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BOOK REVIEW

Photosynthesis in Algae

Larkum, A. W. D., Douglas, S. E., and Raven, J. A. [Eds.] 2003. **Photosynthesis in Algae**. Kluwer, Dordrecht, The Netherlands. US$255. ISBN: 0-792-36333-7.

The study of photosynthesis has always involved a range of organisms, from photosynthetic bacteria, cyanobacteria, and algae to higher plants. Many features of photosynthesis are highly conserved among this set of otherwise quite dissimilar organisms; for example, a landmark in the field of photosynthesis was the resolution of the bacterial reaction center from the *Rhodopseudomonas viridis* that was instrumental in developing structural models of PSII in plants and algae. The availability of numerous model systems has certainly contributed to the accelerating progress in the field of photosynthesis, as documented in the 15 volumes of the "Advances in Photosynthesis and Respiration" series as well as many other books over the last decade. Nevertheless, phototrophs, especially algae, differ significantly in how the photosynthetic apparatus is structured and how it functions. So an objective of this volume, number 14 in the aforementioned series, is to highlight the broad diversity of pigments, membrane structure, chloroplast evolutionary origin, and so forth that are found within the algae. As in other volumes in the series, this is an edited book with topics covered in 19 chapters written by the editors and 26 other authors. The book is organized into four sections. The target audience is graduate students and researchers in the field.

The introductory section of the book provides background on eukaryotic algae and their plastids (Chapter 1 by Douglas et al. and Chapter 2 by Larkum and Vesk). These chapters emphasize the chimeric nature of algae resulting from endosymbiosis of a photosynthetic prokaryotic with a eukaryotic host, with increasing evidence for secondary symbioses in the evolution of some groups. This raises an important point that is followed up in subsequent chapters—that the diversity in structure and function within the algae is as much a function of the various hosts as the various sources for the plastid-producing symbionts. Chapters 1 and 2 efficiently sketch the breadth of the algal world. The treatment is succinct, but I found the figure legends rather skimpy; for example, no detail is provided on how to interpret a rather elaborately annotated phylogenetic tree in Chapter 1.

The general overview chapters are followed by the more specific Chapter 3 (Partensky et al.) on the photosynthetic apparatus of "green oxyphotobacteria" (chl *b* containing photolithotrophic bacteria, e.g. *Prochlorococcus*). I found this chapter an informative update on a group of organisms whose importance has only recently been realized. However, I was struck that photosynthesis in non-phycobilisome containing bacteria would be covered in such detail, whereas other phycobilisome containing cyanobacteria, acknowledged to be allied to the algae in a broad sense, receive varying, but generally secondary, attention in the rest of the book. They were covered in Volume 1, "Molecular Biology of Cyanobacteria," of this same series, though the volume is now 10 years old.

The second section is entitled "Molecular Genetics of Algae." Actually, the only chapter in this section with a primary focus on genetics is Chapter 5 (Rochaix) on finding the function of plastid genes in *Chlamydomonas reinhardtii*. This will be useful to those interested in reverse genetic approaches, but the description of the photosynthetic role of the genes in question is a small part of the chapter. On the other hand, the reviews of algal light harvesting genes (Chapter 4, Durnford) and chl biosynthetic pathways (Chapter 6, Cahoon and Timko) are fairly comprehensive. The latter chapter maps out the biochemistry of the chls, pointing out what genes are involved along the way, and the former chapter is as much about the structure of the light harvesting complexes as their genetic basis. In fact, most other chapters in the volume incorporate some mention of the relevant genes where known. Also, it is obvious that the assembly of the book encompassed a period of rapid expansion in the availability of sequence data, a situation that is inconsistently reported between chapters. For example, Chapter 1 laments that "no algal nuclear genome is currently the focus of a major sequencing project," whereas Chapter 4 points to the recent completion of genome sequences for *Chlamydomonas reinhardtii* and *Thalassiosira pseudonana*.

