Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

1

General features of the plant kingdom

Characteristics of the living state

The living state is characterized by instability and change. The numerous chemical reactions, called collectively metabolism, within a living cell both consume (in the form of foodstuffs) and release energy. Metabolism is indicative of life. Even the apparently inert cells of seeds show some metabolism, but a mere fraction of that which occurs during germination and subsequent growth. Metabolism depends upon the interaction of molecules in an ordered sequence. If this order is destroyed (for example by poisons or heat) metabolism ceases and the cell dies. In some instances it is possible to arrest metabolism without death. With yeast and some tissue cultures, for example, this can be achieved by very rapid freezing at temperatures of −160 °C (−265 °F) or lower. The cells can then be preserved in liquid nitrogen (−195 °C; −319 °F), in an apparently genuine state of "suspended animation", indefinitely. With yeast up to 95 percent of cells of rapidly frozen cultures resume metabolism and growth following careful thawing.

The sources of energy a cell requires to maintain its dynamic state are predominantly compounds of carbon. In addition a cell requires water, since much of the metabolism takes place in the aqueous phase in the cell. Also essential are those materials necessary for the maintenance of its structure which it is unable to make for itself. Prominent amongst these are the nitrogen of the proteins, the commoner minerals (including phosphorus), and certain other metals and elements which, although needed only in traces, are essential components of a number of enzymes and associated molecules. Occasionally, in isolated cultures of cells, complex organic molecules called vitamins or growth factors must also be supplied from outside.

Autotrophic and heterotrophic nutrition

It is useful to divide organisms into two classes according to the manner in which their needs for organic carbon are met. Those able to utilize simple molecules with single carbon atoms are termed *autotrophs*; those requiring more complex carbon compounds rich in energy (such as sugars) are termed *heterotrophs*. Some organisms are able to switch between these alternative forms of nutrition, depending upon the environment in which they find themselves. These are called *mixotrophs*.

The assimilation of simple carbon compounds by autotrophs, and their transformation into more complex molecules, require an external source of energy. This may be chemical or physical, depending upon the organism. Very many autotrophs (including the whole of the plant kingdom) utilize the energy of light, and are consequently known as photoautotrophs (or simply as *phototrophs*) and the process of assimilation as *photosynthesis*. Only the phototrophs have acquired extensive morphological diversity. Autotrophs utilizing energy from chemical sources (*chemotrophs*)

Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

for the assimilation of carbon are found solely amongst the bacteria.

Phototrophic life is made possible by two unique biological molecules, chlorophyll and bacteriochlorophyll. The chemical differences between them are not profound, but their absorption spectra are distinct, as is their distribution amongst the phototrophs. Bacteriochlorophyll is found only in bacteria and functions mostly anaerobically. Photosynthetic systems based upon bacteriochlorophyll are unable to use water as an electron donor, and consequently there is no evolution of oxygen (***anoxygenic photosynthesis***). Those organisms which contain chlorophyll and which photosynthesize aerobically with the evolution of oxygen constitute the plant kingdom. So defined the plant kingdom is distinct from all other organisms (including the fungi).

Chlorophyll is a complex pigment. It is green in colour, and absorbs light in the blue and to a smaller extent in the red region of the spectrum. The molecule is in part similar to the active group of the blood pigment hemoglobin, but contains at its center magnesium in place of iron. A number of different forms are known (*a*, *b*, *c*, *d* and perhaps *e*), each with its characteristic absorption spectrum. Chlorophyll *a*, which is present in all plants, has the remarkable property of temporarily losing electrons when illuminated. Chlorophyll *b*, which is found in all land plants, assists in the light-harvesting process, but the functions of chlorophylls *c*, *d* and *e* (p. 77), present in some algae, are not so well known. Chlorophyll is always accompanied by accessory pigments (either carotenoids or phycobilins (biliproteins), or in a few organisms both). The light energy absorbed by these additional pigments can be transferred to the chlorophyll.

As a result of the remarkable photochemical properties of chlorophyll *a* the energy of the incident light is transformed into chemical energy. This leads to the generation in the cell of ATP, and reducing power in the form of $NADPH + H^+$ (the light reactions). These two products then bring about the reductive assimilation of atmospheric carbon dioxide in the illuminated cells, the assimilation being initiated by the enzyme ribulose bisphosphate carboxylase (RUBISCO), leading to the production of carbohydrates (the dark reactions). The ability to utilize atmospheric carbon dioxide in this photosynthetic manner releases the organisms concerned from the necessity of an external source of carbohydrate, and their nutritional demands are consequently relatively simple.

