Algal Cell Walls

Secondary article

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Algal cell walls constitute a rich array of fibrillar, matrix and crystalline chemicals. These complex extracellular coverings are formed by complex interactions of intracellular and cell surface events.

Article Contents

Introduction

The algae are a diverse group of primitive photosynthetic eukaryotes that inhabit most littoral freshwater, marine and terrestrial ecosystems. The morphology exhibited by algae includes microscopic unicells, colonies, filaments and large and complex seaweeds. Various classification schemes have been used to group the algae and members are found in both the Protista and the Thallophyta. Modern phycological treatises (e.g. Sze, 1998) will help the reader interpret the history and complexity of algal taxonomy. In this article, the four major groups of algae, the green algae, the red algae, the brown algae and golden algae, will be considered.

Most algae have an extracellular covering comprising anything from multiple layers of elaborate scales to highly mineralized coats to complex cell walls consisting of structural fibrils enmeshed in complex matrices. The structure, chemistry and development of the algal cell wall and related coverings have long fascinated life scientists. For example, early microscopists often studied the elaborate silica-based cell walls of diatoms. Also, various extracted biopolymers of algal cell walls, including alginates and carrageenans, are used extensively today in the medical, pharmaceutical and food industries. Today, modern biochemical extraction methodologies and electron microscopic techniques have elucidated the structure and function of these complex coverings. In the future, the addition of molecular analyses should contribute significantly to our understanding of their synthesis and organization as well as providing improved ways of yielding important, algal-derived wall biopolymers.

Green Algae

The green algae (Chlorophyta) are the ancestral lineage to land plants and comprise a large and diverse group of organisms. Like higher plants, these algae possess chlorophylls *a* and *b*, double membrane-bound chloroplasts and, in most cases, starch as the main food reserve. Current molecular analyses are providing new insights into the evolution and taxonomy of green algae (Melkonian and Surek, 1995). At least four distinct classes have been recognized in the green algae: the Prasinophyceae (or Micromonadophyceae), the Chlorophyceae, the Ulvaphyceae and Charophyceae. Within each class, there exists considerable variation in cellular structure and morphological types as well as extracellular coverings.

Composition and structure

In the most primitive class of the green algae, the Prasinophyceae, cells are typically covered by a series of variously shaped and sized scales or a 'single' covering that represents a fusion of scales called the theca. Scales may also be found on the surface of the flagellar membrane. In scaly prasinophytes, the scales consist primarily of both neutral and acidic sugars including unusual 2-keto sugars such as 3-deoxylyxo-2-heptulosaric acid (Becker *et al*., 1991). Some of these sugars may be sulfated and some scale types appear to be complexed with calcium and phosphate (Domozych *et al*., 1991). Similarly, small amounts of protein/glycoprotein have also been detected, especially in flagellar scales. The theca of prasinophytes like *Tetraselmis* and *Scherffelia* is also rich in acidic sugars including several unusual 2-ketodeoxy sugars (Becker *et al*., 1991). The various scale types of prasinophytes can be spectacular both quantitatively and qualitatively. *Pyramimonas tetrarhynchus* has several distinct layers of variously shaped scales. The outermost layer consists of large scales numbering roughly 7000 per cell, while the innermost layer is made up of up to 300 000 small scales per cell (Moestrup and Walne, 1979). In the freshwater flagellate *Mesostigma viride* the number of layers and types of scales are considerably less than in *Pyramimonas*, but the outermost layer of 'body scales' consists of large and spectacular basket scales which are made of an intricately woven lattice positioned on a flat base and supported by struts (Domozych *et al*., 1991; **Figure 1**).

The class Chlorophyceae contains an assortment of unicellular to multicellular, motile to nonmotile forms. The best-studied members within this class are the volvocalean flagellates (Volvocales) represented by such distinct genera as the unicellular *Chlamydomonas*, and the colonial *Volvox* (Harris, 1989; Kirk, 1998). These organisms and their relatives possess a distinct and unique type of cell wall based upon aggregates of hydroxyproline- and glycine-rich glycoproteins. In the well-studied representative, *Chlamy-*

