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Minireview

Photosynthesis research in the People's Republic of China[1]

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Abstract

The first research paper on photosynthesis in China was published by T.T. Li[2] in 1929. Two photosynthesis laboratories were established in Shanghai and Beijing in the 1950s and the 1960s, respectively. A photophosphorylation 'intermediate' was discovered after the energy conversion process was separated into light and dark phases in the 1960s. Since the 1980s, research has accelerated at several different levels through efforts of a large number of scientists in China.

Abbreviations: ATP – adenosine triphosphatase; CP – chlorophyll protein; D1 – the 32-kDa polypeptide subunit of Photosystem II; LHC – light-harvesting complex; LHCP – light-harvesting chlorophyll protein; NADPH – nicotinamide adenine dinucleotide phosphate (the reduced form); Rubisco – ribulose bisphosphate carboxylase oxygenase

The early days: 1929–1960

The first research on photosynthesis in China, 'The immediate effect of change of light on the rate of photosynthesis,' was published in a British journal (T.T. Li 1929). Hung-Chang Yin found that the photosynthetic rate of *Elodea* changed transiently at the very moment when the light was changed from one wavelength to a different wavelength, in Ji-Tung Li's Laboratory at Nankai University. This could be the precursor of the so-called Blinks effect, discovered later by Lawrence Blinks in 1957, and related to the discovery of the two photosystems in oxygenic photosynthesis (see French 1961). After a one-year co-operation with Pei-sung Tang studying single-celled green algae, Yin worked with the late Robert Emerson at California Institute of Technology from 1935 to 1937. In the 1930s, many plant physiologists, including Tang and Yin, returned to China after receiving their PhDs in America and Europe, and started to set up laboratories of Plant Physiology. The earnest wishes in photosynthesis research of Yin and Tang were realized when two photosynthesis laboratories were established in the Shanghai Institute of Plant Physiology and the Institute of Botany (in Beijing) in 1950s and 1960s, respectively. Both professors became the Lab directors, Yin at Shanghai, and Tang at Beijing (Figure 1).

The next phase: 1960–1970 – a major discovery and growth of research

In the 1960s, comprehensive study in photosynthesis from the molecular to the community level was organized (see Shen 1994). On the molecular level, the study was mainly concentrated on energy conversion, and the quantum requirement of photophosphorylation (Yin 1961). Shen and Shen (1962) convincingly showed the existence of a 'photophosphorylation intermediate' after separating the energy conversion process into light and dark phases (see also Jagendorf 2002). Relationships among photophosphorylation,

Figure 1. Hong-Chang Yin (left, 1908–1992) and Pei-sung Tang (right, 1900–2001).

chlorophyll (Chl) a fluorescence and Mn content were later investigated (Chow et al. 1963; Kuang et al. 1966). Natural problems of photosynthesis, such as community structure and light utilization, also became main areas of research (Yin et al. 1959).

Since 1970, several photosynthesis groups have been organized at Bejing University, Sichuan University, Beijing Agricultural University, Beijing Forest University, Institute of Oceanology, Nanjing Agricultural University, Zhejiang University and Shangdong Agricultural University, South China Institute of Botany, and Institute of Chemistry and Institute of Biophysics, both in Beijing.

The modern period: 1980 and beyond

In the 1980s, research in the area of photosynthesis was greatly accelerated. The first national conference of photosynthesis was held in Xiamen in 1981. More than forty scientists participated in this conference. Govindjee and Bacon Ke, however, joined us at the second conference in Yangzhou in 1984 (Figure 2). In 1981, Bacon Ke held the first training course of primary reactions in photosynthesis in Beijing. Forty scientists attended his course. In 1985, the United Nations Environment Programme organized a training course on bio-productivity and photosynthesis in Shanghai. More than 10 international professors taught 40 young scientists to solve problems in photosynthesis. In 1988, more than 20 reputed scientists participated in an international symposium on 'regulation and efficiency of photosynthesis.' Since then, a great number of outstanding international photosynthesis scientists have visited universities or institutes in China and many reputed Labs have accepted hundreds of Chinese scientists, many of whom have made outstanding discoveries, and are now teaching at US and other universities. Meanwhile, excellent research has also been accomplished in China.

