Photosynthesis

Sixth edition

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and

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Importance and role of photosynthesis

1.1 Ultimate energy source

Hardly a day goes by without the importance of photosynthesis being brought to our attention. All our food and our fossil and biological fuels (biomass) are derived from the process of photosynthesis, both past and present. Increasingly, the products of photosynthesis are being sought to feed and fuel the world and also to provide chemicals and fibres. How our changing environment will affect plants and their productivity has become a topic of great interest. Thus, an understanding of the fundamental and applied aspects of photosynthesis is now essential to a wide range of scientists and technologists – from agriculture and forestry through ecology and biology to chemistry, genetics and engineering. It is this universality that attracts varied approaches to studying photosynthesis and makes it such an exciting field of work to so many different types of people. We hope that this becomes evident in our book.

The term photosynthesis literally means building up or assembly by light. As used commonly, photosynthesis describes the process by which plants synthesize organic compounds from inorganic raw materials in the presence of sunlight. All forms of life in this universe require energy for growth and maintenance. Algae, higher plants and certain types of bacteria capture this energy directly from the solar radiation and utilize it for the synthesis of essential food materials. Animals cannot use sunlight directly as a source of energy; they obtain the energy by eating plants or by eating other animals that have eaten plants. Thus, the ultimate source of all metabolic energy in our planet is the sun, and photosynthesis is essential for maintaining all forms of life on earth.

We use coal, natural gas, petroleum, etc. as fuels. All these fuels are decomposition products of land and marine plants or animals, and the energy stored in these materials was captured from the solar radiation millions of years ago. Solar radiation is also responsible for the formation of wind and rain, and hence the energy from windmills and hydroelectric power stations could also be traced back to the sun.

The major chemical pathway in photosynthesis is the conversion of carbon dioxide and water to carbohydrates and oxygen. The reaction can be respresented by the equation:

$$CO_2 + H_2O \xrightarrow[\text{plants}]{\text{sunlight}} \underset{\text{carbohydrate}}{[CH_2O]} + O_2$$

The carbohydrates formed possess more energy than the starting materials, namely CO_2 and H_2O. By the input of the sun's energy, the energy-poor compounds, CO_2 and H_2O, are converted to the energy-rich compounds, carbohydrates and O_2. The energy levels of the various reactions that lead up to the overall equation above can be expressed on an oxidation–reduction scale ('redox potential' given in volts), which tells us the energy available in any given reaction – this is discussed in Chapter 4. Photosynthesis can thus be regarded as a process of converting radiant energy of the sun into chemical energy of plant tissues.

1.2 The carbon dioxide cycle

The CO_2 content of the atmosphere remained almost constant for millenia in spite of its depletion during photosynthesis. However, there has been a 27% increase since the Industrial Revolution in the last century, resulting in the so-called greenhouse effect. All plants and animals carry out the process of respiration (in mitochondria) whereby O_2 is taken from the atmosphere by living tissue to convert carbohydrates and other tissue constituents eventually to CO_2 and H_2O with the simultaneous liberation of energy. The energy is stored in adenosine triphosphate (ATP) and is utilized for the normal functions of the organism. Respiration thus causes a decrease in the organic matter and O_2 content and an increase in the CO_2 content of the planet. Respiration by living organisms and combustion of carbonaceous fuels consume on average about 10000 tonnes of O_2 every second on the surface of the earth. At this rate, all the O_2 of the atmosphere would have been used up in about 3000 years. Fortunately for us, the loss of organic matter and atmospheric O_2 during respiration is counterbalanced by the production of carbohydrates and

