Red Algae

Introductory article

Carlos Frederico Deluqui Gurgel, *Smithsonian Marine Station, Fort Pierce, Florida, USA*

Juan Lopez-Bautista, *University of Alabama, Tuscaloosa, Alabama, USA*

Red algae are ancient aquatic plants with simple organization, noteworthy colour variation, vast morphological plasticity, challenging taxonomy and most extant species (about 6000 worldwide) are marine. They include species with complex life cycles, significant ecological importance and extensive economical applications.

Article Contents

doi: 10.1002/9780470015902.a0000335

Introduction: Definition and Characterization

Red algae (Rhodophyta) are a widespread group of uni- to multicellular aquatic photoautotrophic plants. They exhibit a broad range of morphologies, simple anatomy and display a wide array of life cycles. About 98% of the species are marine, 2% freshwater and a few rare terrestrial/subaerial representatives. Planktonic unicellular species have simple life cycles characterized by regular binary cell division. Advanced macroscopic species exhibit the characteristic trichogamy, triphasic, haplo-diplobiontic life cycle, with one haploid (gametophytic) and two diploid (carposporophytic and tetrasporophytic) stages. Red algae are true plants in the phylogenetic sense since they share, with the green lineage (green algae and higher plants), a single common ancestor (Adl *et al*., 2005). However, the features that distinguish red algae from any other algal group refer to the absolute lack of flagella and centrioles, presence of phycobilisomes and unstacked thylakoids in the chloroplast, absence of parenchyma and presence of pit-connections between cells (i.e. incomplete cytokinesis). The characteristic red colour and its many variations are the result of a variety of photosynthetic pigments (chlorophylls and carotenoids) plus phycobilisomes, the light harvesting complex composed of three main classes of water-soluble protein-based pigments (phycobiliproteins): phycoerythrin (red), phycocyanin (blue) and allophycocyanin (blue–greenish) (Grossman *et al*., 1993). **See also**: Algal Chloroplasts; Algal Metabolism; Algal Photosynthesis; Algal Pigments; Phycology

The growth in length of macroscopic species is governed by a single apical cell or by a group of multiaxial apical cells. Intercalary cell divisions are common and account for most of the growth in width and thickness of thalli in many red algal groups. No specialized growth tissues or meristems exist and, therefore, a true parenchyma is never developed. In this view, all red algal thalli can be interpreted as a group of filaments held together by cell-wall interactions, mucilage and pit-connections (pseudoparenchyma). Red algal cell walls are composed of cellulose fibrils (rarely xylan fibrils) and a matrix of hydrocolloids. Cell wall hydrocolloid matrixes in red algae are formed by sulfated polysaccharides classified in two main groups: agar and carrageenan. Some taxa present calcium carbonate deposits whose crystal state can be found in two forms, either calcite or aragonite. **See also**: Algal Calcification and Silification; Algal Cell Walls

Red algae are one of the oldest eukaryotic groups in the world, with fossil evidence dating back from the late Pre-Cambrian, about 2 billion years ago (Tappan, 1976). The oldest multicellular eukaryotic fossil record is of a red alga dated 1.8 billion years ago. We also know that red algae share a single common ancestor with green algae (Chlorophyta) and the land plants (Embryophyta), and these three groups, together with the Glaucophytes define the current Plant Kingdom (Keeling, 2004). **See also**: Algal Taxonomy: Historical Overview; Eukaryotes and Multicells: Origin

Sexual Reproduction

The basic scheme of sexual reproduction includes the development of a specialized female filament called the carpogonial branch. The female gamete (carpogonium) is easily recognizable by the presence of the trichogyne, an elongated extension responsible for receiving the male gametes (spermatium). After fertilization, the zygotic nucleus develops, directly or indirectly, into a diploid phase, the carposporophyte, which grows parasitically on the female gametophyte. During the direct development, the fertilized carpogonium matures into a carposporophyte usually composed of gonimoblastic filaments (vegetative diploid cells) and carposporangia (reproductive diploid cells). Mature carposporangia release diploid carpospores into the water column. However, in many groups with indirect development, the zygotic nucleus undergoes nuclear divisions and these nuclei are transferred to other specialized cells, called auxiliary cells, where they will, in turn, develop into carposporophytes remote from the original fertilization site. The auxiliary cell can be located or originated in close proximity to the carpogonial branch, in a short distance to receive the zygotic nucleus (procarpic condition), or away from it, in another vegetative independent filament (non-procarpic condition). In the latter case, a complex network of connecting filaments (ooblast filaments) can develop to deliver the diploid nuclei to several auxiliary cells.