The next section ("Biochemistry and Physiology") deals with the nuts and bolts of the photosynthetic apparatus' structure and functions. PSI and PSII are the primary complexes in photosynthetic electron transport, and in Chapter 7 Nugent et al. show that a great deal has been learned about photosystem structure and function using algae as model systems—though algae in this instance is mainly certain cyanobacterial strains and *C. reinhardtii*. Coverage of other, especially "non-green," algae is sparse, mostly noting where peripheral polypeptides differ. I was also struck that no structural depictions were included given that the

three-dimensional structures of the reaction centers and other complexes are some of the most recent results to emerge. On the other hand, Chapter 8 (Beardall et al.) on photorespiration and chlororespiration is amply illustrated with diagrams that help distinguish between the subtle differences in these processes between algal groups. The chapter also makes the point that these processes are more than just minor pathways and instead play important roles in regulating electron carriers and carbon metabolism under variable environmental conditions. Likewise, Chapter 9 (Miyake and Asada) deals with oxygen acting as an electron acceptor for photosynthetic electron transport, forming superoxide. This is commonly called the Mehler reaction, but the authors use an alternate term, the water–water cycle, because water is both the source and ultimate sink for electrons in the cycle. Chapter 10 (Raven and Beardall) extends the discussion of metabolic pathways to respiration. This might seem peripheral to the topic of photosynthesis but is consistent with respiration as the co-theme of the series. However, the detailed coverage given to "dark" as well as photo- and chlororespiration stands in contrast to the apparent omission of any detailed treatment of the photosynthetic carbon reduction cycle—surely as important to understanding photosynthesis in algae as these other topics. Only the key enzyme in that cycle, RUBISCO, which exists in several forms in algae, is mentioned in several chapters, most extensively in Chapter 11 (Raven and Beardall) on carbon concentrating mechanisms (CCMs). Indeed, the latter chapter seems to focus more on the characteristics of RUBISCO (i.e. why CCMs are needed) than on inorganic carbon transport per se, with only a brief discussion of most common CCMs based on the active transport of bicarbonate or CO_2. It would have been useful to see more detail about transport mechanisms and perhaps not as much about the less common C_4 or acid types of CCMs. There is also relevant material on environmental regulation of CCMs in other chapters, like Chapter 17, but cross-references to this are absent in Chapter 11.

The third section of the book treats light harvesting systems and is led off by Chapter 12 on modeling excitation energy capture (Trissl). This chapter provides a good introduction to energy transfer within light harvesting complexes and the mechanistic basis for variable fluorescence, but the primary focus is the author's mathematical model, the understanding of which requires some fluency in calculus and linear algebra. Moreover, the analytic approach is only applied to the red algal phycobilisome antenna and two algae with unusual chl pigments, but little is said about light harvesting in the environmentally more important chromophyte systems. The follow-up Chapter 13 (Larkum) also discusses the structure and function of light harvesting, taking in a much broader view of the algae groups and discussing regulatory mechanisms. Several schematic diagrams are helpful in explaining the latter. The two final chapters in this section focus specifically on the phycobiliproteins, mainly as found in the rhodophytes and cryptophytes (Chapter 14) and carotenoids (Chapter 15). Again, coverage of cyanobacterial phycobilisomes is conspicuous in its absence (the reader is referred to a 1999 review by Glazer); otherwise, Chapter 14 (Toole and Allnutt) gives a thorough presentation of what is known at the levels of gene, chromophore, protein, and pigment-complex structure and function. The structural and functional diversity in algal carotenoids, particularly the xanthophylls, is mentioned repeatedly in the volume (Chapters 3, 10, 13, and 16–19). In Chapter 15, Mimuro and Akimoto do a good job of showing the mechanistic basis for carotenoid diversity with a discussion of how structure determines energy transfer. The chapter is amply illustrated with structural diagrams as well as theoretical and experimental results. Overall, this section provides good coverage of the most diverse aspect of algal photosynthesis.

