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Volume 4



ENERGETICS AND  
TRANSPORT IN  
AQUATIC PLANTS

John A. Raven

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# **ENERGETICS AND TRANSPORT IN AQUATIC PLANTS**

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**Volume 4**

**Energetics and Transport in Aquatic Plants**

John A. Raven

**To my parents and Linda**

## Preface

The immediate impetus to write this book came from my being chief instructor for a course held at the Marine Biology Laboratory, Woods Hole, Massachusetts in August 1982. That course bore the same title as does this book. Over a longer period my teaching and research has been emphasising aspects of the functioning of aquatic plants for which no comprehensive text was available. To the extent that authors must, in a preface, rationalise their efforts, that is my justification. However, if this book is not its own justification, no amount of preparatory pontificating will rationalise its publication.

A more important use for a preface is to acknowledge help which the author has received. The following alphabetical list acknowledges those who have, by talking and listening, made this book better than it would otherwise have been: S. Allen, J.M. Anderson, M.C. Anderson, M. Andrews, T. ap Rees, M.R. Badger, M. Bassett, J. Beardall, D.S. Bendall, F.L. Bendall, J.A. Berry, M.A. Bisson, G. Bowes, D.J. Bowles, R. Box, M.J. Canny, D.T. Clarkson, W.G. Chaloner, G.A. Codd, E.J.H. Corner, I.R. Cowan, W.J. Cram, R.M.M. Crawford, J. Dainty, I.R. Davison, M.I. De Michelis, I.K. Deshmukh, D. Edwards, G.C. Evans, G.D. Farquhar, D.S. Fensom, G. Findenegg, G.E. Fogg, A. Fyson, P.B. Garland, R.J. Geider, C. Glidewell, S.M. Glidewell, H. Griffiths, N.M. Griffiths, J.P. Grime, M.R. Groom, P.J. Grubb, B.E.S. Gunning, J.L. Harper, A.E. Hill, R. Hill, A.B. Hope, H.A.P. Ingram, H.D. Jayasuriya, A.M. Johnston, A. Kaplan, J.E. Keeley, G.O. Kirst, A.W.D. Larkum, D.H. Lewis, U. Lüttge, J.J. MacFarlane, E.A.C. MacRobbie, A.L. Miller, T.H. Nicolson, B.A. Osborne, C.B. Osmond, J.B. Passioura, G.D. Price, T. Preston, M.L. Reed, R.H. Reed, K. Richardson, J.B. Robinson, R. Rybova, H.D.W. Saddler, G. Samuelsson, D. Sanders, R. Scott, B. Shachar-Hill, F.A. Smith, J.A.C. Smith, S.E. Smith, R.M. Spanswick, D.H.N. Spence, K.R. Sporne, J.I. Sprent, W.D.P. Stewart, J.M. Sutherland, P.J. Syrett, R.J. Thomas, M.T. Tyree, E.A. Vigrow, N.A. Walker, J.D.B. Weyers, R.E. Williamson and R.G. Wyn Jones. I am especially indebted to Drs. E.A.C. MacRobbie and K. Richardson. Enid MacRobbie, who supervised my postgraduate work, was and is a great source of inspiration. Katherine Richardson has read the entire book as a near-final draft, and her wise counsel has greatly improved both the science and its exposition. Finally, the good humour, celerity, and accuracy of Anne Cameron (typist) and Shona McInroy (draughtswoman) have solaced me when only darkness seemed to inhabit the end of the authorial tunnel.

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# Chapter One

## The Physical and Chemical Background

### INTRODUCTION

Aquatic plants are organisms which use electromagnetic radiation as their sole (or major) energy source for growth and survival, which use inorganic solutes as their sole (or major) sources of the chemical elements needed for growth and survival, and which normally live submerged in water. This definition defines the external milieu and resources of the aquatic plant; the other leg of the energy-materials-information tripod on which the organisms' survival and continuation is (precariously) balanced is, of course, provided by the information in the organism's genome interacting with the intracellular and extracellular environment, and refined by natural selection. This book will, as befits its title, say little about the informational transactions of aquatic plants, although the primacy of information in a realistic definition of life cannot be gainsaid.