The arrangement, morphology and number of cells that make up the carpogonial branch, and the shape, origin and location of auxiliary cells are prime characters for the taxonomy of red algae. In many red algae the fully mature first diploid stage is called carposporophyte. The cystocarp is composed of the carposporophyte plus all protective sterile haploid tissue of the female gametophyte encircling and interacting with it (pericarp). Carpospores develop into a second free-living phase called tetrasporophyte, which can be morphologically similar (isomorphic alternation of generations) or different (heteromorphic alternation of generations) from the gametophytes. Tetrasporophytic plants produce tetrasporangia by meiosis, which release tetraspores. This pattern of meiotic cell division in the tetrasporangium is stable in red algae and can be one of three types: cruciate (including decussate), tetrahedral and zonate. When released, each tetraspore will give rise to either a male or a female haploid gametophyte.

Vegetative Reproduction

Vegetative reproduction is quite common in red algae. Thallus fragmentation is considered by many as the most significant kind of vegetative reproduction in red algae due to the huge drifting biomass mats observed, many times accumulating and piling high at beaches. In many places, such as the intracoastal waterways along the Eastern coast of the USA, bottom deposits of drifting populations of seaweeds are constant components of the benthic community. Key species in this case include *Hypnea cervicornis*, *Spyridia hypneoides* and *Acanthophora spicifera*. Some species produce propagules such as spores from bisporangia (e.g. *Caloglossa apomeiotica*) monospores from monosporangia (e.g. *Monosporus* sp., Ceramiaceae), and frail branchlets designed to break apart, disperse and develop into new plants (e.g. star-shaped branchlets of *Hypnea cornuta*). Vegetative growth and fragmentation is the primary mode of reproduction in many invasive species of red seaweeds such as *Gracilaria salicornia* and *Hypnea musciformis* in Hawaii (Davidson *et al*., 2003). **See also**: Algal Spores

Major Groups

Traditionally, red algae can be morphologically separated in three major groups: (1) a unicellular group with reproduction by binary cell division only, (2) a multicellular group where a carpogonial branch is absent or incipient (Bangiophyceae *sensu lato*) and (3) a multicellular group with well developed carpogonial branches (Florideophyceae). The taxonomy of red algae is a dynamic field with new classification schemes at different levels of biological organization being proposed frequently and many new species being described every year (especially with the advent of molecular-based phylogenetic analyses). The two most recent and complete classification systems of the red algae at higher levels of biological organization were proposed by Saunders and Hommersand (2004) and Yoon *et al*. (2006). Both works recognized the red algae as the first divergence in the Plant Kingdom, with at least five major red algal internal evolutionary lineages, and the monophyly between the Florideophyceae and a redefined Bangiophyceae *sensu stricto* (Bangiales only). However, the phylogenetic relationships among the unicellular red algal groups (e.g. Porphyridiales lineages) remain partially unresolved, despite a plethora of physiological, morphological and molecular data available. Currently, there are approximately 32 orders of red algae but more are expected to be proposed. The evolutionary relationships and taxonomic classification systems in red algae, across all levels of biological organization, have been extensively advanced in the last 15 years with the aid of molecular-based phylogenetic analyses. Among the most common phylogenetic markers used with this purpose are the chloroplast-encoded *rbc*L (1467 base pair single copy gene that codes for the large subunit of the ribulose 1,5-bisphosphate carboxylase/oxygenase enzyme), and the nuclear-encoded ribosomal cistron encoding 18S, ITS1, 5.8S, ITS2 and the 28S rDNA (e.g. Freshwater *et al*., 1994; Harper and Saunders, 2001).

