Green Algae

Advanced article

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Article Contents

The green algae are a large and diverse group of photosynthetic eukaryotes. They comprise many ancient and diverse lineages, including land plants. Through evolutionary time, green algae have formed a number of symbiotic associations with fungi and animals and their chloroplasts have been incorporated into other eukaryotic organisms through secondary endosymbioses. Green algae display many degrees of organismal complexity: from microscopic unicells to macroscopic, multicellular thalli more than a metre in length. They are critical components of almost all aquatic ecosystems and many terrestrial ecosystems as well. Green algae are commercially important as feed and as a source of many industrial and pharmaceutical chemicals. Available chloroplast, mitochondrial and nuclear genomic data have contributed greatly to our understanding of their biology and evolutionary history. Scientists are still discovering new species and lineages of green algae as well as novel biological and chemical characteristics.

Introduction

Green algae are diverse phototrophic eukaryotes that live in aquatic habitats, including open ocean, coastal waters, reefs, estuaries, hypersaline environments and freshwater ponds and streams. They also occur commonly in soils and attached to natural and man-made surfaces. Green algae are key primary producers and they form complex biological interactions with other organisms. Green algae include about 15 000 named species, although this number is increasing as more habitats are investigated, and as a result of the use of molecular markers and phylogenetic methods in assessing species. Green algae serve as important model organisms and provide valuable commercial products. Embryophyte land plants evolved from a green algal ancestor. The characteristics and major groups of green algae are summarised in the following sections. **See also**: Algal Ecology; Algal Symbioses; Embryophyta (Land Plants)

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Cellular, Biochemical and Reproductive Characteristics

Green algae are phototrophic eukaryotic organisms characterised by cells with 1 or more primary chloroplasts (photosynthetic organelles evolutionarily derived from a cyanobacterial endosymbiont and surrounded by two membranes) containing chlorophyll a, b and carotenoids. Starch is commonly stored in the chloroplasts of green algae as an energy reserve. Pyrenoids, chloroplast localisations rich in the carbon-fixing enzyme rubisco, are present in most species. Vegetative cells may be nonmotile or motile by 1-2-4-several flagella that are inserted anteriorly in the cell and usually of equal length. Motile cells occur also as sexual cells (gametes) and asexual swimming cells (zoospores). Cellular coverings may be absent, as in the unicellular flagellates *Dunaliella* and *Ostreococcus*. In some (e.g. *Pyramimonas*) the motile cells (and sometimes the flagella) are covered with organic scales, whereas most species possess cell walls that are dominated by cellulose, mannans, glycoproteins, some including deposits of calcium carbonate (e.g. *Nitella*, *Halimeda*) or with minor compounds such as sporopollenin (e.g. *Scenedesmus*). Cells of green algae can be uninucleate or multinucleate. Some green algal cells have large vacuoles. Green algae have three major life histories: diplontic, haplontic and diplohaplontic (alternation of generations). Asexual