This introductory chapter outlines the energy and chemical resources available to, and used by, aquatic plants, and some general physicochemical constraints on the way plants can manipulate these resources (see Fig. 1.1).

### LIGHT IN THE AQUATIC ENVIRONMENT

The light used by aquatic plants (excluding the photosynthetic bacteria but including Cyanobacteria) is in the wavelength range 400–700 nm; this is termed “photosynthetically active radiation” (PAR). The photon flux density incident on the surface of a water body will not generally exceed 2 mmol photons  $\text{m}^{-2} \text{s}^{-1}$ , equivalent to some 400  $\text{W m}^{-2}$  in energy units [see Jeffrey, 1981; Spence, 1982], in the 400–700-nm range. If all of this light were absorbed by plants, and used at the highest widely accepted efficiency of photosynthetic energy conversion—i.e., the fixation of one mol of carbon dioxide per ten mol photons absorbed [see Clayton, 1980; Halliwell, 1981]—



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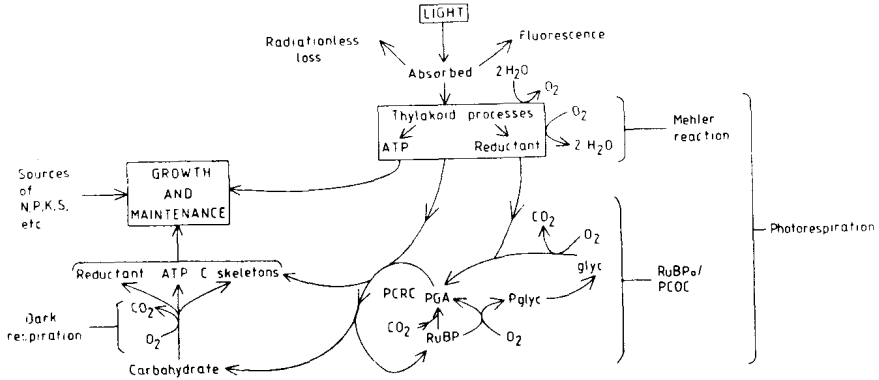


Fig. 1.1. Outline of the pathways of energy, carbon, and oxygen in photosynthesis, photorespiration, dark respiration, and growth of a phytoplankter. No attempt is made to represent stoichiometries. (Abbreviations: Glyc, glycolate; PCOC, photorespiration carbon oxidation cycle; PCRC, photosynthetic carbon reduction cycle; PGA, 3-phosphoglycerate; Pglyc, phosphoglycolate; RuBP, ribulose biphosphate; RuBPo, ribulose biphosphate oxygenase. [after Raven and Beardall, 1981b].

then gross productivity would be  $200 \text{ mmol carbon m}^{-2} \text{ s}^{-1}$ . In an idealized situation of 12 h illumination per day at  $2 \text{ mmol photons m}^{-2} \text{ s}^{-1}$  being used with the efficiency quoted above, yearly gross productivity would be  $38 \text{ kg carbon m}^{-2}$ , equivalent to 760 tonnes of organic dry weight per hectare. This is more than ten times the highest measured gross productivities in aquatic communities [e.g., Mann, 1982].

Among the factors which account for the discrepancy for both terrestrial and aquatic plants are incident photon flux densities lower than the high value of  $2 \text{ mmol photons m}^{-2} \text{ s}^{-1}$  quoted above, and the inability of plants, constrained by lack of nutrients in addition to the intrinsic physics and chemistry of their catalytic systems, to absorb all of the incident radiation and transform it at the efficiency quoted earlier; light saturation can occur in communities as well as in individual organisms. Aquatic plants are additionally disadvantaged by the absorption of light by their fluid medium, and certain organic compounds dissolved therein. In a terrestrial community the absorption of photosynthetically active radiation by air in the plant canopy is negligible relative to absorption by the plants themselves, while in many aquatic communities, particularly phytoplankton communities, the medium in which the plants live absorbs much more light than do the plants themselves [Jeffrey, 1981; Spence, 1982; Dring, 1981]. Thus the aquatic plants are disadvantaged relative to land plants in the availability of photosynthetically active radiation.

