

## 5. REFERENCES

- Ahlbrink, R., M. Haumann, D. Cherepanov, O. Bogershausen, A. Mulkidjanian, and W. Junge. 1998. Function of tyrosine Z in water oxidation by photosystem II: electrostatical promotor instead of hydrogen abstractor. *Biochemistry* 37(4):1131-1142.
- Allakhverdiev, S.I., Y.M. Feyziev, A. Ahmed, H. Hayashi, J.A. Aliev, V.V. Klimov, N. Murata, and R. Carpentier. 1996. Stabilization of oxygen evolution and primary electron transport reactions in Photosystem II against heat stress with glycinebetaine and sucrose. *Journal of Photochemistry and Photobiology B* 34:149-157.
- Ananyev, G.M., and G.C. Dismukes. 1996a. Assembly of the tetra-Mn site of photosynthetic water oxidation by photoactivation: Mn stoichiometry and detection of a new intermediate. *Biochemistry* 35(13):4102-4109.
- Ananyev, G.M., and G.C. Dismukes. 1996b. High-resolution kinetic studies of the reassembly of the tetra-manganese cluster of photosynthetic water oxidation: proton equilibrium, cations, and electrostatics. *Biochemistry* 35(46):14608-14617.
- Ananyev, G.M., and G.C. Dismukes. 1997. Calcium induces binding and formation of a spin-coupled dimanganese(II,II) center in the apo-water oxidation complex of photosystem II as precursor to the functional tetra-Mn/Ca cluster. *Biochemistry* 36(38):11342-11350.
- Ananyev, G.M., A. Murphy, Y. Abe, and G.C. Dismukes. 1999. Remarkable affinity and selectivity for Cs<sup>+</sup> and uranyl (UO<sub>2</sub><sup>2+</sup>) binding to the manganese site of the apo-water oxidation complex of photosystem II. *Biochemistry* 38(22):7200-7209.
- Ananyev, G.M., L. Zaltsman, C. Vasko, and G.C. Dismukes. 2001. The inorganic biochemistry of photosynthetic oxygen evolution/water oxidation. *Biochim Biophys Acta* 1503(1-2):52-68.
- Andreasson, L.E., I. Vass, and S. Styring. 1995. Calcium ion depletion modifies the electron transfer on both donor and acceptor sides in Photosystem II from spinach. *Biochim. Biophys. Acta* 1230:155-164.
- Babcock, G.T., B.A. Barry, R.J. Debus, C.W. Hoganson, M. Atamian, L. McIntosh, L. Sithole, and C.F. Yocum. 1989. Water Oxidation in Photosystem II: From Radical Chemistry to Multielectron Chemistry. *Biochemistry* 28(25):9557-9565.
- Baranov, S.V., G.M. Ananyev, V.V. Klimov, and G.C. Dismukes. 2000. Bicarbonate accelerates assembly of the inorganic core of the water-oxidizing complex in manganese-depleted photosystem II: a proposed biogeochemical role for atmospheric carbon dioxide in oxygenic photosynthesis. *Biochemistry* 39(20):6060-6065.
- Barber, J. 2002. Photosystem II: a multisubunit membrane protein that oxidises water. *Curr Opin Struct Biol* 12(4):523.
- Barber, J. 2006. Photosystem II: an enzyme of global significance. *Biochem Soc Trans* 34(Pt 5):619-631.
- Barber, J., K.N. Ferreira, K. Maghlaoui, and S. Iwata. 2004. Structural model of the oxygen-evolving centre of photosystem II with mechanistic implications. *Phys Chem Chem Phys* 6:4737-4742.
- Barra, M., M. Haumann, and H. Dau. 2005. Specific loss of the extrinsic 18 KDa protein from photosystem II upon heating to 47 degrees C causes inactivation

- of oxygen evolution likely due to Ca release from the Mn-complex. *Photosynth Res* 84(1-3):231-237.
- Beck, W.F., J.C. de Paula, and G.W. Brudvig. 1985. Active and resting states of the O<sub>2</sub>-evolving complex of photosystem II. *Biochemistry* 24(12):3035-3043.
- Bergmann, U., M.M. Grush, C.R. Horne, P. DeMarois, J.E. Penner-Hahn, C.F. Yocum, D.W. Wright, C.E. Dubé, W.H. Armstrong, G. Christou, H.J. Eppley, and S.P. Cramer. 1998. Characterization of the Mn Oxidation States in Photosystem II by K, X-ray Fluorescence Spectroscopy. *J. Phys. Chem. B* 102:8350-8352.
- Bernat, G., S. Padhye, C. Barta, L. Kovacs, and S. Demeter. 2001. Chemical probes for water-oxidation: synthetic manganese complexes in photoactivation of water splitting complex and as exogenous electron donors to photosystem II. *Z Naturforsch [C]* 56(9-10):755-766.
- Berry, J., and O. Björkmann. 1980. Photosynthetic responses and adaptation to temperature in higher plant. *Ann Rev Plant Physiol* 31:491-543.
- Biesiadka, J., B. Loll, J. Kern, K.D. Irrgang, and A. Zouni. 2004. Crystal structure of cyanobacterial Photosystem II at 3.2 Å resolution: A closer look at the Mn-Cluster. *Phys Chem Chem Phys* 6:4733-4736.
- Blankenship, R.E. 2001. Molecular evidence for the evolution of photosynthesis. *Trends Plant Sci* 6(1):4-6.
- Blankenship, R.E. 2002. *Molecular Mechanism of Photosynthesis*. Blackwell Science, U.K.
- Blubaugh, D.J., and G.M. Cheniae. 1992. Photoassembly of the Photosystem II Manganese Cluster. In *Research in Photosynthesis*. Murata N, editor. Kluwer Academic Publishers. 361-364.
- Boussac, A., J.L. Zimmermann, and A.W. Rutherford. 1989. EPR signals from modified charge accumulation states of the oxygen evolving enzyme in Ca<sup>2+</sup>-deficient photosystem II. *Biochemistry* 28(23):8984-8989.
- Bowes, J.M., and A.R. Crofts. 1978. Interactions of protons with transitions of the water splitting enzyme of photosystem II as measured by delayed fluorescence *Z Naturforsch [C]* 33c:271-275.
- Bricker, T.M., and R.L. Burnap. 2005. The Extrinsic Proteins of Photosystem II. In *Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 95-120.
- Bricker, T.M., and L.K. Frankel. 1998. The structure and function of the 33 kDa extrinsic protein of Photosystem II: A critical assesment. *Photosynth Res* 56:157-173.
