Oxygenic Photoautotrophic Growth and Photosystem I

J. W. Lee *et al.* (*1*) state that the minimum quantum requirement for photosystem II (PSII) photosynthesis should be four photons per O_2 molecule, because PSII photosynthesis uses a single light reaction (PSII) instead of two (both PSI and PSII). This statement is not correct because photosynthesis requires adenosine triphosphate (ATP) in addition to reducing power such as that provided by nicotinamide adenine dinucleotide phosphate ($NADP^+ \rightarrow NADPH$).

If one assumes textbook values, the reduction of one CO_2 molecule by the enzymes of the Calvin cycle requires 2NADPH and 3ATP. The reduction of two molecules of nicotinamide adenine dinucleotide phosphate ($2NADP^+$) by $2H_2O$ requires only four photons in PSII photosynthesis, but the formation of 3ATP requires another two-and-a-half photons.

Here is the calculation: 3ATP requires nine protons to pass through ATP synthase. Four of those protons are provided by the splitting of H_2O:

$$2H_2O \rightarrow 4H^+ + 4e^- + O_2$$

The other five protons are assumed to be provided by cyclic electron flow through the cytochrome b/f complex. The requirement is one electron (one photon) for every two protons pumped by the cytochrome b/f complex. Thus, an additional two-and-a-half photons are required for the synthesis of ATP and a total of six-and-a-half photons is the theoretical minimum required to drive PSII CO_2 fixation by the Calvin cycle.

John M. Olson
Department of Biochemistry and Molecular Biology, University of Massachusetts, Amherst, MA 01003–4505, USA

REFERENCES

1. J. W. Lee, C. V. Tevault, T. G. Owens, E. Greenbaum, *Science* **273**, 364 (1996).

31 July 1996; accepted 6 December 1996

Response: Olson correctly points out that fixation of a single molecule of CO_2 in photosynthesis requires a minimum expenditure of three molecules of ATP and two molecules of NADP. He implicitly assumes that the four electrons required to produce the two NADPH molecules are derived from water oxidation through photochemistry in the PSII reaction center. This same reaction releases four protons into the thylakoid lumen. Production of 3ATP requires a total of nine protons, thus five additional protons are required. It is on the production of these five "extra" protons that the discussion of quantum requirement hinges.

Olson explicitly assumes that the five protons are derived from cyclic electron flow through the cytochrome b/f complex, a process that pumps two protons into the lumen for each electron that is passed through the complex (and thus the need for two-and-a-half additional photons). The driving reaction for this cyclic flow was not specified, but must be assumed to be PSII because our mutants lack detectable PSI.

There is an additional assumption in Olson's calculation—that the linear flow from water to $NADP^+$ is not coupled to any additional proton translocation. Photosynthesis in the absence of PSI would require that one define a pathway for reduction of ferredoxin and ultimately $NADP^+$ by electrons derived from PSII. Recent inhibitor studies by Lee and Greenbaum. (*1*) have suggested that the plastoquinone pool and the cytochrome b/f complex may be required in this pathway, but this does not make an understanding of the pathway any clearer. Nevertheless, there is increasing data to support the original observation that some mutants of *Chlamydomonas reinhardtii* lacking PSI exhibit light-dependent CO_2 fixation, or H_2 evolution with simultaneous O_2 evolution, or both. If the cytochrome b/f complex does participate in direct electron flow to ferredoxin, the necessity for the additional two-and-a-half photons may be obviated and a theoretical minimum quantum requirement of four may be approached.

Consideration of quantum requirement is secondary to the problem of establishing the pathway of electrons from PSII to ferredoxin in the absence of PSI. Knowledge of this pathway could then allow one to establish a minimum quantum requirement based on the extent of proton translocation in the pathway. It is on an understanding of this pathway that our efforts should be focused, for herein lies the unique aspects of oxygenic photosynthesis in the absence of PSI.

T. G. Owens
Section of Plant Biology, Cornell University, Ithaca, NY 14853, USA
J. W. Lee
C. V. Tevault
E. Greenbaum
Oak Ridge National Laboratory, Oak Ridge, TN 37831-6194, USA

REFERENCE

1. J. W. Lee and E. Greenbaum, unpublished observations.

23 August 1996; revised 18 December 1996; accepted 10 January 1997