An important concept in aquatic photosynthesis, and one about which some incorrect generalizations have been made, is that of the euphotic zone. This is the surface zone in which the photon flux density is sufficient for net photosynthesis. Accordingly, the bottom of the euphotic zone has a photon flux density of PAR which just permits net photosynthesis by the most shade-adapted phototroph (benthic, or phytoplankter in a stratified water column). While  $10^{-2}$  of surface photon flux density has been widely quoted as the compensation photon flux density which defines the bottom of the euphotic zone, it is now clear that values closer to  $10^{-3}$  are more realistic [Luning, 1981; Richardson et al., 1983]. The depth at which such photon flux densities occur is defined by the Lambert-Beer law, which can be expressed as equation 1.1:

$$I_d = I_0 e^{-Kd}, \quad (1.1)$$

where  $d$  = depth (m),  $I_0$  = photon flux density incident upon the surface of the water body ( $\text{mol photon m}^{-2} \text{s}^{-1}$ ),  $I_d$  = photon flux density at depth  $d$  ( $\text{mol photon m}^{-2} \text{s}^{-1}$ ), and  $K$  = extinction coefficient ( $\text{m}^{-1}$ ).

It is possible, and desirable, to partition  $K$  into components which relate to water itself, to solutes in the water which absorb in the wavelength range 400–700 nm, to plants which absorb photosynthetically active radiation, and to other particles which absorb and scatter visible radiation. To give some feel for the magnitude of the  $K$  which sums all of these components, a “typical” value of  $K$  would be 0.04 in clear oceanic waters, and 0.15 in temperate coastal waters.  $K$  is very wavelength-dependent; in the two cases quoted above, the attenuation in the oceanic water would largely result from absorption by water itself which is more pronounced in the long-wavelength regions, so the radiation at depth would be largely blue and blue-green. In coastal waters, by contrast, there are additional components of absorption owing to “Gelbstoff” (yellow substance: organic substances absorbing blue light) and, related to the higher nutrient availability in many coastal waters, photosynthetic pigments absorbing blue and red light, leaving green light as the most deeply penetrating radiation. Jeffrey [1981] and Dring [1981] discuss the significance of these differential attenuations of various wavelengths for aquatic plants.

## PHOTOSYNTHESIS

Phototrophs use the process of photosynthesis to convert electromagnetic radiation into the ATP and reductant which can be used for growth (nutrient

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assimilation) and maintenance processes. As has been indicated above, the highest efficiency of phototrophic growth which is widely accepted involves the use of 10 mol photons for growth corresponding to the assimilation of 1 mol of carbon dioxide. When we look at the efficiency with which the energy of these ten photons is used in terms of the energy content of the cell material produced we find that less than 0.3 of the absorbed light energy appears in the final cell product. Thus even the most efficient use of light energy leaves more than 0.7 of the energy "wasted." However, this apparent waste of energy is *qualitatively* essential if the growth process is to proceed at a finite rate [cf. Odum and Pinkerton, 1955; Caplan, 1971] and thus is essential to the perpetuation of the individual phototroph. The tradeoff between the efficiency of a process (running costs) and the rate at which it occurs (related to capital investment in catalytic machinery) will be a recurring theme [cf. Raven, 1980a, 1981a], as will the extent to which the balance struck between rate and efficiency is modified by considerations of controllability and safety of the catalyzed processes. A further very important implication of this apparent waste of energy is seen when the significance of solar heating of the surface layers of water bodies, resulting from light energy absorption by plants, water, dissolved solutes, and nonliving solid material, is considered in relation to the phenomena of thermal stratification and of the production of bulk water movements. The role of stratification and water movement is considered below in the context of "energy subsidies" to phototrophs, i.e., increases in the availability of resources for growth of phototrophs which are energized by processes other than photosynthesis and photosynthesis-dependent processes in the individual phototrophs.