- Britt, R.D. 1996. Oxygen Evolution. In *Oxygenic Photosynthesis: The light reactions*. Ort DR, Yocum CF, editors. Kluwer Academic Publishers, The Netherlands. 213-247.
- Britt, R.D., K.A. Campbell, J.M. Peloquin, M.L. Gilchrist, C.P. Aznar, M.M. Dicus, J. Robblee, and J. Messinger. 2004. Recent pulsed EPR studies of the photosystem II oxygen-evolving complex: implications as to water oxidation mechanisms. *Biochim Biophys Acta* 1655(1-3):158-171.
- Britt, R.D., J.M. Peloquin, and K.A. Campbell. 2000. Pulsed and parallel-polarization EPR characterization of the photosystem II oxygen-evolving complex. *Annu Rev Biophys Biomol Struct* 29:463-495.
- Buchel, C., J. Barber, G. Ananyev, S. Eshaghi, R. Watt, and C. Dismukes. 1999. Photoassembly of the manganese cluster and oxygen evolution from monomeric and dimeric CP47 reaction center photosystem II complexes. *Proc Natl Acad Sci U S A* 96(25):14288-14293.

- Burnap, R.L. 2004. D1 protein processing and Mn cluster assembly in light of the emerging photosystem II structure. *Phys Chem Chem Phys* 6:4803-4809.
- Burnap, R.L., M. Qian, and C. Pierce. 1996. The manganese stabilizing protein of photosystem II modifies the in vivo deactivation and photoactivation kinetics of the H<sub>2</sub>O oxidation complex in *Synechocystis* sp. PCC6803. *Biochemistry* 35(3):874-882.
- Calderone, V., M. Trabucco, A. Vujicic, R. Battistutta, G.M. Giacometti, F. Andreucci, R. Barbato, and G. Zanotti. 2003. Crystal structure of the PsbQ protein of photosystem II from higher plants. *EMBO Rep* 4(9):900-905.
- Campbell, K.A., D.A. Force, P.J. Nixon, F. Dole, B.A. Diner, and R.D. Britt. 2000. Dual-mode EPR Detects the initial Intermediate in Photoassembly of the Photosystem II Mn Cluster: The influence of Amino Acid Residue 170 of the D1 Polypeptide on Mn Coordination. *J. Am. Chem. Soc.* 122:3754-3761.
- Chen, C., J. Kazimir, and G.M. Cheniae. 1995. Calcium modulates the photoassembly of photosystem II (Mn)<sub>4</sub>-clusters by preventing ligation of nonfunctional high-valency states of manganese. *Biochemistry* 34(41):13511-13526.
- Cheniae, G.M. 1972. Effects of Hydroxylamine on Photosystem II. *Plant Physiol.* 50:87-94.
- Cheniae, G.M., and I.F. Martin. 1967. Photoreactivation of manganese catalyst in photosynthetic oxygen evolution. *Biochem Biophys Res Commun* 28(1):89-95.
- Cheniae, G.M., and I.F. Martin. 1970. Sites of function of manganese within photosystem II. Roles in O<sub>2</sub> evolution and system II. *Biochim Biophys Acta* 197(2):219-239.
- Cheniae, G.M., and I.F. Martin. 1971. Photoactivation of the manganese catalyst of O<sub>2</sub> evolution. I. Biochemical and kinetic aspects. *Biochim Biophys Acta* 253(1):167-181.
- Chow, W.S., and E.M. Aro. 2005. Photoinactivation and mechanisms of recovery. In *Photosystem II; The Light-driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 627-648.
- Cinco, R.M., K.L. McFarlane, J.H. Robblee, J. Yano, S.A. Pizarro, E. Bellacchio, K. Sauer, and V.K. Yachandra. 2004. Calcium EXAFS Establishes the Mn-Ca Cluster in the Oxygen-Evolving Complex of Photosystem II. *Biochemistry* 41:12928-12933.
- Clausen, J., W. Junge, H. Dau, and M. Haumann. 2005. Photosynthetic water oxidation at high O<sub>2</sub> backpressure monitored by delayed chlorophyll fluorescence. *Biochemistry* 44(38):12775-12779.
- Cole, J.L., V.K. Yachandra, R.D. Guiles, A.E. McDermonnt, R.D. Britt, S.L. Dexheimer, K. Sauer, and M.P. Klein. 1987. Assignment of the g = 4.1 ERP signal to manganese in the S<sub>2</sub> state of the photosynthetic oxygen-evolving complex: An X-ray absorption edge spectroscopy study. *Biochim Biophys Acta* 890:395-398.
- Coleman, W.J., G. Govindjee, and H.S. Gutowsky. 1988. The effect of chloride on the thermal inactivation of oxygen evolution. *Photosynth Res.* 16:261-276.
- Dau, H., A. Grundmeier, P. Loja, and M. Haumann. 2007. *Philos Trans R Soc Lond B Biol Sci.*
- Dau, H., and M. Haumann. 2003. X-Ray absorption spectroscopy to watch catalysis by metalloenzymes: status and perspectives discussed for the water-splitting manganese complex of photosynthesis. *Journal of Synchrotron Radiation* 10:76-85.
- Dau, H., and M. Haumann. 2005. Considerations on the mechanism of photosynthetic water oxidation - dual role of oxo-bridges between Mn ions in (i) redox-

- potential maintenance and (ii) proton abstraction from substrate water. *Photosynth Res* 84(1-3):325-331.
- Dau, H., and M. Haumann. 2006. Reaction Cycle of photosynthetic water oxidation. *Science* 312:1471-1472.
- Dau, H., and M. Haumann. 2007a. Eight steps preceding O-O bond formation in oxygenic photosynthesis-A basic reaction cycle of the Photosystem II manganese complex. *Biochim Biophys Acta* 1767(6):472-483.
- Dau, H., and M. Haumann. 2007b. Time-resolved X-ray spectroscopy leads to an extension of the classical S-state cycle model of photosynthetic oxygen evolution. *Photosynth Res* 92(3):327-343.
- Dau, H., L. Iuzzolino, and J. Dittmer. 2001. The tetra-manganese complex of photosystem II during its redox cycle - X-ray absorption results and mechanistic implications. *Biochim Biophys Acta* 1503(1-2):24-39.
- Dau, H., P. Liebisch, and M. Haumann. 2003. X-ray absorption spectroscopy to analyze nuclear geometry and electronic structure of biological metal centers—potential and questions examined with special focus on the tetra-nuclear manganese complex of oxygenic photosynthesis. *Anal Bioanal Chem* 376(5):562-583.
