Book Review by Anthony W.D. Larkum (*Phycologia,* 2006, in press)

Chlorophyll a Fluorescence A Signature of Photosynthesis
Editors G.C. Papageorgiou and Govindjee
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Why should a book on chlorophyll *a* (Chl *a*) fluorescence appeal to people who work on algae? At first sight there might seem to be a nexus between the two subjects. However, on reflection the two are intimately bound up. The algae are *par excellence* the great players in the field of photosynthetic pigments. After all, we still classify several groups of algae on their colouration. Just imagine if we tried to classify other protists in the same way! And whether they use red pigments, brown or green, all algae use Chl *a* as their central photochemical pigment. If you count cyanobacteria as algae there is now one possible exception to this rule: *Acaryochloris marina* (see below), where Chl *d* may totally replace Chl *a*. However, apart from that they all use Chl *a*. As a result the many types of other photosynthetic pigments in algae perform all kinds of dances with the central Chl *a* and the result is that by studying Chl *a* fluorescence one can learn a multitude of information that can be of help all the way from taxonomy, to productivity, to global warming.

From the foregoing, it is therefore of no surprise that this is a large book. There are thirty-one chapters, by the world's experts in the field, and the book weighs in at 2.2 Kg and covers 818 pages. This, unfortunately, is too many chapters to pick out each one for special mention, much as the high quality and interest of this book demands it.

The book begins with two indispensable chapters by the Editors on the basics of fluorescence in photosynthetic organisms and its history. Luminescence, delayed light emission, goes back a long way; but not the word: it dates from 1897. Undoubtedly the ancients knew about bioluminescence from such things as fireflies, glow worms, particles in the sea (*Noctiluca*), fish, mushrooms and rotting meat, to name a few; but the ancients used the loose term "phosphorescence" (in various forms), and it is often difficult to pin down exactly what phenomenon was being referred to. Fluorescence, or prompt re-emission of light, is a much more recent word of Victorian origin; the phenomenon was first observed by Sir David Brewster in about 1834 and the word itself was coined by Sir G.G. Stokes in 1852 (from the mineral fluor-spar, which can be made to fluoresce). Based on the multiple associations that this word now conjures up, we have come a long way in 150 years!

Many of the chapters in this book are for specialist interested in the physics and biophysics of fluorescence in photosynthetic apparatus, since the reaction centres of each and every photosystem and many of their light-harvesting proteins contain chlorophylls, which fluoresce. Thus there are chapters outlining the basic aspects of excitation energy migration, i.e., how the energy is distributed between the pigments, before fluorescence occur (R.M. Clegg) and trapping of excitation (R. van Grondelle; W.J. Vredenburg) and fluorescence in Photosystem I (S. Itoh and K. Sugiura). Other chapters which need not detain us here deal with such specialist areas as fluorescence in fruit and leaves (L. Nedbal and J. Whitmarsch), water stress (N.G. Bukhov and R. Carpentier), heavy metals toxicity (M.K. Joshi and P. Mohanty), light adaptation and senescence in plants (H.K. Lichtenthaler aand F. Babani) and a global analysis of fluorescence in plants (A Gilmore). Suffice it to say that few areas of interest to the eclectic reader are absent and what is present is of a very high standard.

We will now deal with those chapters of particular appeal to anyone interested in algae.

One would have to begin here with the chapter on Photosystem II (PS II) (Shinkarov), unlikely as it might seem, because it is PS II that gives out the most fluorescence and, that if probed in the right way, can give so much information about the partial-reactions of photosynthesis in algae. From here one can go to the two basic chapters for any algologist in this field "Pulse amplitude modulation (PAM) fluorometry" (U. Schreiber) and "Variable chlorophyll fluorescence techniques in marine ecosystems" (P Falkowski, M. Koblizek, M Gorbunov and Z. Kolber).

The Diving-PAM developed by R Gademann and U. Schreiber and made by Walz GMB for aquatic studies is the most widely used instrument in this field at the present time and works well. Thus the chapter by Schreiber is particularly welcome. It describes, in many ways for the first time, the underlying logic of the PAM fluorimetric approach. Using the PAM instrument one can measure the maximum (optimal), dark-adapted quantum yield, a measure of whether PS II is working unconstrained – or is working under some kind of stress. More importantly the effective quantum yield can be measured – and this leads to a measure of absolute rate of photosynthetic electron transport, by use of the Genty equation. In effect this yields the rate of photosynthesis, arguably the most sought after parameter in all algal and plant studies. Moreover, it is a measurement that can be achieved in seconds. Compare this with the time of minutes to hours needed to measure photosynthesis by oxygen evolution or carbon dioxide fixation methods. Furthermore the box of tricks does not end there, as the PAM fluorometer has proven exceptionally good at measuring non-photochemical quenching, that is the measure of the amount of light that is deliberately diverted into heat by a photosynthetic organism, most notably by the xanthophyll cycle [dealt with in two other chapters (G.H. Krause and Peter Jahns; W.W. Adams and B. Demmig-Adams)].