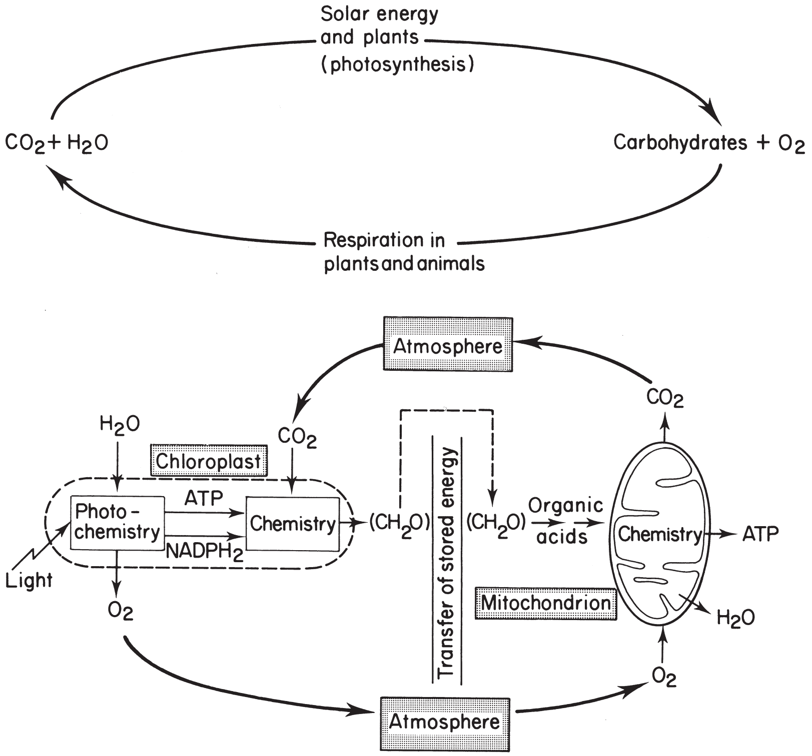

Fig. 1.1 The CO_2 and O_2 cycle in the atmosphere and the cell.

O_2 during photosynthesis. Under ideal conditions, the rate of photosynethesis in the green parts of plants is about 30 times as much as the rate of respiration in the same tissues. Thus, photosynthesis is very important in regulating the O_2 and CO_2 content of the earth's atmosphere. The cycle of operations can be represented as shown in Fig. 1.1. Current estimates suggest a mean residence time of 12.5 years for a CO_2 molecule in the atmosphere before it is captured via photosynthesis by land plants; the residence time decreases to five years for the total flux of CO_2 from the atmosphere (the sum of land and ocean uptake). The recycling time of O_2 is approximately 4000 years.

It should be made clear that the energy liberated during respiration is finally dissipated from the living organism as heat and is not available for recycling. Thus, for millions of years, energy has been constantly removed from the sun and wasted as heat in the earth's atmosphere. But fortunately there is still enough energy available from the sun for photosynthesis to continue for many hundreds of millions of years.

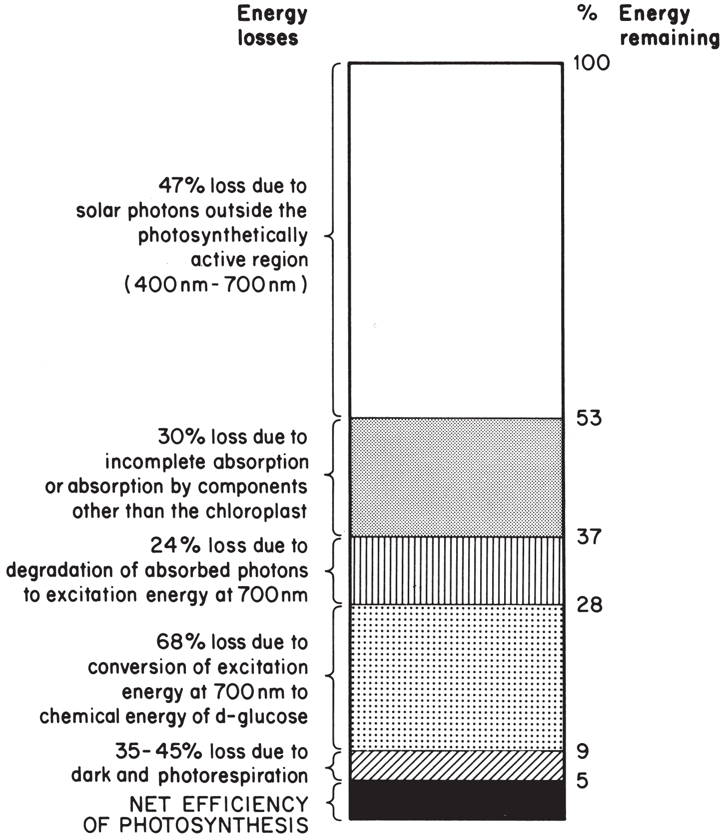

Fig. 1.2 Summary of the energy losses in photosynthesis as sunlight falls on a leaf at 25 °C.

