}{I + I_\alpha} \right)$
Smith (1936) ⁵	$P_{max} \left(\frac{I}{\sqrt{I^2 + I_\alpha^2}} \right)$
Talling (1957) ¹¹	$P_{max} \ln(2I/I_\alpha)$
Vollenweider (1958) ¹	$P_{max} \ln \left(\frac{I}{I_\alpha} + \sqrt{1 + (I/I_\alpha)^2} \right)$
Webb et al. (1974) ⁹	$P_{max} (1 - e^{-I/I_\alpha})$
Jassby & Platt (1976) ¹⁰	$P_{max} \tanh (I/I_\alpha)$
Prioul and Chartier (1977) ^{‡6}	$\frac{P_{max}}{2\gamma} \left(1 + I/I_\alpha - \sqrt{(1 + I/I_\alpha)^2 - 4\gamma I/I_\alpha} \right)$
Bannister (1979) ⁷	$P_{max} I (I^\gamma + I_\alpha^\gamma)^{-1/\gamma}$

Table S2.

Expressions for saturation irradiance (I_{sat}) and photosynthetic capacity (P_{max}) in terms of model parameters for six models from Table 1. These models have a parameter for a hypothetical maximum photosynthetic rate, P_s , which can be used to compute photosynthetic capacity (P_{max}). Note also that $I_{\alpha}^s = P_s / \alpha$ and $I_{\beta}^s = P_s / \beta$.

Name	Saturation irradiance, I_{sat}	Photosynthetic capacity, P_{max}
Steele 1962	$\frac{P_s}{\alpha}$	P_s
Peeters & Eileers 1978	$\frac{P_s}{\sqrt{\alpha\beta}}$	$\frac{P_s}{1 + 2\sqrt{\beta/\alpha}}$
Platt et al. 1980	$\frac{P_s}{\alpha} \ln\left(\frac{\alpha + \beta}{\beta}\right)$	$\frac{P_s}{\alpha} \left(\frac{\alpha}{\alpha + \beta}\right) \left(\frac{\beta}{\alpha + \beta}\right)^{\beta/\alpha}$
Neale & Richerson 1986	$\frac{P_s}{2\alpha} \ln\left(\frac{2\alpha}{\beta} + \sqrt{\left(\frac{2\alpha}{\beta}\right)^2 + 1}\right)$	$P_s \tanh\left(\frac{I_{\text{sat}}}{I_{\alpha}^s}\right) \exp\left(-\frac{I_{\text{sat}}}{I_{\beta}^s}\right)$
Baly 1935*	$\frac{P_s}{2\alpha} \left(\sqrt{1 + \frac{4\alpha}{\beta}} - 1\right)$	$P_s \left(\frac{I_{\text{sat}}}{I_{\text{sat}} + I_{\alpha}^s}\right) \exp\left(-\frac{I_{\text{sat}}}{I_{\beta}^s}\right)$
Smith 1936*	$I_{\text{sat}}^3 + \left(\frac{P_s}{\alpha}\right)^2 I_{\text{sat}} - \left(\frac{P_s}{\alpha}\right)^2 \left(\frac{P_s}{\beta}\right) = 0$	$P_s \left(\frac{I_{\text{sat}}}{\sqrt{I_{\text{sat}}^2 + (I_{\alpha}^s)^2}}\right) \exp\left(-\frac{I_{\text{sat}}}{I_{\beta}^s}\right)$

Table S3.

The number and percentage of PI curves, out of 1808 exhibiting photoinhibition, with the lowest RMSE, BIC, and AICc from any model with a plateau compared to any model without a plateau. The models with a plateau are Fasham & Platt (1983), the piecewise linear (Blackman) function, and the six new models developed in this manuscript. The non-plateau models are all the remaining models in Table 1.

Model set	RMSE (%)	BIC (%)	AICc (%)
Plateau	1574 (87%)	1340 (74%)	1350 (75%)
Non-plateau	234 (13%)	468 (26%)	458 (25%)

Table S4.

Summary statistics for three parameters fit to PI curves with photoinhibition using the Amirian model and four derived irradiance parameters. Reported statistics are median, geometric mean, and standard deviation reported as a percentage. Parameters are log normally distributed, so the mean and standard deviation are computed on the log of the parameters and then exponentiated. We report the standard deviation as $100(10^\sigma - 1)$ where σ is the standard deviation of the log transformed parameter values. I_α^* and I_β^* are the irradiance at which $P = 90\% P_{\max}$.

