

O. Marchal

AQUATIC PHOTOSYNTHESIS



Paul G. Falkowski, PhD

Senior Scientist

Oceanographic and Atmospheric Sciences Division

Brookhaven National Laboratory

Upton, New York

John A. Raven, PhD, FRSE, FRS

John Boyd Baxter Professor of Biology

Department of Biological Sciences

University of Dundee

Dundee, Scotland

b

Blackwell
Science

Contents

Preface	vii
CHAPTER 1	
An Introduction to Photosynthesis in Aquatic Systems	1
CHAPTER 2	
Light Absorption and Energy Transfer in the Photosynthetic Apparatus	33
CHAPTER 3	
The Photosynthetic Light Reactions	65
CHAPTER 4	
Photosynthetic Electron Transport and Photophosphorylation	96
CHAPTER 5	
Carbon Acquisition and Assimilation	128
CHAPTER 6	
The Molecular Structure of the Photosynthetic Apparatus	163
CHAPTER 7	
Photosynthesis in Continuous Light	193
CHAPTER 8	
Making Cells	228
CHAPTER 9	
Photosynthesis and Primary Production in Nature	263
CHAPTER 10	
Aquatic Photosynthesis in Biogeochemical Cycles	300
Index	360

Preface

Photosynthesis is one of the oldest and most fascinating processes in biology. The subject has attracted physicists, physical chemists, organic chemists, biochemists, geneticists, molecular biologists, physiologists, ecologists, geochemists, and evolutionary biologists. Indeed, research on photosynthesis can lend itself to so many lines of investigation that not only students but professional researchers and teachers as well are hard pressed to assimilate it all.

There are many textbooks on photosynthesis, and a few even discuss photosynthesis in aquatic ecosystems as part of a curriculum in aquatic science. For the most part, these texts consider flowering plants and green algae as the "norm." While many aspects of photosynthesis are common to all oxygen-evolving photosynthetic organisms, there is a great deal of taxonomic diversity in aquatic photosynthetic organisms that is manifested in photosynthetic processes. We have not found an introductory textbook that integrates biophysical, biochemical, and physiological concepts of photosynthesis in the context of the ecology and evolution of aquatic organisms. We felt, therefore, that it was time to write an accessible text that takes as the norm the diversity of taxa that contribute to primary productivity in aquatic systems.

Terrestrial plants are so much a part of the human experience that aquatic photosynthetic organisms are often overlooked. All terrestrial plants are derived from a single class of a single division of algae. There are a dozen divisions of eukaryotic algae that we know of, and at least one prokaryotic division. A division is the taxonomic equivalent of phylum. (To illustrate the depth of evolutionary diversity in the algae, it is humbling to consider that humans, birds, dinosaurs, and fish are all in the same phylum, Chordata.) The diversity in algae is manifested in many aspects of the photosynthetic apparatus. Perhaps the most obvious is the wide range of colors observed in algae. In fact, differences in color are often a clue to the taxonomic classification of the organism. In addition, however, aquatic photosynthetic organisms often differ from higher plants in choices of metals used in photosynthetic electron transport, the enzymes used to fix carbon dioxide, the location of genes encoding proteins in the photosynthetic system, and the architecture of the organisms themselves. A discussion of photosynthesis in aquatic organisms puts diversity at the center of the consideration of mechanisms, the ecology of natural populations, and the geochemical and paleoecological consequences of aquatic photosynthesis on the evolution of life on Earth.

This text is not meant to be a reference book that reviews all the latest discoveries in photosynthesis. Rather, it is our attempt to explain fundamental concepts, especially biochemical and biophysical mechanisms, not only in terms of molecular processes, but also in terms of underlying physical and chemical processes. We hope that this physico-chemical approach will help readers less familiar with physics and chemistry to understand and appreciate the biochemical and biophysical discussion. Similarly, our discussion of the phylogeny and structure of the aquatic photosynthetic organisms should help readers with less background in biology.

The book was written for advanced undergraduate or postgraduate students with a general scientific background. We presume no previous knowledge of pho-

tosynthesis. Each of the ten chapters, written in what we believe is a logical sequence, can be read on its own, used in a course, or assigned as supplemental reading for a course. Each successive chapter builds upon information in the preceding chapter, but each can also be read as a self-contained essay. We have provided references not only to review papers, but also to original research papers that we think will help an interested reader explore a specific subject in depth. We would consider the book a success if it helped the reader understand virtually any paper written on any topic related to photosynthesis.

