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*Minireview*

# Early research on the role of plastocyanin in photosynthesis

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**Abstract**

A review is presented of the early history of investigations into the function of the blue copper-protein plastocyanin in photosynthesis. The controversy or confusion that arose as to the function of plastoycanin in conjunction with cytochrome *f* and cytochrome $c_6$ is discussed and investigations contributing to the establishment of the role of plastocyanin as the mobile electron carrier between the Photosystem I reaction center complex and the cytochrome $b_6/f$ complex are described.

*Abbreviations:* cyt – cytochrome; DCIP – 2,6-dichlorophenolindophenol; PS I – Photosystem I; PS II – Photosystem II; DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea; NADP –ṅicotinamide adenine dinucleotide phosphate

## Introduction

An involvement of copper in photosynthesis was suggested as early as 1939 when it was found that photosynthesis was more sensitive than dark respiration to specific inhibitors of copper enzymes (Greene et al. 1939) and that a major portion of copper in green leaves was located in chloroplasts (Neish 1939). An investigation into the function of copper in photosynthesis was, however, initiated two decades later when the actual status of copper in the photosynthetic apparatus was elucidated. In 1960, a blue copper protein, that could undergo reversible oxidation and reduction reactions but had no oxidase activity, was discovered in *Chlorella ellipsoidea* (Katoh 1960a; see Katoh 1995). The copper protein was also found in higher plants, present in green leaves but not in non-chlorophyllous tissues; it was located in broken chloroplasts or thylakoids in the ratio of 1 protein per 300 chlorophyll molecules, or one protein per 'photosynthetic unit' (Katoh et al. 1961). In view of its localization in chloroplasts and its characteristic blue color in the oxidized state, the copper protein was named plastocyanin (Katoh and Takamiya 1961). Plastocyanin was rapidly reduced in the light but not in the dark by thylakoid membranes (Katoh and Takamiya 1961). These data suggested that the copper protein is related to photosynthesis but not to respiration.

This historical minireview focuses on the early stage of investigation at which time the role of plastocyanin in photosynthetic electron transport was established. For the studies on the structure–function relationship of the protein which have greatly advanced since the crystal structure of poplar plastocyanin was analyzed (Coleman et al. 1978), see reviews of Freeman (1981), Sykes (1985, 1991), Gross (1993, 1996), Redinbo et al. (1994), Sigfridsson (1998), Hope (2000) and Ke (2001, pp. 605–621).

Although the structure of plastocyanin is not the main theme of this article, for historical reasons, I show in Figure 1, a photograph of a greeting card I received in 1980 from Hans Freeman's research group in Sydney, Australia. Figure 2 shows a rendition of plastocyanin from poplar (*Populus nigra*) (see