Parameter	Units	Median	Mean	SD (%)
$P_{\max}$	mg C (mg chl <i>a</i>) ⁻¹ d ⁻¹	1.92	1.71	130
α	mg C (mg chl <i>a</i>) ⁻¹ d ⁻¹ (μmol m ⁻² s ⁻¹) ⁻¹	0.0122	0.0118	110
β	mg C (mg chl <i>a</i>) ⁻¹ d ⁻¹ (μmol m ⁻² s ⁻¹) ⁻¹	0.000 980	0.000 898	150
I_α	μmol m ⁻² s ⁻¹	152	145	100
I_β	μmol m ⁻² s ⁻¹	2015	1900	98
I_α^*	μmol m ⁻² s ⁻¹	228	217	103
I_β^*	μmol m ⁻² s ⁻¹	1710	1620	98

Table S5.

Statistical summary of 1807 light-saturating model fits for PI curves without photoinhibition, ordered by increasing median root mean squared error (RMSE). The number of parameters is p . Statistics are median adjusted R^2 , median RMSE, mean RMSE, and the standard error of the mean RMSE. The mean RMSE for Smith (1936) and Webb et al (1974) are not significantly different from mean RMSE for Jassby & Platt (1976) (t-test, $p > 0.05$).

Name	p	Median R^2_{adj}	Median RMSE	Mean RMSE	s.e.
Prioul et al. (1976)	4	0.981	0.158	0.188	0.0031
Bannister (1979)	4	0.981	0.159	0.191	0.0032
Smith (1936)	3	0.979	0.168	0.202	0.0033
Webb et al. (1974)	3	0.979	0.170	0.206	0.0034
Jassby & Platt (1976)	3	0.979	0.170	0.201	0.0033
Blackman (1905)	3	0.969	0.211	0.242	0.0037
Baly (1935)	3	0.967	0.217	0.259	0.0042

Performance of the two models with lowest **mean** RMSE for each number of parameters, p , assessed as the number of times (and percentage) each model had the lowest BIC and AICc over all PI curves without photoinhibition.

Model	p	BIC	BIC (%)	AICc	AICc (%)
Jassby & Platt (1976)	3	1041	58	1052	58
Prioul et al. (1976)	4	766	42	755	42

Alternate version of the previous table comparing models with lowest **median** RMSE, which was the criterion used in Table 3.

Model	p	BIC	BIC (%)	AICc	AICc (%)
Smith (1936)	3	1102	61	1111	61
Prioul et al. (1976)	4	705	39	696	39

Table S6.

Median relative differences in parameter estimates for PI models compared to the reference formulations. The Jassby & Platt 1976 equation (Eq. 1a, Table S1) serves as the reference for light-saturating models, while the Amirian equation (Table 1) is used for photoinhibition models. Models with additional shape parameters are excluded from this comparison. Models capable of capturing the plateau are denoted with †. The Median Absolute Deviation (MAD) as a robust measurement used to mitigate outlier impact, instead of Standard Deviation.

Name	$P_{\max} \pm \text{MAD}$	$\alpha \pm \text{MAD}$	$I_{\alpha} \pm \text{MAD}$	$\beta \pm \text{MAD}$	$I_{\beta} \pm \text{MAD}$
<i>Light-saturating Models</i>					
Blackman (1905)	-0.06 ± 0.01	-0.22 ± 0.06	0.21 ± 0.08		
Baly (1935)	0.25 ± 0.03	1.09 ± 0.22	-0.41 ± 0.07		
Smith (1936)	0.05 ± 0.01	0.11 ± 0.02	-0.06 ± 0.02		
Webb et al. (1974)	0.05 ± 0.01	0.39 ± 0.04	-0.25 ± 0.02		
<i>Photoinhibition Models</i>					
Steele 1962	0.01 ± 0.05	-0.81 ± 0.09	4.14 ± 1.98	...	...
Peeters & Eilers 1978	0.28 ± 0.17	1.87 ± 1.23	-0.58 ± 0.20	0.60 ± 0.57	-0.21 ± 0.37
Platt et al. 1980	0.13 ± 0.11	0.23 ± 0.32	-0.06 ± 0.25	0.18 ± 0.36	-0.05 ± 0.34
Neale & Richerson 1987	0.13 ± 0.12	-0.09 ± 0.21	0.25 ± 0.31	0.05 ± 0.34	0.08 ± 0.39
Baly 1935*	0.03 ± 0.09	1.14 ± 0.70	-0.52 ± 0.17	0.27 ± 0.29	-0.16 ± 0.22
Smith 1936*	0.11 ± 0.10	-0.02 ± 0.23	0.16 ± 0.32	0.24 ± 0.37	-0.10 ± 0.28
exp-tanh [†]	0.01 ± 0.01	0.40 ± 0.04	-0.28 ± 0.02	0.01 ± 0.01	0.00 ± 0.01
tanh-exp [†]	0.53 ± 0.20	0.42 ± 0.42	0.01 ± 0.26	0.25 ± 0.28	0.14 ± 0.29
exp-exp [†]	0.53 ± 0.20	0.80 ± 0.49	-0.26 ± 0.19	1.11 ± 4.87	0.12 ± 0.29

Figure S1.