The book was a collaboration between us, extending, in fits and starts, over a period of three years. During that time, we learned a great deal from each other and from discussions with numerous colleagues, students, and collaborators. We especially thank Richard Barber, John Beardall, Mike Behrenfeld, John Berges, William Cramer, Bruce Diner, Zvy Dubinsky, Dion Durnford, Diane Edwards, Jack Fajer, Graham Farquhar, Anthony Fielding, Elizabeth Gantt, Richard Geider, Sheila Glidewell, Howard Griffiths, Linda Handley, Garmen Harbottle, Geoffrey Hind, Andy Johnston, Todd Kana, Jon Keeley, John Kirk, Andrew Knoll, Zbignew Kolber, Janet Kubler, Claire Lamberti, Julie LaRoche, Jeff MacFarlane, Enid MacRobbie, David Mauzerall, Michael McKay, Linda Medlin, Andre Morel, François Morel, Jack Myers, Bruce Osborne, Barry Osmond, Ondrej Prasil, Katherine Richardson, Slim Samulesson, Andrew Smith, Bob Spicer, Janet Sprent, Norman Sutin, Alan Walker, David Walker, Doug Wallace, John Whitmarsh, and Kevin Wyman for sharing their thoughts. We take full responsibility for any errors in fact or interpretation. We are indebted to our families for their patience and support, without which this project could not have been completed. We both thank our parents for their nurturing and guidance. JAR thanks his primary school teacher, the late Mrs. F. Ridgewell. PGF thanks the late Bill Siegelman for his encouragement and counsel through the years.

PGF
JAR

1

An Introduction to Photosynthesis in Aquatic Systems

Photosynthesis is the biological conversion of light energy to chemical bond energy that is stored in the form of organic carbon compounds. Approximately 40% of the photosynthesis on Earth each year occurs in aquatic environments (Falkowski 1994). Because we live on land, however, and the aggregate biomass of aquatic plants amounts to less than 1% of the total plant biomass on Earth, terrestrial plants are much more a part of the human experience (Table 1.1). Consequently, the role and importance of aquatic photosynthetic organisms are not appreciated by most students of photosynthesis.

Most of the detailed biochemical, biophysical, and molecular biological information about photosynthetic processes comes from studies of higher plants and a few model algae such as *Chlamydomonas* and *Chlorella* (Harris 1989; Rochaix 1995). Traditionally, model organisms have been chosen because they are easily grown or can be genetically manipulated rather than because they are ecologically important. There are significant differences between terrestrial and aquatic environments that affect and are reflected in photosynthetic processes. These differences have led to a variety of evolutionary adaptations and physiological acclimations of the photosynthetic apparatus in aquatic organisms that are without parallel in terrestrial plants. Moreover, there is sufficient knowledge of the basic mechanisms and principles of photosynthetic processes in aquatic organisms to provide a basic understanding of how they respond to changes in their environment. Such interpretations form the foundation of aquatic ecophysiology and are requisite to understanding both community structure and global biogeochemical cycles.

We strive here to describe some of the basic concepts and mechanisms of photosynthetic processes, with the overall goal of developing an appreciation of the adaptations and acclimations that have led to the abundance, diversity, and productivity of photosynthetic organisms in aquatic ecosystems. In this introductory chapter we briefly examine the overall photosynthetic process, the geochemical and biological evidence for the evolution of oxygenic photosynthetic organisms, and the concepts of life-forms and nutritional modes. Many of these themes are explored in detail in subsequent chapters.

A DESCRIPTION OF THE OVERALL PHOTOSYNTHETIC PROCESS

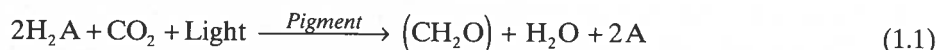
The biological economy of Earth is based on the chemistry of carbon. The vast

Table 1.1 Comparison of global net productivity/living biomass in marine and terrestrial ecosystems

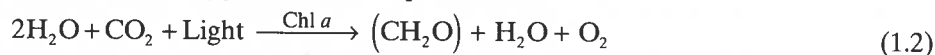
Ecosystem	Net Primary Productivity (10 ¹⁵ grams/year)	Total Plant Biomass (10 ¹⁵ grams)	Turnover Time (years)
Marine	35–50	1–2	0.02–0.06
Terrestrial	50–70	600–1000	9–20

majority of carbon on Earth is in an oxidized, inorganic form;¹ that is, it is combined with molecular oxygen and is in the form of the gas carbon dioxide (CO₂) or its hydrated or ionic equivalents, namely bicarbonate (HCO₃⁻) and carbonate (CO₃²⁻). These inorganic forms of carbon are interconvertible but thermodynamically stable. They contain no biologically usable energy, nor can they be used directly to form organic molecules without undergoing a chemical or biochemical reaction. In order to extract energy from inorganic carbon or to use the element to build organic molecules, the carbon must be chemically reduced, which requires an investment in free energy. There are only a handful of biological mechanisms extant for the reduction of inorganic carbon; on a global basis photosynthesis is the most familiar, most important, and most extensively studied.

