The Diversity of Green Plants

Third Edition

Peter Bell and Christopher Woodcock

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Preface to the third edition

In the almost twenty years since *Diversity of Green Plants* was first written striking advances in our knowledge of plants have put Botany well ahead in the Biological Sciences. At the fundamental level of membranes, the use of electron spin resonance spectroscopy is revealing the secrets of the extremely fast reactions which bring about the transfer of energy in photosynthesis. In plant cytology studies of the differentiation of the helical gametes of the lower land plants have shown the crucial role of microtubules in bringing about fundamental change in cell shape. It seems likely that these remarkable cells will also reveal the origin and composition of centrioles, a problem to which animal cytology has been able to give no firm answer. Genetical maps of chloroplasts are now as familiar as those of mitochondria, and the discovery that key nucleotide sequences are common to each has thrown new light on the possible evolutionary origins of these organelles. Even concerning the ancient plants exciting discoveries continue to be made. New knowledge of the curious forms at the end of the Palaeozoic which may have paved the way for the ultimate appearance of the flowering plants has come from Australian deposits. These examples from widely different aspects of the science are representative of the active research which is bringing outstanding liveliness and enthusiasm to current Botany.

As teachers we have been confronted with the problem of how this new knowledge is to be presented to the student. We remain convinced that a basic knowledge of plant morphology and evolution provides the structure essential for the orderly development of our science. Not only does an awareness of the inter-relationships of the organisms used in current research facilitate an understanding of the significance of the results, it also stimulates the recognition of new lines of profitable enquiry. Our purpose, therefore, is to promote our discipline in all its aspects by providing a concise account of the structure and reproduction of the varied groups of photoautotrophic plants, both living and extinct, proceeding from the simple to the complex.

Although we have adopted a form of classification as a framework for our account, we have thought of the photoautotrophic plants as a whole. Each is the morphogenetic expression of inherited information, much of it presumably common to all photoautotrophs. The fossil record does, however, give undeniable evidence of an evolutionary progression. We have therefore discussed the likely origin of each level of organization and its possible selective advantages, but unwarranted phylogenetic speculation has naturally been avoided. We have referred throughout to experimental work relevant to the problems of growth and form, and to the detection of evolutionary affinities, but detailed consideration of these topics has had to be omitted as beyond the scope of this book.

The Diversity of Green Plants is intended primarily for undergraduate students, but it will also be useful to all those seeking information about the relationships of the photoautotrophs familiar to the experimental botanist. Fuller accounts of the plants we describe can be found in the standard works to which our superscripts refer.

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P.R.B.
C.L.F.W.

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1

The principles governing the evolution of autotrophic plants

Significance of autotrophic nutrition

The living state is characterized by instability and change. A living cell consumes and releases energy by means of numerous chemical reactions, called collectively metabolism, taking place within it. Metabolism is synonymous with life. Even the apparently inert cells of seeds show some metabolism, but admittedly only a fraction of that which occurs during germination and subsequent growth. At normal temperatures, only in a dead cell, provided it remains sterile, does metabolism stop.

To maintain the dynamic state of a living cell it must be provided with sources of energy. The most usual sources are chemical and frequently consist of sugars. Together with these sources of energy, a cell also requires water, since much of metabolism is dependent on the maintenance of an aqueous phase in the cell, and those materials necessary for the repair and maintenance of its structure which it is unable to make for itself. These vary with the nature of the cell, but examples are certain metals which are essential components of important enzymes, the nitrogen of the proteins, and in some instances certain complex molecules called vitamins. All these nutritional requirements of the cell must be met; if not, the dynamic state we call life ultimately ceases.

It is a remarkable property of a large part of the Plant Kingdom that the cells, or in a multicellular plant at least some of the cells, are able to incorporate the energy of incident light into their metabolism. The energy, absorbed by the pigment chlorophyll, is used to generate ATP and reducing power in the form of NADPH + H^+ (the light reactions). These two products then bring about the reduction and assimilation of carbon dioxide in the form of carbohydrate (the dark reactions). The ability to metabolize atmospheric carbon dioxide in this way (***photosynthesis***) releases the organisms concerned from the necessity of an external source of carbohydrate, and their nutritional demands are consequently relatively simple. Photosynthetic plants are therefore examples of ***autotrophs***, the general term for organisms which require only simple molecules with single carbon atoms for their organic nutrition. Organisms which require complex carbon compounds (such as sugars) are termed ***heterotrophs***.