Light harvesting complex: structure and function

Correlating structure with function of pigment-protein complexes, the 21 kD protein of light harvesting complex (LHC) I was demonstrated to be responsible for long-wavelength fluorescence of LHC I (Kuang et al. 1984). (For a historical review on Chl *a* fluorescence, see Govindjee 1995.) In higher plants, it was shown that: (1) association of the Chl proteins with the light-harvesting complex follows the order: LHCP 1, LHCP 2 and LHCP 3 (Z.D. Zhang et al. 1981); (2) the cation-induced membrane stacking of thylakoid does not necessarily cause a corresponding change in Chl a fluorescence (Zhou et al. 1982); (3) two proteins on the outer surface of the thylakoid membrane might serve as regulators of energy distribution (Li et al. 1986); and (4) Mg^{2+} ions could induce structural or conformational alteration of thylakoid membranes through electrostatic neutralization of LHC II, and thereafter cause changes in excitation energy distribution between the two photosystems (L.B. Li et al. 1987). It was also shown that during state transitions in wheat leaf, both spillover and changes in absorption cross-section are involved (Tan et al. 1998; for further information on this topic, see Allen 2002).

In the chloroplast of *Codium fragile*, the cation-induced change of excitation energy distribution between PS II and PS I is not controlled by the electrostatic property on the thylakoid surface (L.B. Li et al. 1992).

The two-dimensional structure of LHC II crystals was determined at 1.5 nm resolution by electron microscopy and image processing. By comparing 2-D crystal formations, similar but not identical structural

Figure 2. Participants at the 1984 Yangzhou Symposium on Photosynthesis, *Front row (from left to right):* Su-Jun Li, Ming-Qi Li, Yun-Kang Shen, Eric Lam, Govindjee, Hong-Chang Yin, Bacon Ke, Wah Soon Chow, Yu-Zhu Gao, Ting-Yun Kuang, Pei-Zhen Zhou, and Yun-Lin Dai.

Figure 3. Authors (from left to right) Liang-Bi Li, Ting-Yun Kuang, Yun-Kang Shen and Chunhe Xu.

features were shown for LHC IIs of cucumber and spinach (W. Xu et al. 1998).

Isolation, crystallization and analysis of crystal structure of a phycobiliprotein: R-phycoerythrin was obtained for *Porphyra yezoensis* (Chang et al. 1995). The importance of exciton transfer in antenna systems was discussed after measuring the time-resolved excitation density-dependent fluorescence for R-phycoerythrin (H.Z. Wang et al. 1994). Ordered 2-D arrays of the photodynamic pigment protein allophycocyanin were also obtained (J. He et al. 1996).

Using a ChlL-depletion mutant of the cyanobacterium *Synechocystis* 6809, energy transfer from phycobilisome to the two photosystems was related to certain aspects of chlorophyll synthesis (J.J. Yu et al. 1999). After long-term adaptation of the photosynthetic apparatus, a cyanobacterial mutant PR 6008 was found to be unable to synthesize phycocyanin and thus unable to assemble peripheral rods (Zhao et al. 2001).

The 77K fluorescence spectra of wheat thylakoids showed that LHC II trimer in thylakoid membrane could be aggregated and transformed into macroaggregates on a large scale in the presence of Mg^{2+} (Wen et al. 1999).

A comparative study was made on structure and function of incompletely and fully developed membranes of wheat chloroplasts. It was found that cations did not cause decrease in the Soret and the red absorption bands in the incompletely developed chloroplast membranes. The so-called flattening effect (or the 'sieve' effect; see Rabinowitch 1956) on the light absorption spectrum of unsuspended particles in the incompletely developed chloroplast membranes was not observed. Changes of absorption spectrum were related to changes in membrane structure (Kuang et al. 1980).

The reaction center and the core complexes

Magnetic circular dichroism spectrum of Photosystem (PS) II reaction center (RC) was obtained and its relative components were assigned to related pigments (K.Y. Yang et al. 1997). After analyzing picosecond kinetics by time-resolved absorption spectroscopy, a possible energy transfer between β-carotene or pheophytin (Pheo) and P680 was demonstrated within PS II RC (Hou et al. 1997).

Derivative and difference absorption spectra showed that two groups of Chl a exist in both CP43 and CP47 (chlorophyll protein complexes with masses of 43 and 47 kDa, respectively). One with peaks in the shorter wavelength region was designated as CP43-669 or CP47-669, and the other as CP43-682 or CP47-680, the numbers reflect the red absorption maximum, in nm. CP43-669 and CP47-669 may exist as monomers, whereas CP43-682 and CP47-680 exist as dimers (Shan et al. 2001). CP47 is more heat stable than CP43 but the native state of Chl a of CP47 is more light sensitive than that of CP43 during light- and/or heat-induced denaturation of PS II (J.S. Wang et al. 1999).