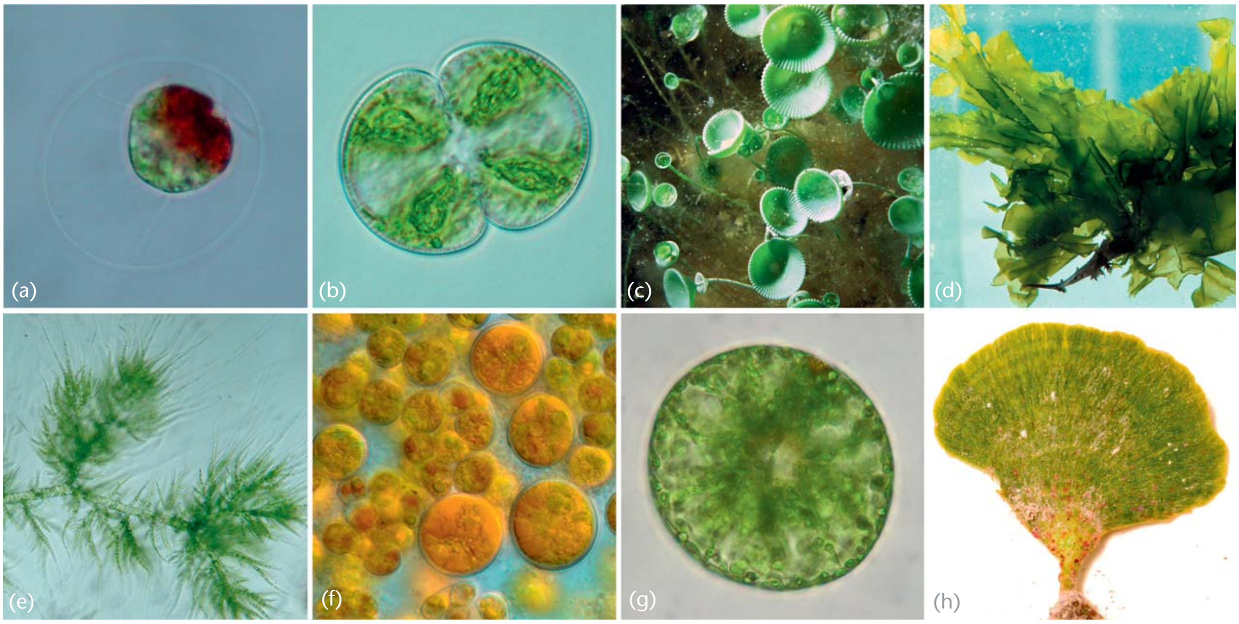

Figure 1 Sampling of vegetative morphology seen in different member of the green algae: (a) *Haematococcus*, Chlorophyceae, microscopic; (b) *Cosmarium*, Zygnemophyceae, microscopic; (c) *Acetabularia*, Ulvophyceae, macroscopic; (d) *Ulva*, Ulvophyceae, macroscopic; (e) *Draparnaldia*, Chlorophyceae, microscopic; (f) *Scenedesmus*, Chlorophyceae, microscopic; (g) *Eremosphaera*, Trebouxiophyceae, microscopic; (h) *Udotea*, Ulvophyceae, macroscopic.

reproduction is common and occurs by binary fission, fragmentation and production of motile or nonmotile spores. **See also**: Algal Calcification and Silification; Algal Carbon Dioxide Concentrating Mechanisms; Algal Cell Walls; Algal Chloroplasts; Algal Flagella; Gametophyte and Sporophyte; Plant Peroxisomes and Glyoxysomes; Plant Reproduction

Green algae range in size from approximately 1 μm to 1 m in length (**Figure 1**). They are morphologically diverse, with vegetative thalli that are unicellular motile or nonmotile cells, packets of cells, motile or nonmotile colonies, unbranched and branched filaments, parenchymatous, pseudo-parenchymatous and coenocytic.

Characteristics of dividing cells of green algae and motile cells help to diagnose some of the major groups. Cell division includes mitosis and cytokinesis. In some green algae the nuclear membrane remains intact during most of mitosis (closed), and in others the nuclear envelope breaks down (open). Modes of cytokinesis include infurrowing, a phycoplast or a phragmoplast; infurrowing is more common than either the phycoplast or phragmoplast systems. Phragmoplasts occur in embryophyte land plants and related green algae. **See also**: Plant Microtubules: Their Role in Growth and Development; Plant Mitosis, Cytokinesis and Cell Plate Formation

Motile cells of green algae typically have flagella oriented apically (anteriorly) or subapically. By convention, the flagellar apparatus (basal bodies and anchoring microtubular roolets) is compared from an apical view – as if looking directly at the apex of the cell. Across green algae, motile cells can be described as symmetrical, having a cruciate or cross-like organisation of basal bodies and supporting proteinaceous rootlets, or as asymmetrical. **See also**: Algal Flagella

Major Groups

The green algae can be divided into two main phyla, the Chlorophyta and Charophyta (**Figure 2**), which also includes the embryophyte land plants (itself formally given phylum status, Embryophyta). Major groups of green algae are distinguished by ultrastructural features of the cells, including their modes of cytokinesis and the architecture of their motile cells and more recently using molecular data. **Figure 2** illustrates the phylogenetic relationships of major green algal groups, as currently assessed by phylogenetic analysis of molecular and morphological evidence.

Most major groups include species with diverse morphological forms, indicating that vegetative morphology of green algae is less useful for classification than ultrastructural features and that the basic morphological forms have evolved independently in different evolutionary lineages. A brief discussion of the better-known groups is presented, but for more complete summaries see Further Reading. **See also**: Algae: Phylogeny and Evolution; Algal Taxonomy: Historical Overview; Embryophyta (Land Plants); Molecular Phylogeny Reconstruction