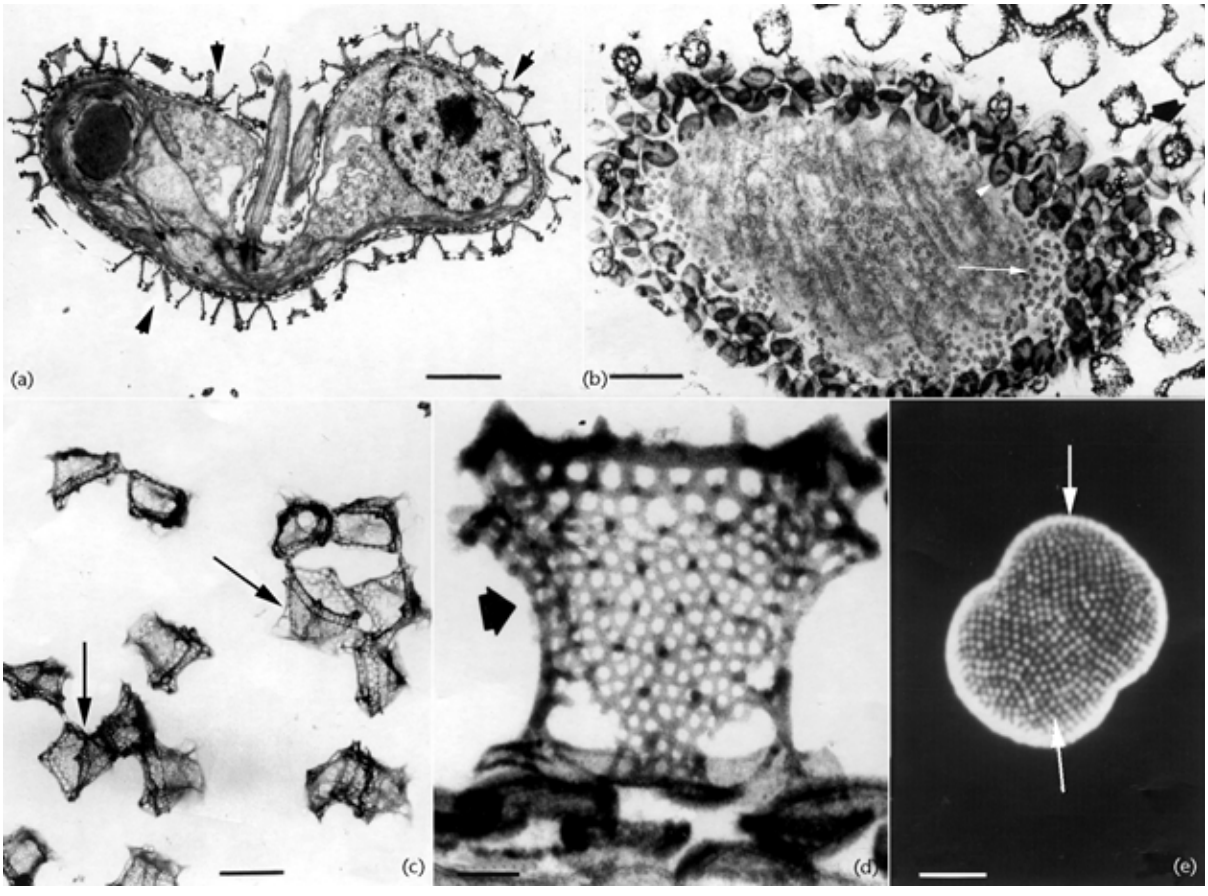

Figure 1 The scaly extracellular covering of the green alga, *Mesostigma viride*. (a) View through the flattened, biflagellated cell showing the noticeable scale-covering (arrowheads). Bar = 1 μm. (b) Glancing section of the cell surface. Note the three layers of the scales, the small underlayer of scales (long arrow), the middle layer, oval scales (small arrowhead) and the large basket scales (wide arrow). Bar = 500 nm. (c) View through a preparation of isolated basket scales (arrows). Bar = 500 nm. (d) Magnified view of the basket scale (arrow) revealing the intricate design of the lattice and supporting struts. Bar = 60 nm. (e) A whole cell labelled with a fluorescent-labelled antibody raised against the basket scale. Note the linear array of scales (arrows) upon the cell surface. Approximately 800 scales can cover a typical cell. Bar = 3 μm. (a)–(d) were processed for conventional transmission electron microscopy while (e) was processed for immunofluorescence light microscopy.

domonas reinhardtii, 17–30 of these glycoproteins are found in the wall complex, arranged into interlocking fibrillar and granular elements, some of which are in crystalline strata (**Figure 2**). In the complex colonial flagellate *Volvox*, the extracellular matrix consists of at least four distinct zones and some of the inclusive glycoproteins are extensively sulfated. A few of these glycoproteins have elaborated into an extensive mucilaginous sheath which holds daughter cells together.