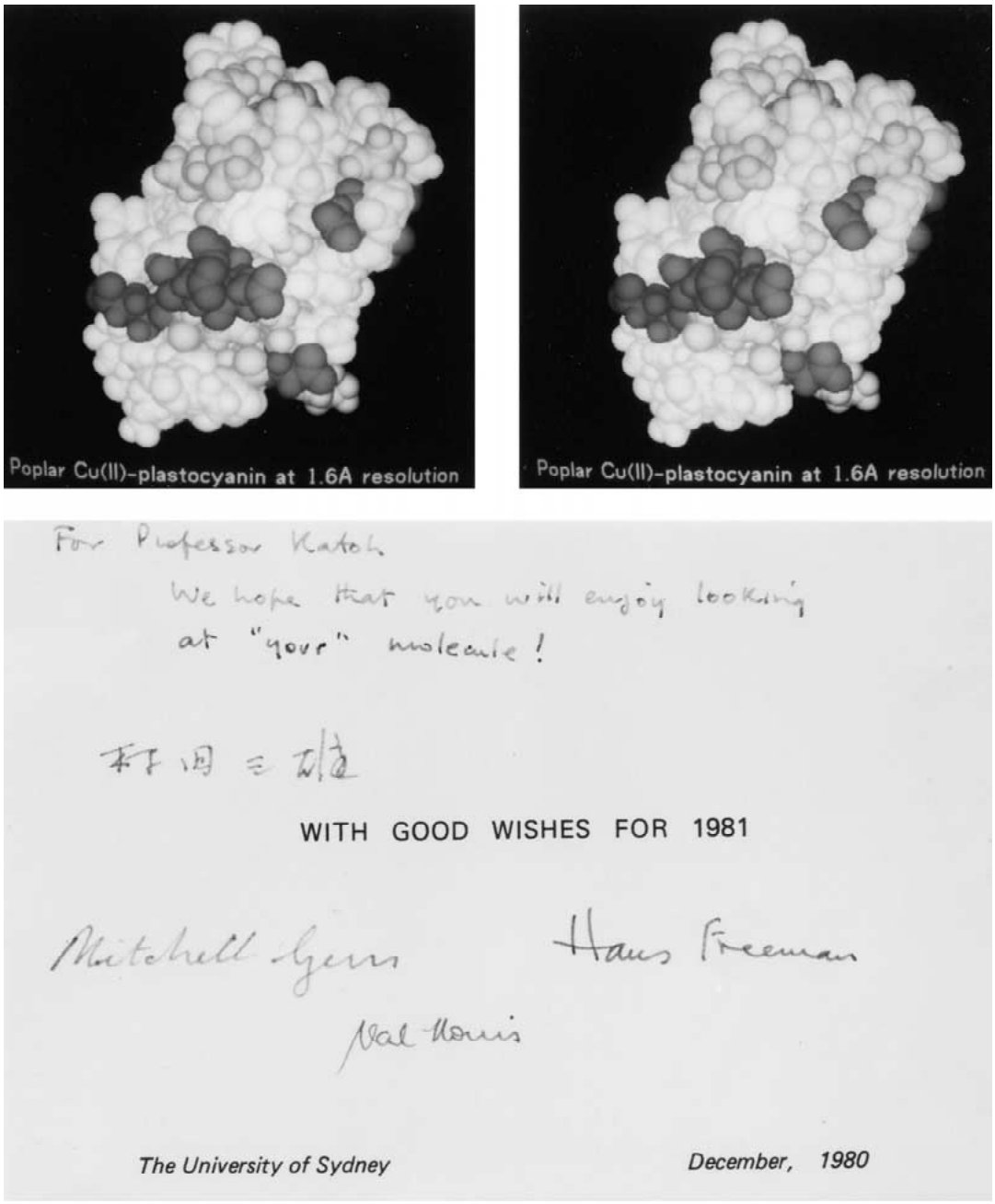


*Figure 1.* A greeting card from H.C. Freeman's laboratory sent to the author (SK) in 1980. For a color version of this figure, see color section in the front of the issue. The black and white rendition here does not show the colors mentioned in the legend. *Top*: stereoscopic picture of the poplar plastocyanin molecule viewed from the side of the negative patch (orange). Tyrosine-83 is near the center of the picture and Histidine-87 (bluish) is visible at the top of the molecule. *Bottom*: signatures of Freeman and his group members.

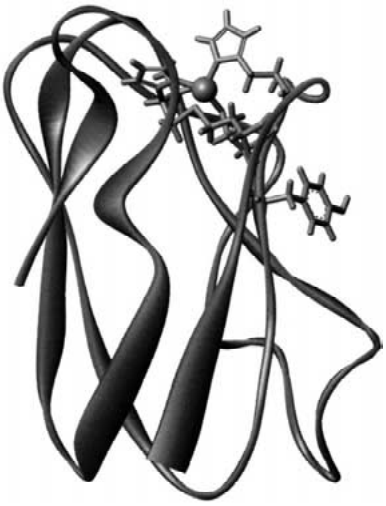

*Figure 2.* A rendition of the structure of poplar (*Populus nigra*) plastocyanin by Blankenship (2002, p. 140) from the Protein Data Bank file 1 PLC, using Web Lab viewer from Molecular Simulations, Inc. This figure shows the amino acids that ligand to the copper (shown as a ball) as well as the tyrosine.