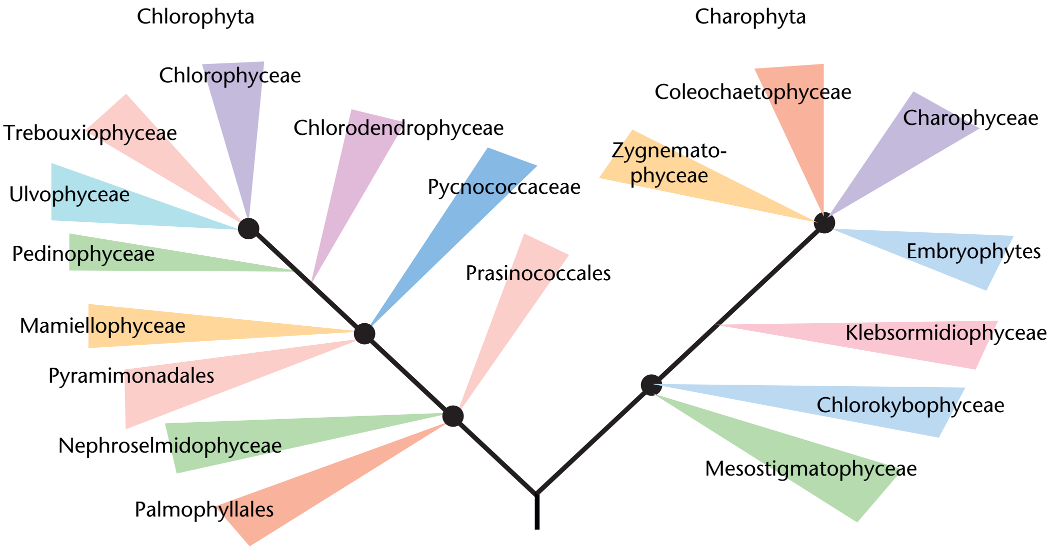

Figure 2 Diagrammatic summary of the phylogenetic relationships of major groups of green algae (plus embryophytes).

The Chlorophyta

Members of Chlorophyta have diverse vegetative morphologies, and motile cells with symmetrical and asymmetrical flagellar apparatuses. The symmetrical flagellar apparatus is found in the later-diverging lineages, classes Chlorodendrophyceae, Chlorophyceae, Trebouxiophyceae and Ulvophyceae. With some exceptions, members of Chlorophyta have a closed mitosis, and contain peroxisomes with the photorespiratory enzyme, glycolate dehydrogenase. Ten lineages are mentioned below, with a focus on the four later-diverging lineages because they are the best-studied groups.

- Class Nephroselmidophyceae. Algae in this group have cells with two flagella of unequal length, two body scale layers and two flagellar scale layers. The flagellar apparatus is complex, having three flagellar roots. Example: *Nephroselmis*.
- Order Prasinococcales. This early diverging group includes the coccoid species *Prasinococcus* and *Prasinoderma* (Guillou *et al*., 2004; Turmel *et al*., 2009b).
- Order Palmophyllales. This group was previously classified with more derived freshwater forms in the Chlorophyceae due to their similar thallus morphology. Their multicellular thalli display palmelloid organisation (i.e. small spherical cells embedded in mucilage). Comparative DNA sequence analysis (Zechman *et al*., 2010) now suggests these algae are a distinct lineage and among the earliest diverging green algae. Unlike the freshwater chlorophyceans they were once allied with, these algae form dark green crusts or cushions in deep (>200 m) or dimly lit tropical and temperate waters. Flagellate stages have never been observed and thus may have implications for understanding the nature of the ancestral green plant. Mitosis and cytokinesis have never been described in detail via electron microscopy. Examples: *Palmophyllum* and *Verdigellas*.
- Class Pycnococcaceae. This is a small group of unicellular marine algae whose evolutionary affinities are still uncertain. Members of the genus *Pseudoscourfieldia* have two unequal flagella and organic scales on the body and flagella. The coccoid taxon *Pycnococcus* is also supported in this group on the basis of molecular data.
- Class Mamiellophyceae. Widely distributed in marine habitats and also with freshwater members. These algae are unicellular, either motile by 1–2 subapical flagella or coccoid. Cells lack covering or have scales (Marin and Melkonian, 2010). Sexual reproduction has not been observed directly, although evidence of recombination indicates that sexual exchanges occur (in *Ostreococcus*, Grimsley *et al*., 2010). Asexual reproduction is by binary fission.
- Order Pyramimonadales. This group includes quadriflagellate taxa living in both marine and freshwater. The cells of some species are covered with complicated scales. Some members produce a cyst or phycoma stage, which is likely the result of sexual reproduction. Phycomata, with their resistant walls, appear in the fossil record in the Early Cambrian and perhaps earlier (Tappan, 1980). Examples: *Halosphaera*, *Pyramimonas*.
- Class Pedinophyceae. This class contains a small number of very small flagellates that occur in marine, brackish and freshwater habitats. The cells lack scales and have a single emergent flagellum and a second basal body. The arrangement of basal bodies is interpreted as counterclockwise, and mitosis is closed. The eyespots are located at the opposite end of the cells from the flagella (Moestrup, 1991). Examples: *Pedinomonas*, *Resultor*.
- Class Chlorodendrophyceae. Mostly marine, unicellular flagellates or branched colonies. The cells are covered by a theca, formed by fusion of individual small scales, and

individual scales also cover the four flagella of motile cells. Motile cells have basic symmetry, with counter clockwise orientation of the flagellar root. Division of the cell is mediated by a phycoplast. Example: *Tetraselmis*.