Oxygenic photosynthesis, the defining characteristic of the plant kingdom, involves two photosystems. The first (photosystem I) leads to the formation of $NADPH + H^+$, and the second (photosystem II) provides a supply of electrons to the chlorophyll of photosystem I. Photosystem II involves the photolysis of water with the production of oxygen. The evolution of oxygenic photosynthesis probably occurred in marine photosynthetic bacteria inhabiting waters close to oceanic thermal vents. At these sites there is a rich supply of minerals, including manganese, a component of the enzyme in photosystem II responsible for the splitting of the water molecule and the release of oxygen. Photosystem II may have appeared only once, or (in geological time) more or less coincidentally at several sites. In any event it was an innovation of immense significance since it made possible the evolution of all subsequent oxygen-requiring organisms, both plant and animal. It is legitimate, therefore, to regard the simplest organisms showing this form of photosynthesis, based upon chlorophyll *a* (as distinct from bacteriochlorophyll), as the earliest plants, opening up a whole new vista of evolution. These early plants, whose living descendants are to be found in the Cyanophyta (p. 24), and Prochlorophyta (p. 38), naturally retained some of the features of their bacterial origins. Nevertheless, freed from the constraints of bacterial photosynthesis, the earliest plants had an evolutionary potential denied to their retarded cousins.

Structure of the phototrophic cell

Chlorophyll does not occur freely in cells, but is always associated with lipoprotein membranes. These membranes surround flattened sacs called ***thylakoids***. When the membranes are seen in surface view in the electron microscope (made possible by the special technique of freeze-frac-

Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

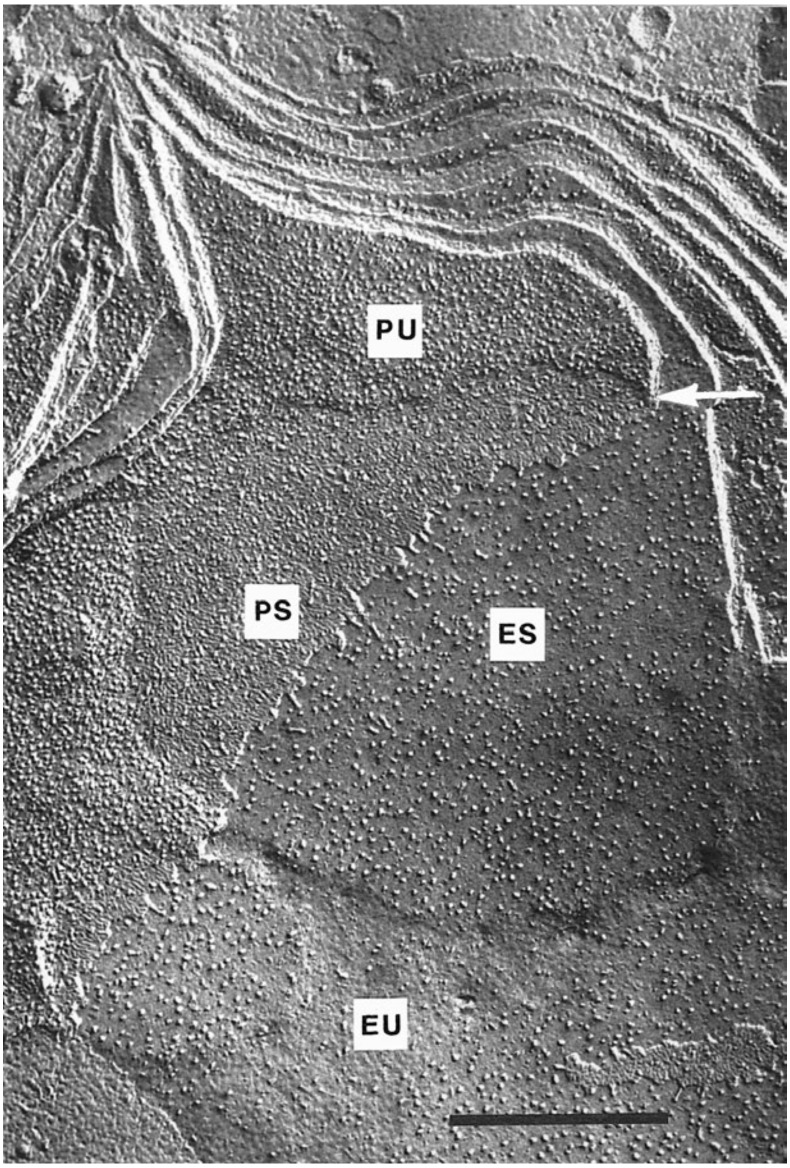

Figure 1.1 Shadowed replica of the thylakoid membranes of the chloroplast of *Euglena* exposed by freeze-fracture. The thylakoids are either single ("unstacked") or paired ("stacked"). Because in the conditions of freeze-fracture membranes are pulled apart, two complementary faces (E and P) are represented in the replica. This reveals that the particles are asymmetrically placed in the membrane (cf. Fig. 1.2). There are also differences in the frequencies of particles in stacked (S) and unstacked (U) membranes. The arrow indicates where the membranes of two adjacent thylakoids come together to form a stack. Scale bar 0.5 μm. (From Miller and Staehelin. 1973. Reproduced from *Protoplasma* 77, by permission of Springer-Verlag, Vienna.)