Ecological Importance

General importance

In many tropical and subtropical intertidal communities red algae are the primary component of the flora in terms of biomass and species diversity. As primary producers and conspicuous members of the benthic marine community, red algae serve as a source of oxygen for the environment, food for heterotrophic species, substrate for many epiphytic species of animals and plants and as a refuge, nesting and egg depository site for many other organisms. In the marine environment red algae can be found inhabiting the upper littoral zone to the deepest benthic region of the continental shelves. As littoral organisms, many species can endure severe abiotic stresses such as nutrient limitation, intensive light exposure, osmotic pressures and desiccation, e.g. *Bostrychia* sp. growing on mangrove prop roots. The deepest known marine plant in the world is a crustose coralline red alga growing at about 265–268 m deep, offshore the Bahamas, at the limit of the photic zone, where the light available for photosynthesis is only 0.0001% of the surface irradiance (Littler *et al*., 1985). **See also**: Algal Ecology

Reef builders

In coral reefs, crustose coralline red algae play a paramount role in coral recruitment, being the primary settlement substratum for several coral larvae. Crustose growth of coralline red algae unite rubble, other specimens of crustiform algae and pieces of dead coral, thus helping to build the reefs. It can be said that red algae work as a biological cement helping to integrate coral reef structures. Deep-water regions of many continental shelves around the world (usually between 40 and 200 m) are characterized by large deposits of rhodoliths. Rhodoliths can be defined as unattached nodules of several size classes composed of a variable number of calcareous crustose red algal conglomerates. These rhodolith-based deep water hard-bank communities harbour an abundant, diverse and unique benthic biota. Offshore rhodolith deposits are also associated with gas and petroleum deposits. When such deposits occur in shallow waters, they are called *maërl*. **See also**: Algal Symbioses; Marine Communities; Zygomycota

Invasive species

Human-mediated introductions of nonindigenous red seaweeds have been reported in several parts of the world: Australia, Brazil, Europe, USA, among others. Compared to other seaweeds, in the USA alone, red algae account for twice the number of algal species introduced in coastal marine communities (Ruiz *et al*., 2000). In general, these introductions can be classified in two major groups: deliberate and nondeliberate introductions. Deliberate introductions have the purpose to develop local aquaculture practices of economically important exotic seaweed species, notoriously among this kind of imports, is the introduction of *Kappaphycus alvarezii* in many tropical coastal marine environments (Ask *et al*., 2003). Nondeliberate introductions may occur as the result of marine practices such as ballast water carry over and the international animal aquaculture trade; in particular the importation, introduction and farming of the Japanese oyster, *Crassostrea gigas*. This latter scenario includes species such as *Gracilaria vermiculophylla* in Northern Europe (Rueness, 2005) and *Grateloupia* spp. in Europe and Eastern USA (Verlaque *et al*., 2005). In Hawaii, invasive species of red algae are a threat to coastal coral reefs and cause major ecosystem changes with conspicuous losses in biodiversity (Davidson *et al*., 2003).

Economical Importance

Red algae have a wide array of economic applications supporting a diversified industry worth billions of dollars every year. At least 125 different species of red algae are used worldwide with different applications. The two most important uses in terms of annual economic value, aquaculture intensity, and biomass production are first food, and second in hydrocolloid production (agar and carrageenan – discussed in more details below). From the estimated 125 species with economic application, 79 are used as food for human consumption, 33 in agar production and 27 in carrageenan production. The aquaculture industry of *Porphyra* (nori) alone generates the major monetary volume and annual metric ton of cultured algal biomass produced by any species of red algal worldwide (Zemke-White and Ohno, 1999). Exploitation of natural stocks of red algae is also common and accounts for about 50% of red algae annually. Besides the food and hydrocolloid usages, other known red algal applications include the production of paper, silage for animal aquaculture (e.g. *Palmaria palmata* in abalone farming), water nutrient removal from natural (ponds) and artificial (tanks) containments in animal aquaculture, energy production (e.g. methane gas), phycobiliproteins as fluorescent tags, fertilizers and pH control for agricultural soils (i.e. calcareous species are washed, crushed and added to acid soils to correct the pH) and as a potential source of natural products with pharmaceutical relevance. Examples of biologically active substances extracted from red algae include several lectins with haemagglutinating, cell migrating and anticoagulation properties; domoic and kainic acids have anthelmintic, insecticide and medical research applications (the latter as a neuronal agonist). Certain secondary metabolites found in red algae are poisonous (e.g. manauealide and polycavernoside found in Pacific members of Gracilariaceae), showing either antitumour or tumour promoting activities, or display viral inhibitory activity. A plethora of other substances with pharmaceutical applications are extracted from red algae (see review in Smit, 2004).