- Chlorophyceae. Predominantly freshwater, with some marine and terrestrial forms. These algae include haplontic, microscopic unicellular motile and nonmotile forms, packets of cells, motile or nonmotile colonies and microscopic and macroscopic unbranched and branched filaments. Cells are uninucleate or multinucleate, most possess walls. Cytokinesis involves a phycoplast and cells sometimes have plasmodesmata. In most species, motile cells have a symmetrically arranged flagellar apparatus with basal bodies in the directly opposite or clockwise orientation. Cells divide asexually to produce single cells, zoospores or autospores. Examples: *Chlamydomonas*, *Scenedesmus*.
- Ulvophyceae. Predominantly marine macroscopic seaweeds, but also found in terrestrial or freshwater habitats. Thalli of multicellular species may be filamentous, or mono- or distromatic blades and tubes. Macroscopic forms may also display siphonous construction in which nuclear division and cytokinesis are decoupled. Siphonous thalli may be uniaxial (as individual siphons) or multiaxial with many siphons woven into a larger, more complex thallus (free or intertwined in a complex matrix). Cytokinesis is by infurrowing, without a phycoplast. Motile cells have a symmetrically arranged flagellar apparatus with basal bodies in the counter clockwise orientation. Cells are walled and can divide asexually to produce single cells or clusters of cells. Sexual reproduction involves haplontic diplontic, or haplodiplontic. Examples: *Ulva*, *Caulerpa*, *Acetabularia*, *Trentepohlia*.
- Trebouxiophyceae. Predominantly freshwater and terrestrial forms, but some marine species occur. These are microscopic, unicellular or filamentous, some form macroscopic blades. Many are symbionts with lichen fungi. Cells are uninucleate or multinucleate, with walls. Cytokinesis involves a phycoplast. Motile cells have a symmetrically arranged flagellar apparatus with basal bodies in the CCW orientation, and lack scales. Cells divide asexually to produce single cells, zoospores or autospores. Their life cycle is haplobiontic. Examples: *Trebouxia*, *Chlorella*.

The Charophyta

The Charophyta are freshwater or terrestrial algae, characterised by motile cells with two or more laterally inserted flagella, and with an asymmetric set of flagellar roots. One flagellar root is associated with a multilayered structure or MLS. Most members of the Charophyta exhibit an open mitotic spindle, and in some the mitotic spindle persists throughout mitosis. The motile stages of most charophytes lack scales. All charophytes have peroxisomes with glycolate oxidase. The six classes within the Charophyta are briefly described below.

- Class Mesostigmatophyceae. This class has only two known species *Mesostigma viride* and *Mesostigma grande*. These freshwater species are vegetatively motile with two laterally inserted flagella, and covered with organic scales (Melkonian, 1989). Cytokinesis is accomplished through infurrowing.
- Class Chlorokybophyceae. This order is monotypic. The vegetative thalli are packets of cells that grow in water or subaerially (Rogers *et al*., 1980) that produce biflagellate, scaled zoospores. Cytokinesis occurs through infurrowing.
- Class Klebsormidiophyceae. This class includes algae with simple unbranched filaments or elongated unicells that produce zoospores with two flagella. Cytokinesis by infurrowing. Examples: *Klebsormidium*, *Entransia*, *Interfilum*.
- Class Zygnematophyceae. This species-rich group contains thousands of freshwater species. Thalli may be unicellular, colonial or uniseriate or branched filaments. They live predominantly in freshwater habitats but can also be found in subaerial habitats, soils and in snow and ice. They completely lack flagella (and the associated basal bodies). Many species produce thick-walled zygospores. Examples: *Micrasterias*, *Spirogyra*.
- Class Charophyceae. This group of freshwater algae contains several hundred species, sometimes called stoneworts. The macroscopic thallus is made of a main axis with large, multinucleate, internodal cells and multicellular nodes with whorled branches. Plants exhibit meristematic growth in which a single meristematic cell initiates growth at the apex. Motile cells are the sperm, which lack scales and have a complex morphology (Garbary *et al*., 1993). Sexual reproduction is oogamous and the egg cell is enveloped in jacketing cells. Examples: *Chara*, *Nitella*.
- Class Coleochaetophyceae. This group contains about 20 species of branched filaments that sometimes form disc-shaped thalli. Some cells in each thallus have distinctive hair-like extensions. Motile cells lack scales. Sexual reproduction is oogamous with various degrees of jacketing over the egg cells. Asexual reproduction by zoospores is common. Example: *Coleochaete*.