Using the *ab initio* method of calculation at the minimal basis set and the restricted Hartree-Fock level, the electronic structure of the primary electron donor, P_{960}, in RC of *Rps. viridis*, was studied (X.D. Zhang et al. 2000). Theoretical investigation was also made on the primary electron donor P_{870} of *Rb. sphaeroides* (C.X. Zhang et al. 1999) and peripheral ligands of the PS II oxygen-evolving center (C.X. Zhang et al. 2000).

Studies on the manganese stabilizing protein

Modification by N-bromosuccinimide was done to explore the role of Trp241, the only tryptophan in the manganese stabilizing protein (MSP) of PS II. Results showed that Trp241 is important in maintaining MSP structure and function in oxygen evolution (Y. Yu et al. 2001). FT-IR (Fourier Transform-Infra Red) study showed that the amide I line shape of MSP was affected by La (L.X. Zhang et al. 1996), indicating a change in β sheets of MSP of between 36 and 50%. MSP shows a reversible two-state unfolding transition from one atmosphere to 180 MPa, much lower than those for most proteins so far studied. The change in standard free energy at pH 6.0 and 20 °C is –14.6 kJ/mol, an order of magnitude lower than conventional proteins. (K.C. Ruan et al. 2001), supporting the theory that MSP lacks a well-defined structure.

Cytochrome b6/f complex and Photosystem I complex

Yan et al. (2001) demonstrated that the β-carotene in cytochrome (Cyt) b_6f complex predominantly takes a 9-cis configuration in both dissociated and native states, suggesting that 9-cis β-carotene is an authentic component and may play a unique physiological role.

FT-IR study demonstrated that the transmembrane structure of proteins in PS I complex is more resistant to delipidation than that in the PS II complex (X. Ruan et al. 2000). The binding of phosphatidylglycerol to PS II particles induced changes in conformation and micropolarity of the phenol ring in tyrosine (Z.L. Yang et al. 2000). Upon reconstitution of lipid-depleted spinach Cyt b_6f complex with the spinach membrane lipids, the electron transfer activity of Cyt b_6f was stimulated, following the order: monogalatosyldiglyceride, digalatosyldiglyceride, phosphatidylcholine, phosphatidylglycerol and sulphoquinovosyldiglyceride. The extent of stimulation of electron transfer was related to the lipid charge (Yan et al. 2000).

Photophosphorylation

Regarding photophosphorylation, besides that previously stated (Shen 1994), new progress has been made. Spraying 1–2 mM $NaHSO_3$ on the wheat leaf resulted in enhancement of photosynthesis through stimulation of cyclic photophosphorylation (H.W. Wang et al. 2000). A previous study had suggested an involvement of a localized proton gradient in photophosphorylation (see Shen 1994). It was found that under low temperature and isotonic conditions, the proton released from water oxidation was liable to be distributed in a localized manner. This localized distribution could be used to synthesize ATP (Wei et al. 1998) (see R. Dilley, Part 3 of these special history issues, forthcoming). Subunit interactions among the chloroplast ATP synthase subunits were studied using a yeast two-hybrid system. Results suggested the existence of specific and strong interactions between γ and ϵ, α and β, α and ϵ, β and ϵ as well as β and δ subunits, but only weak and transient interactions between δ and ϵ, δ and γ subunits (Shi et al. 2000). Deletion of as few as three amino acid residues from the N-terminus or six residues from the C-terminus of ϵ subunit significantly affected the ATPase-inhibitory activity (Shi et al. 2001), suggesting that both N- and C-termini are important in the regulation of ATPase activity. A new membrane system was reconstituted (S.J. Li et al. 1984) by combining thylakoids deficient in CF_1 of spinach chloroplasts with cristae vesicles of rat liver mitochondria. The activity of photophosphorylation in the reconstituted membranes increased with the increase in light intensity. Investigation into the molecular properties and physiological function of thylakoid membrane-bound NAD(P)H dehydrogenase complex (NDH) was carried out in cyanobacteria and higher plants (Mi et al. 2000, 2001).

Rubisco

When tobacco Rubisco, covalently linked to CNBr-activated Sepharose 4B, was treated with urea, the small subunit was dissociated at a urea concentration of 2–2.5 M, while the large subunit remained bound. When the urea concentration was lowered to 0.5 M, the dissociated small subunit could almost completely rebind (L.R. Li et al. 1988). Fructose 1,6-bisphosphate specifically protects the α-subunit of pyrophosphate-dependent 6-phosphofructo-1-phosphotransferase against proteolytic degradation (Y.H. Wang and Shi 1999).