The process of photosynthesis may be divided into three time domains, which correspond to different catalytic and structural entities in the plant. Light absorption ( $10^{-15}$  s) and excitation energy transfer within antenna pigment-protein complexes to the reaction centres ( $10^{-15}$ – $10^{-10}$  s) involve pigment-protein complexes which absorb and transfer energy and (unless deleterious processes such as photo-oxidation occur) which do not themselves undertake photochemistry. These complexes are on, or in, membranes (see chapters 2, 4). Primary photochemistry occurs within  $10^{-9}$  s; otherwise competing reactions (fluorescence, radiationless deexcitation) consume an appreciable fraction of the excitation energy. The primary photochemistry occurs in reaction centres which are integral pigment-protein complexes, and results in electron transfer in terms of energy (uphill, from a relatively high potential donor to a relatively low potential acceptor) and in space (across some fraction of the width of a bilayer membrane). Subsequent processes take  $10^{-6}$  s or longer, and include the range of secondary redox and trans-

membrane proton transfer reactions which result in the generation of reductant and ATP and the dehydrogenation of water to produce oxygen which are associated with the photosynthetic membrane, and the use of reductant and ATP in energy-requiring biosyntheses based on such nutrients as carbon dioxide, nitrate, sulphate, and phosphate which involve water-soluble rather than membrane-associated protein catalysts.

While the details of these reactions will be considered in chapters 4–6, two important points may be made at this juncture which are related to the comparability of the light-acquisition and chemical nutrient-acquisition processes (see below). One is that, in order for the processes to proceed at a finite rate, the energy used in a process must exceed the energy stored in that process; i.e., free energy decreases. Thus the absorption and transfer of light energy involves decrements of usable energy as the excitation energy migrates from pigments whose excited states correspond to shorter wavelengths of absorbed light (i.e., large energy contents in terms of J/mol photon) to pigments whose excited state corresponds to longer wavelengths of absorbed light (i.e., smaller molar energy content); the energy per mol of the excited state of the reaction centre lowest of all. Similar considerations apply with respect to the decrement of usable energy which occurs in the coupling of the exergonic de-excitation of the excited state of the reaction centre pigment to the endergonic primary redox reaction, and the coupling of the products of primary photochemistry (via reactions which restore the reaction centre to a state in which it can undergo another photochemical reaction) to the endergonic secondary redox and proton transport reactions. These reactions are all spontaneous in that, granted the existence of the photosynthetic apparatus in the presence of an appropriate photon flux density (at an appropriate temperature), they will occur at a finite rate without coupling to an extraneous exergonic reaction. This is, of course, a *sine qua non* of phototrophy. However, the existence of the photosynthetic apparatus (whose synthesis requires material as well as energy), the occurrence of the phototroph in the euphotic zone, and the occurrence of an appropriate ambient temperature, may all be related to the “energy subsidies” mentioned below.

The other point to be emphasized relates to the dilute nature of the energy resource, and the consequent importance of a “concentrating” process prior to the primary photochemical reaction if a high specific reaction rate (mol excitation energy transformed (mol reaction centre)<sup>-1</sup> s<sup>-1</sup> is to be attained, thus maximizing the use to which the energy and material resources devoted to the construction of the reaction centre. Furthermore, at low photon flux densities where “leak” or “slippage” reactions (chapters 3–7) might consume a large fraction of the absorbed energy, such a concentration process can help

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profitable reactions to compete with the unprofitable, parasitic reactions. In practice (see chapter 4) of the order of a few hundred antenna pigment molecules are, on average, associated with a reaction centre [see Raven and Beardall, 1982].

The absolute light-absorption potential of a pigmented plant in a given radiation field will be discussed later in the context of maximal resource supply rates to aquatic plants.