So far as is known, photoautotrophs utilize for photosynthesis principally that radiant energy falling within the wave-band called 'visible light'. Consequently, photoautotrophs can exist only in an environment continuously or intermittently illuminated. Some small photoautotrophs can, it is true, also exist as heterotrophs, so we may distinguish between obligate photoautotrophs, such as higher plants, normally unable to utilize sugar supplied externally, and facultative heterotrophs which, although normally photoautotrophs, can adapt their metabolism to the nature of their environment.

Chlorophyll is a complex pigment, existing in a number of slightly different forms. The molecule is in part similar to that of the active group of the blood pigment haemoglobin, but chlorophyll contains magnesium instead of iron. The photosynthetic pigment is not free in the cells, but is always associated with lipoprotein membranes, which seem generally to contain arrays of particles of two distinct size classes (Fig. 1.1). Pure chlorophyll is green, and absorbs particularly in the red part of the spectrum. In cells its colour may be masked by accessory pigments. Although the function of these is not precisely known, in certain instances part of the energy which they absorb is undoubtedly transmitted to the chlorophyll and contributes to its excitation. Chlorophyll, however, is the pigment principally concerned in photosynthesis. It is present in all photoautotrophs, and absent from all obligate heterotrophs, including the whole of the Animal Kingdom.

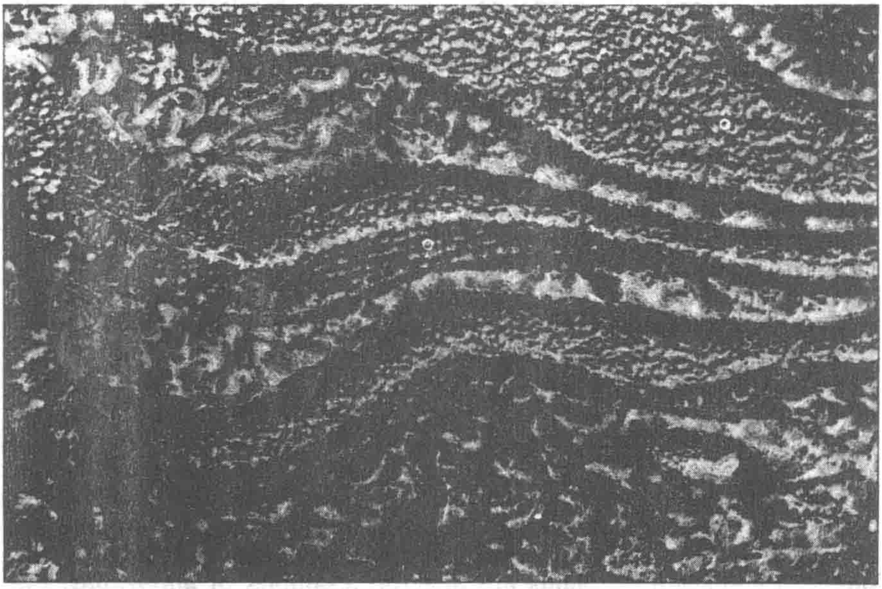

Fig. 1.1 Part of a granum in a chloroplast of spinach fractured obliquely. The replica has been prepared by the freeze-etch technique. The larger particles (indicated by arrow), sometimes in regular arrays, may be the sites at which light energy is transformed into chemical energy. (× 94 000)

The possession of chlorophyll and the consequent ability to utilize the sun's energy clearly bestow a great advantage on photoautotrophs. There is no necessity to forage for a supply of carbohydrates and Mereschkowsky's image[28] of the restless lion and the placid palm as contrasting the consequences of heterotrophic and autotrophic nutrition respectively, although poetic, is nevertheless apt. Photoautotrophs, of course, as all living organisms, remain dependent upon a supply of water and minerals, but such motility as occurs is in relation to light rather than mineral sustenance. Green unicellular organisms, for example, often show marked positive phototaxis.

