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Minireview

The Laboratory of Photosynthesis and its successors at Gif-sur-Yvette, France*

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Abstract

This article is not a survey of all the research made during the last half century at the 'Laboratoire de Photosynthèse' of the 'Centre National de la Recherche Scientifique' (CNRS) in Gif-sur-Yvette, but rather some personal recollections, as faithful as possible. Not all people could be mentioned and the scientists named here are mainly those who, at different stages of the laboratory's evolution, created their research teams, within or outside the laboratory. The laboratory, closed now as an administrative entity, was founded in 1953 by the CNRS in Gif-sur-Yvette, near Paris. Besides the emerging research groups in Paris and at Saclay, it was then the only one in France to be entirely dedicated to photosynthesis. Initially, the focus was on metabolic biochemistry of photosynthesis in whole plants and unicellular algae. In 1959, biophysics of primary and associated processes was added and in 1966, the laboratory was enlarged to include molecular genetics and, somewhat later, structural biology. Most of the early members of the laboratory have now gone offstage, but the research goes on, in Gif and elsewhere, thanks to the numerous high-level scientists that have been trained there. Most of the basic questions have now been answered, and interest has shifted in two directions, atomic and integrated, while many other facets of research are no longer specific to photosynthesis but part of more general biological problems, a normal situation for an area that has reached its maturity.

Introduction

Until the late 1960s, the French educational system was quite centralized and rather conservative, a situation that affected some areas of scientific research at universities, especially in biology. The role of the National Center for Scientific Research (Centre National de la Recherche Scientifique, CNRS) was – and still is – to initiate modern research in highly competitive, emerging or, on the contrary, dormant but essential fields, and so to enliven the academic world. The Laboratory of Photosynthesis was thus founded in 1953 on a CNRS campus about 30 km southwest of Paris, with Alexis Moyse as its first director. In 1958, it moved into an independent laboratory adjacent to the newly constructed Phytotron (Figure 1). These buildings are now shared by the Institute of Plant Sciences and the Center of Molecular Genetics.

Different sections of this paper do not always follow a chronological order but sometimes a thematic one; thus, some of the publications selected here may be scattered over time.[1]

The early days: 1953–1959

At the time of its creation, the Laboratory of Photosynthesis was the only one in France fully devoted to

* This paper is dedicated to the scientists, technicians, students and visitors who could not all be cited here, but who contributed so much to the life of the laboratory.

Figure 1. A view of the Laboratory of Photosynthesis (now part of the Center for Molecular Genetics) in the early 1960s. The large emerging vertical block in the middle and the long greenhouses on the right are part of the former Phytotron (now Institute of Plant Sciences), whereas in the background, buried in the wood, is the old Genetics building where the laboratory was housed from 1953 till 1958 (CNRS photograph).

photosynthesis, in addition to the research groups in Paris (Pierre Joliot, in René Wurmser's laboratory) and Saclay (Eugène Roux, later Paul Mathis) that were on the rise. The initial goal of Alexis Moyse was twofold: to treat all aspects of photosynthesis, especially at the fundamental level, and to develop outdoor large-scale algal cultures as a first step towards a pilot-plant. The idea behind this was to offer a balanced diet to 'under developed' regions (Moyse 1956a, b). Twenty years later, a similar utopia, in which the laboratory also had to be involved, was the massive use of solar energy bioconversion to circumvent the oil crisis. Anyway, once a reasonable harvest yield of *Chlorella*, a freshwater unicellular green alga, was reached in cubic-meter batches, the subject went out of fashion.

