

Chapter 2

Production: The Formation of Organic Matter

Primary producer organisms can form organic matter by acquiring and metabolically making use of energy and carbon (plus a variety of other essential elements). In terms of energy and carbon acquisition, some definitions may be useful. Obligate autotrophs carry out photosynthesis; hence they need light as the energy source (and will not grow in the dark) and fix carbon dioxide as the source of carbon. Facultative autotrophs may carry out photosynthesis, using light and CO_2 , as well as use organic carbon compounds as energy and carbon sources (so may grow in the dark if organic compounds are available). Some autotrophs may carry out chemosynthesis, in which a reduced compound is the source of energy. Heterotrophs can only use organic compounds as energy and carbon sources: these are basically consumers of materials fixed by primary producers, and are treated in other chapters below.

In this chapter, we first deal with photosynthesis, the use of light energy, and fixation of carbon dioxide for production, then dwell on chemosynthesis, by which energy contained in reduced compounds is acquired by producer organisms. This is followed by a brief examination of methods available to measure biomass and production, and of the rates of production by various kinds of producers.

2.1 Photosynthesis

Carbohydrates and other organic compounds are synthesized by photosynthetic autotrophs through the activity of the photosynthetic apparatus and associated biochemical pathways. The basic photosynthetic equation can be expressed as

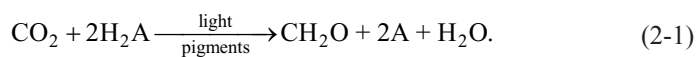


TABLE 2-1. Major electron donors, acceptors, and end products for three major types of primary production. From Fenchel and Blackburn (1979) and Parsons et al. (1977).^a

	Electron donor (reductants)	Electron accep- tor (oxidants)	Oxidized end products
<i>Photosynthesis</i>			
Oxygenic	H ₂ O	CO ₂ ^b	O ₂
Anoxygenic	H ₂ S, H ₂	CO ₂ ^b	S ⁰
<i>Chemosynthesis</i>			
Nitrifying bacteria	NO ₂ ⁻ , NH ₄ ⁺ , NH ₂ OH	O ₂ , NO ₃ ⁻	NO ₃ ⁻ , NO ₂ ⁻
Sulfur bacteria ^c	H ₂ S, S ⁰ , S ₂ O ₃ ⁻	O ₂	S ⁰ , SO ₄ ⁻²
Hydrogen bacteria ^c	H ₂	O, SO ₄	H ₂ O
Methane bacteria ^c	CH ₄	O ₂	CO ₂
Iron bacteria ^c	Fe ²⁺	O ₂	Fe ³⁺
Carbon monoxide bacteria ^c	CO	H ₂	CH ₄

^a There are many other possible chemosynthetic reactions and end products (see Tables 16-1, 16-2). These reactions connect primary production and the carbon cycle to the cycles of other nutrients, as discussed in Chaps. 16 and 17.

^b Takes place if light furnishes the large amounts of energy needed to reduce the CO₂.

^c These groups may also live heterotrophically, using a variety of organic compounds manufactured by other organisms as sources of energy (or electron donors), and with CO₂, H₂O, or more oxidized organic compounds as the end products.

The actual details of photosynthesis are far more complicated than those that appear in Eq. (2-1) (see review in Falkowski and Raven 2007); here, we limit discussion to some essential principles. Photosynthesis is a multistep process comprised of two independent series of reactions. The “light” reactions take place only when light is available and depend on the capture of photons by the photosynthetic pigments. In this process, an electron donor, H₂A, is split, liberating two electrons. In the case of oxygenic photosynthesis, the electron donor is water, and two H₂O molecules are split to form an O₂ molecule and four protons. The energy in the excited electrons released in this reaction is transferred by a series of oxidation–reduction reactions involving various electron “carriers,” to produce adenosine triphosphate (ATP) and a strong reductant, NADPH₂.