Blankenship 2002, p. 140); amino acids (histidine-87 (top of the diagram); histidine-37; cysteine-84; and methionine–92) are liganded to the copper ion; tyrosine-83 (shown on the right end of the diagram) is implicated in the electron transfer events.

## Functional site of plastocyanin

Participation of plastocyanin in photosynthetic electron transport was first indicated by extraction-reconstitution techniques because the protein was readily extracted from thylakoid membranes by detergent and sonic treatments. Detergent treatment of the membranes resulted in loss of PS I activities such as photooxidation of cytochrome *c* and photoreduction of nicotinamide adenine dinucleotide phosphate ($NADP^+$) with the dichlorophenolindophenol (DCIP)-ascorbate couple as electron donor, and the lost activities were effectively restored by addition of plastocyanin (Katoh and Takamiya 1963; Kok et al. 1964; Wessels 1965). Sonication of chloroplasts which released plastocyanin without a severe effect on Photosystem (PS) II electron transport showed that plastocyanin is required for the whole-chain electron transport: NADP photoreduction with water as electron donor was largely recovered by the addition of the copper protein to sonicated preparations (Katoh and Takamiya 1965; Katoh and San Pietro 1966a). These data showed that plastocyanin is an essential member of photosynthetic electron transport and functions near PS I.

Plastocyanin has a redox potential of 370 mV, which is consistent with its location near PS I (Katoh et al. 1962). Because cytochrome *f* (cyt *f*) has a nearly identical redox potential (365 mV), different functional sites of plastocyanin in relation to cyt *f* have been proposed in the decade that followed the discovery of plastocyanin. The view that cyt *f* is located before plastocyanin and donates electron directly to $P700^+$ was proposed based on the assumption that plastocyanin is inactivated by salicylaldoxime, an inhibitor of copper enzymes. This reagent inhibited PS II and whole chain electron transport but not PS I activity, NADP photoreduction with the DCIP/ascorbate couple (Trebst 1963). It was suggested, therefore, that cyt *f* is the electron donor to P700 because at that time the DCIP/ascorbate couple was thought to donate electrons at the level of cyt *f* (Witt et al. 1961). Spectroscopic studies also showed that salicylaldoxime suppressed cyt *f* photoreduction by PS II and a light-induced absorption change near 600 nm which was postulated to represent photooxidation of plastocyanin in the thallus of *Ulva* (Fork and Urbach 1965). Salicylaldoxime also inhibited photoreduction by PS II but not photooxidation by PS I of cyt *f* in spinach chloroplasts (Avron and Chance 1967). The scheme was, however, not supported subsequently because salicylaldoxime was shown to inhibit PS II electron transport but not plastocyanin itself under the conditions employed in these experiments (Katoh and San Pietro 1966b; Katoh 1972a).

The notion that plastocyanin serves as a direct electron donor to P700 was suggested by Davenport (1965) who found that sonically disrupted thylakoid membranes which retained cyt *f* were unable to photoreduce $NADP^+$ unless plastocyanin was resupplied. The different roles of the two electron carriers were more clearly demonstrated by the following two experiments. Digitonin-treatment of thylakoid membranes resulted in release of both plastocyanin and cyt *f,* concomitant with the loss of the NADP photoreducing activity, and the lost activity was restored on the addition of plastocyanin, but not of cyt *f* (Wessels 1966). A *Chlamydomonas* mutant strain, ac208, which is deficient in plastocyanin but not in membrane - bound cyt c 553, later shown to be cyt *f* (*vide infra*), was unable to photoreduce $NADP^+$ with either water or reduced DCIP as electron donor and the activities were restored by the addition of plastocyanin

(Gorman and Levine 1966). Cytochrome *f* bound to the mutant thylakoids was reduced by PS II light but its oxidation by PS I light required plastocyanin. Another *Chlamydomonas* mutant strain, ac206, which has plastocyanin but lacks cyt *c553*, was inactive in the whole-chain electron transport but performed photoreduction of NADP when the ascorbate/ DCIP couple was supplied. All these data are consistent with the notion that the site of plastocyanin function is located between P700 and cyt *f*. Nevertheless, a series of experiments which cast doubt on the location of the two proteins appeared at the end of the 1960s.