Another instrument is also available to measure photosyntheitc rate in phytoplankton and potentially other algae and plants as well. This is the Fast Repetition Rate Fluorescence Fluorometer developed by M. Gorbunov and Z. Kolber in the laboratory of P. Falkowski and this is described in a chapter on the FRRF fluorometer. While the PAM fuorometer operates by giving a single saturating flash, the FRRF fluorometer gives series of single turnover flashes (that is, it is a pump probe device). The outcome is not the same as the PAM fluorometer and thus the F_m (maximum fluorescence yield) is not the same as that measured by the PAM fluorometer. The difference between the two instruments hinges on the reduction by PS II of Q_A and Q_B and their back reactions with the oxidised side of PS II. Both chapters argue that their instrument measures the correct Fm, but the reader must choose. The FRRF fluorometer has the advantage that it measures the absorption cross-section of PS II, a very useful parameter, as well as all those offered by the PAM fluorometer. However, it is much more expensive, has been deployed by less groups and requires a greater knowledge of photosynthetic partial reactions for it's correct use. Nevertheless the chapter on the FRRF fluorometer offers valuable insights into its use in assessing nutrient limitation in the ocean, in estimating primary production and in applications to benthic organisms, including corals.

These chapters are fleshed out by a number of others that demonstrate in greater detail how fluorescence can be used to measure photosynthetic productivity (N.R. Naker and K. Oxborough; K Oxborough; J. A Raven and S.C. Maberley), remote sensing (I. Moya and Z.G. Cerovic; J. Cavender and F.A. Bazzaz), effects of stress (D. Bruce and S. Vasil'ev), and ultra-violet radiation effects (M. Tevini). The chapter on plant productivity of inland waters

(J.A. Raven and S.C. Maberley), somewhat inappropriately entitled because it also deals with phytoplankton and benthic algae, gives a particularly useful overview of how to approach photosynthesis and productivity in freshwater ecosystems. It also gives a useful survey of the primary producers present (planktophytes, pleustophytes, haptophytes and rhizophytes).

The cornucopia provided by this book goes on and on. There is an excellent chapter devoted to fluorescence in cyanobacteria and red algae (M. Mimuro). Here, the classical transfer pathways through phycobiliprotein and carotenoid pigments are elegantly described. And in addition there is a section on the recently discovered cyanobacteria that rely much more on chlorophyll *b* (prochlorophytes) or almost entirely on chlorophyll *d* (*Acaryochloris marina*).

State transitions are a subject dear to the heart of many algal physiologists, because these effects, although found in plants, are so much more dominant and varied in algae. Therefore it is pleasing to see an excellent article on this topic by researchers who lead the field (J.F. Allen and C.W. Mullineaux). Finally the topic of nutrient limitation is tackled, that is whether fluorescence techniques can be used to assess such limitation (G.C. Papageorgiou and K. Stamatakis). Here the emphasis is on cyanobacteria, but the techniques can be applied to a range of alga as well. There have been a number of attempts to measure NIFTs, Nutrient Induced Fluorescence Transients, to assess limitation by a number of nutrients. The technique holds out potential, but there are many pitfalls in the way to a reliable technique. This chapter carefully documents many of these side effects and concludes that many of the effects are the result of osmo-regulatory adjustment. It will therefore be interesting to see how the results of this model system carry over into effects found in eukaryotic algae.

Are there areas of fluorescence that the book does not deal with? Answer: remarkably few! Of course in any multi-authored volume like this there will be unevenness, in coverage and focus. The general layout of chapters lacks a consistent framework, especially from an algal perspective. Thus the order in which I have mentioned chapters is not at all the order in which they were presented in the book. The “Index” had a number of shortcomings from my perspective, too. I looked up “nutrients” and “nutrient limitation” and did not find any of the chapters, mentioned above, cited. It takes a particular type of mind to second-guess how various subjects will be searched, and this expertise should be cultivated by publishers, but often it is not.

In summary, the editors have assembled a constellation of stars to illuminate the field of chlorophyll fluorescence. Any one even remotely interested in the subject will want to have a copy in their University or Institute Library, if not on their own bookshelves.

Anthony W. D. Larkum
School of Biological Sciences (A08)
and SUBIT - Sydney University Biological Informatics and Technology Centre
(Rm 141, Medical Foundation Building)
University of Sydney, NSW 2006,**Australia**

Tel +612 9351 2069/+612 90363306
Fax +612 9351 4119
Email: alark@mail.usyd.edu.au