Besides this applied research, the main interest of Alexis Moyse and his first co-workers, including Marie-Louise Champigny, was focused on the intricate nitrogen and carbon metabolism in photosynthesis. They thus established how some amino acids were directly derived from the Calvin cycle, while others, the aspartic and glutamic acids, required a second carboxylation followed by cellular oxidations (Champigny 1960). The relationship between photosynthesis and organic acid metabolism in crassulacean (CAM, Crassulacean Acid Metabolism) plants was being established at the same time (Moyse 1955); the study by electron microscopy of leaf and chloroplast ultrastructure and of chloroplast development from etiolated plastids was initiated (Bourdu et al. 1965). Along with Jacques Garnier and others, Alexis Moyse was interested in photosynthetic metabolism and pigment biogenesis in red and 'blue-green' algae (now, cyanobacteria) (Garnier 1958, 1964; Garnier et al. 1965). The photochemical property of phycocyanin was also investigated *in vitro* (Vernotte and Moya 1973). Other topics also received attention in the laboratory, the most important being an investigation of plant hormones and plant cell biology conducted by the group led by Claude Péaud-Lenoël. They will not be mentioned any further here, being outside the scope of the present paper (although some convergences could exist; see Chandler et al. 1972).

The biophysical approach: since 1959

The need to add biophysics to the biochemical approach of photosynthesis was fulfilled in 1959 when Jean Lavorel, returning from his stay with Eugene Rabinowitch at the University of Illinois in Urbana, USA, joined the laboratory (I preceded him by about a year). Soon afterwards, many other young investigators also arrived, including Jean-Marie Briantais, Anne-Lise Etienne, Ismaël Moya and, later, Pierre Sebban, to mention only those who later directed their own research groups. This allowed a blossoming of investigations centered on primary and associated reactions (mainly Photosystem II, PS 2).[2]

Figure 2. Participants at the International Colloquium on Photosynthesis, Gif-sur-Yvette, July 1962. * Indicates the laboratory staff at that time and † indicates deceased, but information sometimes is missing. A partial list follows, from bottom to top and from left to right: [1] G. Oster, [2] D. Burk, [3] D.I. Arnon†, [4] R.G. Hiller, [5] J.-M. Bové, [6] A. Trebst, [7] D.C. Fork, [8] C.P. Whittingham, [9] G. Gingras*, [10] Y. de Kouchkovsky*, [11] L.K. Osnitskaya, [12] J. Lavorel*, [13] C. Lemasson*†, [14] J.B. Thomas†, [15] A.A. Shlyk† (partly masked), [16] J. Garnier*†, [17] J.C. Goedheer, [18] F. Gorski, [19] G. Weber†, [20] J.-M. Briantais (partly masked), [21] H.T. Witt, [22] R. Wurmser† (chairman), [23] N.G. Doman, [24] A. Moyse*†, almost entirely masked by [25] L.N.M. Duysens, [26] J. Amesz†, [27] E.I. Rabinowitch†, [28] W. Vredenberg, [29] E. Tyszkiewicz, [30] M. Calvin†, [31] C. Sironval, [32] G. Hoch, [33] B. Kok†, [34] H. Tamiya†, [35] M. Losada, [36] R.B. Park, [37] M. Avron†, [38] Z. Sestak. Several outstanding participants do not appear in the photograph, such as Otto Warburg†, who had decided to remain outside, sitting on a bench, or C.S. French†, to whom I owe a wonderful post-doctoral stay in Stanford (CNRS photograph).

The research concerns included explanation of the various stages of induction of chlorophyll *a* fluorescence and its correlation with O_2 evolution (Delosme et al. 1959; Lavorel 1959); obtaining separate emission spectra of constant and variable fluorescence (Lavorel 1963); establishment of the relationships between fluorescence and luminescence (Lavorel 1971, 1973); modeling of the oxygen evolving mechanism (Lavorel 1976a, b) and of the connection between PS 2 units (Lavorel and Joliot 1972); analysis of the thermal step of oxygen evolution (Etienne 1968) and of the S-state mechanisms of water oxidation (Delrieu 1974, 1978); demonstration of the absence of any respiratory reaction in chloroplasts – at that time, a controversial question – except for what was subsequently called 'chlororespiration' (de Kouchkovsky 1961, 1963, 1966; see P. Bennoun, this issue); description and interpretation of the O_2 'burst' in isolated chloroplasts as reflecting early thermal events (de Kouchkovsky 1963; de Kouchkovsky and Briantais 1963); obtaining of PS 2 particles [subsequently known as 'BBY (Berthold Babcock Yocum) particles'] by mild detergent treatment of thylakoids, these particles being able to evolve oxygen and to reconstitute a connection with PS 1 (Briantais 1967, 1969a, b); establishment of the role of plastocyanin *in vivo* (de Kouchkovsky and Fork 1964); and rapid induction of PS 2 properties in leaves initially grown under a flash regime (Dujardin et al. 1970).