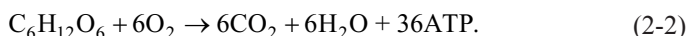
Autotrophs can carry out photosynthesis oxygenically or anoxygenically (Table 2-1). We have been largely discussing the oxygenic pathway associated with phytoplankton and multicellular producers. Photosynthetic bacteria, in contrast, carry out anoxygenic photosynthesis in the low-oxygen environments in which they live. Anoxygenic photosynthesis is carried out by certain groups of bacteria and archaea that use bacteriochlorophyll photosynthetic pigments to capture light energy. The energy is transferred to

ATP without the production of oxygen; water is not used as an electron donor. These organisms are relics of the time when the ancient atmosphere of the earth lacked oxygen; light is the source of energy but the electron donors are reduced inorganic compounds such as hydrogen sulfide or thio-sulfate (in purple and green sulfur bacteria), and organic compounds (in the purple nonsulfur bacteria) (Table 2-1; Fenchel and Blackburn 1979).

The ATP and NADPH₂ provided by the light reactions—for oxygenic as well as anoxygenic photosynthesis—are used to reduce CO₂ into complex organic molecules. These reactions are not light dependent and, hence, are called the “dark” reactions.

There are two major pathways of carbon fixation during the dark reactions. In the “C₃” pathway, the first product of carbon fixation is a 3-carbon compound called 3-phosphoglyceric acid. Primary producers that manufacture this 3-carbon compound as an end product of carbon fixation are referred to as C₃ organisms. In the “C₄” pathway, a 4-carbon compound (malic or aspartic acid) is the first end product of fixation. The malate is decarboxylated, and the CO₂ thus released is fixed through the C₃ pathway (Hatch and Black 1970). There are important physiological differences associated with C₃ and C₄ metabolism, many of which have an ecological significance (cf. Section 11.3.2). C₄ metabolism has been demonstrated in vascular plants but not in phytoplankton.

The organic compounds produced by photosynthesis may be stored or used immediately. The energy contained in the organic compounds is made available by a series of oxidative reactions. This oxidation is called dark respiration, and is the process that provides energy to sustain metabolic needs. The complete oxidation of glucose to carbon dioxide and water, for example, yields 36 ATP¹:

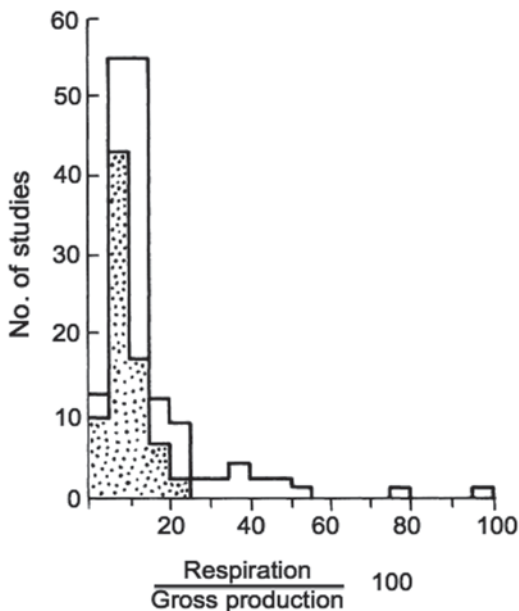


Such oxidation–reduction reactions are not light dependent and, in primary producers, provide the sole source of energy during periods when photosynthesis is not active. Glucose is initially broken down—by glycolysis—to produce NADH and ATP. The electrons in these reduced carriers and those produced by the Krebs cycle are donated to the electron transport chain where they are coupled to phosphorylation of ribulose.

The amount of dark respiration by producers relative to photosynthesis varies and is difficult to measure in the sea because rates are low, and also because bacteria and small zooplankton also respire in the seawater where the producers are suspended. Dark respiration varies widely as a percent of gross production, but most values fall around 10% for benthic microalgae

¹ Respiration, of course, occurs in all organisms. In animals or many microbes, ingested or absorbed carbon compounds serve as the principal substrate that supplies energy needed for respiration (cf. Chap. 15 and 16).