The final section of the volume, "General Aspects" (Chapters 16–19), discusses algal photosynthesis in the context of environmental variations, primarily light, but also other factors like nutrients and temperature. The effects of high light (PAR) and UV have recently attracted much interest, and the topic has some coverage in each chapter of this section (as well as elsewhere in the volume). Chapter 16 (Franklin et al.) is entirely devoted to photoinhibition and UV-B effects. Perhaps one sign of an active topic of research is a diversity of viewpoints. This seems to be the case for work on photoinhibition, as the term is used somewhat differently by different authors. The reader will need some care to thread through this "semantic minefield" (quoting Franklin et al.). Although they recommend a way out of the minefield by using a simple concise set of definitions and avoiding terms like "dynamic" and "chronic," the latter terms are still used in Chapters 18 and 19. Chapter 17 (Raven and Geider) recaps the fundamental features of algal photosynthesis and then examines how they change in response to the environment at the levels of adaptation, acclimation, and regulation. This might be the first chapter read by those with an environmental orientation, after which cross-references can be followed to more detailed discussions in other chapters about particular mechanisms of interest. The mechanism of PSII variable fluorescence was discussed in the previous section, but here we find much more about using variable fluorescence as a tool for exploring environmental responses *in situ*, especially for macroalgae in Chapter 18 (Hanelt et al.). The final chapter (19) by Yellowlees and Warner surveys photosynthesis by algae in symbiotic associations, most notably the dinoflagellate–coral association so important for growth and maintenance of tropical reef ecosystems, but also numerous other systems like lichens. The host cell adds an extra level of complexity to the system, which can be viewed in the case of coral–dinoflagellate as a tertiary endosymbiosis. Interestingly, questions about host–symbiont interactions in regulating photosynthesis have parallels with

questions about plastid–cellular interactions for algal photosynthesis in general. Particularly fascinating is the suggestion, now confirmed by more recent results, that coral hosts select among many strains of symbionts with different tolerances to optimize performance in the host environment.

Overall, the volume covers an enormous amount of material but still falls somewhat short of the comprehensive treatment claimed in the publisher's cover note. This is particularly the case for research based on the rapidly expanding algal sequence database as well as many other subjects as noted above. However, viewed as a series of monographs relevant to the main theme, the volume will be most useful as a reference to researchers who will mainly read the chapter(s) relating to their specialty. In most instances there are cross-references to relevant material in other chapters. The chapters vary in depth of coverage, at some points unnecessarily detailed on a topic that may only interest a few readers, whereas other topics get only a cursory treatment. The quality of editing also varies; some chapters have an inordinately high number of typographical errors, incomplete sentences, and scrambling of text. A particularly glaring example is the statement (on page 404) that a limited supply of Fe relative to Cu leads to the expression of [iron containing] cytochrome c_6 rather than [copper containing] plastocyanin (when it should be the reverse). The specialist reader will find these mistakes mainly irritating, but the volume could prove confusing at times to the beginning graduate student. The latter audience probably is better served by an introductory text such as Falkowski and Raven's *Aquatic Photosynthesis*.

On the other hand, the specialist researcher and the graduate student ready to move beyond *Aquatic Photosynthesis* will profit from taking a look at this book. It is quite successful in depicting the diversity of algae in many aspects of photosynthesis. I recommend anyone seriously interested in algal photosynthesis to read it through, though making it through all 479 pages will take some dedication. Having the characteristics of the different groups gathered together on one stage helps to clarify the similarities and differences in a way that will be useful for many phycologists. Important areas where knowledge is lacking are noted, and this will guide future research. The book also shows that there are many surprises out there, and caution is required in extrapolating results from a few model systems to algal photosynthesis in general. Keeping an open mind as to the possible differences among species and groups will be key to future progress.

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