ture), it is clear that they bear closely packed particles (Fig. 1.1). The larger of these, about 18 nm ($1\,\mathrm{nm} = 10^{-3}\,\mu\mathrm{m}$) in diameter, are probably the site of the chlorophyll and carotenoids (which, like chlorophyll, are lipid soluble). The anchoring of the chlorophyll and carotenoids in a lipoprotein membrane ensures that they are held in a particular order (Fig. 1.2). Electrons can then flow along well-defined paths to the reaction center at which the radiant energy is converted into chemical energy. The thylakoid membrane is thus the site of the light reactions of photosynthesis, and forms the basis of plant life. In turn the animal kingdom is entirely dependent upon the activity of this membrane, not only for its sustenance, but also for the oxygen of its respiration.

Two distinct kinds of cellular organization are found amongst the phototrophs as a whole. In the first, termed ***prokaryotic***, the cell possesses no distinct nucleus, although a region irregular in outline and of differing density occurs at the center of the cell. This is referred to as a nucleoid, and the genetic material lies therein. In the electron microscope this region appears fibrillar rather than granular, and the fibrils indicate the site of the deoxyribonucleic acid (DNA). The protoplast of such cells is bounded by a membrane. In phototrophic cells this membrane invaginates into the cytoplasm and forms the thylakoids. Their full development depends upon light. If the cells are grown in the dark the thylakoids disappear or become very reduced. This primordial kind of

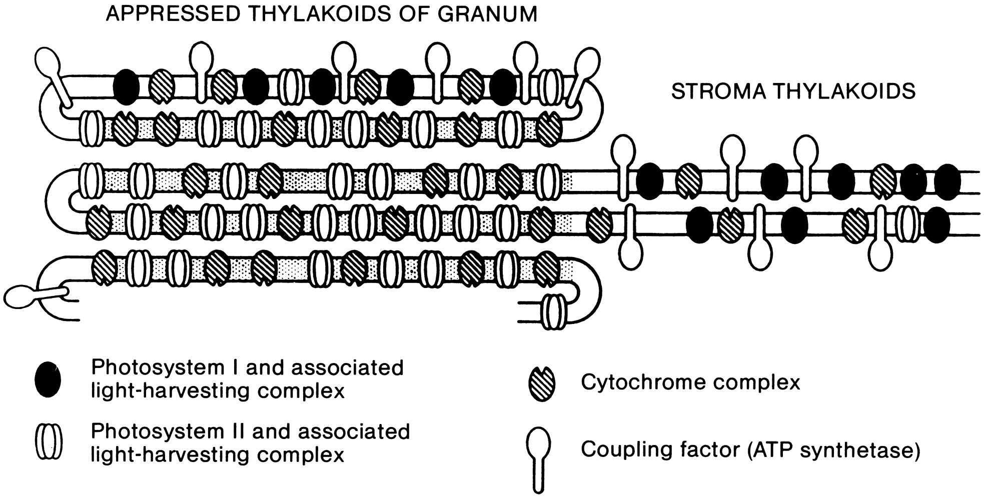

Figure 1.2 The molecular architecture of the thylakoid membrane of a higher plant. The photosystem I complexes are confined to the outer membranes of the grana and to the stroma thylakoids. The stippled regions indicate the appressed membranes of the granum. (From Anderson, Chow and Goodchild. 1988. *Australian Journal of Plant Physiology* 15, modified.)

phototrophic cell is found in both the photosynthetic bacteria and the simplest plants. The fossil record supports the view that the original phototrophs were of this prokaryotic kind. Geochemical evidence of photosynthesis, and remains very suggestive of bacteria and simple cyanophytes, some resembling the living *Oscillatoria* (p. 29), come from early Archaeozoic rocks of South Africa and Australia believed to be $3.3–3.5 \times 10^9$ years old (Table 1.1).

In the cells of all other phototrophic plants the nucleus, the photosynthetic apparatus, and the membranes incorporating the electron transport chain of respiration are separated from the remainder of the cytoplasm by distinct envelopes. Such cells, termed ***eukaryotic***, have evidently been capable of giving rise to much more complicated organisms than the prokaryotic ones. The photosynthetic apparatus, which consists of numerous lamellae running parallel to one another, is contained in one or more ***plastids***. The envelope of the plastid consists of two (in some algae three or four) unit membranes, the inner of which invaginates into the central space (***stroma***) and generates the thylakoids. The thylakoids in the fully differentiated plastid (***chloroplast***) are usually stacked. In the chloroplasts of land plants the thylakoids are also fenestrated. Consequently numerous small stacks, called ***grana***, are formed in place of a single stack, the grana being held together by stroma lamellae (Fig. 1.3). The grana appear in the light microscope as green dots, each about $0.5\,\mu\text{m}$ in diameter. Although most photosynthesis takes place in the grana, the thylakoids in the stroma also contribute.