Location and timing of phytoplankton samples used to quantify PI curves.

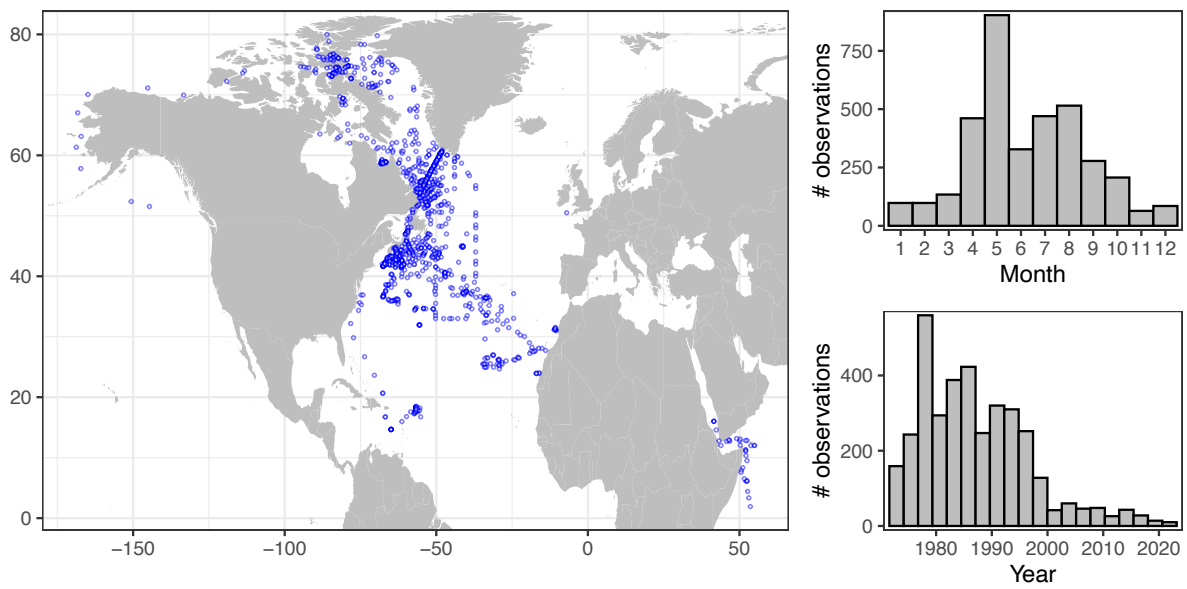


Figure S2.

Visualization of the Amirian model (Eq. 3, with $\gamma = \cosh^2(1)$) illustrating photosynthetic response with and without photoinhibition. The gray dashed line represents the case without photoinhibition ($\beta = 0$), while the black solid line includes photoinhibition ($\beta > 0$). Model parameters are $P_{\max} = 1$, $\alpha = 0.1$, $\beta = 0.01$, and $I_\beta = P_{\max} / \beta$. The red dashed line indicates the rate of photoinhibition, equal to $-\beta$ at the onset of photoinhibition (I_β).

