MODELLING THE FAST FLUORESCENCE RISE OF PHOTOSYNTHESIS

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We construct an ODE model for the fast fluorescence rise of photosynthesis by combining the current reaction scheme of the PS II two-electron-gate with a quasi steady-state description of the fast processes of excitation energy transfer and primary charge separation. The model is fitted to measured induction curves with a multiple shooting algorithm, and remarkably good approximations of the data are obtained. Model refinements are discussed focusing on PS II heterogeneity, and on PS I.

1. Introduction. The fluorescence of the photosynthetic apparatus is a gift of nature to those studying photosynthesis. It emerges from the chlorophylls which absorb light and, while largely converting it into chemical energy, re-emit a small fraction as fluorescence.

With the onset of photosynthesis (after a longer dark interval, for example), conspicuous changes in the chlorophyll fluorescence take place which can be measured easily and precisely. This is why these phenomena were discovered very early and have remained irreplaceable in photosynthesis research until today.

One of the most well-known induction effects is the “fast fluorescence rise” observed during the first second(s) of illumination (see Fig. 1). Although described as early as 1931 by Kautsky (1931), its prominent biphasic behaviour (to which it owes its name of “OIDP-kinetics”—origin, inflection point, dip, peak) has remained a Gordian knot until today. From numerous papers, some working hypotheses have emerged which remain ultimately contradictory: the two most favoured explanations ascribe the phenomenon to photosystem I (PS I), and to the PS II non-B-type centres, respectively (for reviews, see Briantais et al., 1986; Duysens, 1986; Govindjee and Satoh, 1986; Krause and Weis, 1991).

On the other hand, the OIDP rise is most important as an experimental tool both in basic photosynthesis research and in practical applications (for a review, see Renger and Schreiber, 1987). Many external factors (e.g. freezing stress, herbicides) give rise to characteristic changes in the fast fluorescence rise
which provoke qualitative and quantitative conclusions. Such interpretations must, however, be considered with scepticism as long as the phenomenon itself is ultimately unresolved.

Some light may be thrown onto the conflicting qualitative ideas by modelling the proposed mechanisms and comparing them with the experimental data quantitatively. Previous models of fluorescence kinetics have either focused on electron transport through the two-electron-gate on the millisecond timescale (Renger and Schulze, 1985), or on the fast (nano–microsecond timescale) processes of light absorption, transfer of excited states, and charge separation (Schatz et al., 1988; Leibl et al., 1989). In this paper, whose main results are taken from Baake (1989), we modify these and bring them together in a consistent way, which yields our "core model" of fluorescence induction. We then illustrate the procedure of fitting the model to measured induction curves. Finally, the core model is extended according to the aforementioned hypotheses for the OIDP rise and again compared to the data. The results are discussed with respect to our current understanding of the light reaction and fluorescence.

2. Basic Mechanisms and the Core Model. The fluorescence commonly measured in induction experiments (wavelengths around 685 nm) originates nearly exclusively from photosystem II (see Krause and Weis, 1991), so a core model for its description is naturally a model of PS II reaction kinetics. Two different time scales must be considered.

What happens at the slow (millisecond) time scale is depicted in Fig. 2 (adapted from Renger and Schulze, 1985), the reaction scheme of PS II electron transport through the so-called "two-electron-gate" (Crofts and Wraith, 1983). Charges generated at the primary acceptor $Q_A$ by the light-driven charge separation (see below) move on to the secondary acceptor $Q_B$ which, after two such steps, exchanges two electrons with a mobile pool of