Evolution

The green algae are a monophyletic group that includes land plants. They represent one of three extant lineages containing primary plastids, the other lineages being the red algae (Rhodophyta) and the Glaucocystophyta. These three lineages were thought to share a common ancestor and thus represent a single, ancient endosymbiotic event (Delwiche and Palmer, 1997). However, some evidence suggests that these three lineages may not be a monophyletic group (e.g. Kim and Graham, 2008). Relationships among red algae, green algae and glaucocystophytes remain unresolved. **See also**: Glaucocystophytes; Red Algae

Fossil green algae are represented in ancient sediments. Some of the oldest fossils are from the Proterozoic and include both unicellular forms similar to prasinophytes (Colbath, 1983) and filamentous forms similar to the ulvophycean *Cladophora* (approximately 800 Ma; Butterfield *et al*., 1988). Green algal fossils have been found in both marine and freshwater sediments from Ordivician, Silurian and more recent sediments (Tappan, 1980; Colbath, 1983).

Molecular phylogenetic analyses have shown that many of the living species represent ancient lineages that diverged long ago. Resolving the branching order at the deepest nodes has proved challenging (Cocquyt *et al*., 2009; Karol *et al*., 2001; Turmel *et al*., 2009b). In fact, ancient lineages of green algae are still being discovered (e.g. Guillou *et al*., 2004; Zechman *et al*., 2010).

From an ancient green ancestor, many structurally diverse and species-rich lineages evolved. Among the extant lineages of Chlorophyta, many of the earliest diverging lineages are unicellular coccoid or flagellates collectively called prasinophytes. These are predominantly marine planktonic organisms. However, not all the early diverging lineages are unicellular prasinophytes. Recent phylogenetic data suggest that some deep-sea-dwelling organisms – *Palmoclathrus*, *Palmophyllum* and *Verdigellas* – represent one of the earliest-diverging lineages of the Chlorophyta (Zechman *et al*., 2010). These are colonial organisms with spherical cells embedded in a common, stiff mucilaginous matrix. Their placement as an early diverging lineage calls into question the nature of the ancestor of all green algae. Ancient chlorophytes also gave rise to at least three lineages that have undergone considerable subsequent structural diversification: the Chlorophyceae, Trebouxiophyceae and Ulvophyceae. The exact relationships among these lineages and the inclusion of various taxa in these lineages remain controversial. However, some recent studies suggest that the Trebouxiophyceae and Ulvophyceae may form a natural group sister to the Chlorophyceae (Pombert *et al*., 2005; Turmel *et al*., 2009a).

The charophytes comprise at least six algal lineages (see above) as well as land plants. Most of the algal lineages are species-poor and, in contrast to the lineages of the Chlorophyta, living representatives do not have as much structural diversity. The exception to both of these generalisations is the Zygnematophyceae (conjugating green algae), which has many thousands of structurally diverse species (Hall *et al*., 2008). Phylogenetic relationships among these groups remain controversial, particularly with regards to which lineage is sister to land plants. Some molecular data sets suggest that the Charophyceae are sister to land plants (e.g. Karol *et al*., 2001), whereas others indicate the Coleochaetophyceae (e.g. Finet *et al*., 2010) or the Zygnematophyceae are sister to land plants (e.g. Turmel *et al*., 2007). Resolving this and other deep relationships will greatly improve our understanding of evolutionary patterns in green plants.

Genomic Studies of Green Algae

Studies of green algal genomes have greatly expanded our understanding of both the biology and the evolution of green algae and land plants. A variety of genomic techniques have been applied to green algae resulting in many complete chloroplast and mitochondrial genomes as well as a few complete nuclear genomes. In addition, sequencing of expressed sequence tags (ESTs) has provided information about the gene content and physiological capabilities of some green algae.