For historical reasons, and to introduce a personal aspect into this narrative, I show here a photograph (see Figure 3), taken in 1967, at Hakone, Japan. It shows some of the scientists involved in photosynthesis research, including the author, enjoying Sukiyaki dinner.

## Two light reactions *versus* three light reactions

In 1969, a new hypothesis which assumes that plastocyanin is located in a linear electron transport mediated by two PS II light reactions with cyt *f* functioning in a cyclic electron transport driven by a PS I light reaction was forwarded based upon, among others, the observation that plastocyanin was required for the photooxidation of cyt $b_{559}$ by PS II light (Knaff and Arnon 1969). Because this three-light-reaction hypothesis challenged the widely held view that PS I and PS II light reactions are involved in photosynthesis, the functional sites of plastocyanin and cyt *f* suddenly became a matter of heated debate. Supporting the new model was the observation that chloroplasts depleted of plastocyanin by sonication were active in photooxidation of cyt *f* by PS I, whereas PS II-dependent photoreduction of the Cyt required addition of plastocyanin (Knaff and Arnon 1970). In contrast, other investigators showed that plastocyanin was effective in accelerating photooxidation of cyt *f* in sonically disrupted (Avron and Shneyour 1971) and detergent-treated thylakoid preparations (Hind 1968). The plastocyanin content in PS I particles prepared by French pressure cell treatment (Michel and Michel-Wolwertz 1969) also became the focus of attention because the particles were active in cyt *f* photooxidation and $NADP^+$ photoreduction in the absence of added plastocyanin. Investigators in two laboratories independently found that the particles essentially lacked plastocyanin and claimed that the copper protein is not required for PS I activities (Arnon et al. 1970; Murata and Fork 1971). Other investigators found, however, that the PS I particles still retained plastocyanin in an amount sufficient to account for the PS I activities (Baszynski et al 1971; Arntzen et al. 1971; Sane and Hauska 1972). Consensus could not be reached due to the contradicting data obtained by these extraction-reconstitution experiments.

The controversy was, however, settled by several laboratories, which employed different approaches. Plastocyanin was specifically inactivated by treatment of chloroplasts with $HgCl_2$, which resulted in replacement of the copper of plastocyanin by $Hg^{2+}$ (Kimimura and Katoh 1972). Consistent with the location of plastocyanin between P700 and cyt *f,* the inactivation of the protein was accompanied by inhibition of photooxidation of cyt *f* and postillumination reduction of $P700^+$, while leaving photooxidation of P700 unaffected. Treatment of chloroplasts with a high concentration of KCN also led to inhibition of electron transport between P700 and cyt *f* (Izawa et al. 1973) and the inhibition was ascribed to removal of the copper from plastocyanin by KCN (Berg and Krogmann 1975). EPR spectroscopy, which monitors the redox state of plastocyanin *in situ*, showed that, as expected from the two-light-reaction model, the protein was oxidized by PS I light and reduced by PS II light (Malkin and Bearden 1973). Flash spectroscopy revealed the occurrence of an electron donor that transfers electron to $P700^+$ with a half time of 20 $\mu$s and hence more rapidly than cyt *f* that donates an electron to $P700^+$ with a half time of 200 $\mu$s (Haehnel et al. 1971). The 20 $\mu$s donor was later identified as plastocyanin (Hippler et al. 1989). All these data indicated that plastocyanin is the electron donor to $P700^+$.

