



OBITUARY

Tribute to Jean Lavorel (1928–2021), an outstanding experimenter and a brilliant theorist of photosynthesis

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Here, we pay tribute to Jean Lavorel (16 March 1928–12 January 2021), a pioneer of the ‘*Light Reactions of Photosynthesis*’ (see Fig. 1). He was known not only for his ingenuity in devising new instruments but in thoroughly analyzing all the available data theoretically and mathematically – mostly all by himself. He measured, elegantly, oxygen evolution and light given off by photosynthetic organisms, both prompt and delayed chlorophyll fluorescence. He ingeniously used these data to understand how light energy is converted to chemical energy in natural systems. We present below a summary of his life and research. For further information, we refer to de Kouchkovsky (2022).

Prologue

Jean Lavorel was born in a village in France near Grenoble; he studied science as well as humanities, earning high-school degrees in both. In 1947, he was accepted at the Institut National Agronomique (INA, now AgroParisTech), an engineering school accessible by highly competitive examination. After graduation, he was briefly at the Versailles center of the Institut National de la Recherche Agronomique pour l'Agriculture, l'Alimentation et l'Environnement (INRAE, formerly INRA). Then, he worked at the renowned Institut de Biologie Physico-Chimique (IBPC) in Paris, where he obtained his doctorate on ‘*Photoinhibition of catalase in chloroplasts*’ (Lavorel 1956). During 1955–1957, Jean was a Rockefeller fellow at the University of Illinois at Urbana-Champaign (UIUC), working in the ‘*Photosynthesis Project*’ with the topmost authorities on the *Light Reactions of Photosynthesis*: Robert Emerson (1903–1959) and Eugene Rabinowitch (1898–1973).



Fig. 1. Jean Lavorel doing two things he liked most: *left*: as an experimenter (early 1950s, France); *right*: as an amateur photographer (mid-1970s, USA). Source: Lavorel family archives, provided by one of the authors (Y. de Kouchkovsky).

Research

The 1950s–1960s: Right after his 1956 Doctorat d'Etat, on catalase, mentioned above, Jean's first research involved an understanding of how the concentration of fluorophores

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(e.g., fluorescein) affects its absorption and excitation spectra (Lavorel 1957). The idea of dimers was explored as it seems that it may be related to chlorophylls *in vivo*. Soon thereafter, Lavorel (1959) studied chlorophyll (Chl) *a* fluorescence transient, the Kautsky effect, and correctly labeled its phases as 'O' (for 'origin'), 'P' (for 'peak'), and 'S' (for 'steady state'); for a discussion, see Govindjee (1995). Also, he carefully examined the heterogeneity of chlorophyll *a* fluorescence *in vivo* through its emission spectra (Lavorel 1962), and its excitation and polarization spectra (Lavorel 1964). Soon thereafter, Jean provided a novel way to measure the 'O' (minimum fluorescence, F_0) and 'P' (maximum fluorescence F_p or F_m), by using an ingenious 'stop-and-flow' method for algal suspensions (Lavorel 1965). During the late 1960s, he happily collaborated with Jacques Garnier and Yaroslav de Kouchkovsky in examining photosynthetic mutants they had screened by their fluorescence properties from unicellular green algae (Garnier *et al.* 1968). With Henk de Klerk, in Martin Kamen's laboratory (Department of Biochemistry and Molecular Biology, also in Laboratoire de Photosynthèse, Gif-Sur-Yvette), he further determined the effect of age on fluorescence from anoxygenic photosynthetic bacteria (de Klerk *et al.* 1969); this was done with Govindjee (an author of this tribute), and the results were attributed to age-related switching from cyclic to noncyclic electron flow pathway. (For a tribute to Martin Kamen, see Govindjee and Blankenship 2021.)

The 1970s: When Rajni Govindjee and Govindjee visited Jean Lavorel from the University of Illinois at Urbana-Champaign, USA (UIUC), they, together with Jean-Marie Briantais, examined Chl *a* fluorescence transients in wet and dry heptane-extracted chloroplasts and discovered that in the latter case, variable Chl *a* fluorescence disappears – which was later useful in proving that absorption changes due to 'P₆₈₀' (reaction center of PSII) were not a fluorescence artifact (Govindjee *et al.* 1970a,b). Soon thereafter, together with Pierre Joliot, Lavorel presented his theoretical and analytical 'connected model' of Emerson and Arnold's 'photosynthetic unit' (Lavorel and Joliot 1972). It was in the mid-1970s that Lavorel's interest turned to understanding the phenomenon of delayed light emission (luminescence, DLE) in algae (Etienne and Lavorel 1975, Lavorel 1975) and chloroplasts of plants (Haveman and Lavorel 1975). In addition, Lavorel (1976a) provided a new mathematical analysis of the oxygen-evolving system and presented an alternative model to that proposed by Bessel Kok for the same (Lavorel 1976b). The latter was followed by a thorough analysis of anomalies, especially obtained by the addition of uncouplers of phosphorylation (Lavorel and Lemasson 1976). Jean was always analytical and thorough.