The structure of the photoautotrophic cell

Two fairly distinct kinds of cellular organization occur amongst the photoautotrophs as a whole. In the first, termed ***prokaryotic***, [13, 44] the cell possesses no distinct nucleus, although a region irregular in outline and of differing density occurs at the centre 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. The protoplast of such cells is bounded by a membrane and in photoautotrophic cells this membrane here and there invaginates into the cytoplasm (Fig. 1.2). These membranous invaginations are the sites of photosynthesis, and they disappear or become very reduced if the cells are grown in the dark. This simple kind of photoautotrophic cell is found in both the photosynthetic bacteria and the Cyanophyta, perhaps representative of the most primitive kind of photosynthesizing organisms. Remains very suggestive of photoautotrophic prokaryotes have been found in Canadian rocks believed to be about 2000×10^6 years old. Geochemical evidence of photosynthesis, together with what are possibly remains of bacterial cells, comes from even more ancient rocks in South Africa and Australia. The evidence for cellular life now extends as far back as 3500×10^6 years.

In the cells of all other photoautotrophic 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. The photosynthetic apparatus, which consists of numerous lamellae running parallel to one another, is contained in one or more ***plastids*** (or chromatophores). The envelope of the plastid consists of two unit membranes, the inner of which invaginates into the central space and generates the internal lamellar system. The respiratory membranes and enzymes are contained within another distinct organelle, the ***mitochondrion***. Both plastids and mitochondria contain nucleic acids, and have a prokaryote-like biochemistry. They possess genetic systems of their own, partly independent of that of the nucleus.

The simplest eukaryotic photoautotroph is thus a single cell containing a

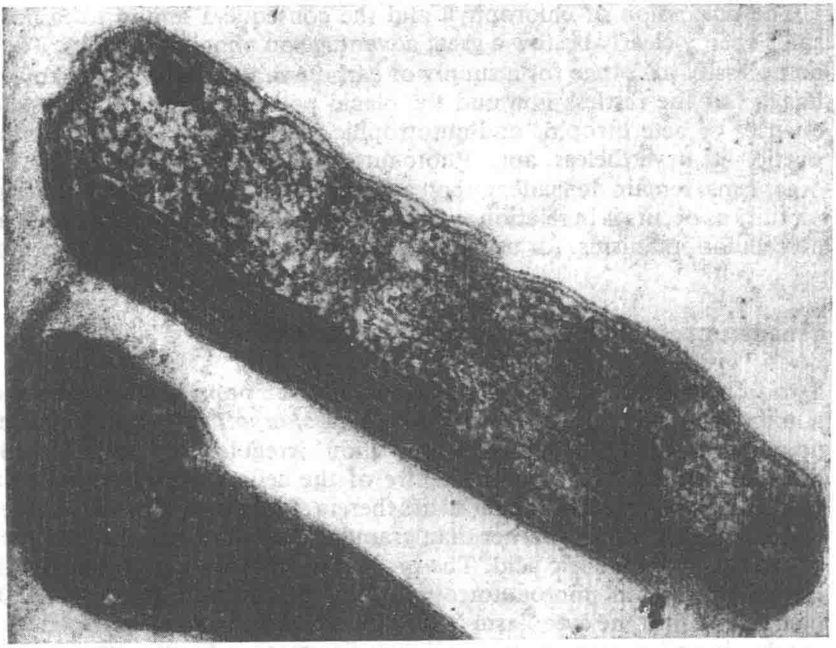

Fig. 1.2 Median section of a photosynthetic bacterium, *Rhodopseudomonas viridis*. The chromatophore is formed from an invagination of the cell membrane (plasmalemma). The folding of the membrane gives rise to a stack of lamellae, similar to the grana seen in the chloroplasts of higher plants. (× 95 000)

plastid and a mitochondrion. This condition is represented in *Micromonas pusilla* (Fig. 1.3), a minute alga ubiquitous in the sea. Electron micrographs of this organism undergoing fission show the plastid and mitochondrion dividing at the same time.