### PHOTOTROPHS, HETEROTROPHS, AND CHEMOLITHOTROPHS

The vast majority of aquatic plants are photolithotrophs, i.e., use inorganic solutes to supply their requirements for carbon, nitrogen, sulphur, and phosphorus. Many of them are apparently obligate photolithotrophs, in that it is not possible to culture them in media supplying an energy source other than light and/or a carbon source other than inorganic carbon species (carbon dioxide, bicarbonate): see Table 1.1. This definition of photolithotrophy provides a good example of the falsification principle of testing scientific hypotheses: how many unlikely substrates at osmotically embarrassing concentrations must be tested and shown *not* to act as carbon and energy sources for dark growth before an organism is deemed to be an obligate photolithotroph? Undoubtedly such investigations are justified in that they might help to explain the basis of obligate photolithotrophy (see below), although their ecological significance is not clear. An example is the painstaking work of Cheng and Antia [1970] who showed that the marine flagellates *Prymnesium parvum* and *Chroomonas salina* could grow in the dark with glycerol at high concentrations (optimally about  $500 \text{ mol m}^{-3}$ ), as their carbon and energy source. In unpolluted waters the glycerol concentration is likely to be several orders of magnitude less than  $500 \text{ mol m}^{-3}$ , although a possible ecological niche for these two flagellates would be as endosymbionts in glycerol-accumulating algae such as *Dunaliella* [f. Ben-Amotz, 1980].

The range of algae which (from the laboratory culture point of view) are obligate photolithotrophs is exemplified by the compilations of Droop [1974] and Neilsen and Lewin [1974] for microalgae, and work on macroalgae by Fries [1963] and Forsberg [1965a]; the availability of vascular macrophytes in axenic culture [Forsberg, 1965b] opens the way for tests of their trophic status. It may be noted that many algae which are obligate photolithotrophs with respect to bulk supplies of energy and nutrient elements nevertheless require (are auxotrophic for) various organic growth factors, usually one or more of cobalamin, biotin, and thiamine [Droop, 1966; Swift, 1980; Fries and Petterson, 1968].

The enigma of obligate photolithotrophy will be discussed in more detail in chapter 6; the enigma lies in the inability of exogenous organic solutes to substitute for organic solutes generated endogenously in photosynthesis for growth processes. Clearly obligate photolithotrophs must be able to *survive* the dark period of the diel cycle, and many can survive for much longer periods in the dark [Antia, 1976; Raven, 1976a,b], so they must be able to generate enough ATP from stored organic compounds in the dark to provide for maintenance processes. Furthermore, obligate photolithotrophic macrophytes often have nonphotosynthetic cells which must be able to grow as well as survive by heterotrophic metabolism, albeit using substrates generated by photosynthetic cells in the same organism [Raven, 1976a,b]. Even though obligate photolithotrophs cannot *grow* with organic solutes as their sole carbon and energy source, many of them can take up, and metabolize, organic solutes. The extent to which such metabolism increases the survival of photolithotrophic microalgae at subcompensation photon flux densities has been validly questioned by Richardson and Fogg [1982].

The other category of photolithotrophic organisms is that of facultative photolithotrophs, i.e., the organisms which can grow on organic compounds in the light (photoorganotrophy) or the dark (chemoorganotrophy) in addition to their ability to grow photolithotrophically. The organotrophic growth rates of the various facultative photolithotrophs as a fraction of their photolithotrophic growth rate, and the extent to which the presence of an organic growth substrate represses the synthesis of the photosynthetic apparatus, is quite variable [Raven, 1976a]. The extent to which the organotrophic (heterotrophic) potential of facultative photolithotrophs is expressed under most natural conditions has been questioned [e.g., by Whittenbury and Kelly, 1977] on the grounds that facultative heterotrophs are unlikely to be able to compete successfully with specialist, obligate heterotrophs under natural conditions. Be that as it may, the coexistence of obligate and facultative photolithotrophs in nature suggests that the ability to grow on organic compounds need not greatly reduce the fitness of an organism when growing photolithotrophically in competition with obligate photolithotrophs. The study of the “facultative *versus* obligate” question in terms of competition experiments has been carried much further with chemolithotrophic [Gottschal and Kuenen, 1981] than with photolithotrophic organisms (cf. the lucid exposition of the rigorous tests which must be applied before a given attribute can be termed “adaptive” in a given environment in Osmond et al. [1980]).