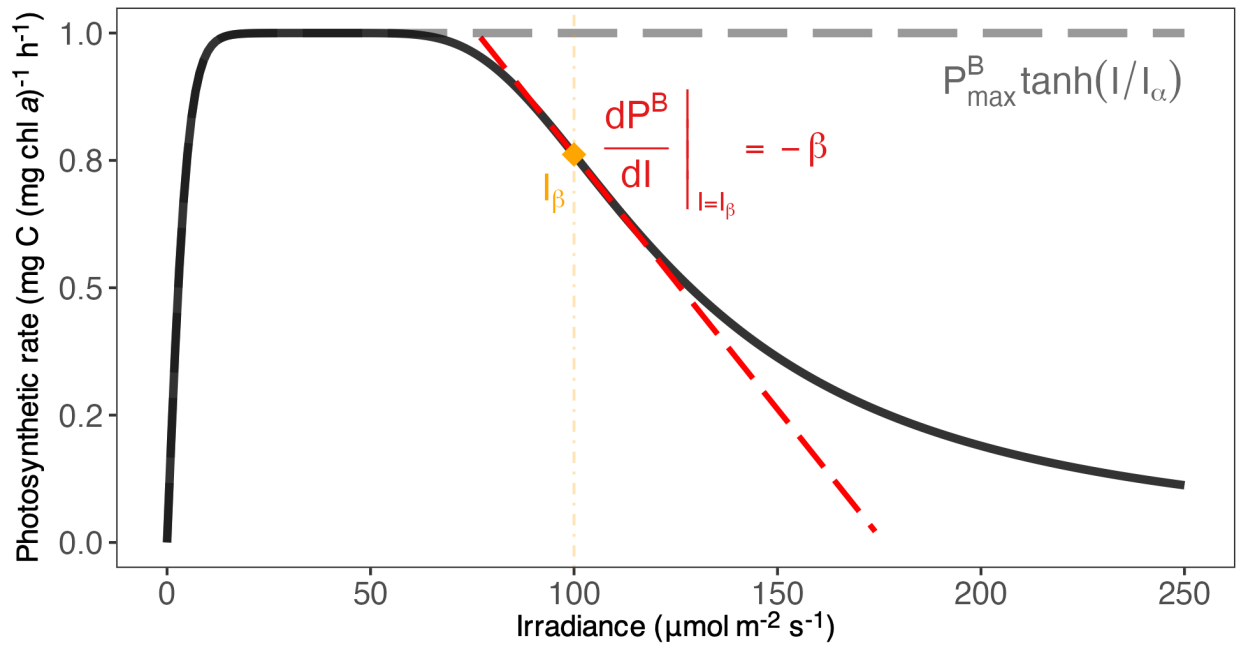


Figure S3.

Median root mean squared error difference (RMSED) for 10 photoinhibition models relative to the Amirian model (points with 95% confidence interval) over all PI curves. The upper horizontal axis is a dimensionless RMSED scaled by the median RMSE of the Amirian model. The mean RMSE (not shown) is significantly larger (t-test, $p < 0.0001$) for all models compared to the Amirian model. The dotted line indicates the location of the Amirian model (0 RMSED).

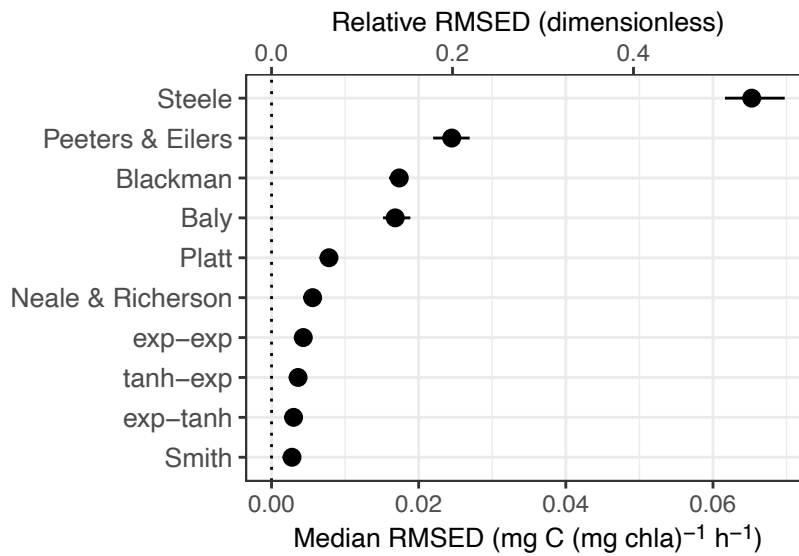


Figure S4.

Distribution of α , β ($\text{mg C (mg chl a)}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1} \text{h}^{-1}$), I_α , I_β ($\mu\text{mol m}^{-2} \text{s}^{-1}$), $I_\beta/I_\alpha = \alpha/\beta$ (dimensionless) and $I_\beta - I_\alpha$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$) on log scales. Parameter values are from fits to the Amiran model for PI curves with photoinhibition where β is significantly larger than 0 ($n = 1701$).