The 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. Although the early forms of life were probably heterotrophic, photosynthesis undoubtedly originated in an aquatic environment, probably in organisms similar to the existing purple bacteria. The plants which later evolved in this aquatic environment, and still in the main exploit it, have many biochemical and structural features in common, and are collectively termed algae. Our treatment of the autotrophic plants consequently begins at this level of organization (Chapters 2 and 3).

At some stage, possibly in the Silurian period (Table 1.1) or even earlier, vegetation began to colonize the land. These early colonists, and conse-

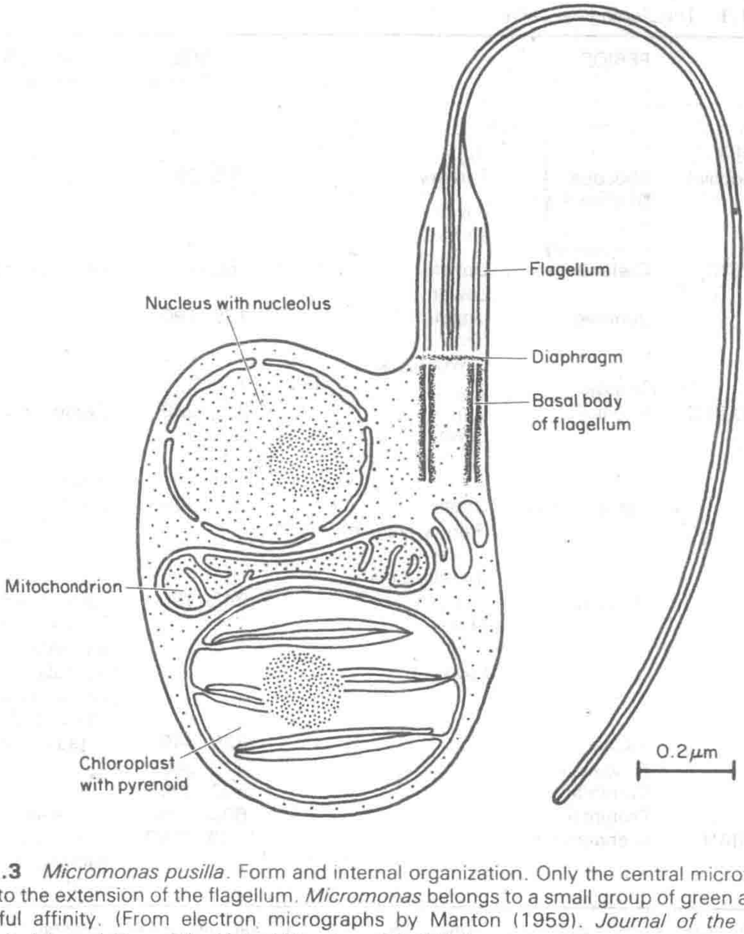

Fig. 1.3 *Micromonas pusilla*. Form and internal organization. Only the central microtubules run into the extension of the flagellum. *Micromonas* belongs to a small group of green algae of doubtful affinity. (From electron micrographs by Manton (1959). *Journal of the Marine Biological Association of the United Kingdom*, **38**, 319.)

quently the whole of our existing land flora, almost certainly emerged from that group of aquatic plants today represented by the green algae (Chlorophyta).[8] The Chlorophyta and the land plants (a term which means plants suited to life on land and not merely plants growing on land) have the same photosynthetic pigments, and basically the same photosynthetic apparatus. Moreover, at least one green alga (*Cladophorella*; see p. 39) which grows on damp mud is covered on its upper surface by a material which, judging from its resistance to acids and oxidizing agents, closely resembles cutin. This perhaps indicates the way in which the cuticle, ubiquitous in land vegetation, was derived.