Figure 3. Partial view of the audience at the International Colloquium on Photosynthesis, Gif-sur-Yvette, July 1962. * Indicates the laboratory staff at that time and † indicates deceased, but information sometimes is missing. Starting from bottom to top and from left to right, first row: [1] D.I. Arnon†; second row: [2] J.F.G.M. Wintermans, [3] B. Kok†; third row: [4] C. Vernotte*, [5] J.-M. Briantais*, [6] J.S. Brown, [7] G. Weber†; fourth row: [8] H. Gaffron†, [9] E.I. Rabinowitch†, [10] C.P. Whittingham, [11] R.G. Hiller, [12] A. Faludi-Daniel†, [13] Z. Sestak; fifth row: [14] W. Vredenberg, [15] J. Amesz†; sixth row: [16] C. Lemasson*†, [17] D.C. Fork, [18] C. Sironval; standing in the background, on the right: [19] Y. de Kouchkovsky*, next to [20] N.G. Doman, sitting (CNRS photograph).

The continuous blend of theoretical approaches, experimental advances and instrumental innovations brought the laboratory to the forefront of the field. As early as 1962, the laboratory had organized an international colloquium (Figures 2 and 3) that was the seminal meeting of the now well established International Congresses of Photosynthesis. Several outstanding scientists attended this meeting, including the Nobel prize winners Otto Warburg (1931) and Melvin Calvin (1961). Many of the now classical and most fundamental advances of the moment, primarily the discovery of the two photosystems, were then presented and vividly discussed. The book of proceedings reproduces these oral exchanges (CNRS 1963). The most stubborn opponent[3] to many new concepts was Warburg who, for example, rejected the quantum yield of oxygenic photosynthesis established by Robert Emerson and presented his indefensible model of a carbonic 'photolyte' as a precursor of oxygen. This 'imperial' attitude sometimes affected the social ambiance (see the legend to Figure 2) that otherwise was relaxed. Nevertheless, Warburg, a great spirit above all, could also be thoughtful, as witnessed by his closing address.[4]

The molecular biology approach: since 1966

In 1966, Jean Lavorel succeeded Alexis Moyse as director of the laboratory, when the later was appointed professor at the University of Paris-South at Orsay, where he started a new laboratory devoted to plant metabolism.

Obviously, a dozen years after its inception, the laboratory's image had changed. It changed even more when, following the advice of Jacques Monod, then a recent Nobel Prize winner, the CNRS decided to open, within the laboratory, a department of molecular biology of photosynthesis. It was placed, from 1966 until 1971, under the direction of Martin Kamen, one of the discoverers of carbon isotopes, whose laboratory in La Jolla (University of California at San

Diego, USA) was working on photosynthetic bacteria. I assisted him in this endeavor until a post-doctoral fellow from Kamen's laboratory, Françoise Reiss-Husson, accepted the responsibility. At the same time, Roger Stanier, a Canadian-born internationally renowned molecular microbiologist interested in cyanobacteria, was appointed as the new director of the former Laboratory of Hydrobiology nearby, and worked in close conjunction with Kamen's group. (A few years later, Marcelle Lefort-Tran, an ultrastructural plant cytologist, replaced him and headed, until the middle 1980s, a Laboratory of Cytophysiology of Photosynthesis.)

Thanks to Kamen and Stanier and to the sustained visit of high-level scientists, all the research groups of the laboratory flourished. Françoise Reiss-Husson began a fruitful investigation on the reaction centers of *Rhodobacter sphaeroides* (Jolchine et al. 1969), ultimately leading to their crystallization and molecular analysis (Ducruix and Reiss-Husson 1987). At the same time, Françoise Espardellier, collaborating with Chantal Astier, started to work on the molecular biology of cyanobacteria, introducing facultative phototrophic strains of *Synechocystis* as new models in the photosynthetic field (Astier et al. 1979, 1984).