- Dau, H., P. Liebisch, and M. Haumann. 2004. The structure of the manganese complex of Photosystem II in its dark-stable S<sub>1</sub>-state—EXAFS results in relation to recent crystallographic data. *Phys Chem Chem Phys* 6:4781 - 4792.
- De Las Rivas, J., M. Balsera, and J. Barber. 2004. Evolution of oxygenic photosynthesis: genome-wide analysis of the OEC extrinsic proteins. *Trends Plant Sci* 9(1):18-25.
- Debus, R.J. 1992. The manganese and calcium ions of photosynthetic oxygen evolution. *Biochim Biophys Acta* 1102(3):269-352.
- Debus, R.J., C. Aznar, K.A. Campbell, W. Gregor, B.A. Diner, and R.D. Britt. 2003. Does aspartate 170 of the D1 polypeptide ligate the manganese cluster in photosystem II? An EPR and ESEEM Study. *Biochemistry* 42(36):10600-10608.
- Debus, R.J., K.A. Campbell, W. Gregor, Z.L. Li, R.L. Burnap, and R.D. Britt. 2001. Does histidine 332 of the D1 polypeptide ligate the manganese cluster in photosystem II? An electron spin echo envelope modulation study. *Biochemistry* 40(12):3690-3699.
- Debus, R.J., M.A. Strickler, L.M. Walker, and W. Hillier. 2005. No evidence from FTIR difference spectroscopy that aspartate-170 of the D1 polypeptide ligates a manganese ion that undergoes oxidation during the S<sub>0</sub> to S<sub>1</sub>, S<sub>1</sub> to S<sub>2</sub>, or S<sub>2</sub> to S<sub>3</sub> transitions in photosystem II. *Biochemistry* 44(5):1367-1374.
- Dekker, J.P., H.J. van Gorkom, M. Brok, and L. Ouwehand. 1984. Optical characterization of Photosystem II electron donors. *Biochim. Biophys. Acta* 764:301-309.
- Diner, B.A. 2001. Amino acid residues involved in the coordination and assembly of the manganese cluster of photosystem II. Proton-coupled electron transport of the redox-active tyrosines and its relationship to water oxidation. *Biochim Biophys Acta* 1503(1-2):147-163.
- Diner, B.A., and G.T. Babcock. 1996. Structure, Dynamics, and Energy Conversion Efficiency in Photosystem II. In *Oxygenic Photosynthesis: The light reactions*. Ort DR, Yocum CF, editors. Kluwer Academic Publishers, The Netherlands. 213-247.

- Dismukes, G.C., and Y. Siderer. 1981. Intermediates of a polynuclear manganese center involved in photosynthetic oxidation of water. *Proc Natl Acad Sci U S A* 78(1):274-278.
- Enami, I., S. Kikuchi, T. Fukuda, H. Ohta, and J.R. Shen. 1998. Binding and functional properties of four extrinsic proteins of photosystem II from a red alga, *Cyanidium caldarium*, as studied by release-reconstitution experiments. *Biochemistry* 37(9):2787-2793.
- Estabrook, R.W. 1967. Mitochondrial respiratory control and the polarographic measurement of ADP: O ratios. *Methods Enzymol* 10:41-47.
- Ferreira, K.N., T.M. Iverson, K. Maghlaoui, J. Barber, and S. Iwata. 2004. Architecture of the photosynthetic oxygen-evolving center. *Science* 303(5665):1831-1838.
- Förster, V., and W. Junge. 1985. Stoichiometry and kinetics of proton release upon photosynthetic water oxidation. *Photochem Photobiol Sci* 41:183-190.
- Fowler, C.F. 1977. Proton translocation in chloroplasts and its relationship to electron transport between the photosystems. *Biochim Biophys Acta* 459(3):351-363.
- George, G.N., R.C. Prince, and S.P. Cramer. 1989. The manganese site of the photosynthetic water-splitting enzyme. *Science* 243(4892):789-791.
- Ghanotakis, D.F., G.T. Babcock, and C.F. Yocum. 1984. Calcium reconstitutes high rates of oxygen evolution in polypeptide depleted Photosystem II preparations. *FEBS Lett* 167:127-130.
- Ghanotakis, D.F., and C.F. Yocum. 1986. Purification and properties of an oxygen-evolving reaction center complex from Photosystem II membranes. *FEBS Lett.* 197(1,2):244-248.
- Govindjee, and D. Krogmann. 2004. Discoveries in oxygenic photosynthesis (1727-2003): A perspective. *Photosynth Res* 80:15-57.
- Grabolle, M. 2005. Die Donorseite des Photosystems II: Rekombinationsfluoreszenz- und Röntgenabsorptionsstudien. In *FB Physik*. Free Univ., Berlin.
- Grabolle, M., and H. Dau. 2005. Energetics of primary and secondary electron transfer in Photosystem II membrane particles of spinach revisited on basis of recombination-fluorescence measurements. *Biochim Biophys Acta* 1708(2):209-218.
- Grabolle, M., M. Haumann, C. Muller, P. Liebisch, and H. Dau. 2006. Rapid loss of structural motifs in the manganese complex of oxygenic photosynthesis by X-ray irradiation at 10-300 K. *J Biol Chem* 281(8):4580-4588.
- Green, B., and D. Durnford. 1996. The chlorophyll-carotenoid proteins of oxygenic photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 47:685-714.
- Green, B.R., and E. Gantt. 2005. The Distal and Extrinsic Photosystem II Antennas. In *Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 23-44.
- Guiles, R.D., V.K. Yachandra, A.E. McDermott, J.L. Cole, S.L. Dexheimer, R.D. Britt, K. Sauer, and M.P. Klein. 1990. The  $S_0$  state of photosystem II induced by hydroxylamine: differences between the structure of the manganese complex in the  $S_0$  and  $S_1$  states determined by X-ray absorption spectroscopy. *Biochemistry* 29(2):486-496.
- Han, G., J. Li, G. Chen, L. Ling, S. Li, A.A. Khorobrykh, S.K. Zharmukhamedov, V.V. Klimov, and T. Kuang. 2005. Reconstruction of the water-oxidizing complex in manganese-depleted Photosystem II using synthetic manganese complexes. *J Photochem Photobiol B* 81(2):114-120.
- Hasegawa, K., M. Kusunoki, Y. Inoue, and T.A. Ono. 1998. Simulation of  $S_2$ -state multiline EPR signal in oriented photosystem II membranes: structural

- implications for the manganese cluster in an oxygen-evolving complex. *Biochemistry* 37(26):9457-9465.