Any consideration of the evolution of a photosynthesizing land flora must thus necessarily take into account the physiological features of the green algae, and how these may have been modified in the transition to terrestrial

Table 1.1 The Geological Table

ERA	PERIOD		AGE (in 10^6 years)	First authentic appearance
QUATERNARY	Pleistocene and Recent		0–2.5	
TERTIARY	Pliocene	Upper		
(or Cenozoic)	Miocene	Tertiary	2.5–28	
	Oligocene			
	Eocene	Lower Tertiary	28–65	
	Paleocene			
MESOZOIC	Cretaceous	Upper	65–135	Angiosperms*
		Lower		
	Jurassic	Upper	135–190	
		Middle		
		Lower (Lias)		
	Triassic		190–225	
PALAEOZOIC	Permian	Upper	225–280	Cycad- and *Ginkgo*-like plants, *Glossopteris*
		Lower		
	Carboniferous	Upper (Pennsylvanian)	280–345	Conifers
		Lower (Mississippian)		Pteridosperms
	Devonian	Upper	345–395	Ferns, seeds
		Middle		Sphenopsids
				Heterospory
		Lower		Vascular plants: Lycopods and Psilopsids
	Silurian		395–440	Triradiate spores
	Ordovician		440–500	
	Cambrian		500–600	
PRE-CAMBRIAN	Proterozoic		600–1500	Calcareous algae
	Archaeozoic		1500–3000 +	Fungi, algae, bacteria (see p. 3)

*See pp. 326–30 for a discussion concerning the first appearance of the angiosperms

life. Recent research into algal environments is yielding much information relevant to this problem. It is commonly found, for example, that from 5 to 35% of the light striking the surface of a lake or sea is reflected, the actual amount lost depending upon the angle of incidence. The light penetrating the water is then gradually absorbed as it advances, so that up to 53% of the radiation passing the surface may be dissipated as heat in the first metre.[33] Consequently, in warm and temperate regions, the rate of photosynthesis of submerged plants is normally controlled by the amount of light reaching them, and not by the amount of carbon dioxide in the water. We can see at once that the first colonists of land, emerging on to bare mineral surfaces, would almost certainly have had to contend with irradiances strikingly higher than those experienced by their aquatic ancestors. This would have provided opportunities for greatly increased photosynthesis.

Another discovery of recent research, also very relevant to the problem of the colonization of the land, is the surprising extent to which algae release photosynthesized materials into the surrounding water. In Windermere, for example, up to 35% of the total carbon fixed is continuously lost in this way. Losses of this order are clearly possible only from aquatic plants. As vegetation advanced from marshes, or from littoral belts subject to periodic inundation, on to relatively dry substrata, much more of the fixed carbon must have been conserved within the plant body.

The emergence of green plants from seas or lakes must therefore have involved striking changes in carbohydrate metabolism. The increased assimilation of carbon, resulting from the increased irradiances on land, and a diminishing loss of photosynthesized carbohydrates by outward diffusion as plants reached relatively dry areas, could have resulted in embarrassingly large, and possibly toxic, quantities of carbohydrates in the cells. The physiology must therefore have changed simultaneously to meet this new situation.

We have no evidence that adaptation to terrestrial life was accompanied by any reduction in the amount of chlorophyll in the chloroplasts (the term used for plastids that are unambiguously green), or in the efficiency of the photosynthetic apparatus. It is therefore not surprising to find that in addition to the condensation of sugar to starch, already encountered in the algae, the migration of plants on to land was accompanied by other ways of removing fixed carbon from the general metabolism. Rigid cell walls, making possible multicellular plant bodies penetrated by air spaces, are composed of cellulose and hemicellulose, both sugar products segregated more or less permanently in non-metabolizable form. Resin, phlobaphene and lignin are also derived from sugars. In addition to their structural and sealing properties these substances, which are often prominent in the more primitive land plants, are antiseptic and may have been important protectants to the early colonists. Massive plant bodies, which seem to have appeared relatively soon in the evolution of the land flora, also made possible the confinement of photosynthesis to specialized regions, such as leaves, so that the amount of assimilation per unit mass was reduced. Natural selection would, of course, have ensured that those forms survived in which the cells containing the condensed carbohydrates, and the materials derived from them, assisted the functioning of the plant as a whole.

We can envisage how this led to the evolution of xylem, the principal lignified tissue of land plants. Although largely dead, xylem is of paramount importance in the structure of plants since it provides both a skeleton supporting the plant in space, and an effective system for the transport of water and solutes. Cutin and sporopollenin, condensation products of a fatty nature, are also given essential roles in land plants. They serve to lessen the loss of water by evaporation from the living cells and, with the stomata, conserve a saturated atmosphere within the intercellular spaces. Plants were thus able to move into areas of lower humidity.