Phycocolloids

Red algal hydrocolloids (a.k.a. red algal phycocolloids) are polysaccharides with gel-forming capabilities. They can be classified in two classes, each bearing a basic sugar skeleton consisting of 1,3-linked β-D-galactopyranose plus either 1,4-linked 3,6-anhydro-α-L-galactopyranose (i.e. agars) or 1,4-linked 3,6-anhydro-α-D-galactopyranose units (i.e. carrageenans). However, several other sugar residues are present making all natural phycocolloid products (whether agars or carrageenans) a complex mixture of neutral and charged polysaccharides. Phycocolloid gel quality is measured by its rheological properties such as gel strength, density, gelling and melting points. These properties are in turn influenced by the overall chemical composition of the gels, i.e. the ratio among different polysaccharides and modified sugar residues found in it. Some groups of red algae exhibit higher concentrations of one particular class and thus are known as either agarophytes (agar-producers, e.g. Gracilariales, Gelidiales and Ceramiales) or carrageenophytes (carrageenan-producers, e.g. most families currently in the Gigartinales such as Solieriaceae, Hypneaceae, Cystocloniaceae, Caulacanthaceae, Furcellariaceae, Tichocarpaceae, Sphaerococcaceae, Polyideaceae, Kallymeniaceae, Dumontiaceae, Rhizophyllidaceae, to name a few). **See also**: Plant Gums

Agar

Agar was the first phycocolloid discovered and purified, giving rise to a whitish powder product. Agar (or agar–agar) is a word derived from Malay meaning 'seaweed jelly'. At first used as food in Eastern Asia, its applications have multiplied. Agar can be fractionated into two distinct components: agarose and agaropectin. The former is the one with the highest gelling capacity and is a neutral molecule, the latter is charged and can have several of its sugar residues replaced by methylated and sulfated sugar units, among other modifications. The ratio between agarose and agaropectin may vary according to taxonomical, ontogenetical, life-cycle phase, strain selection (genetics) and abiotic factors. In general, the higher the concentration of 3,6-anhydrogalactose, the stronger the gel and higher the quality of the agar.

The current most important economic applications of agar relate to biotechnology, molecular biology and biomedical research industries. Agar gels are the main solidifying agent in microbiological cultures (e.g. bacterial, fungi, viral culture plates), and is used in many electrophoretic applications (e.g. DNA size separation). Agar gelling point usually varies between 35 and 50°C and its melting point is situated between 80 and 100°C.

Carrageenan

Phycocolloids belonging to the carrageenan group are also heterogeneous and complex. Different carrageenan types have traditionally been designated by letters from the Greek alphabet. There are three main commercial classes of carrageenan: κ-, ι- and λ-carrageenans. κ-type may have galactose units esterified with sulfate at the 4-position, κ- and ι-carrageenans contain significant amounts of 3,6-anhydro-D-galactose residues (and can undergo thermally reversible gelation in the presence of potassium and certain other cations) while the λ-type contain smaller amounts to none. Each type of carrageenan exhibits distinct gelling properties and are found in distinct concentrations within red algal cell walls. The amount of a particular kind of carrageenan varies taxonomically, with life-cycle phases, biotic and abiotic factors. The current most economically relevant applications of carrageenan refer to the dairy industry, where it is used as thickening and stabilizing agents in items such as yogurts, heavy and whipping creams, ice creams, chocolates, etc.

Aquaculture

China, Korea and Japan seem to lead the aquaculture of red algae in the world regarding biomass production and economic value generated. Most of their production targets the food market of direct seaweed consumption, making *Porphyra* (nori) the second most cultured seaweed in the planet in terms of biomass produced (Zemke-White & Ohno, 1999). Several indoor and outdoor algal farming techniques and technologies have been developed and tested throughout the world. A significant amount of publications regarding algal aquaculture practices, techniques, management and environmental consequences are available in the literature. Tropical countries such as Indonesia, the Philippines and Tanzania are regarded as major sources of cultured carrageenan-producing species (e.g. *Kappaphycus*, *Betaphycus* and *Eucheuma*) while the temperate coast of Chile is the main source of agar in the world (i.e. from *Gracilaria chilensis*). Other countries recognized as red algal phycocolloid producers include Canada, USA and France. However, seaweed aquaculture for food consumption leads the biomass production and such industries is particularly significant in China, Japan and Korea. **See also**: Biogeography of Marine Algae

References

Adl SM, Simpson AGB, Farmer MA *et al.* (2005) The new higher level classification of eukaryotes with emphasis on the taxonomy of protests. *Journal of Eukaryotic Microbiology* **52**: 399–451.