Plastids contain both DNA and ribonucleic acid (RNA), and both transcription and translation may occur within them. Plastids thus have some resemblance to phototrophic prokaryotes, although most plastid proteins are encoded solely in the nuclear DNA. The enzyme RUBISCO, essential for photosynthesis and probably the commonest protein in the world, consists of a large and a small subunit. In the green algae (Chlorophyta, p. 39) and in all land plants, the large subunit is encoded in the plastid DNA and the smaller in that of the nucleus. Nevertheless, in some eukaryotic algae, namely the Rhodophyta (p. 30), the Cryptophyta (p. 96) and the whole of the heterokont algae (Table 2.1), both large and small subunits are coded for in the plastid genome. In the prokaryotic algae both subunits are coded for in the DNA of the nucleoid. The possibility exists that coding for one or both units of RUBISCO may also be present in the DNA of a plasmid (p. 8), but this has not been demonstrated.

In the commonest form of carbon assimilation, atmospheric carbon dioxide, having been

Table 1.1 The geological time scale. Age estimates of Proterozoic and Archaeozoic ± up to 100 million years.

Eon	Era	Period		Age (in 10^6 years)	First authentic appearance
Phanerozoic	Quaternary	Holocene and Pleistocene		0–1.6	
	Tertiary (Cenozoic)	Pliocene		1.6–5.2	
		Miocene		5.2–23.3	
		Oligocene		23.3–35.4	
		Eocene		35.4–56.5	Grasses
		Paleocene		56.5–65	
	Mesozoic	Cretaceous	Senonian	65–88.5	
			Gallic	88.5–131.8	Carpels, flowers, angiosperms
			Neocomian	131.8–145.6	
		Jurassic	Malm	145.6–157.1	Tectate pollen
			Dogger	157.1–178	
			Lias	178–208	
		Triassic		208–245	Cycadopsida, anthophytes,
	Paleozoic	Permian	Zechstein	245–256.1	Ginkgoopsida, Glossopterids
			Rotliegendes	256.1–290	
		Carboniferous	Pennsylvanian	290–322.8	Pinopsida, Bryopsida, Polypodiopsida
			Mississippian	322.8–362.5	
		Devonian	Upper	362.5–377.4	Seeds, fronds, pteridosperms, progymnosperms, early ferns, Cladoxylopsida, Equisetopsida, Trimerophytopsida, Marchantiopsida, heterospory,
			Middle	377.4–386	Zosterophyllopsida, Lycopodiopsida
			Lower	386–408.5	
		Silurian	Upper	408.5–424	Rhyniopsida, vascular plants, rhyniophytoids
			Lower	424–439	
		Ordovician		439–510	Triradiate spores
		Cambrian		510–570	Phaeophyta
Proterozoic	Sinian	Vendian		570–610	
		Sturtian		610–800	
	Riphean			800–1650	
	Animikean			1650–2200	Various algal groups
	Huronian			2200–2450	
Archaeozoic	Randian			2450–2800	
	Swazian			2800–3500	
	Isuan			3500–3800	Stromatolites and cyanophytes (Cyanobacteria)
	Hadean			3800–4560	