- Hasegawa, K., and T. Ono. 1999. Spin-exchange structures of S<sub>2</sub>-state Mn-cluster in photosynthetic oxygen-evolving complex. *Riken Review* 24:62-63.
- Hasler, L., D. Ghanotakis, B. Fedtke, A. Spyridaki, M. Miller, uuml, S.A. Iler, A. Engel, and G. Tsiotis. 1997. Structural Analysis of Photosystem II: Comparative Study of Cyanobacterial and Higher Plant Photosystem II Complexes. *J Struct Biol* 119(3):273-283.
- Haumann, M., M. Barra, P. Loja, S. Loscher, R. Krivanek, A. Grundmeier, L.E. Andreasson, and H. Dau. 2006. Bromide does not bind to the Mn<sub>4</sub>Ca complex in its S<sub>1</sub> state in Cl(-)-depleted and Br(-)-reconstituted oxygen-evolving photosystem II: evidence from X-ray absorption spectroscopy at the Br K-edge. *Biochemistry* 45(43):13101-13107.
- Haumann, M., O. Bögershausen, D. Cherepanov, R. Ahlbrink, and W. Junge. 1997. Photosynthetic oxygen evolution; H/D isotope effects and the coupling between electron and proton transfer during the redox reactions at the oxidizing side of Photosystem II. *Photosynth Res.* 51:193-208.
- Haumann, M., O. Bogershausen, and W. Junge. 1994. Photosynthetic oxygen evolution: net charge transients as inferred from electrochromic bandshifts are independent of proton release into the medium. *FEBS Lett* 355(1):101-105.
- Haumann, M., and W. Junge. 1994. Extent and rate of proton release by photosynthetic water oxidation in thylakoids: electrostatic relaxation versus chemical production. *Biochemistry* 33(4):864-872.
- Haumann, M., and W. Junge. 1996. Protons and Charge Indicators in Oxygen Evolution *In* Oxygenic Photosynthesis - The Light Reactions. Ort D, Yocum CF, editors. Kluwer Academic Publi., Dordrecht. 165-192.
- Haumann, M., P. Liebisch, C. Muller, M. Barra, M. Grabolle, and H. Dau. 2005a. Photosynthetic O<sub>2</sub> formation tracked by time-resolved X-ray experiments. *Science* 310(5750):1019-1021.
- Haumann, M., A. Mulkidjanian, and W. Junge. 1999. Tyrosine-Z in oxygen-evolving photosystem II: a hydrogen-bonded tyrosinate. *Biochemistry* 38(4):1258-1267.
- Haumann, M., C. Muller, P. Liebisch, L. Iuzzolino, J. Dittmer, M. Grabolle, T. Neisius, W. Meyer-Klaucke, and H. Dau. 2005b. Structural and oxidation state changes of the photosystem II manganese complex in four transitions of the water oxidation cycle (S<sub>0</sub> → S<sub>1</sub>, S<sub>1</sub> → S<sub>2</sub>, S<sub>2</sub> → S<sub>3</sub>, and S<sub>3,4</sub> → S<sub>0</sub>) characterized by X-ray absorption spectroscopy at 20 K and room temperature. *Biochemistry* 44(6):1894-1908.
- Hillier, W., and J. Messinger. 2005. Mechanism of Photosynthetic Oxygen Production. *In* Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 567-608.
- Homann, P.H. 1988. Structural Effects of Cl and Other Anions on the Water Oxidizing Complex of Chloroplast Photosystem II. *Plant Physiol* 88(1):194-199.
- Hsu, B.-D., J.-Y. Lee, and R.-L. Pan. 1987. The high-affinity binding site for manganese on the oxidizing side of Photosystem II. *Biochimica et Biophysica Acta (BBA) - Bioenergetics* 890(1):89-96.
- Ifuku, K., T. Nakatsu, H. Kato, and F. Sato. 2003. Crystallization and preliminary crystallographic studies on the extrinsic 23 kDa protein in the oxygen-evolving complex of photosystem II. *Acta Crystallogr D Biol Crystallogr* 59(Pt 8):1462-1463.

- luzzolino, L., J. Dittmer, W. Dorner, W. Meyer-Klaucke, and H. Dau. 1998. X-ray absorption spectroscopy on layered photosystem II membrane particles suggests manganese-centered oxidation of the oxygen-evolving complex for the  $S_0$ - $S_1$ ,  $S_1$ - $S_2$ , and  $S_2$ - $S_3$  transitions of the water oxidation cycle. *Biochemistry* 37(49):17112-17119.
- Joliot, A., and B. Kok. 1975. Oxygen evolution in photosynthesis. In *Bioenergetics of Photosynthesis*. Govindjee, editor. Academic Press, New York. 387-412.
- Joliot, P., G. Barbieri, and R. Charbaud. 1969. Un nouveau modele des centres photochimiques du systeme II. *Photochem. Photobiol.* 10:309-329.
- Junge, W., M. Haumann, R. Ahlbrink, A. Mulikjanian, and J. Clausen. 2002. Electrostatics and proton transfer in photosynthetic water oxidation. *Phil. Trans. R. Soc. Lond. B.*
- Kamiya, N., and J.R. Shen. 2003. Crystal structure of oxygen-evolving photosystem II from *Thermosynechococcus vulcanus* at 3.7-Å resolution. *Proc Natl Acad Sci U S A* 100(1):98-103.
- Karge, M., K.D. Irrgang, S. Sellin, R. Feinaugle, B. Liu, H.J. Eckert, H.J. Eichler, and G. Renger. 1996. Effects of hydrogen/deuterium exchange on photosynthetic water cleavage in PS II core complexes from spinach. *FEBS Lett* 378(2):140-144.
- Kargul, J., K. Maghlaoui, J.W. Murray, Z. Deak, A. Bousac, A.W. Rutherford, I. Vass, and J. Barber. 2007. Purification, crystallization and X-ray diffraction analyses of the *T. elongatus* PSII core dimer with strontium replacing calcium in the oxygen-evolving complex. *Biochim Biophys Acta* 1767(6):404-413.
- Kelley, P.M., and S. Izawa. 1978. The role of chloride ion in photosystem II. I. Effects of chloride ion on photosystem II electron transport and on hydroxylamine inhibition. *Biochim Biophys Acta* 502(2):198-210.
- Kern, J., J. Biesiadka, B. Loll, W. Saenger, and A. Zouni. 2007. Structure of the Mn(4)-Ca cluster as derived from X-ray diffraction. *Photosynth Res* 92(3):389-405.