1.3 Efficiency and turnover

Photosynthetic efficiency on a global basis may be defined as the fraction of photosynthetically active radiation (PAR) that falls on the earth's surface which is converted to *stored* energy by photosynthesis in the biosphere.

The solar energy striking the earth's atmosphere every year is equivalent to about 56×10^{23} joules (J) of heat. Of this, roughly half is reflected back by the clouds and by the gases in the upper atmosphere. Of the remaining radiation that reaches the earth's surface, only 50% is in the spectral region of light that could bring about photosynthesis, the other half being weak infra-red radiation (Fig. 1.2). Thus, the annual influx of energy of photosynthetically active radiation, i.e. from violet to red light, to the earth's surface is equivalent to about 15×10^{23} J. However, some 40% of this is reflected by ocean surface, deserts, etc. and only the rest can be absorbed by the plant life on land and sea. Recent estimates of the total annual amount of biomass (plant matter) produced by photosynthesis are about 2×10^{11} tonnes of organic matter, which is equivalent to about 4×10^{21} J of energy. Thus, the average coefficient of utilization of the incident photosynthetically active radiation by the entire flora of the earth is only about 0.27% ($4 \times 10^{21}/15 \times 10^{23}$). The annual food intake by the human population (approximately 5800 million at present) is about 1000 million tonnes, or 16×10^{18} J, which is only 0.4% ($16 \times 10^{18}/4 \times 10^{21}$) of the annual biomass produced. It is interesting that the total consumption of energy by the world, including biomass in 1991 was about 3.9×10^{20} J – this was only a tenth of the energy stored by photosynthesis! In fact, the energy content of the biomass standing on the earth's surface today (80% trees) is equivalent to about two-thirds of our proven reserves of fossil fuel (36×10^{21} J), i.e. oil, gas and coal. The total resources of fossil fuel stored under the earth's surface (260×10^{21} J) represent only 60 years of net photosynthesis.

1.4 Spectra

Light is a form of electromagnetic radiation. All electromagnetic radiation has wave characteristics and travels at the same speed of 3×10^8 ms^{-1} (c, the speed of light). But the radiations differ in wavelength, the distance between two successive peaks of the wave. Gamma rays and X-rays have very small wavelengths (less than one thousand millionth of a centimetre, 10^{-11} m), while radio waves are in the order of 10^4 cm. Wavelengths of visible light are conveniently expressed by a unit called a nanometre. One nanometre is one thousand millionth of a metre ($1\,\text{nm} = 10^{-9}$ m). It has been known since the time of Isaac Newton that white light can be separated into a spectrum, resembling the rainbow, by passing light through a prism. The visible portion of this spectrum ranges from the violet at about 380 nm to the far red at 750 nm (Fig. 1.3).

The atmosphere of the sun consists mainly of hydrogen. The energy of the sun is derived from the fusion of four hydrogen nuclei to form a helium nucleus. The fusion process is a multistep reaction that can be simplified as $4\text{H} \rightarrow \text{He} + h\nu$ (energy). The mass of the He nucleus is less than the total mass of 4H; the mass lost during fusion is converted to energy and emitted as photons or quanta. It has been estimated that 4.3×10^{12} g of H per second are transformed to He in the cosmos; the mass difference is radiated as photons,