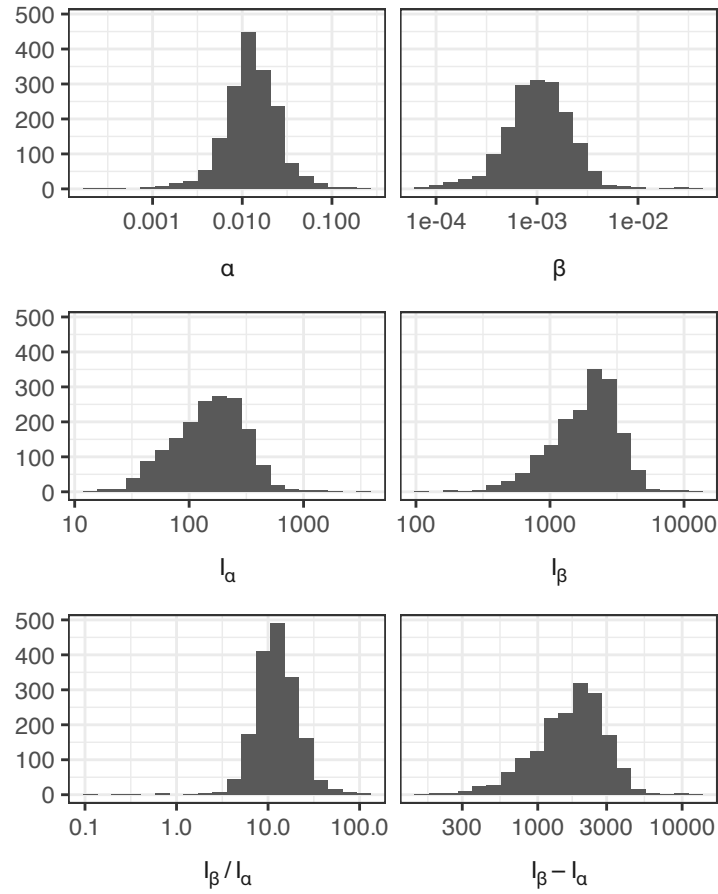


Figure S5.

Two-dimensional histograms of pairs of $P_{\max}$, α , and β on log scale from PI curves with photoinhibition fit to the Amiran model. Pairwise correlations of logarithm of these parameters are: $\text{cor}(P_{\max}, \alpha) = 0.57$, $\text{cor}(\alpha, \beta) = 0.68$, $\text{cor}(P_{\max}, \beta) = 0.74$.

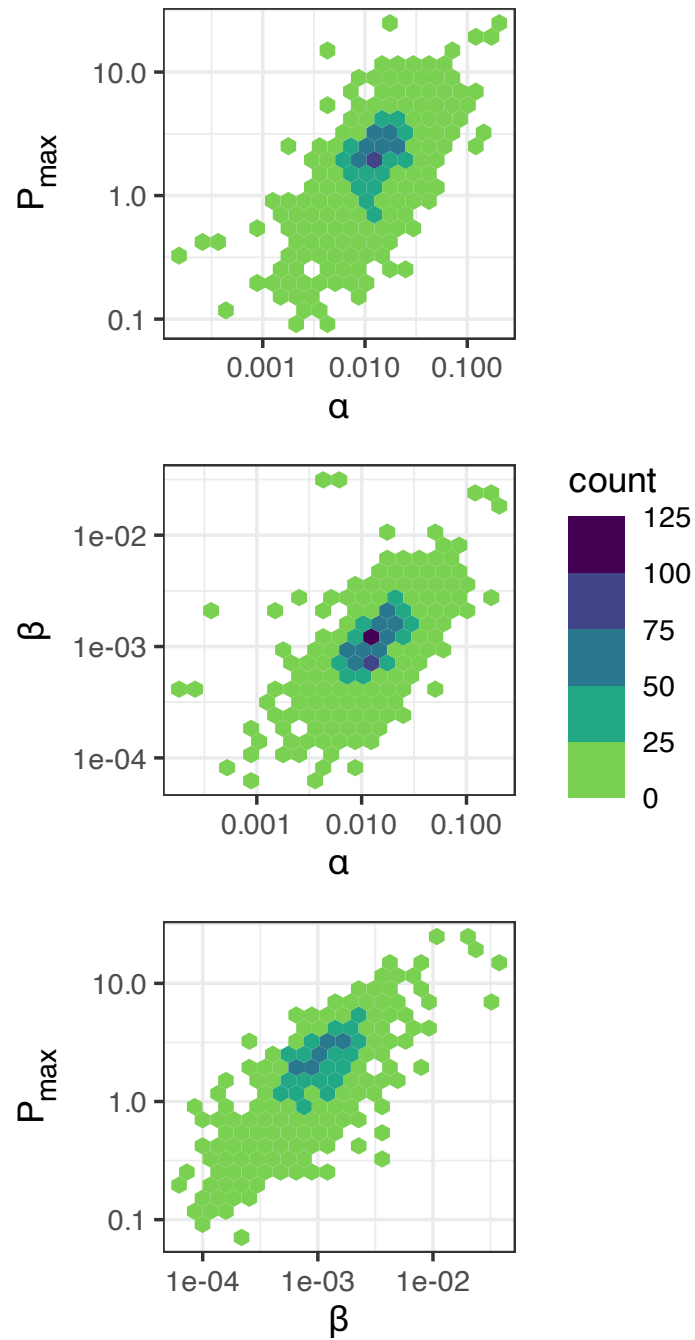


Figure S6.