Ask EI, Batibasaga JA, Zertuche-Gonzalez JA and de San M (2003) Three decades of *Kappaphycus alvarezii* (Rhodophyta) introduction to non-endemic locations. *Proceedings International Seaweed Symposium* **17**: 49–58.

Davidson K, Hamnet M, Minato C (2003) The first four years: Hawaii Coral reef Initiative Research Program (1998–2002). Social Science Research Institute, University of Hawaii at Manoa. 72 pp.

Freshwater DW, Fredericq S, Butler BS, Hommersand MH and Chase MW (1994) A gene phylogeny of the red algae (Rhodophyta) based on plastic *rbc*L. *Proceedings of the National Academy of Sciences of the USA* **91**: 7281–7285.

Grossman AR, Schaefer MR, Chiang GG and Collier JL (1993) The Phycobilisome, a light-harvesting complex responsive to environmental conditions. *Microbiology Reviews* **57**: 725–749.

Harper TJ and Saunders GW (2001) Molecular systematics of the Florideophyceae (Rhodophyta) using nuclear large and small subunit rDNA sequences data. *Journal of Phycology* **37**: 1073–1082.

Keeling PJ (2004) The diversity and evolutionary history of plastids and their hosts. *American Journal of Botany* **91**: 1481–1493.

Littler MM, Littler DS, Blair SM and Norris JN (1985) Deepest known plant life is discovered on an uncharted seamount. *Science* **227**: 57–59.

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ and Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Reviews of Ecology and Systematics* **31**: 481–531.

Rueness J (2005) Life history and molecular sequences of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta), a new introduction to European waters. *Phycologia* **44**: 120–128.

Saunders GW and Hommersand MH (2004) Assessing red algal supraordinal diversity and taxonomy in the context of contemporary systematic data. *American Journal of Botany* **91**: 1494–1507.

Smit AJ (2004) Medicinal and pharmaceutical uses of seaweed natural products: A review. *Journal of Applied Phycology* **16**: 245–262.

Tappan H (1976) Possible eukaryotic algae (Bangiophycidae) among early Proterozoic microfossils. *Geological Society of America Bulletin* **87**: 633–639.

Verlaque M, Brannock PM, Komatsu T, Villard-Bohnsack M and Marston M (2005) The genus *Grateloupia* C. Agardh (Halymeniaceae, Rhodophyta) in the Thau Lagoon (France, Mediterranean): a case study of marine plurispecific introductions. *Phycologia* **44**: 477–496.

Yoon HS, Müller KM, Sheath RG, Ott FD and Bhattacharya D (2006) Defining the major lineages of red algae (Rhodophyta). *Journal of Phycology* **42**: 482–492.

Zemke-White WL and Ohno M (1999) World seaweed utilization: an end-of-century summary. *Journal of Applied Phycology* **11**: 369–376.

Further Reading

Cole KM and Sheath RG (1990) *The Biology of Red Algae*, 517pp. Cambridge, MA: Cambridge University Press.

Guiry MD and Guiry GM (2007) *AlgaeBase version 4.2*. Worldwide electronic publication, National University of Ireland, Galway. http://www.algaebase.org.

McHugh DJ (2003) *A Guide for Seaweed Industry*, 105pp. FAO Fisheries Technical Paper no. 441. Rome, FAO.

Oliveira EC, Alveal K and Anderson RJ (2000) Mariculture of agar-producing gracilarioid red algae. *Reviews in Fisheries Sciences* **8**(4): 345–377.

Pueschel CM and Cole KM (1982) Rhodophycean pit plugs: an ultrastructural survey with taxonomic implications. *American Journal of Botany* **69**: 703–720.