

Response to Reviewer Comments for DOI: 10.5194/bg-2023-163

Anonymous Referee #1: *The manuscript by Neri et al. explored how maximum PSII yield changes with PFT and climate using data collected from the literature. The research topic was of great importance for the global carbon cycle, and implementing the idea in terrestrial biosphere models will help improve the model predictions. The manuscript was overall well written, and ideas were well-delivered. While I am convinced about the importance of the idea, I have some concerns about the research and analyses performed. Below are two primary issues I found, and I hope they are useful for the authors.*

Response: We appreciate this reviewer's comments and careful reading of the manuscript, and the insights provided to us. We have carefully considered each question raised and will revise the manuscript accordingly. Our responses to each specific comment are as follows.

1. *Simply modifying $\Phi_{PSII_{max}}$ is not adequate for photosynthesis and thus fluorescence models. For example, if the change of $\Phi_{PSII_{max}}$ is due to those of the rate constants, such as K_d , K_f , K_n , and K_{pmax} , prescribing $\Phi_{PSII_{max}}$ will only impact the calculation of electron transport rate J and thus A_j and A_{gross} . However, the subsequent q_L , NPQ , and Φ_f calculations will not be accurate as the $K_d/f/n/pmax$ are not changing accordingly. Therefore, a more process-focused model to explain $\Phi_{PSII_{max}}$ will be more useful. For example, the van der Tol et al. (2013) fluorescence model assumed that K_d is temperature-dependent to explain the temperature dependency of Φ_f on temperature. A similar approach, such as a revised K_n (temperature) function, can be taken here.*

Response: We agree with the reviewer that prescribing $\Phi_{PSII_{max}}$ as a function of temperature only directly impacts the estimation of A_j , and a more process-focused model, such as the van der Tol et al. (2013) or the Gu et al. (2023) approach, will be more useful for parameterizing overall effects of temperature on photosynthesis and thus fluorescence models. Following the van der Tol et al. (2013) approach, integrating our global-scale PAM datasets to parameterize the temperature- $K_d/f/n/pmax$ function is straightforward. For example, the temperature function of $\Phi_{PSII_{max}}$ developed in our study can be directly applied into the x function in van der Tol et al. (2013), which would enable the simulation of K_n variation with temperature.

However, as already alluded by this reviewer, photosynthesis is a multi-stage phenomenon. Gu et al. (2023) separated photosynthesis into three stages of reactions – photophysical reactions, photochemical reactions, and biophysical reactions. These three stages have both mutually dependent and independent reactions, including temperature responses. This means that a temperature response in one stage can appear as if it is in a response in another stage. The ability to distinguish independent from dependent temperature responses is essential in this approach and will have to be achieved through mechanistic process understanding. Enzymatic reactions of biochemistry, e.g., carboxylation and oxygenation, have both well-understood and well-quantified temperature responses (*i.e.*, the Farquhar biochemical model of photosynthesis). The Marcus theory of electron transfer in proteins can be used to similarly describe the temperature response of the photochemical reactions (Gu et al. 2023). Currently, however, the precise mechanisms of temperature response of photophysical reactions, which include those of different rate constants that directly affect $\Phi_{PSII_{max}}$ and thus are important to the present study, are not well understood.

We believe that an empirical parameterization of the independent temperature response of $\Phi_{PSII_{max}}$ is an effective strategy for modeling the temperature effects of photophysical reactions because $\Phi_{PSII_{max}}$, which is equal to $K_{pmax}/(K_f + K_d + K_{ni} + K_{pmax})$, is an integrative quantity of photophysical reactions and is key to modeling J , A_j , and A_{gross} . Here K_f , K_d , K_{ni} , and K_{pmax} are the rate constants for fluorescence,

constitutive heat dissipation, energy-independent non-photochemical quenching (NPQ), and photochemistry when PSII reaction centers are fully open. Without an understanding of the processes that may control the dynamics of these rate constants, we are concerned that empirically parameterizing temperature responses of individual rate constants may run into the risk of mixing the independent and dependent temperature responses and lead to erroneous interpretations. This is a legitimate concern because none of the rate constants can be monitored directly under natural conditions. $\Phi_{\text{PSII}_{\text{max}}}$ can be monitored directly, however. A conservative strategy at present is to treat K_f and K_d as physical properties of pigment molecules and assume they are insensitive to temperature under typical physiological conditions (see for example curve a in Fig 1 of Pospisil et al. 1998; Fig 6 of Tesa et al. 2018). Note that even if K_f or K_d have no temperature dependence, the energy allocated to fluorescence or constitutive heat dissipation *in vivo* can still be temperature dependent because of the coupling between different energy dissipation pathways and because of the feedbacks from the photochemical and biochemical reactions on the photophysical reactions.