Photolithotrophy is clearly of importance to the photolithotrophs themselves in that it is the “energy” leg of the information-energy-materials tripod. It is also of very great importance to the rest of the aquatic biota in

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TABLE 1.1. Resources Used by Aquatic Plants [From Raven, 1976a,b; 1980a,b; chapters 3-9]

Resource	Form in which nutrient enters cell	Constitutive repressible ability to use nutrient
Energy	Light for phototrophs	Photosynthetic apparatus repressible in facultatively organotrophic phototrophs (by presence of usable organic carbon source), derepressed by absence of usable organic carbon source, presence of light
	Organic carbon for organotrophs	Organic carbon transport mechanism repressible by light in some facultatively organotrophic phototrophs; derepressible by presence of exogenous substrate in others
Carbon	CO <sub>2</sub> for photolithotrophy and for anaplerotic pathways in organotrophy	Entry nonmediated and hence constitutive
	HCO <sub>3</sub> <sup>-</sup> for many photolithotrophs	Entry repressible by high CO <sub>2</sub> , inorganic N availability; capacity to transport HCO <sub>3</sub> <sup>-</sup> may parallel reduced permeability to CO <sub>2</sub>
Nitrogen	Organic carbon	See under Energy above
	N <sub>2</sub> in N <sub>2</sub> -fixers (Cyanobacteria, associative relations between phototrophs and N <sub>2</sub> -fixing prokaryotic organotrophs)	N <sub>2</sub> entry nonmediated and hence constitutive; metabolism repressed by fixed N sources
	NH <sub>4</sub> <sup>+</sup>	NH <sub>4</sub> <sup>+</sup> entry repressed at high external concentrations of NH <sub>4</sub> <sup>+</sup> /NH <sub>3</sub> ; NH <sub>3</sub> entry constitutive
	NO <sub>3</sub> <sup>-</sup> (not used by some algae, e.g., <i>Euglena</i> )	Entry, assimilation repressible by reduced N sources
	Organic nitrogen (urea, ureides, amino acids, amides, purines, etc.)	Entry, assimilation repressible (except for nonmediated entry of urea, and assimilation of protein-amino acids, nucleic acid bases)
Phosphorus	Phosphate	Entry constitutive (some repression of high affinity system at high external concentrations); assimilation by oxidative phosphorylation constitutive, photophosphorylation repressible. See under Energy above
	(Polyphosphate, organic phosphates)	Generally hydrolyzed prior to entry
Sulphur	Sulphate	Entry, assimilation constitutive (partial repression of entry at high sulphate concentrations)
	Organic sulphur compounds	See organic nitrogen above.
Non-metabolized	K <sup>+</sup> , Na <sup>+</sup> , Ca <sup>2+</sup> , Mg <sup>2+</sup> , Cl <sup>-</sup>	Probably all constitutive

that the energy for the growth of almost all other aquatic organisms is derived from photosynthetic reactions. This dependence is most clearly seen for biophages (organotrophs which consume live organic material)—e.g., herbivores, carnivores, and biotrophic parasites—and for necrophages (organotrophs which consume organic material post mortem)—e.g., “decomposers” and necrotrophic parasites [see Wiegert and Owen, 1971; Lewis, 1973a,b; cf. Rigler, 1975]. The dependence is rather less obvious for chemolithotrophs (i.e., those organisms which couple their endergonic growth and maintenance processes to exergonic *inorganic* chemical reactions: see Whittenbury and Kelly [1977]; Quayle and Ferenci [1978]). Taking the example of nitrifying and sulphide-oxidizing bacteria, the oxygen which acts as terminal electron acceptor in the ammonium-, nitrite-, or sulphide-oxidizing reaction is itself very largely a result of the activity of photolithotrophs over the course of geological time [Levine, 1982], with free oxygen representing some of the photosynthetic oxidant left over when some of the reduced products of photosynthesis escaped respiratory reoxidation [Cloud, 1972]. The ammonium or nitrite which is oxidized, together with most of the sulphide (an exception being sulphide from hydrothermal vents [Felbeck and Somero, 1982]) owes its origin to the decomposition of organisms whose complement of reduced nitrogen and sulphur derived ultimately from phototrophs or, particularly in the case of sulphide, to the anoxic generation of ATP by necrotrophs using oxyanions such as nitrate and, especially, sulphate as terminal electron acceptors for the oxidation of phototroph-derived reduced carbon.