## Location of plastocyanin in the thylakoid membranes

Controversial data have also been reported as to the location of plastocyanin in the thylakoid membranes. The occurrence of plastocyanin in the interior of the membranes was suggested by Hauska et al. (1971) who showed that (1) sonic treatment of the thylakoids in the presence of a high concentration of plastocyanin prevented net loss of plastocyanin from the membranes and preserved activities of electron transport and coupled phosphorylation, and (2) plastocyanin in the membranes was not accessible to a specific antibody raised against the protein. The observation

*Figure 3.* A photograph of the Sukiyaki party at the symposium on Comparative Biochemistry and Biophysics, held from August 12 through 15, 1967, at Hakone, Japan. Shown here are, in the first row, C. Stacy French (smoking cigar) and Hiroshi Tamiya (hands in the air), among others. In the second row (4th from left) is the author (SK), smoking a cigarette, and looking down. At that time, the ills of smoking were not so clearly known, or accepted, by many scientists. A portrait of the author appears in Katoh (1995).

that $P700^+$ could not receive electrons from exogenously added plastocyanin unless thylakoid membranes were disrupted was in line with this model (Katoh 1972b). There appeared, however, data suggesting that plastocyanin is at least partly exposed to the exterior surface of the membranes. Polycations (Brand et al. 1972) and an antiserum to plastocyanin (Schmid et al. 1975) selectively inhibited photosynthetic electron transport at the level of plastocyanin. Plastocyanin was modified by treatment of thylakoids with several chemical reagents that also do not cross the membranes (Smith et al. 1977). The location of plastocyanin inside the membranes was, however, strongly supported by studies on the structural organization of photosynthetic electron transport. P700 and cyt *f,* the reaction partners of plastocyanin, are located on the PS I reaction center complex (Bengis and Nelson 1975) and the cyt $b_6/_f$ complex (Nelson and Neuman 1972), respectively. P700 is present on the lumenal side of the membranes (Witt 1971; Bengis and Nelson 1977). The globular portion of the cyt *f* molecule containing the heme is also exposed to the interior of the membranes (Willey et al 1984). It is now widely accepted that plastocyanin serves as a mobile electron carrier that connects the PS I reaction center complex and the cyt $b_6/f$ complex in the lumen of the thylakoid (Golbeck 1987).

**Plastocyanin and cytochrome** $c_6$

The role of plastocyanin is analogous to that of cyt *c* which shuttles electrons between the cyt $b/c_1$ complex and the cytochrome oxidase complex in the mitochondorial respiratory electron transport chain. In this respect, of particular interest is cyt $c_6$, which is present in algae and cyanobacteria but not in higher plants. Cytochrome $c_6$, which was originally called cyt *c552*, or *c553* according to the maximum absorption of the $\alpha$ band of the reduced protein, was discovered in the red alga *Porphyra tenera* and originally considered as a complex of two cytochromes due to a shoulder of the $\alpha$ band at 550 nm (Yakushiji 1935). *Porphyra* cytochrome was purified, crystallized and shown to be a single protein with a molecular weight of about 10,000 and a redox potential of 355 mV (Katoh 1960b, c). *Euglena* cyt $c_6$ restored whole-chain electron transport from water to NADP in *Euglena* chloroplasts that had lost the cyt during preparation (Katoh and San Pietro 1967). Thus, cyt $c_6$ resembles plastocyanin in both molecular and functional respects. Nevertheless, cyt $c_6$ was considered as the algal equivalent of higher plant cyt *f* due to similarity in the absorption spectrum and redox potential. For instance, because plastocyanin and *Euglena* cyt $c_6$ were rapidly photooxidized by detergent-treated chloroplasts, parallel

electron transfer to $P700^+$ from plastocyanin and cyt *f* was proposed (Kok et al. 1964). The confusion was settled by Wood (1977,1978) who showed that soluble cyt $c_6$ is distinctly different from membrane-bound cyt *f* and functions as the electron donor to $P700^+$ in place of plastocyanin in algae and cyanobacteria. All algae and cyanobacteria contain either plastocyanin or cyt $c_6$, or both. In the organisms that have both proteins, the levels of the cytochrome and plastocyanin are reciprocally regulated by concentrations of copper in the growth medium (Wood 1978; Bohner and Böger 1978). It was Merchant and Bogorad (1987) and Merchant et al. (1991) who showed that cells were measuring copper. It is suggested that plastocyanin replaced the soluble cytochrome in the course of evolution from cyanobacteria to higher plants.

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