A full modeling of temperature responses of photosynthetic variables, including q_L , NPQ, and Φ_F , can be achieved by coupling the photophysical reactions (Gu et al., 2019), photochemical reactions (Gu et al., 2023), and the Farquhar biochemical model (Farquhar et al., 1980), with the support of the temperature dependence modeling of $\Phi_{\text{PSII}_{\text{max}}}$ provided by this study. We are currently still working on this coupling, which is a large undertaking, and is beyond the scope of this current study. **The present specific study aims** to (1) provide a global scale parameterization of temperature responses of $\Phi_{\text{PSII}_{\text{max}}}$ and its variability across plant functional types and illuminate a so-far poorly understood dynamic trade-off between tolerance and resilience of the temperature- $\Phi_{\text{PSII}_{\text{max}}}$ relationship and (2) demonstrate how incorporating climatology into analysis of the temperature- $\Phi_{\text{PSII}_{\text{max}}}$ relationship can improve the prediction of $\Phi_{\text{PSII}_{\text{max}}}$. Acquiring this knowledge is important for understanding and predicting temperature regulation on electron transport rates and A_J , which has been underrepresented in the current photosynthesis model (e.g., Farquhar model, Collatz model), compared with the thorough consideration of temperature controlling photosynthetic capacity parameters (V_{cmax}) and biochemical kinetics parameters. Moreover, understanding the differences in tolerance and resilience of the temperature- $\Phi_{\text{PSII}_{\text{max}}}$ relationship among different PFTs will facilitate our assessment of the photosystem II efficiency of diverse PFTs under climate change and climate extremes.

Considering this manuscript is already fairly long, we prefer not to include integrated parameterization of the temperature- $K_d/f/n/p_{\text{max}}$ function. Instead, we will integrate the reviewer's suggestion with our ongoing effort, which is employing the global-scale PAM dataset and temperature- $\Phi_{\text{PSII}_{\text{max}}}$ functions from this study to parameterize the integrated temperature effects on light partitioning and photosynthesis in the fluorescence-enabled photosynthesis model, as described in our previous study (Gu et al., 2019). To respond to the reviewer's comment, we will revise the introduction (L105-115) to better refine the scope and aim of this study. We will also revise the discussion section: 4.5 Uncertainty and future work (L773-777) to highlight that this is only the first step on the road of mechanistic fluorescence-enabled photosynthesis modeling. We will outline the subsequent work built upon this study.

Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980) "A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species." *Planta* **149**: 78-90.

Gu, L., et al. (2019). "Sun-induced Chl fluorescence and its importance for biophysical modeling of photosynthesis based on light reactions." *New Phytologist* **223**(3): 1179-1191.

Gu L, Grodzinski B, Han J, Marie T, Zhang Y-J, Song YC, Sun Y. 2023. “An exploratory steady-state redox model of photosynthetic linear electron transport for use in complete modeling of photosynthesis for broad applications.” Plant, Cell and Environment **46**: 1540-1561.

Pospíšil P, Skotnica J, Nauš J (1998) Low and high temperature dependence of minimum F0 and maximum FM chlorophyll fluorescence in vivo. Biochimica et Biophysica Acta 1363 1998 95–99.

Tesa M, Thomson S, Gakamsky A (2018) Temperature-dependent quantum yield of fluorescence from plant leaves. AN P41, Edinburgh Instruments.

According to our responses, the revised texts in the manuscript will include:

On lines 105-115: “Our previous effort (Gu et al., 2019) has modelled the leaf-level SIF-GPP dynamics as a function of NPQ, q_L , $\Phi_{PSII_{max}}$, and the absorbed photosynthetically active radiation (APAR). That study pointed out a need for mechanistic descriptions of how NPQ, q_L , and $\Phi_{PSII_{max}}$ respond to environmental conditions to accurately predict environmental regulation on the GPP-SIF relationship at the leaf level. By empirically fitting the NPQ rate coefficient with a function of relative light saturation and combining it with the biochemical reactions-centered photosynthesis model, van der Tol (2013) estimated the responses of leaf-level fluorescence yield to changing temperature, light, and CO₂ concentration, indicating that quantifying environmental responses of photochemical yield is the key step of addressing the integrated environmental impacts on SIF-GPP dynamics. Therefore, here we present a novel model of $\Phi_{PSII_{max}}$ response to temperature variation by collecting and applying a global-scale database of published PAM measurements, with an emphasis on parameterizing the different temperature resilience and tolerance of various plant functional types (PFTs) and investigating how habitat climatology may affect this temperature- $\Phi_{PSII_{max}}$ relationship. This study will deliver the first global-scale quantification of temperature impact on photosystem II efficiency and its variability across PFT and habitat climatology and build a theoretical basis for assessing vegetation light utilization potential for carbon sequestration under climate change and climate extremes. Modeling temperature regulation on $\Phi_{PSII_{max}}$ is important for assessing extreme temperature impacts on the maximum electron transport rate (J_{max}) in biochemical reactions-centered photosynthesis models. Moreover, characterizing the temperature response of $\Phi_{PSII_{max}}$ will allow us to connect other light partitioning mechanisms to temperature change, building the first step of resolving coupled SIF and GPP responses to temperature change. With the support of the temperature dependence modeling of $\Phi_{PSII_{max}}$ provided by this study, a full modeling of temperature responses of photosynthetic variables, including q_L , NPQ, and Φ_F , can be achieved by coupling the photophysical reactions (Gu et al., 2019), photochemical reactions (Gu et al., 2023), and the Farquhar biochemical model (Farquhar et al., 1980).