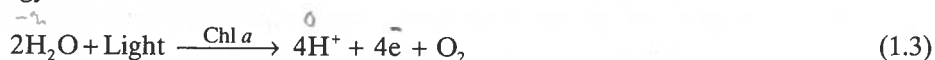
Photosynthesis can be written as an oxidation-reduction reaction of the general form:



Note that in this representation of photosynthesis light is specified as a substrate; some of the energy of the absorbed light is stored in the products. All photosynthetic bacteria, with the important exceptions of the cyanobacteria and prochlorophytes, are obligate anaerobes and are incapable of evolving oxygen. In these organisms compound A is, for example, an atom of sulfur and the pigments are bacteriochlorophylls (Blankenship et al. 1995; Van Niel 1941). All other photosynthetic organisms, including the cyanobacteria, prochlorophytes, eukaryotic algae, and higher plants, are oxygenic; that is, Equation 1.1 can be modified to:



where Chl *a* is the ubiquitous plant pigment chlorophyll *a*. Equation 1.2 implies that somehow chlorophyll *a* catalyzes a reaction or a series of reactions whereby light energy is used to oxidize water:



(yielding gaseous, molecular oxygen. Equation 1.3 represents the so-called “light reactions”) of oxygenic photosynthesis. The processes that constitute the light reactions will be discussed in Chapters 2 and 3.

Equation 1.3 describes an oxidation process. Specifically, it is a *partial reaction*, where electrons are extracted from water to form molecular oxygen. This process is the heart of one of two groups of reactions in oxygenic photosynthesis.

1. The terms *inorganic* and *organic* are archaic, originating from the time when inorganic carbon compounds were obtained from minerals and organic compounds were obtained from plant or animal sources. For our purposes, we assume that an organic molecule contains a carbon atom that is directly, covalently linked to a hydrogen atom.

The other reaction, the reduction of CO₂, also can be described by:



As free electrons are normally not found in biological systems, the reaction described by Equations 1.3 and 1.4 requires the formation of an intermediate reducing agent that is not shown explicitly. The form of, and mechanism for, the generation of reductants will be discussed in Chapter 4.

Although the biological reduction of CO₂ may be thermodynamically permitted on theoretical grounds, by, for example, mixing a biological reducing agent such as NADPH with CO₂, the reaction will not spontaneously proceed. Enzymes are required to facilitate the reduction process. Given the substrates and appropriate enzymes, the reactions that lead to carbon reduction can proceed in the dark as well as the light. These so-called "dark reactions" are coupled to the light reactions by common intermediates and by enzyme regulation. Although there are variations on the metabolic pathways for carbon reduction, the initial dark reaction, whereby CO₂ is temporarily "fixed" to an organic molecule, is highly conserved throughout all photosynthetic organisms.² We will examine the dark reactions in Chapter 5.

AN INTRODUCTION TO OXIDATION-REDUCTION REACTIONS

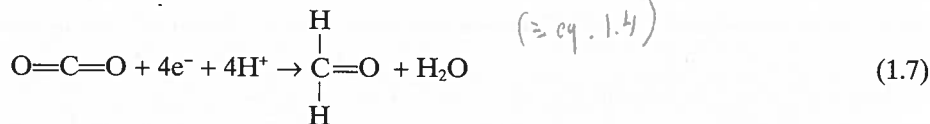
The term *oxidation* was originally proposed by chemists in the latter part of the 18th century to describe reactions involving the addition of oxygen to metals, forming metallic oxides. For example:



The term *reduction* was used to describe the reverse reaction, namely the removal of oxygen from a metallic oxide, for example, by heating with carbon:



Subsequent analysis of these reactions established that the addition of oxygen is accompanied by the removal of electrons from an atom or molecule. Conversely, reduction is accompanied by the addition of electrons. In the specific case of organic reactions that involve the reduction of carbon, the addition of electrons is usually balanced by the addition of protons. For example, the reduction of carbon dioxide to formaldehyde requires the addition of four electrons *and* four H⁺, that is, the equivalent of four hydrogen atoms.



2. Historically, the term *fixation* means to make nonvolatile. It is a term applied to the biochemical or chemical, but not physical, sequestration of a gas. Thus, adsorption of a gas by activated charcoal is not fixation, while the chemical reaction of CO₂ with an amine to form a carbamate is a form of fixation. Strictly speaking, the term fixation is not synonymous with chemical reduction, although the two terms often are used interchangeably in the vernacular.