Density of PI parameters $P_{\max}$ and α from the Amiran model for PI curves with and without photoinhibition in the data. Median values of $P_{\max}$ (1.92 with and 3.42 without photoinhibition) are 44% smaller when photoinhibition is detected, while median values of α (0.056 with and 0.062 without photoinhibition) are 9% smaller when photoinhibition is detected. Mean values are statistically different between PI curves with and without photoinhibition for both parameters (t-test, $p < 0.01$).

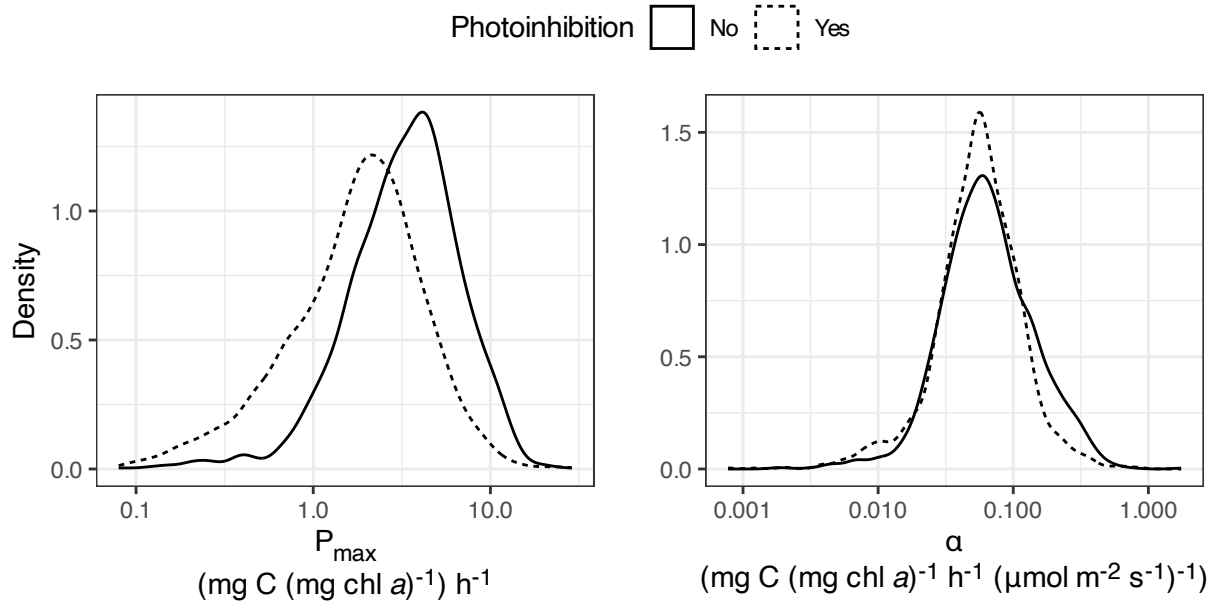


Figure S7.

Comparison of model outputs from the commonly used Platt model (Eq. 2; red lines) and the Amirian model (Eq. 3, with $\gamma = \cosh^2(1)$; black lines), each with associated 95% prediction confidence intervals. The models are fit to data from two photosynthesis-irradiance experiments exhibiting different degrees of photoinhibition¹².