- Kimura, Y., N. Mizusawa, A. Ishii, and T.A. Ono. 2005. FTIR detection of structural changes in a histidine ligand during S-state cycling of photosynthetic oxygen-evolving complex. *Biochemistry* 44(49):16072-16078.
- Kirby, J.A., R. A.S., J.P. Smith, A.C. Thompson, S.R. Cooper, and M. Klein. 1981. State of Manganese in the Photosynthetic Apparatus. 1. Extended X-ray Absorption Fine Structure Studies on Chloroplasts and Di-p-oxo-Bridged Dimanganese Model Compounds. *J. Am. Chem. Soc.* 103:5529-5537.
- Kok, B., B. Forbush, and M. McGloin. 1970. Cooperation of charges in photosynthetic  $O_2$  evolution-I. A linear four step mechanism. *Photochem Photobiol* 11(6):457-475.
- Kretschmann, H., E. Schlodder, and H.T. Witt. 1996. Net charge oscillation and proton release during water oxidation in photosynthesis. An electrochromic band shift study at pH 5.5–7.0. *Biochim Biophys Acta* 1274:1-8.
- Kretschmann, H., and H.T. Witt. 1993. Chemical reduction of the water splitting enzyme system of photosynthesis and its light-induced reoxidation characterized by optical and mass spectrometric measurements: A basis for the estimation of the states of the redox active manganese and of water in the quaternary oxygen-evolving S-state cycle. *Biochim Biophys Acta* 1144:331-345.
- Kruse, O., J. Rupprecht, J.H. Mussnug, G.C. Dismukes, and B. Hankamer. 2005. Photosynthesis: a blueprint for solar energy capture and biohydrogen production technologies. *Photochem Photobiol Sci* 4(12):957-970.

- Kulik, L., B. Epel, J. Messinger, and W. Lubitz. 2005. Pulse EPR, 55Mn-ENDOR and ELDOR-detected NMR of the S<sub>2</sub>-state of the oxygen evolving complex in photosystem II. *Photosynth Res* 84(1-3):347-353.
- Kuzek, D., and R.J. Pace. 2001. Probing the Mn oxidation states in the OEC. Insights from spectroscopic, computational and kinetic data. *Biochim Biophys Acta* 1503(1-2):123-137.
- Laemmli, U.K. 1970. Cleavage of structural proteins during the assembly of the head of bacteriophage T4. *Nature* 227(15):680-685.
- Lavergne, J., and W. Junge. 1993. Proton release during the redox cycle of the water oxidase. *Photosynth Res* 39:279-296.
- Lee, C.B., H. Hayashi, and B.Y. Moon. 1997. Stabilization by glycinebetaine of photosynthetic oxygen evolution by thylakoid membranes from *Synechococcus* PCC7002. *Mol Cells* 7(2):296-299.
- Lehninger, A.L., D.L. Nelson, and M.M. Cox. 2000. Principles of Biochemistry. Worth Publishers Inc., New York.
- Liu, B., P.P. Shen, W. Shi, Y.G. Song, W. Li, Z. Nie, and Y. Liu. 2006. Highly efficient photoactivation of Mn-depleted photosystem II by imidazole-liganded manganese complexes. *J Biol Inorg Chem* 11(5):636-632.
- Loll, B., J. Kern, W. Saenger, A. Zouni, and J. Biesiadka. 2005. Towards complete cofactor arrangement in the 3.0 Å resolution structure of photosystem II. *Nature* 438(7070):1040-1044.
- Lundberg, M., and P.E. Siegbahn. 2004. Theoretical investigations of structure and mechanism of the oxygen-evolving complex in PSII. *Phys Chem Chem Phys* 6:4772-4780.
- Magnuson, A., P. Liebisch, J. Hogblom, M.F. Anderlund, R. Lomoth, W. Meyer-Klaucke, M. Haumann, and H. Dau. 2006. Bridging-type changes facilitate successive oxidation steps at about 1 V in two binuclear manganese complexes—implications for photosynthetic water-oxidation. *J Inorg Biochem* 100(7):1234-1243.
- McEvoy, J.P., and G.W. Brudvig. 2004. Structure-based mechanism of photosynthetic water oxidation. *Phys Chem Chem Phys* 6:4754-4763.
- McEvoy, J.P., J.A. Gascon, V.S. Batista, and G.W. Brudvig. 2005a. The mechanism of photosynthetic water splitting. *Photochem Photobiol Sci* 4(12):940-949.
- McEvoy, J.P., J.A. Gascón, E.M. Sproviero, V.S. Batista, and G.W. Brudvig. 2005b. Computational Structural Model Of The Oxygen Evolving Complex In Photosystem II: Complete Ligation By Protein, Water And Chloride. In *Photosynthesis: Fundamental Aspects to Global Perspectives*. Bruce D, van der Est A, editors, The Netherlands. 278-280.
- Meinke, C., V.A. Sole, P. Pospisil, and H. Dau. 2000. Does the structure of the water-oxidizing photosystem II-manganese complex at room temperature differ from its low-temperature structure? A comparative X-ray absorption study. *Biochemistry* 39(24):7033-7040.
- Messinger, J. 2004. Evaluation of different mechanistic proposals for water oxidation in photosynthesis on the basis of Mn<sub>4</sub>O<sub>x</sub>Ca structures for the catalytic site and spectroscopic data. *Phys Chem Chem Phys* 6(4767-4771).
- Messinger, J., M. Badger, and T. Wydrzynski. 1995. Detection of one slowly exchanging substrate water molecule in the S<sub>3</sub> state of photosystem II. *Proc Natl Acad Sci U S A* 92(8):3209-3213.
- Messinger, J., J.H. Robblee, U. Bergmann, C. Fernandez, P. Glatzel, H. Visser, R.M. Cinco, K.L. McFarlane, E. Bellacchio, S.A. Pizarro, S.P. Cramer, K. Sauer, M.P.

- Klein, and V.K. Yachandra. 2001. Absence of Mn-centered oxidation in the S(2) → S(3) transition: implications for the mechanism of photosynthetic water oxidation. *J Am Chem Soc* 123(32):7804-7820.
- Messinger, J., J.H. Robblee, W.O. Yu, K. Sauer, V.K. Yachandra, and M.P. Klein. 1997. The S<sub>0</sub> State of the Oxygen-Evolving Complex in Photosystem II Is Paramagnetic: Detection of an EPR Multiline Signal. *J. Am. Chem. SOC.* 119:11349-11350.