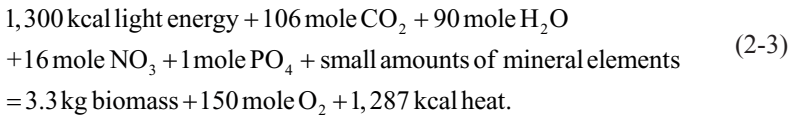
FIGURE 2-1. Frequency distribution of measurements of respiration by benthic microalgae, expressed as percent of gross production. Stippled data obtained by ^{14}C method, rest of data by oxygen method. Adapted from Foreman (1985).



(Fig. 2-1) and for phytoplankton (Gerard 1986). Only a small proportion of photosynthetically fixed carbon is therefore lost via dark respiration (Kelly 1989).

In C_3 plants, there is an additional light-dependent respiration activity—referred to as photorespiration—that consumes oxygen and produces carbon dioxide (Tolbert 1974; Harris 1980). Under high partial pressures of oxygen, the apparent rate of photosynthesis by plant cells declines. When the intracellular concentrations of O_2 are high, one of the enzymes responsible for CO_2 fixation in the C_3 dark reactions—ribulose-bisphosphate carboxylase—can also catalyze the oxidation of a Calvin cycle intermediate, initiating a series of reactions that produce CO_2 and glycine as end products. Hence, when the splitting of water during the light reaction furnishes oxygen, photorespiration takes place. The function of photorespiration is not known. It has also proven difficult to ascertain the degree to which these reactions occur, and there is much contradictory information on the relative rates of photorespiration and photosynthesis by marine algae and angiosperms (Banse 1980). Results showing that O_2 concentrations do not affect photosynthesis rate (Kelly 1989) suggest that photorespiration may be of modest importance in aquatic producers (Falkowski and Raven 2007).

The generalized equation for photosynthesis [Eq. (2-1)] is incomplete, because producers require a variety of inorganic nutrients to provide the building blocks for the synthesis of the many compounds present in cells. A more inclusive equation would be



The biomass yield of Eq. (2-3) would contain, on the average, 13 kcal of energy, 106 g C, 180 g H, 46 g O, 16 g N, 1 g P, and 825 g of mineral ash. These values are based on the average contents of phytoplankton cells (Odum 1971), but there is a considerable variation in these elemental ratios. Although more comprehensive than Eq. (2-1), Eq. (2-3) still gives a very simplified picture of biomass production by producers. For example, phytoplankton may use ammonium rather than nitrate to satisfy their nitrogen requirement, and in the case of diatoms, substantial amounts of silica are required for growth since this element is a major component of their cell wall.

Despite the intricacy of photosynthetic processes, the efficiency in capture of light energy is low. Variable but rather low percentages (1.5–2.4%) of incident light energy are converted into energy stored in cells (Kelly 1989). Light-use efficiency by phytoplankton, while usually low, varies under different conditions in the water column, and may be affected to some degree by differences in irradiance, temperature, or nutrient supply (Babin et al. 1996; Falkowski and Raven 2007).

2.2 Chemosynthesis

Box 2-1. A serendipitous revolution in ocean sciences

Long ago, the Russian soil microbiologist Sergei Vinogradskii (1856–1953) found that certain microorganisms could live by use of inorganic compounds of sulfur, iron, and nitrogen. This novel process, known as chemosynthesis, remained as an arcane technical detail, mainly of interest to soil researchers, until the 1970s. Then, in 1977, the hydrothermal deep-sea vents in the Galapagos Rift were discovered, and most ocean sciences underwent a radical jolt. Ideas about plate tectonics, deep-sea geology and hydrodynamics, biogeochemical cycles, and biology were about to be revised.