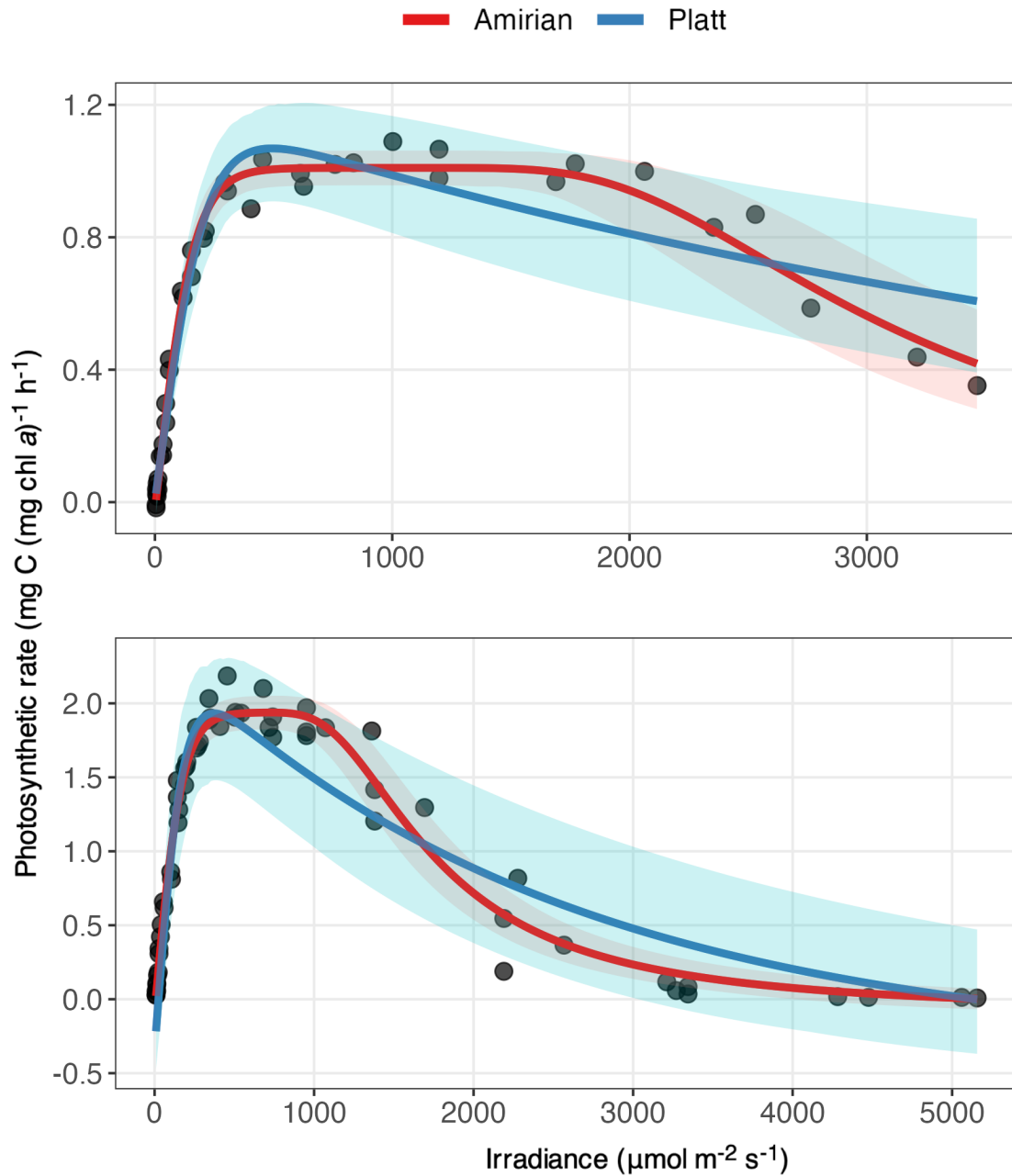


Figure S8.

Display of Amirian model (Eq. 3, with $\gamma = \cosh^2(1)$), decoupled into light saturated and photoinhibited components.