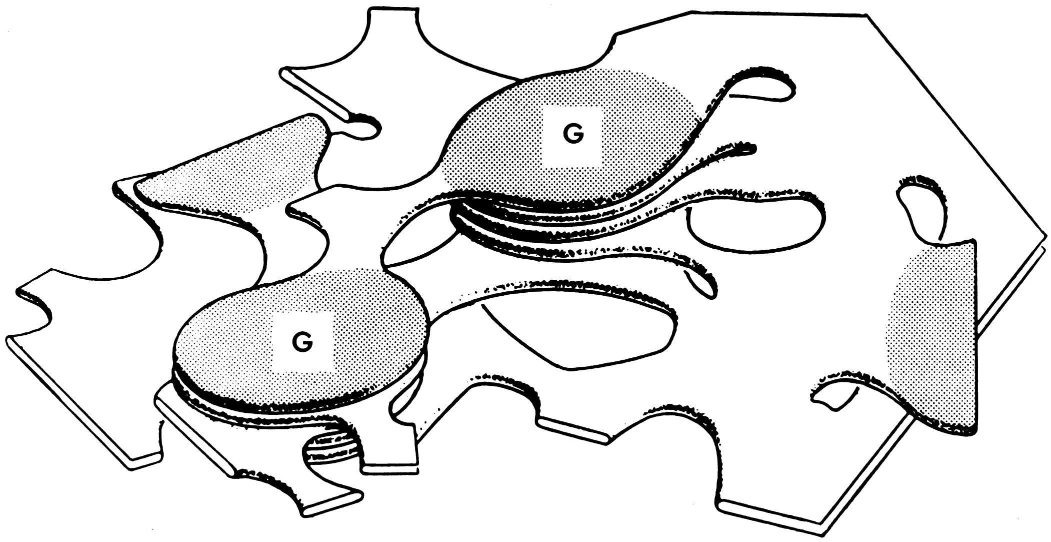

Figure 1.3 Diagram showing the arrangement of the thylakoids in the chloroplast of a higher plant. The stacked regions (grana, G) are visible as green dots in the light microscope. (From an original drawing by Wehrmeyer. 1964. *Planta* 63, modified.)

taken in the presence of RUBISCO into a pentose sugar (ribulose bisphosphate), yields two molecules of triose phosphate. These are reduced by the NADPH + H^+ and ATP, yielding two molecules of glycerin aldehyde. These then enter a complex cycle of reactions (the C3, or Calvin cycle) leading to fructose and other sugars. A mixture of fairly simple carbohydrates probably leaves the chloroplast, further transformations taking place enzymically in the ground cytoplasm. The disaccharide sucrose, for example, the commonest form in which sugar is transported in the plant, is incapable of traversing the chloroplast envelope and is necessarily formed outside. If the rate of photosynthesis exceeds the rate of outflow of fixed carbon, condensation occurs and starch is deposited in the chloroplast. This may become very conspicuous, the organelle then being termed an ***amyloplast***. In some land plants (known as C4 plants) atmospheric carbon dioxide is taken initially in the chloroplasts of the mesophyll cells into phosphoenolpyruvate (PEP), the enzyme involved in this case being PEP-carboxylase. This leads to the formation of oxaloacetic acid, which is then transformed enzymically into malate or aspartate. These products migrate to special chloroplasts in the bundle sheath cells, which are distinguished from those of the mesophyll by lacking grana, but they do contain RUBISCO. Here the malate and aspartate are reconverted into oxaloacetic acid. The carbon dioxide is thereby freed and, as in C3 plants, is assimilated into ribulose bisphosphate and enters directly into the Calvin cycle (Fig. 1.4). PEP-carboxylase has a higher affinity for carbon dioxide than RUBISCO, and can withstand higher temperatures. Further, the combined C4/C3 systems have less need of water in relation to the quantity of carbon assimilated. Consequently vegetation of hot and dry (including "physiologically dry") habitats, such as deserts and salt marshes, often contains a high proportion of C4 plants. A few plants are ambivalent. *Eleocharis vivipara* (a marsh plant), for example, is a C4 plant under terrestrial conditions but C3 when submerged.

The organelle in eukaryotic cells containing the respiratory membranes is termed a ***mitochondrion***. Although there are structural and organizational similarities between mitochondria and plastids, in most photosynthesizing cells the mitochondria have far less internal differentiation. So far as carbon is concerned, the functions of these two organelles are opposed: that of the chloroplast is ***reductive carboxylation***, that of the mitochondrion ***oxidative decarboxylation***. In certain conditions (notably with a low partial pressure of carbon dioxide) RUBISCO can act as an oxidase,

Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

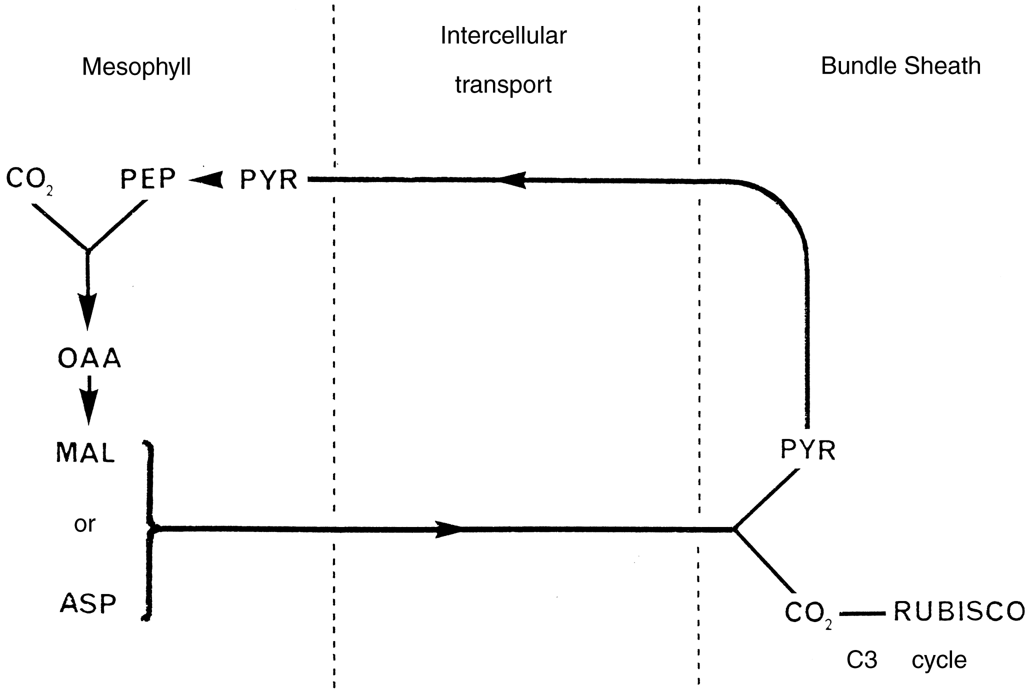

Figure 1.4 The essential features of C4 photosynthesis. PEP, phosphoenolpyruvate; OAA, oxaloacetic acid; MAL, malate; ASP, aspartate (aspartic acid is the amino acid corresponding to malic acid); PYR, pyruvate. There are biochemical variations between species, but the general pattern is retained.

resulting in a loss of fixed carbon (photorespiration). This may have had a significant ecological effect at certain periods of the evolution of land plants in geological time.

Origin of the eukaryotic condition

Although it seems beyond doubt that the prokaryotic condition preceded the eukaryotic (the first eukaryotic algae probably appeared about 2.1×10^9 years ago), the manner in which the transition occurred is by no means clear. A commonly accepted, and little criticized, view (originally put forward in 1905) is that mitochondria and plastids are derived from prokaryotes which entered as endosymbionts into a primordial cell, itself prokaryotic and presumably heterotrophic. The presence in the cytoplasmic organelles of a nucleoid, their possession of transcription and translation systems closely resembling those found in bacteria, and the similarity in size between the ribosomes of organelles and those of bacteria (the ribosomes of eukaryotic ground cytoplasm tend to be larger) provide strong evidence in support of this theory. Further, organisms which appear to have arisen by endosymbiosis are well known. In *Glaucocystis* (Fig. 2.9) and *Cyanophora*, unicellular organisms found occasionally in shallow fresh water, for example, the photosynthetic component of the cell is made up of one or more units resembling blue-green algal cells. These have accordingly been termed "cyanelles" (p. 27). Other possible examples of endosymbiosis are found in the Cryptophyta (p. 97). Here the chloroplast contains a "*nucleomorph*", which, since it is surrounded by a double membrane, may represent the remnant of, in this case, a eukaryotic endosymbiont.

The theory (in its modern form) envisages that, in the primordial eukaryotes, the prokaryotic endosymbionts became integrated into the physiology of the composite cell, contributing some of their genetic information to that in the nucleus, and in so doing losing their individual identity and sacrificing much of their autonomy.

Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

Attractive though this theory is, it has obvious difficulties. Organisms, such as *Glaucocystis*, which appear to be undoubtedly endosymbiotic in origin, are evidently exploiting successfully an ecological niche, and have probably done so since early in the diversification of cellular life. They can therefore be legitimately regarded as models of stability, and, far from being an indication of how the eukaryotic condition arose, are splendid examples of "dead ends" without evolutionary potential. Evidence of selective pressure favoring the complete assimilation of the invasive organisms, although conceivable, is so far lacking. Also required is a credible mechanism for the transfer of essential components of the invaders' genomes, through an alien cytoplasm to the nuclei or nucleoids of the hosts and the incorporation of this information in a (to them) foreign DNA. Further, is the nucleus itself of endosymbiotic origin? There are so many unanswered questions that it would be unjustified to fail to consider alternative possibilities.

The principal alternative view rests upon the occurrence in prokaryotes of plasmids, circles of DNA lying in the cytoplasm apart from the nucleoid. The genetic information in the plasmid is commonly represented also in the DNA of the nucleoid. The nucleotide sequences in a plasmid frequently code for a specific function. Photosynthetic membranes, and also respiratory membranes (mesosomes), are features of many prokaryotes. These membranes arise as invaginations of the plasmalemma. The cyanophytes and prochlorophytes (or their antecedents), the only prokaryotes displaying oxygenic photosynthesis, are obvious candidates for the origin of chloroplasts, a view strengthened by the many molecular similarities between them. Plasmids are indeed widespread in cyanophyte cells (but not yet reported in those of the prochlorophytes). Although it has not yet been possible to ascribe any precise function to the plasmids of the cyanophytes, it is not unreasonable to envisage a plasmid being associated with a photosynthetic membranous invagination in a primitive cyanophyte, and containing genes modulating its development and function. This possibility is strengthened by the evidence for the presence of regulatory genes on a plasmid regularly associated with the photosynthetic membrane system of the bacterium *Rhodospirillum rubrum*. If the peripheral complex of a cyanophyte, similarly endowed, were taken into the body of the cell, a rudimentary chloroplast would result. A similar translation affecting a peripheral respiratory membrane associated with an appropriate plasmid would lead to a rudimentary mitochondrion. Each would contain genetic information shared wholly or partly with that in the nucleoid or nucleus, a feature of mitochondria and plastids. No substantial transfer of essential genetic information would be required following the internalization of these membranous complexes into the body of the cell. It would follow that the correspondence between the genome of a plastid and that of the nucleus of its cell was analogous to that between a plasmid and the nucleoid in a prokaryote. This relationship would represent the persistence of an ancient feature, not the emergence of a new one.