The discovery was a completely unforeseen result of an expedition, made possible by use of the deep-diving submarine *Alvin*², to search for springs of hot water at plate boundaries known as mid-ocean

² Narratives of the *Alvin* discoveries in the Galapagos Ridge can be found in Ballard (1977), Luiggi (1977), and Crane and Keener-Chavis (<http://oceanexplorer.noaa.gov>), and a review of the field in Van Dover (2000). In 2012, Time magazine included the Galapagos Rift as one of the most influential places in history (T. Onstott 23 April 2012).

ridges, which were expected by physical scientists to balance the oceans' heat budget. On that dive, guided by previous evidence of a buoyant plume of water with higher temperatures, and following a trail of large dead clam shells, *Alvin* came upon springs through which shimmering, extremely hot water was actively flowing, the first deep-sea hydrothermal vent seen by humans. Even more surprising, the hydrothermal vents were surrounded by dense populations of animals never before seen (Fig. 2-2). This was a surprise because the usual notion had been that, by being so distant from the surface waters where production took place, the abyssal regions of the oceans had to be deserts, largely devoid of life. How was it possible for the exceedingly abundant fauna seen around the hydrothermal vents to survive in these environments?

Concerted study revealed that many of the vent species, particularly the mouthless giant tube worms, took up sulfides emerging from vents in hemoglobin and transferred the sulfide to their gut, where large populations of symbiotic bacteria use energy in these reduced sulfur compounds to convert carbon dioxide to organic matter:



The bacteria manufactured carbohydrates and other organic compounds, which in turn were taken up by the worms (and other species) as food. The bacterial conversion of a 1-carbon compound to a multiple-carbon carbohydrate is an example of chemosynthesis, the process that Vinogradskii had described all those years ago. Subsequent work showed that methane could also be fixed into organic compounds by chemosynthetic bacteria (Fisher 1990; Stewart et al. 2005).

The result of much work (Jannasch and Wirsén 1979; Karl et al. 1980; Cavanaugh 1983; Cavanaugh 1994; Lee et al. 1999) therefore answered the question: the high chemosynthetic bacterial production near the vents served as the food base for the complex community of deep-sea vent organisms (Lonsdale 1977). The newly found hydrothermal vent consumer species supported their metabolism by symbiotic relationships and/or by direct ingestion of the chemosynthetic bacteria.

Study of the hot water flowing from the vents revealed that there were significant fluxes and deposits of valuable minerals surrounding the vents. These additional discoveries added economic and political dimensions, as nations began to be interested in vents within territorial waters (Fig. 2-3), because these are likely sites to find deposits of mineral resources to mine, an activity that might conflict with interests in conservation of rift regions (Van Dover 2011).



FIGURE 2-2. Top left and middle: Images of the research submarine *Alvin* being deployed from its mother ship, research vessel *Atlantis*, on its way to a deep dive to a rift zone. Top right: “smoker” vents, showing active release of materials from deep-sea rift sediments. Bottom left: Pogonophoran worms (left bottom), *Riftia pachyptila*, whose tubes can reach up to 1.6 m in length, and that represented a previously unknown family. Bottom right: a field of large clams (up to 30 cm in length), *Calyptogena magnifica*, which were a new genus of bivalves. Images courtesy of Daniel Fornari and the Woods Hole Oceanographic Institution.

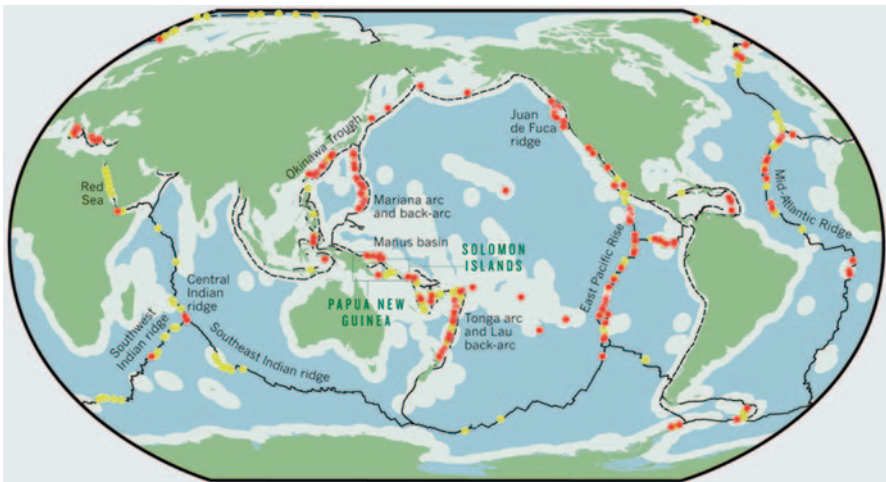
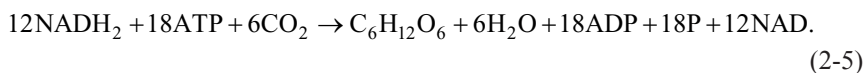