Photoinhibition

Studies on the operation and regulation of the photosynthetic apparatus, started with the effects of humidity on the midday depression of photosynthesis (D.Q. Xu and Shen 1984). Study showed the relative contributions of different mechanisms in protecting the photosynthetic apparatus from photodamage during leaf development (Hong et al. 1999). Under natural conditions, photoinhibition of photosynthesis in soybean can be attributed to reversible inactivation of PS II reaction centers, involving the dissociation of LHC II (Hong and Xu 1999). During photoinhibition, photodamage of histidine was discovered in PS II RC (Kuang et al. 1993). The photodamage of Pheo and P680 subsequently occurred: Pheo is first damaged under strong illumination; and a Pheo photo-protective scheme was proposed for PS II RC (Hou et al. 1996).

In vivo studies demonstrated that PS II is rather resistant to water stress, as a mild water deficit in leaves did not significantly affect PS II activity. However, extreme water stress caused an obvious reduction in photosynthetic O_2 evolution (J.X. He et al. 1995). At moderate water stress, the apoproteins of LHC II decreased more rapidly than the Chl content. However, the contents of both Chl and apoproteins of LHCII decreased markedly in severely water-stressed maize leaves (Hao et al. 1996).

Inhibition of D1 synthesis by treatment with lincomycin induced a parallel blockage on both zeaxanthin epoxidation and PS II recovery from a damaged state (C.C. Xu et al. 2000a). The role of the xanthophyll cycle in the protection against PS II photoinhibition induced by chilling in moderate light was investigated, and it was suggested that the xanthophyll cycle might play a critical role in the protection of the thylakoid lumen against over-acidification and the resulting photoinhibition of PS II RC (C.C. Xu et al. 2000b). The xanthophyll cycle plays a role in protection of PS II from photoinhibition in senescent leaves by dissipating excess excitation energy, in particular when the leaves are exposed to high light levels (Lu et al. 2001a, b). (See a historical account by B. Demmig-Adams, this issue, for xanthophyll-dependent photoprotection by loss of heat.) H. Yu et al. (2000) demonstrated that LHC I was more sensitive than the PsaA/B subunits to degradation after 40 min illumination.

Studies abroad by the authors

Two of us (C. X. and T.-Y. K.) have not only worked in the People's Republic of China, but have also done collaborative research in the USA. The work of T.-Y. K., in the laboratory of Charlie Arntzen has been already discussed above (Kuang et al. 1984). C. X. worked in the laboratory of Govindjee for his doctoral degree. It is an interesting coincidence that Govindjee was a student of Robert Emerson, with whom Hung-Chang Yin had earlier studied. Together with others, C. Xu discovered the unique and differential role of chloroacetates on both the acceptor (Xu 1992; Govindjee et al. 1997) and the donor side of Photosystem II (PS II) (C. Xu et al. 1995; Y. Yu et al. 1997). Further, he observed the differential stimulatory role of bicarbonate on chloroacetate- and formate-treated photosynthetic samples, and related it to the well-established bicarbonate effects on PS II (C. Xu et al. 1991; C. Xu 1992; for historical reviews on the bicarbonate effect, see Stemler 2002; van Rensen 2002). Following the observations of Fatima El-Shintinawy in Govindjee's laboratory, C. Xu made one of the earliest measurements on the bicarbonate-reversible formate inhibition effect on both the donor and acceptor sides of PS II (El-Shintinawy et al. 1990). Importantly, Vladimir Shinkarev et al. (1997) were able to measure the kinetics of oxygen evolution from the Chl a fluorescence decay data obtained by one of us (C.X.), after single flashes.

Concluding remarks

Among eight plant functional types along a precipitation gradient in northeast China, their net photosynthesis (Pn) showed the following order from lowest to highest: meadow steppe grasses > typical steppe grasses > steppe shrubs > desert grasses > forest tree > forest shrubs > desert shrubs > forest grasses ($P < 0.05$) (Jiang et al. 1999). Different plant functional types gave different responses of photosynthesis to enviromental changes.

Study of photosynthesis in China has been only briefly summarized above. Currently, a national scientific program is being carried out among universities and institutes, in attempts to correlate the productivity of crops, especially super-rice with photosynthetic activity. Hopefully, promising results will be obtained after the co-operation is completed.

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Notes

[1]Editor's note: this article does not contain information on work done in Taiwan (The Republic of China), only in mainland China.

[2]In the Chinese custom, the last name of an individual is written first, but for consistency and indexing, Photosynthesis Research uses the international convention.

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