

Comment to the Editor

Response to Kinetic Models of Photosystem II Should Incorporate a Role for Q_B -Nonreducing Reaction Centers

The light-dependent photosynthetic reactions occurring in thylakoid membrane are very complex phenomena. Among others, chlorophyll *a* fluorescence, oxygen yield, or rate of its production, caused by single turnover flashes (STF) or continuous excitation, are the measuring techniques used to study this phenomena. However, many mechanisms have been suggested to play a role as it is known, e.g., for the case of the chlorophyll *a* fluorescence rise (for a recent review, see Lazar (1)). A mathematical model is very often used to check the correctness of a suggested mechanism. Therefore, any model is restricted to its assumptions, which are thought by its author to play a significant role in the explanation of explored experimental data; usually, a model describing only a particular mechanism is constructed. However, another model including another mechanism usually satisfactorily describes the same experimental data also. To avoid doubts about which model or which mechanism is proper, combination of the particular models into a very complex and robust model is a possible solution. Although the use of this solution for description of the light-dependent photosynthetic reactions is not without problems, e.g., a lack of detailed knowledge of particular mechanisms or high computational demands to perform the simulations (even thousands of differential equations to be solved), such a general model may give key information about the function and regulation of photosynthetic reactions.

In a recent article (2), we introduced the so-called intermediate S-states of the oxygen evolving complex based on theoretical modeling of period-four oscillations in oxygen evolution and fluorescence signal caused by a series of STF. We assumed a model of homogeneous photosystem II (PSII) for our simulations. On the other hand, there are no doubts that PSII, especially of higher plants, is heterogeneous in many aspects (3), including the Q_B -reducing/ Q_B -nonreducing heterogeneity, which is mentioned by Wim Vredenberg in his comment on our article. However, our model was developed with the main goal being to simulate and explain the STF-induced period-four oscillations in oxygen evolution without an assumption of phenomenological parameters, the misses and the double hits originally suggested by Kok et al. (4) to describe the function of the donor side of PSII. Therefore, we focused on an improvement (with respect to our original model (5)) of the description of the PSII donor side. To avoid mismatching a role

of performed changes in the original model structure of the PSII donor side with a possible role of PSII heterogeneity on resulting simulations, we assumed homogeneous PSII.

The arguments given by Wim Vredenberg in his comment results from the theory given in his recent articles (6–8), which is based on a different kinetic approach for the description of electron transport kinetics (irreversible reactions) and definition of fluorescence (proportional to amount of Q_A^- ; Y_Z^+ quenching) than the approach and definition that we used in our model (reversible reactions; fluorescence is defined as deactivation of excited states via rate constant of fluorescence; no Y_Z^+ quenching). Further, Wim Vredenberg used his theory for description of fluorescence data only, and he was not concerned in the function of the PSII donor side and in the simulation of oxygen evolution caused by a series of STFs as we were. Therefore, Wim Vredenberg's theory might simulate experimental fluorescence data, but it is not known whether his theory will be successful also for the simulations of oxygen evolution data. However, our more (oxygen evolution) or less (fluorescence) successful simulations of experimental data support our assumption of the intermediate S-states in an assumed homogenous system. To support our model approach (i.e., no Q_B -nonreducing PSII and no Y_Z^+ quenching), we note that Belyaeva et al. (9) used a model almost the same as our model (no intermediate S-states were considered in their model, but fluorescence was defined in their model as in our model) and successfully simulated experimentally measured fluorescence response to STF (with $F(1-2\text{ ms})/F_0 > 1$) without consideration of the Q_B -nonreducing PSII and of the Y_Z^+ quenching.

In summary, we admit that consideration of the Q_B -nonreducing PSII might lead to a better agreement of theoretical simulations with experimental data, and therefore a complex PSII model should include the heterogeneity, a statement that was also mentioned in the conclusions of our article (2). However, in view of the state-of-the-art modeling of photosynthetic events (see the first paragraph), many other mechanisms should be considered also, e.g., an effect of transmembrane electric potential on electron transport rates or an effect of electron transport reactions occurring behind PSII (for a review, see Lazar (1)). Such extensions of theoretical models for description of light-dependent photosynthetic reactions are in development in our laboratory.

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Address reprint requests to Dusan Lazar. E-mail: lazard@seznam.cz.

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Dusan Lazar and Jiri Jablonsky

Palacky University
Faculty of Science
Laboratory of Biophysics
Olomouc, Czech Republic