FIGURE 2-3. Global distribution of hydrothermal vent fields. The blue areas are international waters, national economic zones are shown as grey areas. Active vents are shown in red, some unconfirmed vent areas are in yellow. Ridge environments are shown as whole black lines, subsiding trenches as dashed black lines. Adapted from van Dover (2011), based on mapping by S. Beaulieu, K. Joyce, and A. Soule, all of the Woods Hole Oceanographic Institution.

Chemosynthesis is carried out by bacteria whose metabolism allows obtaining energy from simple inorganic compounds (Table 2-1). The biochemical pathways of different kinds of chemosynthetic bacteria are very diverse (Fenchel and Blackburn 1979; Parsons et al. 1977). The basic reaction of chemosynthesis is



where H_2A represents a relatively reduced inorganic compound. Dehydrogenase converts this reduced compound to the oxidized end product, AO , and the reducing power gained is represented as $[\text{H}^+ + e^-]$. Some of the reducing power gained through Eq. (2-4) is devoted to energy production, such as synthesis of ATP via transfer through the cytochrome system to O_2 . Most chemosynthetic bacteria thus require free oxygen to function as the electron acceptor. Obligate anaerobic or facultative bacteria can use oxygen bound in nitrate or sulfate for this purpose. The rest of the reducing power obtained through Eq. (2-4) may be used to reduce NAD to NADH_2 . The ATP and NADH_2 can then be used to assimilate CO_2 and make organic matter:



Chemosynthetic bacteria thus obtain both energy and reducing power from inorganic compounds (Table 2-1). Since the inorganic compounds that function as electron donors are not themselves assimilated by the bacteria, these reactions have been called dissimilative reactions, in contrast to assimilative reactions whose purpose is the uptake of elements or compounds.

Photosynthetic processes have usually been given the spotlight in texts about ecology. This is justified in view of the extent to which photosynthesis today produces organic matter and determines many of the dynamics of contemporary food webs. This book, however, might have been organized differently, giving precedence to bacterial chemosynthesis. This latter approach would be justified because of the pervasive biogeochemical influence of chemosynthesis, as will be seen in Chaps. 15 and 16, and from evolutionary and biogeochemical standpoints. Chemosynthetic transformations took place very early in the history of the earth, when the atmosphere was devoid of oxygen. Photosynthesis taking place today may, in fact, be thought of as a more recent process, derived from the emergence of organisms that had access to light to provide large amounts of energy needed to reduce CO_2 , and have, much belatedly, had supplies of O_2 to take up electrons to complete the process of fixing CO_2 and energy.

2.3 Measurement of producer biomass and primary production³

Box 2-2. Some terms used in discussion of the rates at which organic matter is synthesized and metabolized by primary producers

Photosynthesis can be thought of as the conversion of light energy into energy that can be stored or be metabolizable by organisms. The process fixes CO_2 and releases O_2 .

Gross production (P_g) is used in the production literature as synonymous to photosynthesis.

Net production (P_n) is the difference between P_g and the amount of fixed energy used in respiration (R).

Respiration in photosynthetic organisms is the sum of dark and light respiration ($R = R_d + R_l$). Both light and dark respiration consume O_2 and release CO_2 .

