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HISTORY & BIOGRAPHY

LETTER TO THE EDITOR

On “P750s” in cyanobacteria: A historical perspective

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Prelude

Emerson *et al.* (1957) discovered enhancement of photosynthesis when far-red light (>700 nm) was supplemented with light of shorter wavelengths, and this led to the concept of the two-light reaction two-pigment system scheme for oxygenic photosynthesis (for a perspective, *see* Govindjee 2023; for evidence, by mass spectroscopy, that the effect is on photosynthesis, not respiration, *see* Govindjee *et al.* 1963). In addition, Govindjee *et al.* (1960) showed that in *Porphyridium cruentum* and *Chlorella pyrenoidosa* (but apparently not in *Anacystis nidulans*) “extreme red” light (>720 m) inhibited photosynthesis produced by “far red” light (690–700 nm). From the action spectrum of this phenomenon, it appeared that an unknown pigment, with an absorption band around 745 nm, was, perhaps, behind this phenomenon. This unusual result led to careful measurements of the absorption spectra of dense samples of these organisms, in the 720–780 nm range, using a home-built absorption spectrophotometer (Govindjee *et al.* 1961).

To the surprise of the authors, a clear intense absorption band, at 750 nm, was found in *Anacystis nidulans* (*see* Fig. 1), but only very weak absorption bands in *Porphyridium* and *Chlorella*, but the latter turned out to be mostly “artifacts” (Govindjee and Cederstrand 1963). Further, in a detailed mass spectroscopic study, and by using O^{18}, Govindjee *et al.* (1963) showed that although light affects respiration (oxygen uptake), there was a clear Emerson enhancement effect in photosynthesis. In addition, Owens and Hoch (1963), also by using O^{18} and mass spectrometry, showed that an inhibitory effect, they had observed, of extreme-red light on far red-light photosynthesis in *Anacystis nidulans* was due to the effect of light on O_2 uptake, *i.e.*, respiration, not photosynthesis. It is unclear why in the experiments of Govindjee *et al.*

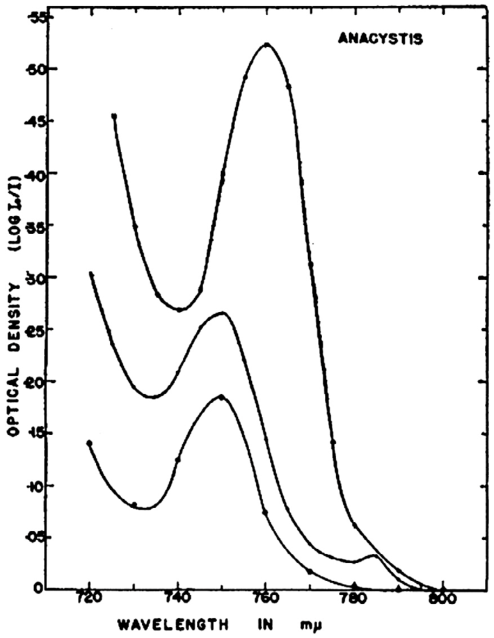

Fig. 1. Absorption spectra of three different “thick” suspensions of *Anacystis nidulans*, grown mainly under white, fluorescent light (Govindjee and Rabinowitch 1960). They all show the presence of a “P750”; reproduced from Govindjee *et al.* (1961). [Note: for the wavelength of light, mμ, millimicrons, was used then in most journals – although nm, nanometers, had already been initiated by Thomas Young (1773–1829) long ago!]

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(1960), *Anacystis* did not show this effect. However, P750, in *Anacystis*, remained a mystery as to its function. It is not possible to know, without further new experiments, if this P750 is due to the recently discovered long wavelength chlorophyll *f* (for Chl *f*, *see* Chen *et al.* 2010, Nürenberg et al. 2018). We now present what we know about P750. It turns out that there are several P750s – not just one!

The P750 or P750s

Aghion *et al.* (1963) showed, through methanol-induced changes in chloroplasts, the formation of a P750, and Govindjee (1963a) showed that a P750 was fluorescent – with an emission peak at 760 nm. In addition, Govindjee (1963b) showed that isolated chlorophyll *a* from *Anacystis* can artificially produce P750A – an aggregate form of Chl *a*. All of this was confirmed, many years later, by Goedheer and Hammans (1975). However, no correlation of this band with photosynthesis was found by Gassner (1962). This seemed to us to be an example of a dead-end research as far as we were concerned. However, Van Baalen (1965) found that a P750 was involved in the photo-oxidation of uric acid in *Anacystis nidulans*; and Fischer and Metzner (1969) suggested that P750, he was looking at, maybe an open chain tetrapyrrole, but not a bacteriopheophytin, and not a chlorin! Several years later, Öquist (1974) found that iron deficiency in *A. nidulans* increased fluorescence at 755 nm, perhaps, due to an increase in the concentration of a P750 there (*cf.* Shubin *et al*. 1991). On the other hand, Goedheer and Hammans (1975), mentioned above, observed excitation energy transfer from several photosynthetic pigments to P750; and then Hammans *et al.* (1977) established that P750, in *Anacystis nidulans*, actually initiated oxygen uptake. Further, Hammans (1978) showed that P750 sensitizes photo-oxidation of several endogenous reductants in the same organism; however, these reductants neither served as electron donors to Photosystem I (PSI), nor they were oxidized in any Chl-sensitized reactions! There was, however, a hint that excitation of both P750 and Chl may cause the formation of singlet oxygen.