With the help of sophisticated optical and EPR techniques, Jean Lavorel's group developed and came to include, among many others, Anne-Lise Etienne, Alain Boussac (now in Saclay) and Jérôme Lavergne (who thereafter moved to Paris and recently to Cadarache) on the one hand, and Ismaël Moya and Pierre Sebban on the other. This group pursued multiple research directions in the biophysical domain. These included: the determination of lifetime and yield of chlorophyll fluorescence in algae and chloroplasts, measured by phase fluorimetry and photon counting (Moya et al. 1977, 1986; Moya and Garcia 1983); excitation transfer in bacteria (Sebban et al. 1984; Sebban and Barbet 1984); two types of reaction centers (B and non-B: Lavergne 1982a, b; not to be confused with the non-Q_B concept: Lavergne and Leci 1992); the redox potential of primary donors of PS 2 (Boussac and Etienne 1984) and the role of Ca^{2+} in water oxidation (Boussac et al. 1985); the experimental and theoretical analysis of prompt and delayed fluorescence (Lavorel 1975, 1980; Etienne and Lavorel 1975; Lavorel et al. 1982); the probabilistic approach of PS 2 kinetics (Lavorel 1986). Of course, this list only mentions a few of the major lines of research.

Jean-Marie Briantais and Claudie Vernotte pioneered a long-term investigation on PS 1–PS 2 balance controlled by membrane state and reversible phosphorylation of the light-harvesting complex (Moya et al. 1977; Briantais et al. 1979; Vernotte et al. 1979; Krause et al. 1982). Jacques Garnier, on the basis of an original suggestion by Jean Lavorel (Garnier 1967; Garnier et al. 1968), isolated numerous *Chlamydomonas* mutants by the fluorescence intensity of their colonies in Petri dishes. He could thus obtain new data on pigment–protein complexes and functional properties of cytochromes *b* (Maroc and Garnier 1979; Garnier et al. 1986, 1987; Trémolières et al. 1991). A collection of these mutants is kept by the Chlamydomonas Genetic Center, Duke University, Durham, North Carolina, USA.

My research group, with some students that became permanent coworkers, such as Francis Haraux, who is now in Saclay, shifted its interest from PS 2 (except a study of S-states kinetic mechanisms: Delrieu and Rosengard 1987, 1988, 1991) to membrane bioenergetics. Thus, in the 1980s, we proposed a microchemiosmotic model able to resolve basic contradictions between Peter Mitchell's 'delocalized' theory and the 'localized' or 'direct-coupling' hypotheses (de Kouchkovsky and Haraux 1981; Haraux et al. 1983; de Kouchkovsky et al. 1984; Sigalat et al. 1988). In the following decade, we also investigated some mechanisms of thylakoid ATP synthesis and hydrolysis by the thylakoid ATP-synthase: dependence of its K_m for ADP and of the kinetic parameters of the proton flux on membrane energization (Bizouarn et al. 1989, 1991); discrimination of 'activating' and 'energetic' proton pathways within the enzyme (Valerio et al. 1992).

Sowing seeds

When Jean Lavorel left Gif-sur-Yvette for Cadarache in 1983, Jean-Marie Briantais replaced him for a couple of years until the CNRS decided to split the laboratory into two independent units. One ('Centre Réactionnels Photosynthétiques') comprised the groups led by Anne-Lise Etienne (who headed the unit), Françoise Reiss-Husson and Françoise Espardellier (who later left for Marseilles and was replaced by Chantal Astier), whereas my research group ('Biosystèmes Membranaires') along with that of Jacques Garnier and Antoine Trémolières, a specialist in plant lipids now at Orsay, constituted the second unit ('Biochimie Fonctionnelle des Membranes Végétales'). These units lasted a few more years before the different groups and individuals dispersed themselves into often more broadly oriented laboratories. Thus, Jean-Marie Briantais moved to the University of Paris-South (Department of Plant Ecology). He often collaborated with Ismaël Moya, who had formed a group for the study of biophysical ecology around the synchrotron facilities in Orsay ('Laboratoire pour l'Utilisation du Rayonnement Electromagnétique', LURE). This group is studying the physiological state of plants, from leaf to population levels, using time-resolved fluorescence methods (Moya et al. 1992).