Light respiration (R_l), also referred to as *photorespiration*, occurs when light is available, and impropitious complexities of C3 photosynthesis consume O_2 rather than produce CO_2 . In aquatic plants and algae, R_l is usually low as compared with R_d .

Dark respiration (R_d) uses fixed energy to sustain metabolic needs, and takes place whether light is available or not.

In discussion of these rates for populations of producers under field conditions, a set of related terms has been used:

Gross primary production (GPP) is the magnitude of photosynthesis by producers, not considering any respiration by the producers or by other organisms present.

Net primary production (NPP) is GPP corrected for respiration (R_l) by the producers themselves.

Net ecosystem production (NEP) is GPP corrected to account for respiration by the entire community of producers and other organisms that may be present (CR).

All these rates are usually expressed in terms of oxygen and carbon, but can be also measured in terms of nitrogen. More detailed descriptions of these processes can be found in Falkowski and Raven (2007) and Vernet and Smith (2007).

³ The literature uses "production" and "productivity" often indiscriminately (Lipkin et al. 1986). Both refer to a measure of accumulation of organic matter across a certain period of time. A distinction that could be made is that "production" might best describe a yield or accumulation that takes place during a period (g C after a day, month, year, etc.); productivity has the sense of a rate of production per unit time, say, g C hour⁻¹.

2.3.1 *Phytoplankton*

2.3.1.1 Measurement of producer biomass⁴

Measurements of producer biomass in water samples—As made apparent by some of the figures in Chap. 1, the most frequently used method to estimate the standing crop of phytoplankton is to extract and measure the amount of chlorophyll *a* in seawater samples (Strickland and Parsons 1968; Holm-Hansen and Rieman 1978). The chlorophyll concentration can be used directly or, if desired, the algal standing crop can be obtained using a calculated ratio between weights of biomass and chlorophyll. For phytoplankton, the ratio of biomass to chlorophyll weights averages about 62 and the extremes span a wide range (22–154), so the conversion of chlorophyll to biomass should be used with some concern (Falkowski and Raven 2007). For benthic microalgae, the ratio of carbon to chlorophyll averages 42, with bounds of 22 and 79 (Foreman 1985). The species composition of the sample, extent and variability of light adaptation, age, and nutritional state of the cells all affect these ratios.

Content of ATP of phytoplankton has also been used to estimate standing crop (Holm-Hansen and Booth 1966). The ATP values are extrapolated to total carbon by multiplying a derived factor of 250, although the ATP content of cells is variable due to the influence of several environmental and growth factors (Holm-Hansen 1970; Banse 1977; Banse and Mosher 1980).

Hobbie et al. (1972) compared several methods of estimating microbial and algal biomass in seawater obtained from nutrient-poor and nutrient-rich stations in the Atlantic from the surface to a depth of 700 m. There were relatively high correlations among measurements of phytoplankton and organic carbon, volume of particulates, concentrations of ATP, DNA, and chlorophyll *a*. Comparisons among these correlated variables, however, are not straightforward, since, for example, not only algal but also fungal and bacterial biomass are included in the organic carbon, particulate volume, ATP, and DNA values. Organic carbon, particulate volume, and DNA may include nonliving materials. Knowledge of the ratio of algal abundance to that of other microbes or detritus would be needed to calculate phytoplankton biomass using these other variables. Hobbie et al. (1972) made an effort to obtain samples of water whose nutrient content ranged from rich to very poor. Their values of standing crops thus varied over a broad range, and they saw high correlations over that range. In any more local study, the

⁴ Here we emphasize biomass measurements, but estimations of cell numbers have been useful in advancing knowledge of the nature and role of phytoplankton. For example, data on cell numbers obtained by counts done by epifluorescence microscopy and flow cytometry led to the discovery of picoplankton, a topic that revolutionized our understanding of the phytoplankton (Waterbury et al. 1979, Chisholm et al. 1988). Flow cytometry, a procedure that allows fast counting (several thousand cells per minute) and sorting of cell types, has become the most widely used method for cell counts.

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