A major question had been as to where any of these P750s are located. Murata *et al.* (1981) showed that a P750 was present in the cell envelope, not in the thylakoids, where there was also a small amount of pheophytin (Pheo)-like pigment with an absorption maximum at 673 nm, and even some carotenoids. This observation explained why this P750 had nothing to do with photosynthesis. Then, Nultsch *et al.* (1983) found that P750 was absent in *Anabaena*, another cyanobacterium, and could not have been involved in phototaxis. Three years later, Worcester *et al.* (1986) related a P750 to an *in vitro* micellar system of aggregated Chls; this correlation was suggested to be with the chlorosomes of green bacteria. Soon thereafter, Gombos *et al.* (1987) showed that a P750, an aggregated form of Chl *a*, was formed during nitrogen starvation of cyanobacteria at ~39°C and that this process was reversible. Interestingly, however, in *Arthospira platensis*, redox titration of P750, using its fluorescence band (F_{758}) showed that it has the same midpoint potential as P700; and, based on available data, it was suggested that its fluorescence quantum yield, measured at 758 nm, is proportional to the concentration of P700. It is not clear how and what this means. However, in contrast, observations of Gombos *et al.* (1987), cited above, suggested a link of P750 to photosynthesis, at least in this organism.

In addition to the various P750 species described above, there is a large literature on highly aggregated chlorophylls *in vitro*, usually involving water. These aggregated chlorophylls typically have absorption maxima in the 730–750 nm region (Jacobs *et al.* 1954, 1957; Ballschmiter and Katz 1972, Strouse 1974). These species are in many ways similar to J-aggregates, which are highly aggregated dyes whose absorption maxima are strongly red-shifted (Würthner *et al.* 2011). It is not clear whether any of these aggregated chlorophyll species have any relationship to the *in vivo* species described above.

In view of all the observations, summarized above, further research is needed to understand the role (or the roles) of the different P750s, *i.e*., where they are exactly located in cyanobacterial cells, and what function or functions they perform, and what is their importance in the evolutionary tree. For general information on photosynthetic pigments, *see* Lichtenthaler (1987). We conclude this "letter" by urging scientists, interested in cyanobacteria, to find the possible location(s) and function(s) of the various P750s there, and in other organisms (if any) after examining different aspects of chlorophylls and bacteriochlorophylls (Grimm *et al.* 2006), as well as the overall molecular mechanisms of photosynthesis (Blankenship 2021).

References

Aghion J., Porcile E., Lippincott J.A.: Solvent-induced changes in the absorbancy of isolated chloroplast fragments. – Nature **197**: 1110-1112, 1963.

Ballschmiter K., Katz J.J.: Chlorophyll-chlorophyll and chlorophyll-water interactions in the solid state. – BBA-Bioenergetics **256**: 307-327, 1972.

Blankenship R.E.: Molecular Mechanisms of Photosynthesis. 3rd Edition. Pp. 352. John Wiley & Sons, Hoboken 2021.

Chen M., Schliep M., Willows R.D. *et al.*: A red-shifted chlorophyll. – Science **329**: 1318-1319, 2010.

Emerson R., Chalmers R., Cederstrand C.N.: Some factors influencing the long-wave limit of photosynthesis. – PNAS **43**: 133-143, 1957.

Fischer K., Metzner H.: On chlorophyll and pigment P750 of *Anacystis nidulans*. – In: Metzner H. (ed.): Progress in Photosynthesis Research. Pp. 547-551. International Union of Biological Sciences, Tübingen 1969.

Gassner E.B.: On the pigment absorbing at 750 mμ occurring in some blue-green algae. – Plant Physiol. **37**: 637-639, 1962.

Goedheer J.C., Hammans J.W.: Efficiency of light conversion by the blue-green alga *Anacystis nidulans*. – Nature **256**: 333-335, 1975.

Gombos Z., Szalontai B., Surányi G., Csatorday K.: Selective alteration of the pigment composition of the blue-green alga, *Anacystis nidulans*. – Photochem. Photobiol. **45**: 399-402, 1987.