Sequences of chloroplast and mitochondrial genomes of green algae were first determined in the 1990s and since then organelle genomes from a couple dozen species have been sequenced from across the green algal tree of life (excluding land plants, for which many dozens of chloroplast genomes are available). These organellar genomes have provided some insight into the evolution of these genomes and the organisms from which they were derived. Although organelle genome architecture tends to be conserved over long evolutionary time scales, gene content, order and density as well as nucleotide composition vary considerably across the green algae (Turmel *et al*., 2009b, a). Chloroplast genomes are generally circular and divided into four parts: one large and one small single-copy region containing protein-encoding genes separated by two inverted repeat regions that often contain ribosomal RNAs and other genes. However, some green algae (such as the charophytes *Staurastrum punctulatum* and *Zygnema circumcarinatum*) do not have inverted repeat regions in the chloroplast genome (Turmel *et al*., 2005). Most mitochondrial genomes are circular, however, some green algae have linear mitochondrial genomes (Smith *et al*., 2010).

Few nuclear genomes have been completely sequenced. To date, only those of *Chlamydomonas reinhardtii*, *Volvox carteri* as well as and two strains each of *Ostreococcus* and *Micromonas* are available. ESTs have been used more broadly to assess nuclear genome content (as well as gene expression). Although few complete genomes are available, it is apparent that green algal nuclear genomes vary considerably in size and content.

Many of these genome-scale studies have been conducted for phylogenetic reconstruction. In particular, chloroplast and mitochondrial genomes have provided important information about the early evolution of green algae and their relationships with one another and land plants. These studies have resolved some relationships, but only increased the uncertainty of others. For example, large data sets of chloroplast, mitochondrial or nuclear (EST) sequences provide conflicting evidence for relationships among charophytes – including the sister relationship to land plants (Karol *et al*., 2001; Turmel *et al*., 2005, 2007; Finet *et al*., 2010). Additional sampling within some lineages may resolve this apparent conflict or reveal other confounding evolutionary processes. The full potential of green algal genomics has yet to be realised, however, published studies have contributed significantly to our understanding of the biology and evolution of these fascinating organisms. For example, EST surveys of green algae revealed the presence of a sexual division-inducing pheromone in a charophyte (Fukumoto *et al*., 2003) and genomic of *Ostreococcus* and *Chlorella* revealed evidence for cryptic sexual reproduction (Derelle *et al*., 2006; Blanc *et al*., 2010). Studies using the genome of *Chlamydomonas reinhardtii* and related algae are providing evidence for the evolution of mating types and multicellularity (e.g. Prochnik *et al*., 2010). The development of single-cell genomic techniques has created tremendous opportunities to study ecology and physiology in organisms that are not amenable to laboratory experimentation. **See also**: Genomics of Algae

Ecology

Green algae are important participants in marine, freshwater and terrestrial ecosystems.

Microscopic green algae are well-known open ocean organisms (*Ostreococcus*, *Prasinococcus*, *Nannochloris* and *Pyramimonas*). Ostreococcus, the smallest known eukaryote, is widely distributed in open oceans (Courties *et al*., 1994; Palenik *et al*., 2007). Recent molecular studies from environmental samples have revealed that many novel species of microscopic planktonic green algae are yet to be cultured and studied (Shi *et al*., 2011). Green algae also are common in freshwater ponds, lakes, rivers and streams. The unicellular genus *Desmodesmus*, and others, exhibit morphological responses to different environmental conditions, including the presence of predators (phenotypic plasticity) (Trainor, 1998), making these organisms very useful in monitoring environmental toxins. **See also**: Algal Ecology; Environmental Impact Assessment; Phytoplankton; Predator-induced Plasticity

Intertidal and shallow subtidal species

The green macroalgae are important and ubiquitous primary producers in benthic marine ecosystems throughout the world. Although primarily associated with rocky shore habitats, these algae also form diverse communities in soft bottom habitats. The majority of these organisms is in the Class Ulvophyceae and possess a diverse array of thalli. *Ulva* (**Figure 1d**) is a cosmopolitan green seaweed found in coastal and estuarine habitats and is know as an indicator of high nutrient levels (as in waters with sewage or fertiliser contamination). *Ulva* and related taxa are common ephemeral species that opportunistically colonise cleared substrate. Because of their ability to withstand broad variation in temperature and salinity, *Ulva* is also common seaweed in high intertidal tide pools where it often forms monospecific populations.

Tropical siphonous marine green algae (e.g. *Caulerpa*, *Halimeda*, *Udotea*, *Penicillus* and *Rhipocephalus*) form vast meadows along with seagrasses that provide important habitat and food for marine animals. These algae are able to survive in these soft bottom habitats with a number of structural adaptations. *Caulerpa* is capable of overgrowing soft sediment with stoloniferous branches and regular rhizoidal branches that penetrate the sediment. Other multiaxial siphonous algae consolidate sediment in a bulbous rhizoidal holdfast that anchors the alga in the sand.