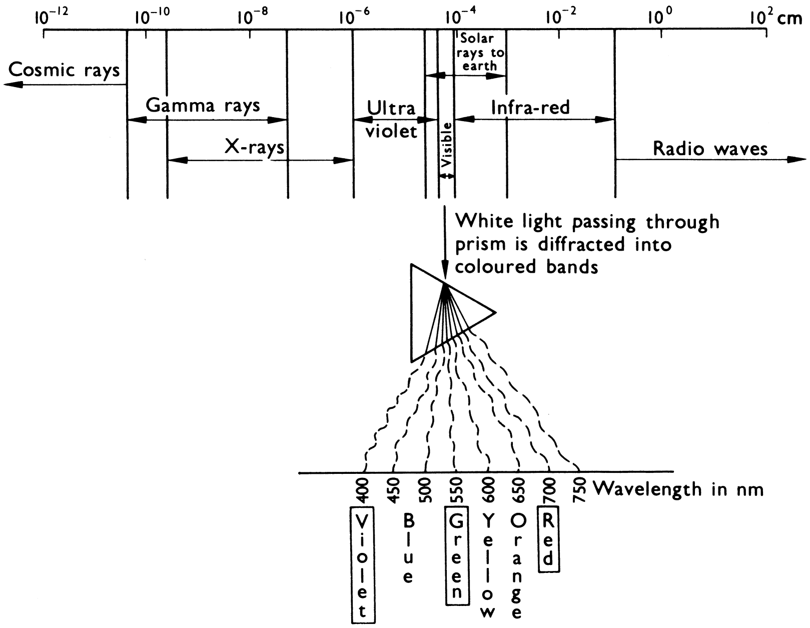

Fig. 1.3 Spectra of electromagnetic radiation and diffraction pattern of visible light.

which reach the earth with an energy of 1353 kwm^{-2}, in the 290–4000 nm spectral region. The energy liberated during the nuclear fusion maintains the surface temperature of the sun at around 6000 K. The sun radiates energy representing the entire electromagnetic spectrum, but the earth's atmosphere is transparent only to part of the infra-red and ultraviolet light and all the visible light. The ultraviolet waves, which are somewhat shorter than the shortest visible light waves, are absorbed by the O_2 and ozone of the upper atmosphere. This is fortunate because ultraviolet radiations are harmful to living organisms. At 6000 K, the temperature of the sun, the maximum intensity of emitted light lies in the orange part of the visible spectrum, around 600 nm.

1.5 Quantum theory

In 1900, Max Planck (Germany) enunciated the theory that the transfer of radiation energy within a hot object occurred in discrete 'units' of energy called quanta. Planck's quantum theory can be expressed mathematically as $E = hv$, where E is the energy of a single quantum of radiation, v is the frequency of the radiation (frequency is the number of waves transmitted per unit time), and *h* a constant. The Planck's constant (*h*) has the dimensions of the product of energy and time and its value is 6.626×10^{-34} J s (joules per second). Planck's theory proposes that an oscillator of fundamental frequency (*v*) would take up energy *hv*, 2*hv*, 3*hv*→*nhv*, but it could not acquire less than a whole number of energy quanta. Five years later, Albert Einstein extended Planck's theory to light and proposed that light energy is transmitted not in a continuous stream but only in individual units or quanta. The energy of a single quantum of light, or *photon* (luxon before 1916), is the product of the frequency of light and Planck's constant, i.e. $E = hv$. Because frequency is inversely related to wavelength, it follows that photons of short-wave light are more energetic than photons of light of longer wavelength, i.e. photons of blue light (400 nm) at one end of the visible spectrum are more energetic than those of red light (700 nm) at the other end.

For photosynthesis to take place, the pigments present in the photosynthesizers should absorb the energy of a photon at a characteristic wavelength and then utilize this energy to initiate a chain of photochemical and chemical events. We will learn later than an electron is transferred from the reaction centre pigment immediately after the absorption of a suitable quantum of light. It should be emphasized that a single photon cannot transfer its energy to two or more electrons, nor can the energy of two or more photons combine to transfer an electron. Thus, the photon should possess a critical energy to excite a single electron from the pigment molecule and initiate photosynthesis. This accounts for the low efficiency of infra-red radiation in plant photosynthesis because there is insufficient energy in the quantum of infra-red light. Certain bacteria, however, contain pigments that absorb infra-red radiation and carry out a type of photosynthesis that is quite different from plant-type photosynthesis in that no O_2 is evolved during the process (see Chapter 7).

1.6 Energy units

According to Einstein's law of photochemical equivalence, a single molecule will react only after it has absorbed the energy of one photon (*hv*). Thus, 1 mole (gram-molecule) of a compound must absorb the energy of N photons ($N = 6.023 \times 10^{23}$, the Avogadro number), i.e. N*hv*, to start a reaction. The total energy of photons absorbed by 1 mole of a compound is called an *Einstein*, i.e. one Einstein $= 6.023 \times 10^{23}$ quanta. One Einstein (*E*) of light quanta is also referred to as one *mol* quanta.

Let us calculate the energy of a mol (or Einstein) of red light of wavelength 650 nm (6.5×10^{-7} m). The frequency, $v = c/\lambda$ = speed of light/wavelength of light. The speed of light is 3×10^{8} m s^{-1}.