The 1980s: Studies on DLE in algae were extended by Lavorel (1980) under conditions where the electron transport was blocked by diuron (DCMU) on the electron acceptor side of PSII, thus providing new insights on multiple processes involved in the slow components of this light emission (Lavorel and Dennerly 1982). However,

one of the most important contributions of Lavorel was when he exploited a Monte Carlo method for simulating kinetic models for photosynthesis (Lavorel 1986). In addition, Jean and his research group helped in understanding the effect of the 33-kDa protein on the mechanism of oxygen evolution through the so-called S-state cycle, establishing the key role of this protein (see Miyao *et al.* 1987); this was aided by the use of the subchloroplast particles (Seibert and Lavorel 1983). In addition, Jean even ventured into understanding the interaction between photosynthesis and respiration in anoxygenic photosynthetic bacteria (Lavorel *et al.* 1989).

The 1990s: This was a period of tremendous analysis and questioning of the information in the literature including his own. Lavorel (1991) discussed, in depth, what had been known as 'sigma analysis' for flash-induced oxygen evolution. Further, Lavorel (1992) improved the existing techniques and determined more precisely and rapidly the time of the release of oxygen in photosynthesis; thanks to a new instrument he had designed, which allowed direct deposition of chloroplasts and algal cells on the cathode by centrifugation.

Epilogue

Although Jean Lavorel made many new instruments, with many new ideas, of which several could have been patented, in his career, he did not bother with them. However, we mention just one exception: an apparatus that could easily measure the presence of intact photosynthetic organisms in aquatic environments by chlorophyll luminescence; it was patented in 1987.

To complement this brief overview, we refer the readers to reminiscences on Jean Lavorel by several of his colleagues or students, available in de Kouchkovsky (2022): Govindjee Govindjee, Jaap Haveman, Pierre Joliot, Ismael Moya, Pierre Sebban, André Verméglio, and Yaroslav de Kouchkovsky, without forgetting the affectionate testimony of his daughter Véronique. We add here two messages, one from Győző Garab (one of the authors), and the other from Péter Maróti (also from Szeged, Hungary). Garab recalled his vivid memories from the years of his early scientific career, when he had an opportunity to show his results to the world-famous scientist, Jean Lavorel, during his short visit, in 1978, to Szeged; he also cherishes memories of the Gif-sur-Yvette seminars which he attended during his fellowship in Pierre Joliot's lab (in Paris) and in Saclay, France. On the other hand, Maróti wrote: 'Jean Lavorel had a deep impact at the beginning of my career, through his invitation to me, in 1976, to the *Laboratoire de Photosynthèse* in Gif-sur-Yvette (France), and by his own visit, in 1978, in Hungary'. Maróti added: 'Lavorel had amazing talent to manage a large research center and to pave the way for the younger generation. During my stay, I learned two French expressions from him, both characteristic of his unique personality. The first is 'bricolage' ('do-it-yourself'), and indeed, he followed it himself. The second is 'effet tiroir' ('drawer effect'), i.e., a manuscript should be kept in a

chest of drawers, and if we still find it worthwhile after a year, we can send it for publication. After this, several of my manuscripts remained there forever, but one did survive: Maróti and Lavorel (1979)'.

We all miss Jean Lavorel; he was an outstanding experimenter and a renowned theorist of photosynthesis.