Pierre Sebban and co-workers are still in Gif, where they are disentangling the pathways of protons in the reaction centers of *Rhodobacter capsulatus*, applying refined biophysical analyses to site-directed amino-acid mutants (Hanson et al. 1992; Maroti et al. 1994, 1995; Miksovska et al. 1999). The group headed by Chantal Astier and Françoise Reiss-Husson, now part of the Center of Molecular Genetics in Gif, uses a combination of biochemical, biophysical and molecular genetic approaches to determine the gene organization and expression of the photosynthetic apparatus in cyanobacteria (Ajlani et al. 1989; Olive et al. 1997) and purple bacteria (Ouchane et al. 1997); at the same time, new data, emphasizing the role of lipids and water, in the reaction center's molecular organization have now been obtained (Roth et al. 1991; Arnoux et al. 1995; Scheuring et al. 2001). Anne-Lise Etienne, who undertook an in-depth investigation of electron transfer between Q_A and Q_B primary acceptors in Gif, as well as studies of herbicides resistance in PS 2 and photoinhibition mechanisms (Miyao et al. 1987; Kirilovsky et al. 1990), has moved to the 'Ecole Normale Supérieure,' in Paris to head a laboratory studying algal photosynthesis ('Membranes Végétales'). Finally, I joined the Institute of Plant Sciences, where I switched from thylakoids to mitochondria. In collaboration with Rosine De Paepe from the Institute of Plant Biotechnology in Orsay, we have investigated molecular genetics and functional properties of respiratory-chain mutants, which incidentally show a mitochondrial control for photosynthetic CO_2 uptake (Gutierres et al. 1997; Sabar et al. 2000).

Figure 4. Photograph of the author taken at the laboratory in 1966 (at the age of 34).

Conclusion

The choice made in this survey was mainly to cite research topics rather than precise results (however, the titles in the bibliography are often explicit). Yet, many subjects – and persons – have not even been mentioned. The overall picture presented above does indeed reflect the evolution of our knowledge about photosynthesis. It is now such a broad area that no single laboratory could treat all its multiple facets. In fact, many of these aspects are not unique to photosynthesis and deserve to be handled together with their counterparts in other fields, some even outside the plant kingdom. The Laboratory of Photosynthesis at Gif no longer exists under this name but, even though many of the group leaders are now retired (Jean-Marie Briantais, Marie-Louise Champigny, Jean Lavorel, and myself) or deceased (Jacques Garnier, Alexis Moyse), its spirit survives thanks to the many scientists still active that were trained there. Nevertheless, I share Lavorel's opinion that if something remains in the future from our scientific contribution, it will certainly be modestly anonymous; and this is well enough.

Acknowledgments

This historical minireview was stimulated by Jean-Marie Briantais in response to a request by Govindjee, who was a visiting fellow of the laboratory in 1968 and then made several other shorter visits. Thanks are due to both of them, as well as to the past colleagues cited above, particularly Marie-Louise Champigny and Chantal Astier, who helped me in the early stages of this paper. Jean Lavorel, former director of the laboratory, is also thanked for his critical reading, but even more for his invaluable support of my early days in photosynthesis research. I am also grateful to Spencer Brown, a good friend now in charge of my former laboratory space, for final correction. However, I take sole responsibility of all errors and omissions, hoping that I will be forgiven for these unintentional shortcomings. This text was edited by Govindjee; at his suggestion, I am also including a photograph of myself taken at an early stage of my career (Figure 4).

Notes

[1]Many earlier publications were in French, at that time widely understood by the scientific community.

[2]The concept of two photosystems had arisen – and was accepted – around 1961.

[3]'New ideas don't convert people, it's just that old men die' (Max Planck).

[4]'When after a long interval of 25 years [i.e., from the rise of the nazi power to the post-war period] I had the opportunity to revisit this country; when I saw in a beautiful summer night the flood-lighted borders of the Seine river with the not destroyed buildings ... I felt that in this world justice still exists. I felt happy too to be again in the country of the great Pasteur ...; it is [his] spirit that has reigned over our meeting.'

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