Table 1.1. *Energy levels of visible light*

Wavelength (nm)	Colour	Energy		
		J/mol	kcal/mol	eV/photon
700	Red	17.10×10^4	40.87	1.77
650	Orange-red	18.40×10^4	43.98	1.91
600	Yellow	19.95×10^4	47.68	2.07
500	Blue	23.95×10^4	57.24	2.48
400	Violet	29.93×10^4	71.53	3.10

$v = 3.0 \times 10^8 / 6.5 \times 10^{-7} = 4.61 \times 10^{14}$
$E = \mathrm{N}hv$

i.e. energy = number of molecules × Planck's constant × frequency

$\therefore\ E = 6.023 \times 10^{23} \times 6.626 \times 10^{-34} \times 4.61 \times 10^{14} = 18.40 \times 10^4\ \mathrm{J}$
= energy of one Einstein (or mol) of red light
or $E = 18.40 \times 10^4 / 4.184 \times 10^3 = 43.98$ kcal.

(One kilocalorie, kcal, is equal to 4.184×10^3 J.) Thus, 1 mol of red light at 650 nm contains 18.40×10^4 J of energy.

The energy of photons can also be expressed in terms of electron volts. An electron volt, eV, is the energy acquired by an electron when it falls through a potential of 1 volt, which is equal to 1.6×10^{-19} J. If 1 molecule of a substance acquires an average energy of 1 eV, the total energy of a mole can be calculated to be 9.64×10^4 J ($1.6 \times 10^{-19} \times 6.023 \times 10^{23}$). Thus, the energy of 1 photon of 650 nm light (Table 1.1) is equal to 1.91 eV ($18.40 \times 10^4 / 9.64 \times 10^4$).

1.7 Measurement of photosynthetic irradiance

Historically, light intensity was measured in terms of *lumens* (lm), a lumen being defined as the luminous flux on a unit surface, all points of which are at unit distance from a uniform point source of one candle. Intensity of illumination (illuminance) was expressed either as foot candles (lm ft^{-2}) or *lux* (lm m^{-2}).

Nowadays, photobiologists prefer to measure light energy incident on a surface, i.e. radiant flux density or *irradiance*, in terms of the units of power as watts per sq metre (W m^{-2}). Because photochemical reactions in photosyn-

Table 1.2. *Terminology for radiation data*

Term	Unit	Definition
Radiant energy	J	Energy in the form of electromagnetic radiation
Radiant flux	$W = J s^{-1}$	Radiant energy emitted or absorbed by a surface per unit time
Radiant flux density	$W m^{-2}$	Radiant flux (of a specific wavelength region) incident on a small sphere divided by the cross-sectional area of the sphere
Irradiance	$W m^{-2}$	Radiant flux incident on a unit area of plane surface per unit time
Fluence	$mol m^{-2}$	Number of photons incident across a unit area of plane surface
Photon flux density (PFD)	$mol m^{-2} s^{-1}$	Photon flux per unit area
Photosynthetically active radiation (PAR)		Solar radiation in the 400 to 700 nm waveband
Photosynthetic photon flux density (PPFD)	$mol m^{-2} s^{-1}$	Flux of 400 to 700 nm solar radiation

thesis depend more on the *number* of photons incident on a surface rather than on the energy content of these photons, it is more logical to express photosynthetic irradiance in terms of the number of quanta (photons) falling on unit surface in unit time, i.e. as the *photon flux density*. The photon (or quantum) flux density (*Q*) in a particular wavelength region is measured in units of $mol\ m^{-2}\ s^{-1}$ where a mol is 6.023×10^{23} (Avogadro's number) quanta or photons. Because an Einstein (E) is defined as 6.023×10^{23} quanta, *Q* can also be expressed as $E m^{-2} s^{-1}$. A more practical unit to express photosynthetic photon flux density (PPFD) is $\mu mol\, m^{-2}\ s^{-1}$ or $\mu E\, m^{-2}\ s^{-1}$. For example, the solar irradiance reaching the earth's surface at ground level in full sunlight is approximately 1000 $W m^{-2}$ or about 100 000 lux, in which the PPFD is 2000 $\mu mol\ m^{-2}\ s^{-1}$ There are no factors to convert radiation data directly between photometric, radiometric and quantum units. Approximate conversion factors are given on pp. 442 and 443 of Hall *et al.* (1993). Some of the terms used in plant physiology to express radiation are summarized in Table 1.2.