References

- de Klerk H., Govindjee G., Kamen M.D., Lavorel J.: Age and fluorescence characteristics in some species of Athiorhodaceae. – P. Natl. Acad. Sci. USA **62**: 972-978, 1969.
- de Kouchkovsky Y.: Jean Lavorel (1928–2021): A great scientist, a model of integrity. – Photosynth. Res. **151**: 205-211, 2022.
- Etienne A.-L., Lavorel J.: Triggered luminescence in dark adapted *Chlorella* cells and chloroplasts. – FEBS Lett. **57**: 276-279, 1975.
- Garnier J., de Kouchkovsky Y., Lavorel J.: Sélection de mutants d'algues vertes unicellulaires pour l'étude de la photosynthèse. [Selection of unicellular green alga mutants for the study of photosynthesis.] – C. R. Soc. Biol. (Paris) **162**: 365-368, 1968. [In French]
- Govindjee G.: Sixty-three years since Kautsky: chlorophyll *a* fluorescence. – Aust. J. Plant Physiol. **22**: 131-160, 1995.
- Govindjee G., Blankenship R.E.: Martin David Kamen (1913–2002): Discover of carbon-14, and of new cytochromes in photosynthetic bacteria. – Photosynth. Res. **149**: 265-273, 2021.
- Govindjee G., Döring G., Govindjee R.: The active chlorophyll *a*₁₁ in suspensions of lyophilized and Tris-washed chloroplasts. – BBA-Bioenergetics **205**: 303-306, 1970a.
- Govindjee R., Govindjee G., Lavorel J., Briantais J.-M.: Fluorescence characteristics of lyophilized maize chloroplasts suspended in buffer. – BBA-Bioenergetics **205**: 361-370, 1970b.
- Haveman J., Lavorel J.: Identification of the 120 μ s phase in the decay of delayed fluorescence in spinach chloroplasts and subchloroplast particles as the intrinsic back reaction. The dependence of the level of this phase on the thylakoids internal pH. – BBA-Bioenergetics **408**: 269-283, 1975.
- Lavorel J.: Photoinhibition de la catalase des chloroplastes. [Photoinhibition of the catalase of chloroplasts.] – Biochim. Biophys. Acta **22**: 226-237, 1956. [In French]
- Lavorel J.: Influence of concentration on the absorption spectrum and the action spectrum of fluorescence of dye solutions. – J. Phys. Chem. **61**: 1600-1605, 1957.
- Lavorel J.: Induction of fluorescence in quinone poisoned *Chlorella* cells. – Plant Physiol. **34**: 204-209, 1959.
- Lavorel J.: Hétérogénéité de la chlorophylle *in vivo* I. Spectres d'émission de fluorescence. [Heterogeneity of chlorophyll *in vivo* I. Fluorescence spectra.] – Biochim. Biophys. Acta **60**: 510-523, 1962. [In French]
- Lavorel J.: Hétérogénéité de la chlorophylle *in vivo* II. Polarisation et spectres d'action de fluorescence. [Heterogeneity of chlorophyll *in vivo* II. Polarisation and fluorescence action spectra.] – Biochim. Biophys. Acta **88**: 20-36, 1964. [In French]
- Lavorel J.: A study of chlorophyll fluorescence *in vivo* by a flow method. – Photochem. Photobiol. **4**: 819-828, 1965.
- Lavorel J.: Fast and slow phases of luminescence in *Chlorella*. – Photochem. Photobiol. **21**: 331-343, 1975.
- Lavorel J.: Matrix analysis of the oxygen evolving system of photosynthesis. – J. Theor. Biol. **57**: 171-185, 1976a.
- Lavorel J.: An alternative to Kok's model for the oxygen evolving system in photosynthesis. – FEBS Lett. **66**: 164-167, 1976b.
- Lavorel J.: A study of dark luminescence in *Chlorella*. Background luminescence, 3-(3,4-dichlorophenyl)-1,1-dimethylurea triggered luminescence and hydrogen peroxide chemiluminescence. – BBA-Bioenergetics **590**: 385-399, 1980.
- Lavorel J.: A Monte Carlo method for the simulation of kinetic models. – Photosynth. Res. **9**: 273-283, 1986.
- Lavorel J.: On the proper use of sigma analysis in the study of flash induced oxygen evolution. – Photosynth. Res. **27**: 15-18, 1991.
- Lavorel J.: Determination of the photosynthetic oxygen release time by amperometry. – BBA-Bioenergetics **1101**: 33-40, 1992.
- Lavorel J., Dennery J.-M.: The slow component of Photosystem II luminescence. A process with distributed rate constant. – BBA-Bioenergetics **680**: 281-289, 1982.
- Lavorel J., Joliot P.: A connected model of the photosynthetic unit. – Biophys. J. **12**: 815-831, 1972.
- Lavorel J., Lemasson C.: Anomalies in the kinetics of photosynthetic oxygen emission in sequences of flashes revealed by matrix analysis. Effects of carbonyl cyanide *m*-chlorophenylhydrazone and variation in time parameters. – BBA-Bioenergetics **430**: 501-516, 1976.
- Lavorel J., Richaud P., Verméglio A.: Interaction of photosynthesis and respiration in Rhodospirillaceae: evidence for two functionally distinct *b-c*₁ complex fractions. – BBA-Bioenergetics **973**: 290-295, 1989.
- Maróti P., Lavorel J.: Intensity- and time-dependence of the carotenoid triplet quenching under rectangular illumination in *Chlorella*. – Photochem. Photobiol. **29**: 1147-1151, 1979.
- Miyao M., Murata N., Lavorel J. *et al.*: Effect of the 33 kDa protein on the S-state transitions in photosynthetic oxygen evolution. – BBA-Bioenergetics **890**: 151-159, 1987.
- Seibert M., Lavorel J.: Oxygen evolution patterns from spinach photosystem II preparations. – BBA-Bioenergetics **723**: 160-168, 1983.