A number of green algae are infamous as invasive species and potentially destructive of native habitats. *Caulerpa taxifolia* is one whose introduction and spread throughout the Mediterranean Sea is well documented. The species was first observed growing in shallow subtidal habitats near the seawater effluent from the Monaco Aquarium, which possessed the nonnative alga in its flow-through displays. The alga now covers vast areas of subtidal marine habitat, displacing numerous native species.

‘Extreme’ Environments

A number of species of green algae are known to grow well outside the average ranges of light, salinity, pH, temperature and desiccation. High levels of photosynthetically active and UV radiation are experienced regularly by intertidal algae at low tide, planktonic algae living near the water’s surface, as well as algae adapted for life at high altitudes and in snow. These species use a variety of mechanisms to reduce photoinhibition (degradation of the photosynthetic apparatus due to photo-oxidative stress), including down regulation of the photosynthetic apparatus enzymes, use of carotenoid pigments that dissipate excess energy and accumulation of mycosporine-like amino acids (especially in trebouxiophyte algae). In contrast, other green algae (e.g. *Halimeda*) are able to grow well in low light habitats, as in deep water and under submarine ledges. The palmophyllophyte, *Verdigellas*, is capable of living at depths in excess of 200 m where light is about 0.05% of surface irradiance. *Ulva* and other siphonous ulvophytes are thought to survive low light conditions by amplifying light absorption with the green light capturing pigments siphonein and siphonoxanthin. In contrast, the Palmophyllalean greens seem to grow in deeper and darker habitats by increasing their ratios of chlorophyll b/a (Sartoni *et al*., 1993). Although productivity under these low light conditions is very low, the algae may benefit from these darker habitats by reduced stress induced by wave action, temperature variation, competition and herbivory.

Snow algae (e.g. *Chlamydomonas nivalis*, Chlorophyceae) accumulate the bright red carotenoid astaxanthin as cytoplasmic deposits, providing an effective screen for excess radiation (e.g. Gordon *et al*., 2001). Halotolerant algae, such as *Dunaliella salina* (Chlorophyceae), have a number of cellular adaptations to reduce osmotic stress, including accumulation of glycerol and sugars (Oren, 2005). Most green algae occur in 4–25°C waters, but some have positive photosynthesis well below freezing and some benthic forms can tolerate 35°C (Yokohama, 1973). Green algae occur in waters of both low and high pH. Desmids (Zygnematophyceae) are common to bogs and other low pH aquatic habitats, and at certain times of the year desmids can account for over 20% of the microscopic photosynthetic species (Domozych and Domozych, 2008). Filamentous *Zygogonium* (Zygnematophyceae) was reported from an acidic stream of pH 2.3–3.3 (Rothschild, 2001), whereas *Nannochloris* (Trebouxiophyceae) is known from the very salty and alkaline Mono Lake, CA (Seckbach and Oren, 2007). Lack of water is a stress on all organisms, but vegetative cells of diverse green algae in classes Chlorophyceae, Trebouxiophyceae, Klebsormidiophyceae and Zygnematophyceae can withstand long intervals without water and possess the ability to recover quickly upon rehydration (e.g. Gray *et al.*, 2007).

Symbiosis

Green algae live symbiotically with bacteria, fungi, diverse animals, the plant *Ginkgo* and protists. Lichen photobionts are diverse; they can be cyanobacteria, brown algae or green algae. Green algae living as fungal photobionts are unicellular members of Trebouxiophyceae (e.g. *Trebouxia*, *Asterococcus*) and Ulvophyceae (*Trentepohlia*). This association occurs most commonly with basidiomycetes and more rarely with ascomycetes. The green algae living in symbiotically with protists (ciliates, foraminifera) and animals (sponges, clams, nudibranchs, sea pens, anemones, hydra, insects and vertebrates) are known commonly as zoochlorellae because the cells are similar morphologically to the unicellular trebouxiophyte, *Chlorella*. Through the use of molecular markers it was shown that many green symbionts are not *Chlorella*, but instead are diverse algae from independent evolutionary lineages of Chlorophyceae and Trebouxiophyceae (e.g. Huss *et al.*, 1999; Letsch *et al.*, 2009). Two genera of ulvophyte green algae, *Cephaleuros* and *Chlorochytrium*, are parasitic on plants such as coffee, Magnolia and citrus. Two other trebouxiophytes, *Helicosporidium* and *Prototheca*, are parasitic in invertebrates and humans, causing protothecosis in humans and domesticated animals. The latter two genera are completely nonphotosynthetic and have drastically modified chloroplast genomes (de Koning and Keeling, 2006). **See also**: Algal Symbioses; Lichens