### ENERGY SUBSIDIES TO PHOTOTROPHS

The other side of the energetic coin for phototrophs is the extent to which the growth and survival of a photolithotroph depends on energy inputs other than from the photosynthetic energy conversion process in that organism. Such “energy subsidies” take a number of forms, with a major distinction possible between those related to current or previous activities of other photolithotrophs (or organisms energetically dependent on them) and those related to the atmospheric or aquatic fluid movements driven more directly by solar energy and other workings of the physics of the solar system. This distinction is not absolute: an example is the influence of terrestrial and aquatic vegetation on the absorption, scattering and subsequent fate (other than as chemical energy in the end-products of phototrophic growth) of solar radiation. However, the distinction is still a useful one, and energy subsidies can, and will, be itemized under these two broad headings; many of these



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items will be mentioned again in later chapters. It will become clear that essentially all of these energy subsidies relate to the supply of chemical resources which often limit aquatic plant growth to a greater extent than does light [Margalef, 1978; Fogg, 1982; see below].

Dealing first with energy subsidies resulting from solar energy interactions other than storage as chemical energy in photosynthesis, and solar system physics, we have tides, ocean circulation (vertical and horizontal), the production and breakdown of thermal stratification, and the occurrence and movement of liquid water bodies above sea level on land. Permanent stratification of a water body (e.g., in many tropical seas and lakes) leads to impoverishment of nutrients in the euphotic zone, since particulate organic matter removes nutrients by sinking faster than diffusion can replace them across the thermocline. When they occur, the bulk water movements are beneficial to photolithotrophs in terms of moving regenerated (see below) nutrients to the euphotic zone. A very well-investigated example is the relationship of the spring and autumn blooms of phytoplankton in temperate water bodies to the establishment and breakdown, respectively, of thermal stratification, with consequent implications of the nutrient availability and depth of mixing for productivity and species composition [see Margalef, 1978]. Upwellings are also very important to phytoplankton in that they *continuously* bring up nutrient-enriched deep waters into the euphotic zone. On a smaller scale the relative movement of water and plant can be very important in decreasing the thickness of unstirred layers around organisms, and thus increasing the rate of supply of nutrients from the bulk medium to the plant surface [Wheeler and Neushul, 1981; Vogel, 1981; Pedley, 1983].

The nub of the unstirred layer problem relates to the decremental nature of the diffusive transfer of solutes: by definition, diffusion is the only mechanism of solute transport in the unstirred layer. Fick's law of diffusion may be written (equation 1.2)

$$J = \frac{D}{\delta}(C_b - C_s), \quad (1.2)$$

where  $J$  = diffusive flux of solute from bulk medium to plant surface ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $D$  = diffusion coefficient of the solute ( $\text{m}^2 \text{s}^{-1}$ ),  $\delta$  = thickness of the unstirred layer (m),  $C_b$  = concentration of solute in the bulk phase ( $\text{mol m}^{-3}$ ), and  $C_s$  = concentration of solute at the plant surface ( $\text{mol m}^{-3}$ ).

Note that this formulation assumes an abrupt transition from the bulk phase concentration ( $C_b$ ) to the start of a linear gradient in solute concentration at a distance  $\delta$  m from the plant surface, and an equally abrupt transition