This Week's Citation Classic

Trebst A. Energy conservation in photosynthetic electron transport of chloroplasts. Annu. Rev. Plant Physiol. 25:423-58, 1974. [Department of Biology, Ruhr-University Bochum, Federal Republic of Germany]

Biochemical data on the accessibility of redox carriers and components gave evidence for a sidedness of the thylakoid membrane and for a location of the donor and acceptor sides of both photosystems on opposite sides of the membrane, i.e., for vectorial electron flow. New vectorial schemes explained conflicting data on 'ATP coupling sites' in cyclic e-flow systems. [The $SC/^{\odot}$ indicates that this paper has been cited over 270 times since 1974.]

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"The editors of Annual Review leave any particular emphasis of the review requested entirely to the author. But perhaps they did think of antibody work with chloroplast systems when they decided on me. In trying to cover this together with the description of the state of knowledge on the electron flow system, an additional quite general point of view emerged. Structural information, like evidence for the location of a functional component on either side of the membrane as obtained by antibody work, was essential to understand the mechanism of coupled electron flow. Assembling such data they together did give biochemical evidence for the theory of a 'chemiosmotic' mechanism for the coupling of photosynthetic electron flow to ATP formation. Vectorial electron flow, of course, had been proposed by Mitchell¹ also for photosynthetic electron flow and there were strong proponents, particularly among the biophysicists, but the biochemists had been hesitant. By writing in the review the old linear e-flow systems vectorial with proton releasing sites instead of

ATP coupling sites, some of the confusion and discrepancies in the literature on 'coupling sites' suddenly disappeared and easily explained the just identified second coupling site by water splitting inside. Artificial energy conservation was coined for artificial proton pumping by the cofactor itself explaining the coupling of simple, but very efficient, cyclic electron flow systems, where it had been impossible to assign a coupling site in the old way. It was the cooperation with Cünther Hauska,² now at Regensburg, on artificial energy conservation in cyclic electron flow and in donor systems for photosystem I that had prepared me for interpreting old results in another additional way.

"The review is probably cited because it combined structural and functional aspects of the thylakoid membrane and made way for the general acceptance of the vectorial nature of photosynthetic electron flow among the photosynthesis community. The review is cited to refer to a long period of photosynthesis research in the now fashionable way of considering structure when discussing function without bothering to look into the detailed results of many contributors.

"The situation in 1980 might look perhaps as unsettled as it did in 1973. The proton motive force as intermediate in ATP formation is no longer questioned, but unsettled how it is generated in the electron flow system. Though there is no objection anymore to the oxygen evolution system on the inside of the membrane, the location of plastocyanin on the inside is still not accepted by some. As reviewed recently,⁵ more important presently is the cytochrome b₆-f complex. This integral protein, spanning the membrane, seemed not essential and was missing altogether in the schemes of 1973. Now it may play a crucial role in aiding proton translocation via plastoquinol across the membrane. Furthermore, the complex may make possible a Q cycle for a higher proton/electron and in this way coupling stoichiometry."

1. Mitchell P. Chemiosmotic coupling in oxidative and photosynthetic phosphorylation. *Biol. Rev.* 41:445-502, 1966.

^{2.} Hauska G, Reimer S & Trebst A. Native and artificial energy-conserving sites in cyclic photophosphorylation systems. *Biochem. Biophys. Acta* 357:1-13, 1974.

^{3.} **Trebst A.** Inhibitors in electron flow: tools for the functional and structural localization of carriers and energy conservation sites. *Meth. Enzvmol.* **69**:675-715, 1980.