In the course of evolution many complex and bizarre forms of growth have appeared in land plants, but the material from which they are fashioned has remained predominantly carbon, extracted from the atmosphere. This diversity can be related to the tetravalent nature of carbon, and the great range of compounds that can be formed from it. Had not the photosynthetic fixation of this versatile element arisen on the Earth's surface, plant life, and that of animals which depend upon it, would have been impossible. Indeed, it is difficult to conceive of any alternative form of life appearing in its absence.

The mobility of plants

Although the earliest plants probably soon acquired motility of the kind seen today in *Chlamydomonas* and *Euglena* (Chapters 2 and 3), this appears to have been rapidly lost in the evolution of higher forms. Photosynthesis, together with the ability to manufacture a skeleton and a vascular system from the assimilated carbon, eventually made the large and firmly anchored terrestrial plant a practical possibility. Such an organism is, of course, immobile, and thus suffers a serious disadvantage, not shared by the higher animal, at times of natural catastrophe, such as volcanic eruption or fire. Plants, however, very frequently possess a remarkable mobility, or at least a ready transportability by agencies such as wind and water, in their reproductive bodies. Fern spores, for example, have been caught in aeroplane traps in quantity at 1500 m and even higher, and the hairy spikelets of the grasses *Paspalum urvillei* and *Andropogon bicornis* have been encountered at 1200 m above Panama. Lakes, seas and the coats and feet of animals also play their part in distributing plants. The immobility of the individual is thus frequently compensated for by the mobility of the species, and devastated areas and new land surfaces become colonized with amazing rapidity and effectiveness.

Life cycles

A life cycle, involving segregation and recombination of the genetic material, is as basic to the evolution of plants as to that of animals. In one part of the cycle the nucleus contains a single set of chromosomes (and is consequently termed ***haploid***), and in the other two sets of chromosomes (and is termed ***diploid***). The cycle is seen at its simplest in the unicellular algae of aquatic environments (Chapters 2 and 3), where haploid individuals in certain circumstances behave as gametes and fuse, so forming a ***zygote***. The zygote, which contains a diploid nucleus, either undergoes meiosis at once, or only after some delay, in which case the diploid condition can be thought of as having an independent existence. Either the haploid or the diploid phase, or both, may be multicellular. The multicellular plant is called a ***gametophyte*** if it produces gametes directly, and a ***sporophyte*** if it produces, following meiosis, individual cells which either behave as gametes immediately or develop into gametophytes. Each phase may also multiply itself asexually. These various possibilities are summarized in Fig. 1.4.