- Messinger, J., W.P. Schroder, and G. Renger. 1993. Structure-function relations in photosystem II. Effects of temperature and chaotropic agents on the period four oscillation of flash-induced oxygen evolution. *Biochemistry* 32(30):7658-7668.
- Miller, A.F., and G.W. Brudvig. 1989. Manganese and calcium requirements for reconstitution of oxygen-evolution activity in manganese-depleted photosystem II membranes. *Biochemistry* 28(20):8181-8190.
- Miller, A.F., and G.W. Brudvig. 1990. Electron-transfer events leading to reconstitution of oxygen-evolution activity in manganese-depleted photosystem II membranes. *Biochemistry* 29(6):1385-1392.
- Miller, A.F., and G.W. Brudvig. 1991. A guide to electron paramagnetic resonance spectroscopy of Photosystem II membranes. *Biochim. Biophys. Acta* 1056:1-18.
- Miyao-Tokutomi, M., and Y. Inoue. 1992. Improvement by benzoquinones of the quantum yield of photoactivation of photosynthetic oxygen evolution: direct evidence for the two-quantum mechanism. *Biochemistry* 31(2):526-532.
- Miyao, M., and Y. Inoue. 1991a. Enhancement by chloride ions of photoactivation of oxygen evolution in manganese-depleted photosystem II membranes. *Biochemistry* 30(22):5379-5387.
- Miyao, M., and Y. Inoue. 1991b. An improved procedure for photoactivation of photosynthetic oxygen evolution: Effect of artificial electron acceptors on the photoactivation yield of NH<sub>2</sub>OH-treated wheat Photosystem II membranes. *Biochim. Biophys. Acta* 1056:47-56.
- Miyao, M., and N. Murata. 1983. Partial desintegration and reconstitution of the photosynthetic oxygen evolution system. Binding of 24 kilodalton and 18 kilodalton polypeptides. *Biochim. Biophys. Acta* 725:87-93.
- Mohanty, P.S., H. Hayashi, G.C. Papageorgiou, and N. Murata. 1993. Stabilization of the Mn-cluster of the oxygen-evolving complex by glycinebetaine. *Biochim. Biophys. Acta* 1144:92-96.
- Müller, C. 2006. Methodenentwicklung und Durchführung fortgeschrittener Röntgenabsorptionsmessungen am Mangan-Calcium-Komplex des Photosystems II. In *FB Biologie, Chemie, Pharmazie, FU Berlin, Berlin*. 145.
- Murata, N., P.S. Mohanty, H. Hayashi, and G.C. Papageorgiou. 1992. Glycinebetaine stabilizes the association of extrinsic proteins with the photosynthetic oxygen-evolving complex. *FEBS Lett* 296(2):187-189.
- Nash, D., M. Miyao, and N. Murata. 1985. Heat inactivation of oxygen evolution in Photosystem II particles and its acceleration by chloride depletion and exogenous manganese. *Biochim Biophys Acta* 807:127-133.
- Nelson, N., and A. Ben-Shem. 2004. The complex Architecture of Oxygenic Photosynthesis. *Nature Reviews Molecular Cell Biology* 5(12):971-982.
- Nixon, B.J., M. Sarcina, and B.A. Diner. 2005. The D1 and D2 Core Proteins. In *Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 71-94.

- Nixon, P.J., and B.A. Diner. 1992. Aspartate 170 of the photosystem II reaction center polypeptide D1 is involved in the assembly of the oxygen-evolving manganese cluster. *Biochemistry* 31(3):942-948.
- Nixon, P.J., and B.A. Diner. 1994. Analysis of water-oxidation mutants constructed in the cyanobacterium *Synechocystis* sp. PCC 6803. *Biochem Soc Trans* 22(2):338-343.
- Ono, T. 2001. Metallo-radical hypothesis for photoassembly of (Mn)<sub>4</sub>-cluster of photosynthetic oxygen evolving complex. *Biochim Biophys Acta* 1503(1-2):40-51.
- Ono, T., S. Izawa, and Y. Inoue. 1992. Structural and functional modulation of the manganese cluster in Ca(2+)- depleted photosystem II induced by binding of the 24-kilodalton extrinsic protein. *Biochemistry* 31(33):7648-7655.
- Ono, T., H. Nakayama, H. Gleiter, Y. Inoue, and A. Kawamori. 1987. Modification of the properties of S<sub>2</sub> state in photosynthetic O<sub>2</sub>-evolving center by replacement of chloride with other anions. *Arch Biochem Biophys* 256(2):618-624.
- Ono, T.A., and Y. Inoue. 1983a. Mn-preserving extraction of 33-, 24- and 16 kDa proteins from O<sub>2</sub>-evolving PSII particles by divalent salt-washing. *FEBS lett.* 164(2):255-260.
- Ono, T.A., and Y. Inoue. 1983b. Requirement of divalent cations for Photoactivation of the latent water-oxidation system in intact chloroplasts from flashed leaves. *Biochim. Biophys. Acta* 723:191-201.
- Ono, T.A., and Y. Inoue. 1984. Ca<sup>2+</sup>-dependent restoration of O<sub>2</sub>-evolving activity in CaCl<sub>2</sub>-washed PSII particles depleted of 33, 24 and 16 kDa proteins. *FEBS lett.* 168(2):281-286.
- Ono, T.A., and Y. Inoue. 1987. Reductant-sensitive intermediates involved in multi-quantum process of photoactivation of latent O<sub>2</sub>-evolving system. *Plant Cell Physiol.* 28(7):1293-1299.
- Ono, T.A., and Y. Inoue. 1988. Discrete extraction of the Ca atom functional for O<sub>2</sub> evolution in higher plant Photosystem II by a simple low pH treatment. *FEBS Lett* 227(2):147-152.
- Papageorgiou, G.C., Y. Fujimura, and N. Murata. 1991. Protection of the oxygen-evolving Photosystem II complex by glycinebetaine. *Biochim Biophys Acta* 1057:361-366.
- Papageorgiou, G.C., and N. Murata. 1995. The unusually strong stabilizing effects of glycine betaine on the structure and function of the oxygen-evolving Photosystem II complex. *Photosynth Res.* 44:243-525.
- Pecoraro, V.L., M.J. Baldwin, M.T. Caudle, W.Y. Hsieh, and N.A. Law. 1998. A proposal for water oxidation in photosystem II. *Pure Appl. Chem.* 70:925-929.