Experiments with monolayers of polar lipid on the surface of water show how movement of membranous complexes from the periphery of a naked cell to the interior might have come about. When a lipid film is compressed, the film folds into the aqueous phase, so reducing its area. This, however, is an unstable situation. The folds in the aqueous phase become instantaneously detached, relieving the surface film of compression and restoring its continuity. The folds, now submerged, coalesce to form spheres and cylinders, themselves filled with water. Since both the inner and outer faces are now clearly hydrophilic, polar groups must be exposed on both surfaces. The lipid faces of the folds must therefore have come together, forming a bimolecular leaflet. One of the essential elements in the collapsing process is seen as the marked difference in viscosity between air and water, allowing air to escape rapidly from the folds, leading to the apposition of the two lipid layers.

It is not unreasonable to envisage a natural membrane, forming the interface between two phases differing in viscosity as sharply as protoplasm and water, behaving, under compression, in a manner analogous to that of a lipid film. If the folds formed adjacent to, or around, an already existing invagination of the bounding mem-

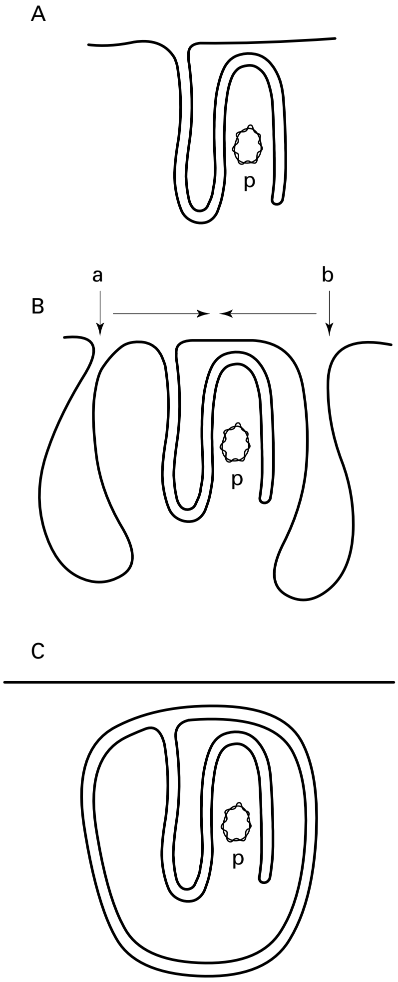

Figure 1.5 Diagrammatic representation of how a peripheral membrane system associated with a plasmid (p) could have become encapsulated and internalized as a consequence of compression of the bounding membrane. (A) Part of the bounding membrane of a prokaryote furnished with a photosynthetic invagination associated with a regulatory plasmid. (B) The bounding membrane is compressed and forms folds. Since the protoplasm adheres strongly to the membrane and is more viscous than the surrounding water, the membrane is dragged inward. If the volume of the cell is shrinking as a consequence of exosmosis, this effect would be enhanced. (C) Excess water is expelled from the folds so that the membranes lie closely parallel to each other, separated only by hydrated surface molecules (possibly glycoproteins). The inner extremities of the folds come together and fuse. Simultaneously the bounding membrane suffers instantaneous collapse. The margins of the folds (a, b) come together, so restoring continuity to the surface, and at the same time releasing a double-membraned inclusion to the interior. The area of the surface is thereby reduced, freed from compression, and structural stability is regained. (Based (by analogy) on experiments by R. J. Goldacre on the collapse of surface films of polar lipid under compression, described in Danielli, Pankhurst and Riddiford (eds.) 1958. *Surface Phenomena in Chemistry and Biology*, pp. 278–98. Pergamon, London.)

brane, the result would be that the invagination was carried, bounded by a double membrane, into the body of the cell (Fig. 1.5). In natural conditions, compression of the bounding membrane could be caused by, for example, exosmosis (if the prokaryote were splashed into a hypertonic pool), or even by mechanical pressure on naked cells arising from turbulence as streams cascaded over rocks. These conditions probably occurred frequently at the beginnings of cellular life.