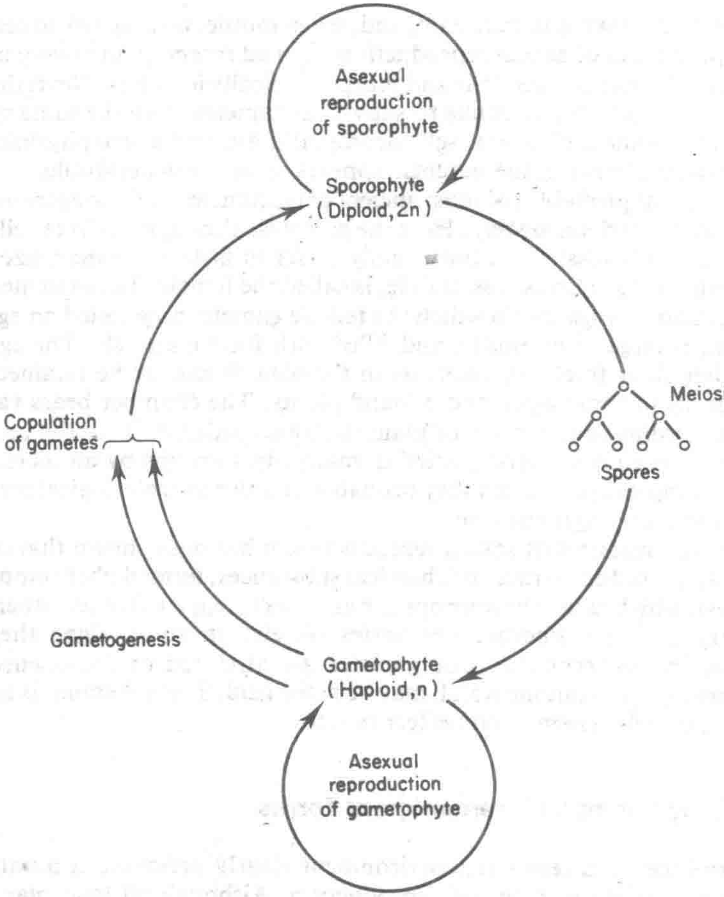

Fig. 1.4 The life cycle of autotrophic plants generalized. The large circle represents sexual reproduction. Only relatively few species display all the reproductive potentialities shown.

A life cycle is thus basically a nuclear cycle, and it is not necessarily accompanied by any morphological change. In the alga *Dictyota* (p. 92), for example, the gametophyte and sporophyte are identical, and it is necessary to observe the manner of reproduction in order to identify the place in the cycle which any individual occupies. Such a life cycle is termed ***isomorphic*** (or homologous). Frequently, however, the two phases of the cycle have different morphologies, one often being less conspicuous than the other, and sometimes parasitic upon it. These cycles are termed ***heteromorphic*** (or antithetic). Although the algae show both isomorphic and heteromorphic life cycles, those of land plants are exclusively heteromorphic. Occasionally there may be a morphological cycle without a corresponding nuclear cycle, as in the apogamous ferns (see p. 220), but this is regarded as a derived condition.

Gametes are always uninucleate, and, when motile, usually naked cells. In the simplest form of sexual reproduction, termed ***isogamy***, the two gametes involved in fusion are free cells and morphologically identical. Nevertheless, detailed investigations continue to show that gametes from the same parent rarely fuse. Some measure of self-incompatibility, and hence physiological differentiation between the parents, appears to be the general rule.

Isogamy was probably the most ancient condition, and this appears to have been succeeded by ***anisogamy***. Here the gametes, although still free cells, are morphologically dissimilar, but usually differ in little more than size. The larger, which may also be less mobile, is called the female. The extreme form of anisogamy is ***oogamy***, in which the female gamete, now called an egg cell or ovum, is large, non-motile, and filled with food materials. The egg cell may either float freely in water, as in the alga *Fucus*, or be retained in a chamber, as in some algae and all land plants. The chamber bears various names according to the group of plants being considered. Since the progression from isogamy is accompanied in many algal groups by an increase in somatic complexity, it seems very probable that this morphological progression is also a phylogenetic one.

In several instances of sexual reproduction it has been shown that one or both gametes produce traces of chemical substances, termed pheromones (or gamones), which cause the appropriate gametes to approach each other. The chemistry of these pheromones varies widely. In some algae they are peptides. In the ferns the male gametes are attracted to the opened egg chambers by a pheromone which may be malic acid. This substance is known to have a striking chemotactic effect *in vitro*.

The life cycles of the transmigrant forms

The transition to a terrestrial environment clearly presented a number of problems in relation to sexual reproduction. Although all land plants are oogamous, and are presumably derived from oogamous algae, fluid was still necessary in the initial land plants to allow the motile male gametes to reach the stationary female. This problem appears to have been met first by the egg becoming enclosed in a flask-shaped chamber, the ***archegonium***, in the neck of which the male gametes accumulate, and second by the male gamete becoming a highly motile cell. The male gametes of the lower archegoniate plants (Chapters 4, 5 and 6), termed ***spermatozoids*** (or antherozoids), are remarkable cytological objects. Each is furnished with two or more highly active flagella, and both the cell and nucleus have an elongated snake-like form, well suited for penetration of the archegonial neck. Dependence upon water is thus reduced to the necessity for a thin film in the region of the sex organs at the time of maturity of the gametes.

The archegonium is common to all the lower land plants, but its origin remains tantalizingly obscure. It may have appeared immediately before the colonization of the land, possibly as a consequence of morphogenetic tendencies seen today in association with the eggs of some Chaetophorales