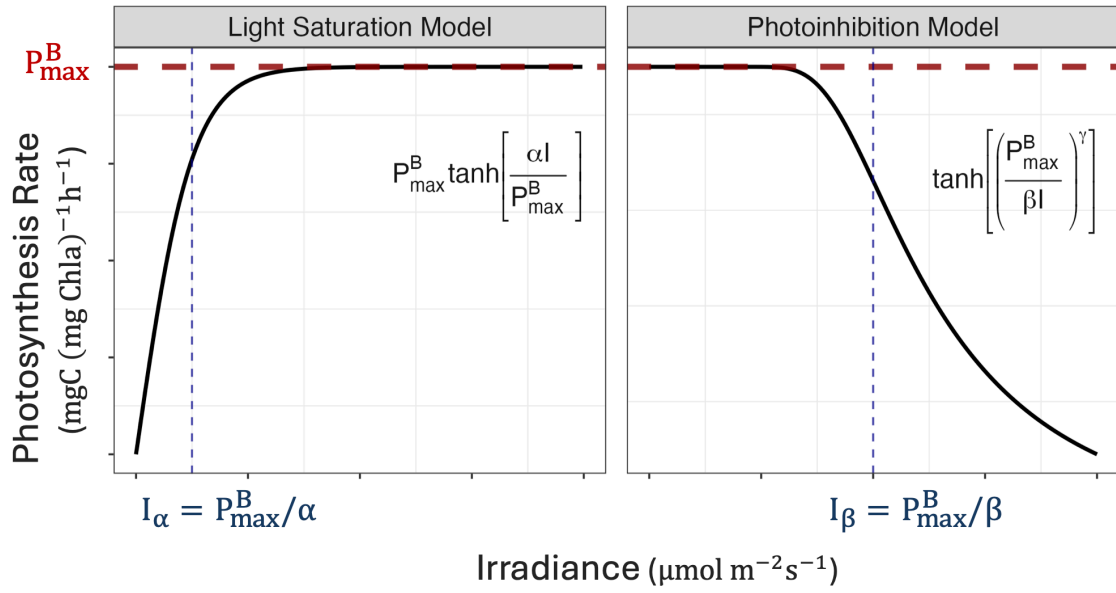
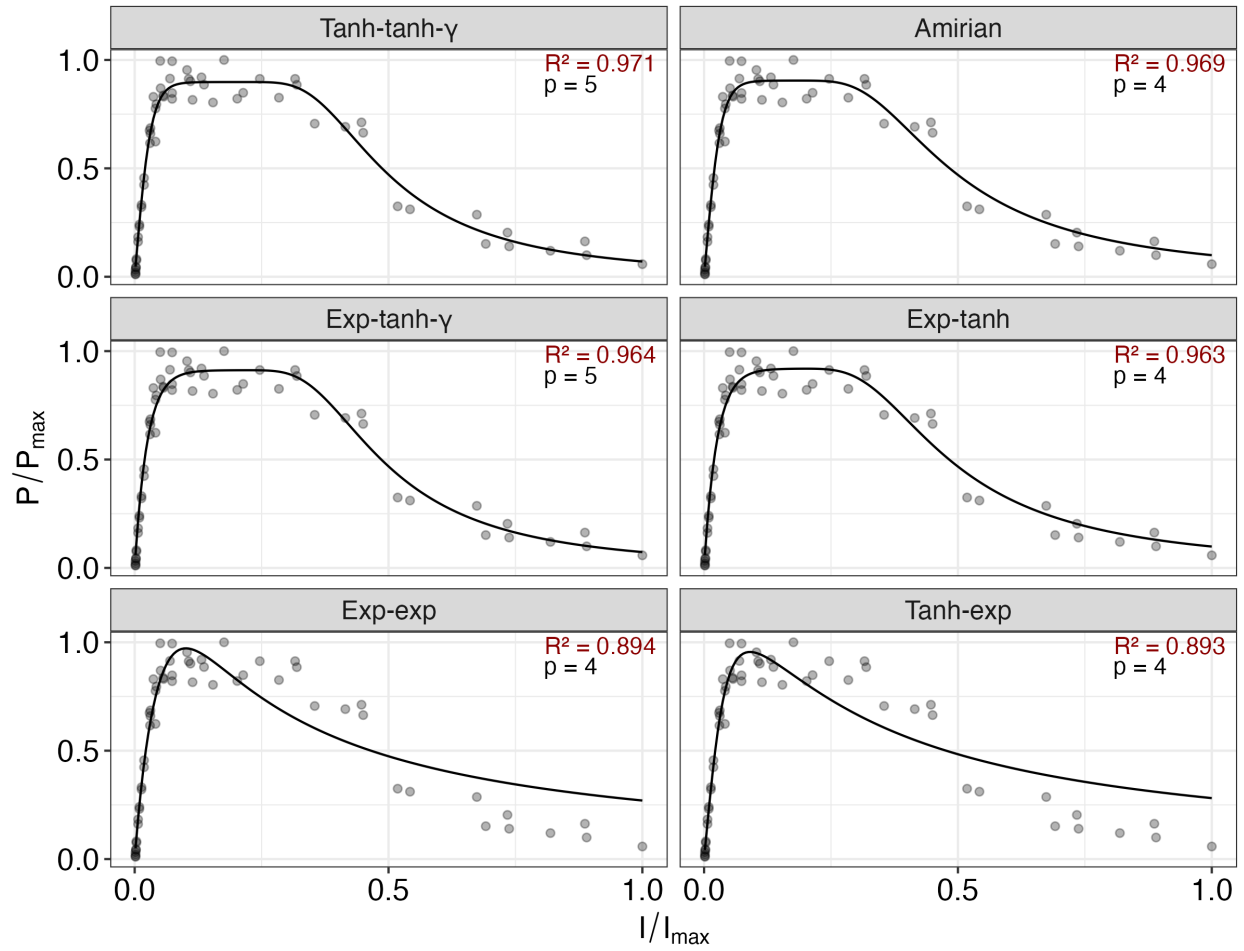


Figure S9.

Comparison of the Amirian model (Eq. 3, with $\gamma = \cosh^2(1)$) with other models developed in this work (Table 1), applied to a photosynthesis-irradiance data sample¹². Models (black lines) are sorted from best to worst based on R^2 performance (shown in red), and the value of p indicates the number of parameters in each model.



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