- Pecoraro, V.L., and W.Y. Hsieh. 2000. Manganese and its Role in Biological Processes. *In* Metal Ions in Biological Systems. Sigel A, Sigel H, editors. Marcel Dekker, New York. 429.
- Peloquin, J.M., and R.D. Britt. 2001. EPR/ENDOR characterization of the physical and electronic structure of the OEC Mn cluster. *Biochim Biophys Acta* 1503(1-2):96-111.
- Peloquin, J.M., K.A. Campbell, D.W. Randall, M.A. Evanchik, V.L. Pecoraro, W.H. Armstrong, and R.D. Britt. 2000. <sup>55</sup>Mn ENDOR of the S<sub>2</sub>-state multiline EPR signal of Photosystem II: implications on the structure of the tetranuclear Mn cluster. *J Am Chem Soc* 122(10926–10942).
- Penner-Hahn, J.E. 1999. Structural Characterization of the Mn Site in the Photosynthetic Oxygen-Evolving Complex. *In* Metal sites in proteins and

- models: redox centres. Hill HA, Sadler PJ, Thomson AJ, editors, Berlin, Heidelberg, New York,. 1-36.
- Popelkova, H., M.M. Im, J. D'Auria, S.D. Betts, N. Lydakis-Simantiris, and C.F. Yocum. 2004. N-Terminus of the Photosystem II manganese stabilizing protein: Effects of sequence elongation and truncation. *Biochemistry* 41:2702-2711.
- Porra, R.J. 1990. The extraction and assay of refractora chlorophylls and a simples method to correct data from Arnon's equations. *In Current Research in Photosynthesis*. Baltscheffsky M, editor. Kluwer Academic Publishers, Netherlands. 237-240.
- Pospisil, P., and H. Dau. 2000. Chlorophyll fluorescence transients of Photosystem II membrane particles as a tool for studying photosynthetic oxygen evolution. *Photosynthesis research* 65:41-52.
- Pospisil, P., M. Haumann, J. Dittmer, V.A. Sole, and H. Dau. 2003. Stepwise Transition of the Tetra-Manganese Complex of Photosystem II to a binuclear  $Mn_2(\mu-O)_2$  Complex in response to a Temperature Jump: A time resolved Structural Investigation Employing X-Ray Absorption Spectroscopy. *Biophys. J.* 84:1370-1386.
- Radmer, R., and G.M. Cheniae. 1971. Photoactivation of the manganese catalyst of  $O_2$  evolution II. A two- quantum mechanism. *Biochim Biophys Acta* 253(1):182-186.
- Rappaport, F., M. Blanchard-Desce, and J. Lavergne. 1994. Kinetics of electron transfer and electrochromic change during the redox transition of the photosynthetic oxygen-evolving complex. *Biochim Biophys Acta* 1184:178-192.
- Razeghifard, M.R., and R.J. Pace. 1999. EPR kinetic studies of oxygen release in thylakoids and PSII membranes: a kinetic intermediate in the  $S_3$  to  $S_0$  transition. *Biochemistry* 38(4):1252-1257.
- Renger, G. 1992. Energy transfer and trapping in Photosystem II. *In The Photosystems: Structure, Function and Molecular Biology*. Barber J, editor. Elsevier Science Publishers B.V. 45-99.
- Riggs, P.J., R. Mei, C.F. Yocum, and J.E. Penner-Hahn. 1992. Reduced derivatives of the Manganese cluster in the Photosynthetic oxygen evolving complex. *J Am Chem Soc* 114:10650-10651.
- Robblee, J.H., R.M. Cinco, and V.K. Yachandra. 2001. X-ray spectroscopy-based structure of the Mn cluster and mechanism of photosynthetic oxygen evolution. *Biochim Biophys Acta* 1503(1-2):7-23.
- Roelofs, T.A., W. Liang, M.J. Latimer, R.M. Cinco, A. Rompel, J.C. Andrews, K. Sauer, V.K. Yachandra, and M.P. Klein. 1996. Oxidation states of the manganese cluster during the flash-induced S- state cycle of the photosynthetic oxygen-evolving complex. *Proc Natl Acad Sci U S A* 93(8):3335-3340.
- Roose, J.L., K.M. Wegener, and H.B. Pakrasi. 2007. The extrinsic proteins of Photosystem II. *Photosynth Res* 92(3):369-387.
- Sandusky, P.O., and C.F. Yocum. 1984. The chloride requirement for photosynthetic oxygen evolution: analysis of the effects of chloride and other anions on amine inhibition of the oxygen-evolving complex. *Biochim. Biophys. Acta* 766:603-611.
- Saphon, S., and A.R. Crofts. 1977. The  $H^+/e$  ration in chloroplasts in 2. Possible errors in its determination. *Z Naturforsch [C]* 32(9-10):810-816.
- Satoh, K., T. Wydrzynski, and Govindjee. 2005. Introduction to Photosystem II. *In Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 11-22.

- Sauer, K., and V.K. Yachandra. 2004. The water-oxidation complex in photosynthesis. *Biochim Biophys Acta* 1655(1-3):140-148.
- Schiller, H., and H. Dau. 2000. Preparation protocols for high-activity photosystem II membrane particles of green algae and higher plants, pH dependence of oxygen evolution and comparison of the S<sub>2</sub>-state multiline signal by X-band EPR spectroscopy. *J Photochem Photobiol B* 55(2-3):138-144.
- Schlodder, E., and H.T. Witt. 1999. Stoichiometry of proton release from the catalytic center in photosynthetic water oxidation. Reexamination by a glass electrode study at pH 5.5-7.2. *J Biol Chem* 274(43):30387-30392.
- Seidler, A. 1996. The extrinsic polypeptides of Photosystem II. *Biochim Biophys Acta* 1277(1-2):35-60.
- Shen, G., J.J. Eaton-Rye, and W.F. Vermaas. 1993. Mutation of histidine residues in CP47 leads to destabilization of the photosystem II complex and to impairment of light energy transfer. *Biochemistry* 32(19):5109-5115.
- Strickler, M.A., L.M. Walker, W. Hillier, and R.J. Debus. 2005. Evidence from biosynthetically incorporated strontium and FTIR difference spectroscopy that the C-terminus of the D1 polypeptide of photosystem II does not ligate calcium. *Biochemistry* 44(24):8571-8577.
- Suorsa, M., R.E. Regel, V. Paakkarinen, N. Battchikova, R.G. Herrmann, and E.M. Aro. 2004. Protein assembly of photosystem II and accumulation of subcomplexes in the absence of low molecular mass subunits PsbL and PsbJ. *Eur J Biochem* 271(1):96-107.