On lines 773-777: “ $\Phi_{PSII_{max}}$ (F_v/F_m) is a ratio composed of the minimum and maximum level of chlorophyll fluorescence from a dark-adapted leaf (Tietz et al., 2017). In future work, we will further isolate the temperature-dependent changes between these two variables and link derived temperature- $\Phi_{PSII_{max}}$ functions in this study with the estimation of relative light saturation and rates of other energy dissipation pathways. These future efforts will allow clarification if the decline in $\Phi_{PSII_{max}}$ is due to a rise in energy-independent NPQ or a change in the availability of PSII reaction centers for photochemistry.”

2. *The authors did not distinguish “response” and “acclimation” in the analyses. For example, let us again assume $\Phi_{PSII_{max}}$ change is due to those of K_d , K_f , K_n , and K_{pmax} here. If*

*Kd = a1*T + b1 for plants grown in the C1 environment and Kd = a2*T + b2 for plants grown in the C2 environment, the function a*T + b is “response” (related to temporary changes in the environment), and shift from a1*x + b1 to a2*x + b2 is “acclimation” (related to long term changes in climate). Therefore, it is likely that the data analyzed is a mixture of “response” and “acclimation”, and attributing all the changes in Phi_PSIImax is inappropriate. Without distinguishing the two, the analyses performed might be biased.*

Responses: Thanks for a clear explanation of “response” vs “acclimation”. This is a great point. Distinguishing response and acclimation is important for clarifying two key results from this manuscript. First, the temperature- $\Phi_{PSII_{max}}$ function developed for each PFT is referred to as the “temperature responses” of a specific PFT (Section 3.1). Second, Section 3.2 (Climatology influence on the temperature- $\Phi_{PSII_{max}}$ function) addresses how PFT-specific temperature- $\Phi_{PSII_{max}}$ responses can “shift” with habitat climatology by quantifying the regression of temperature resilience and tolerance parameters on the climatological temperature index (CTI) (Figure 6) and comparing the differences between these CTI-informed and PFT-specific temperature tolerance metrics and resilience parameters of plant $\Phi_{PSII_{max}}$ values (Figure 10).

The discussion of section 3.2 aims to test a core hypothesis that climatological temperature regulates the temperature tolerance and resilience of $\Phi_{PSII_{max}}$ ‘in the wild’, therefore shifting different PFT’s temperature- $\Phi_{PSII_{max}}$ responses toward converged responses to the climatology of their “similar” local habitat. Considering the collected dataset itself does not clearly address if “this shift” may be related to either plant’s acclimation or adaptation (evolutionary shift) to habitat climatology, we only describe “this shift” as a potential result of plant acclimation and adaptation to habitat climatology (e.g., on lines 685, 695, 725).

By definition, $\Phi_{PSII_{max}}$ is supposed to be measured on dark-adapted leaves for which energy-dependent NPQ is zero and all available PSII reaction centers are fully open. This means that the effects of short-term temperature variation are removed by the measurement protocols. In our data gathering from the published literature, we ensured that the following quality measures were met in the studies included in our dataset: an established toolset was used to perform the PAM fluorometry measurements (e.g., a Walz or other industry-standard technology), and a sufficient dark-adaptation time (generally greater than 2 hours) with preference to over-night length dark adaptation of the material before measurement.

However, we realize that the usage of “acclimation” in some locations of the text (e.g., title, abstract, L17-18, L75, L108, L115, L160-163) is not consistent in meaning with the above points. We will adjust these parts of the texts to “response” or “impact” in a revised version of the manuscript. In addition, we will revise the description of the hypothesis on line 209 as follows.

On line 209: “To test the hypothesis that climatological temperature regulates the temperature tolerance and resilience of $\Phi_{PSII_{max}}$, and therefore shifts different PFT’s temperature- $\Phi_{PSII_{max}}$ responses toward converged responses to the climatology of their “similar” local habitat, we identified...”