Green algae also serve as the ultimate symbiont. Through secondary endosymbiosis green algae have been permanently and obligately incorporated into other eukaryotes as a photosynthetic organelle. Reduced green algae are the ‘chloroplasts’ in euglenoids, green protists known as Chlorarachniophytes and in a small number of dinoflagellates (Rogers *et al.*, 2007; Keeling, 2009). This process resulted in a reduction of most of the cellular contents of the alga, and even in the loss of genes from the algal nucleus or transfer of genes from the symbiont to the host. **See also**: Chlorarachniophytes

Symbiotic associations with bacterial cells have also been described for green algae. It has long been known that *Ulva* grown in axenic culture develop abnormal filamentous cushions rather than their normal membranous thalli. When the naturally occurring epibacterial flora is added to these cultures normal morphology of *Ulva* is restored (Provasoli and Pintner, 1980). The compound produced by these bacteria and responsible for this morphogenetic response is called thallusin. *Caulerpa* sp. growing on soft sediments are also known to contain symbiotic bacteria in their rhizoids capable of fixing nitrogen to facilitate growth.

Model Organisms and Commercial Uses

Green algae serve as important model organisms for the study of a number of biological processes, including photosynthesis (*Chlorella*, *Chlamydomonas* and *Mougeotia*), formation of the plant cell wall (*Micrasterias*, *Penium*), flagellar structure (*Chlamydomonas*), understanding degradation of genomes following loss of photosynthesis, evolution of multicellularity (*Volvox*), cytoplasmic and nuclear interactions (*Acetabularia*, **Figure 1c**), wound healing (*Valonia*) and other processes that would be more difficult to study in larger organisms or those with longer life spans. **See also**: Adhesive Specificity and the Evolution of Multicellularity; Genomics of Algae

Likewise, green algae have important commercial value. Macroscopic green algae have been used as a food source for humans and animals for thousands of years (Spolaore *et al.*, 2006). Marine algae (including green algae) have been used as food and fertilizer in a variety of agricultural settings. Green seaweeds, such as *Ulva*, are also grown as feed for commercial abalone production (Bolton *et al.*, 2009). Since the middle of the twentieth century, microscopic green algae have been used increasingly for food supplementation and chemical production. *Chlorella* and *D. salina* are cultivated on an industrial scale as dietary supplements for humans and animals. These species are good sources of beta-1,3-glucan and beta-carotene, respectively. *Haematococcus pluvialis* (**Figure 1a**) is cultivated for its production of astaxanthin and is often used in salmon aquaculture (Spolaore *et al.*, 2006). There is increased interest in the use of algae (including the green algae *Botryococcus braunii* and *Chlorella*) for the production of biofuels. There is great potential for the use of green algae in the production of food, fibre, fuels and pharmaceuticals. For example, the green seaweed *Bryopsis* is an important source of kahalalide F, which is being investigated as a potential treatment for many human diseases such as cancer and AIDS. A compound from *Ca. taxifolia*, caulerpenyne, was found to have anticancer properties (Smit, 2004). However, relatively few green algae have been thoroughly investigated and therefore represent a significant potential source of useful chemical products. **See also**: Halophiles

Green microalgae are highly promising for use in biofuels due to their potential for higher lipid production per area of land than oleaginous (oil producing) agricultural crops and without competing with food crops in agricultural effort and resource use (Wijffels and Barbosa, 2010). Unlike oil crops and waste coking oil and animal fat, microalgae appear to be the only renewable carbon-neutral biodiesel capable of meeting the global demand for fuel (Chisti, 2007).

Production of microalgae is still largely based on traditional culture methods using a few strains known to produce oils. These include species of *Botryococcus*, *Dunaliella* and *Chlorella*. Maximum growth rates in raceway ponds and photoreactors are dependent upon supplying algae with the nutrients, light and other growth factors necessary for sustained growth. However, these unstressed algae produce lipids mostly in the form of phospholipids founds in cell membranes. Under more stressful conditions (e.g. low nutrients, high light, etc.), some species of microalgae form oil bodies that contain triacylglycerols that are key ingredients in biofuel production. Such stress-induced formation of lipids, however, comes at the expense of growth rates. Efforts to counter this trade-off between growth rate and optimised oil production will no doubt include exploration of diverse algal strains and their culture methods, knowledge of lipid biosynthetic pathways and genetic engineering (Wijffels and Barbosa, 2010). **See also**: Plant Storage Lipids

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