- Tamura, N., and G.M. Chéniaie. 1987. Photoactivation of the water-oxidizing complex in Photosystem II membranes depleted of Mn and Extrinsic proteins. I. Biochemical and kinetic characterization. *Biochim. Biophys. Acta* 890:179-194.
- Tamura, N., Y. Inoue, and G.M. Chéniaie. 1989. Photoactivation of the water-oxidizing complex in Photosystem II membranes depleted of Mn, Ca and extrinsic proteins. II. Studies on the functions of Ca<sup>+</sup>. *Biochim. Biophys. Acta* 976:173-181.
- Tang, X.S., D.W. Randall, D.A. Force, B.A. Diner, and R.D. Britt. 1996. Manganese-Tyrosine Interaction in the Photosystem II Oxygen-Evolving Complex. *J. Am. Chem. Soc.* 118:7638-7639.
- Vander Meulen, K.A., A. Hobson, and C.F. Yocum. 2004. Reconstitution of the photosystem II Ca<sup>2+</sup> binding site. *Biochim Biophys Acta* 1655(1-3):179-183.
- Vass, I., and S. Styring. 1991. pH-dependent charge equilibria between tyrosine-D and the S-states in photosystem II. Estimation of relative midpoint redox potentials. *Biochemistry* 30(3):830-839.
- Vrettos, J.S., J. Limburg, and G.W. Brudvig. 2001. Mechanism of photosynthetic water oxidation: combining biophysical studies of photosystem II with inorganic model chemistry. *Biochim Biophys Acta* 1503(1-2):229-245.
- Whitmarsh, J., and Govindjee. 1999. The Photosynthetic Process. In *Concepts in Photobiology: Photosynthesis and Photomorphogenesis*. Singhal GS, Renger G, Sopory SK, Irrgang K-D, Govindjee, editors. Narosa Publishers, New Delhi. 11-51.
- Wille, B., and J. Lavergne. 1982. Measurement of proton translocation in the thylakoids under flashing light using a spin-labelled amine. *Photochem Photobiol Sci* 4:131-144.
- Williams, W.P., and K. Gounaris. 1992. Stabilisation of PS-II-mediated electron transport in oxygen-evolving PS II core preparations by the addition of compatible co-solutes. *Biochim Biophys Acta* 1100(1):92-97.

- Witt, H.T. 1996. Primary reactions of oxygenic Photosynthesis. *Phys Chem Chem Phys* 100:1923-1942.
- Witt, H.T., and A. Zickler. 1974. Vectorial electron flow across the thylakoid membrane. Further evidence by kinetic measurements with an electrochromic and electrical method. *FEBS Lett* 39(2):205-208.
- Wydrzynski, T.J., and K. Satoh. 2005. The Catalytic Manganese Cluster: Protein Ligation. *In The Light-Driven. Water:Plastoquinone Oxidoreductase*. Govindjee, editor. Springer, The Netherlands. 235-260.
- Yachandra, V.K. 2005. The Catalytic Manganese Cluster: Organization of the Metal Ions. *In Photosystem II: The Light-Driven Water: Plastoquinone Oxidoreductase*. Wydrzynski T, Satoh K, editors. Springer, The Netherlands. 235-260.
- Yachandra, V.K., R.D. Guiles, A.E. McDermott, J.L. Cole, R.D. Britt, S.L. Dexheimer, K. Sauer, and M.P. Klein. 1987. Comparison of the structure of the manganese complex in the  $S_1$  and  $S_2$  states of the photosynthetic  $O_2$ -evolving complex: an x-ray absorption spectroscopy study. *Biochemistry* 26(19):5974-5981.
- Yachandra, V.K., K. Sauer, and M.P. Klein. 1996. Manganese Cluster in Photosynthesis: Where Plants Oxidize Water to Dioxygen. *Chem Rev* 96(7):2927-2950.
- Yano, J., J. Kern, K.D. Irrgang, M.J. Latimer, U. Bergmann, P. Glatzel, Y. Pushkar, J. Biesiadka, B. Loll, K. Sauer, J. Messinger, A. Zouni, and V.K. Yachandra. 2005. X-ray damage to the  $Mn_4Ca$  complex in single crystals of photosystem II: a case study for metalloprotein crystallography. *Proc Natl Acad Sci U S A* 102(34):12047-12052.
- Yano, J., J. Kern, K. Sauer, M.J. Latimer, Y. Pushkar, J. Biesiadka, B. Loll, W. Saenger, J. Messinger, A. Zouni, and V.K. Yachandra. 2006. Where water is oxidized to dioxygen: structure of the photosynthetic  $Mn_4Ca$  cluster. *Science* 314(5800):821-825.
- Yocum, C.F. 1991. Calcium activation of photosynthetic water oxidation. *Biochimica et Biophysica Acta* 1059:1-15.
- Yocum, C.F., C.T. Yerkes, R.E. Blankenship, R.R. Sharp, and G.T. Babcock. 1981. Stoichiometry, inhibitor sensitivity, and organization of manganese associated with photosynthetic oxygen evolution. *Proc Natl Acad Sci U S A* 78(12):7507-7511.
- Zabinsky, S.I., J.J. Rehr, A. Ankudinov, R.C. Albers, and M.J. Eller. 1995. Multiple-scattering calculations of x-ray-absorption spectra. *Physical Review. B. Condensed Matter*. 52(4):2995-3009.
- Zaltsman, L., G.M. Ananyev, E. Bruntrager, and G.C. Dismukes. 1997. Quantitative kinetic model for photoassembly of the photosynthetic water oxidase from its inorganic constituents: requirements for manganese and calcium in the kinetically resolved steps. *Biochemistry* 36(29):8914-8922.
- Zheng, M., and G.C. Dismukes. 1996. Orbital Configuration of the Valence Electrons, Ligand Field Symmetry, and Manganese Oxidation States of the Photosynthetic Water Oxidizing Complex: Analysis of the  $S(2)$  State Multiline EPR Signals. *Inorg Chem* 35(11):3307-3319.
- Zouni, A., R. Jordan, E. Schlodder, P. Fromme, and H.T. Witt. 2000. First photosystem II crystals capable of water oxidation. *Biochim Biophys Acta* 1457(3):103-105.
- Zouni, A., H. Witt, J. Kern, P. Fromme, N. Krauß, W. Saenger, and P. Orth. 2001. Crystal structure of photosystem II from *Synechococcus elongatus* at 3.8 Å resolution. *Nature* 409:739-743.