The nucleus may have arisen in a similar manner, if the DNA of the genome were associated with an invagination of the plasmalemma, as in some existing bacteria. Indeed, internalization of the genome may have happened independently of the formation of plastids and mitochondria. Species of *Gemmata* and *Pirellula*, plancomycete bacteria, have been found in which the nucleoid is surrounded by an envelope. In *Gemmata* this consists of two membranes, the outer of which is connected with the plasmalemma, but in *Pirellula* the envelope is single.

It seems likely that a naked membranous sac, furnished with peripheral invaginations which penetrate contents that are denser than the surrounding medium, presents an unstable biophysical situation, particularly if the bounding membrane is compressed. Stabilization, relieving the membrane of compression, is achieved spontaneously by the internalization of the peripheral complexes. The current development of techniques for the production of compound vesicular bodies, consisting of vesicles bounded by lipoidal membranes lying free within the parent vesicle, raises the possibility of being able to mimic the internalization of peripheral membranous complexes in an experimental system using artificial cells. If it proves possible to explain the origin of the eukaryotic condition in terms of membrane biophysics, based upon a repeatable experimental system, the endosymbiotic hypothesis, which

Cambridge University Press
978-0-521-64673-4 - Green Plants: Their Origin and Diversity: Second Edition
Peter R. Bell and Alan R. Hemsley
Excerpt
More information

rests upon unverifiable evolutionary speculations, can at last be returned to history. The encapsulation and internalization of membrane systems originally attached to the plasmalemma may indeed have occurred many times with primitive cells, unprotected by a wall or mucilage. The emergence in evolution of firm or gelatinous cell walls, protecting a range of the earliest cells from the effects of compression, allowed the persistence of simple prokaryotes with peripheral photosynthetic and respiratory membrane systems into the later eukaryotic times. Although microtubules and actin microfilaments, structural proteins of the cytoplasm, are not found in bacteria, proteinaceous tubular elements ("rhapidosomes"), about 24 nm in diameter, occur in the cytoplasm of some cyanophytes (p. 29). Although not identical with the microtubules of eukaryotes, they may have given the cells of the photosynthetic prokaryotes an additional stability that ensured their survival.

Following the translation of the photosynthetic and respiratory compartments into the body of the cell, these compartments have retained many of their prokaryotic features in subsequent evolution. The invasion of the bounding membrane appears, however, to have led to innovations in the remaining cytoplasm. The endoplasmic reticulum (which retains connections with the outer membrane of the nuclear envelope) and the Golgi bodies are both membranous structures, characteristic of even the smallest eukaryotic cells (e.g., *Osteococcus*, p. 40). The ribosomes, ubiquitous in the cytoplasm, increased in size, reaching diameters some 50 percent greater than those of the ribosomes of mitochondria and plastids, and of prokaryotic cells. Concomitantly, the DNA of the genome became organized into chromosomes, probably a consequence of the nuclear envelope allowing a much closer control of the metabolism and assembly of the proteins (particularly histones) associated with the folding of the DNA. This led to the complex known as chromatin, and its parcelling into a definite number of regularly reproducible bodies, the chromosomes.

Evolutionary consequences of photosynthesis

It seems beyond doubt from the fossil record of life, and from the biological and geological inferences that can be drawn from it, that life began in water. The earliest forms of life remain conjectural, but were probably chemotrophic, accompanied fairly rapidly (in evolutionary time) by heterotrophs feeding upon them. Nevertheless, phototrophs probably also appeared relatively early. Those which contained or acquired chlorophyll (as opposed to bacteriochlorophyll), and which further developed oxygenic photosynthesis, gave rise to the plant kingdom. The descendants of these early aquatic forms, which still in the main exploit the watery environment, are termed algae (Chapters 2, 3 and 4). They have many biochemical, physiological, ecological and structural features in common. For these reasons they include the prokaryotic forms placed in the Cyanophyta and Prochlorophyta, which, although retaining some bacterial features, are clearly superior to these lowly forms in their possession of oxygenic photosynthesis and their general algal characteristics. Although some unicellular algae have attained morphological complexity (e.g., the dinoflagellates; p. 94), others represent the simplest plants still in existence. Apart from the unicellular prokaryotes, such as *Prochlorococcus* (p. 38), some unicellular eukaryotes are also minute. *Osteococcus tauri* (p. 40), for example, is probably the smallest eukaryotic organism known. The cells do not exceed 1 μm in width, lack a cell wall, and contain only a single plastid and a single mitochondrion. *Osteococcus* has so far been found only in the plankton of Mediterranean lagoons, but *Micromonas* (Fig. 1.6), which has a similarly simple cell but is provided with a flagellum, is abundant in the oceans. Relatively early, however, even in the prokaryotes (p. 29), multicellularity appeared in algal evolution, yielding a diversified algal flora whose descendants are still with us today.

At some stage, possibly in the Silurian period (Table 1.1) or even earlier, vegetation began to colonize the land. These early colonists, and consequently the whole of our existing land flora,