Govindjee G.: Emerson enhancement effect and two light reactions in photosynthesis: Dedicated to the memory of late

Professor Robert Emerson. – In: Kok B., Jagendorf A.T. (ed.): Photosynthetic Mechanisms of Green Plants. Publication 1145. Pp. 318-334. National Academy of Sciences-National Research Council, Washington 1963a.

Govindjee G.: Observations on P750A from *Anacystis nidulans*. – Naturwissenschaften **50**: 720-721, 1963b.

Govindjee G.: On the evolution of the concept of two light reactions and two photosystems for oxygenic photosynthesis: A personal perspective. – Photosynthetica **61**: 37-47, 2023.

Govindjee G., Cederstrand C.: Letter to the editor. – Biophys. J. **3**: 507-508, 1963.

Govindjee G., Cederstrand C., Rabinowitch E.: Existence of absorption bands at 730-740 and 750-760 millimicrons in algae of different divisions. – Science **134**: 391-392, 1961.

Govindjee G., Owens O.v.H., Hoch G.: A mass spectroscopic study of the Emerson enhancement effect. – Biochim. Biophys. Acta **75**: 281-284, 1963.

Govindjee G., Rabinowitch E.: Action spectrum of the ‘second Emerson effect’. – Biophys. J. **1**: 73-89, 1960.

Govindjee G., Rabinowitch E., Thomas J.B.: Inhibition of photosynthesis in certain algae by extreme red light. – Biophys. J. **1**: 91-97, 1960.

Grimm B., Porra R.G., Rüdiger W., Scheer H. (ed.): Chlorophylls and Bacteriochlorophylls: Biochemistry, Biophysics, Functions and Applications. Pp. 1-26. Springer, Dordrecht 2006.

Hammans J.W.K.: P750 sensitized photooxidations in *Anacystis nidulans*. – Plant Cell Physiol. **19**: 1457-1463, 1978.

Hammans J.W.K., Hendriks G.M., Teerlink T.: Light dependent oxygen uptake by the blue-green alga *Anacystis nidulans.* – Biochem. Bioph. Res. Co. **74**: 1560-1565, 1977.

Jacobs E.E., Holt A.S., Kromhout R., Rabinowitch E.: Spectroscopic properties of crystals and monolayers of chlorophyll and related compounds. – Arch. Biochem. Biophys. **72**: 495-511, 1957.

Jacobs E.E., Vatter A.E., Holt A.S.: Crystalline chlorophyll and bacteriochlorophyll. – Arch. Biochem. Biophys. **53**: 228-238, 1954.

Lichtenthaler H.K.: Chlorophylls and carotenoids: Pigments of photosynthetic membranes. – Method. Enzymol. **148**: 350-382, 1987.

Murata N., Sato N., Omata T., Kuwabara T.: Separation and characterization of thylakoid and cell envelope of the blue-green alga (cyanobacterium) *Anacystis nidulans*. – Plant Cell Physiol. **22**: 855-866, 1981.

Nultsch W., Schuchart H., Koenig F.: Effects of sodium azide on phototaxis of the blue-green alga *Anabaena variabilis* and consequences to the two-photoreceptor systems-hypothesis. – Arch. Microbiol. **134**: 33-37, 1983.

Nürenberg D.J., Morton J., Santabarbara S. et al.: Photochemistry beyond the red limit in chlorophyll *f*-containing photosystems. – Science **360**: 1210-1213, 2018.

Öquist G.: Iron deficiency in the blue-green alga *Anacystis nidulans*: Fluorescence and absorption spectra recorded at 77°K. – Physiol. Plantarum **31**: 55-58, 1974.

Owens O.v.H., Hoch G.E.: Enhancement and de-enhancement effect in *Anacystis nidulans*. – Biochim. Biophys. Acta **75**: 183-186, 1963.

Shubin V.V., Murthy S.D.S., Karapetyan N.V., Mohanty P.: Origin of the 77 K variable fluorescence at 758 nm in the cyanobacterium *Spirulina platensis*. – BBA-Bioenergetics **1060**: 28-36, 1991.

Strouse C.E.: The crystal and molecular structure of ethyl chlorophyllide $a\cdot 2H_2O$ and its relationship to the structure and aggregation of chlorophyll *a*. – PNAS **71**: 325-328, 1974.

Van Baalen C.: The photooxidation of uric acid by *Anacystis nidulans*. – Plant Physiol. **40**: 368-371, 1965.

Worcester D.L., Michalski T.J., Katz J.J.: Small-angle neutron scattering studies of chlorophyll micelles: Models for bacterial antenna chlorophyll. – PNAS **83**: 3791-3795, 1986.

Würthner F., Kaiser T.E., Saha-Möller C.R.: J-aggregates: From serendipitous discovery to supramolecular engineering of functional dye materials. – Angew. Chem. Int. Ed. **50**: 3376-3410, 2011.