The other members of the Chlorophyceae consists of diverse orders of nonmotile unicellular, coccoid and filamentous forms. The walls of many include the β-1,4-glucan, cellulose, which is arranged in fibrils and is surrounded by a matrix sheath. In more primitive chlorophycean green algae (e.g. *Chlorella*), the microfibrils run in a random meshwork in that cellulose microfibril orientation is not preferentially oriented with respect to the cell surface. Cell wall glycoproteins containing varying amounts of hydroxyproline are also found in these cell walls (Voight *et al*., 1994). In addition, some unicellular members of the Chlorophyceae (e.g. the order of Chlorococcales) contain a 10- to 30-nm-wide, outer wall that has the appearance of a trilamellar sheath. This outer wall stratum is highly resistant to chemical hydrolysis and bacterial enzymatic degradation. The chemicals that make up this layer are called 'algaenans'. They consist of long polymethylenic chains associated with amide groups and minor amounts of *N*-alkyl substituted pyrroles. The role of algaenans appears to be a protective one, especially in conferring resistance to detergents (Corre *et al*., 1996).

The ulvaphycean green algae are represented by many different morphological types ranging from filaments (e.g. *Urospora*) to complex sheets of tissue (e.g. *Ulva*) to siphonous forms (e.g. *Acetabularia*). Most members of this group are marine. The types of cell walls exhibited by the Ulvaphyceae are diverse. Typically, the structure of the

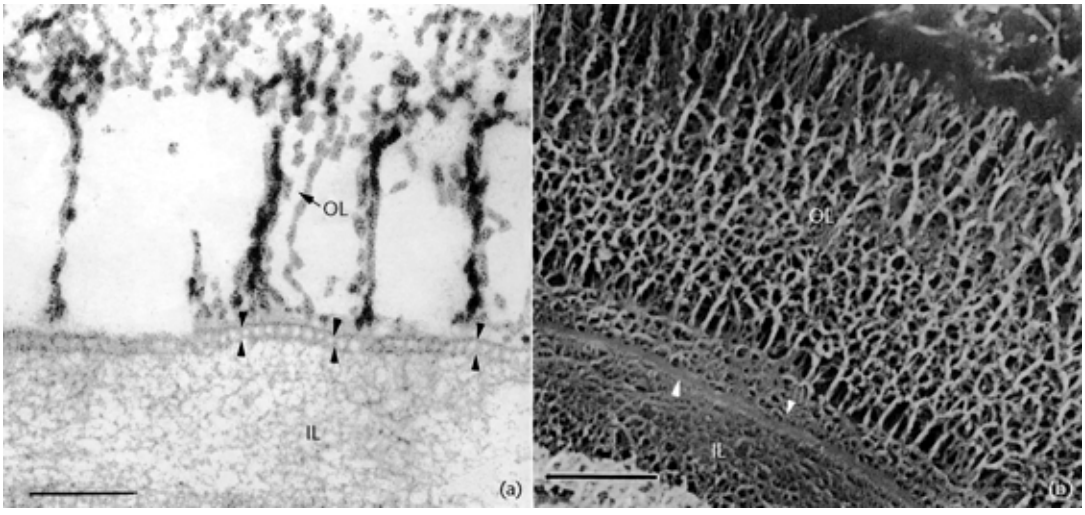

Figure 2 The cell wall of the chlamydomonad green alga, *Gloeomonas kupfferi*. (a) Thin section through the wall; (b) deep etch freeze fracture preparation of the cell wall. For details, see Domozych and Dairman (1993). Note the multilayered nature of the wall with a dense, fibrillar, inner layer (IL), a crystalline median layer (arrowheads) and a fibrous outer layer (OL). The chlamydomonad cell wall consists of an aggregation of hydroxyproline-rich glycoproteins. (a) Bar = 275 nm; (b) Bar = 250 nm.

wall contains a skeletal polysaccharide enmeshed in a matrix that can elaborate into a mucilage (Kloareg and Quatrano, 1988). The skeletal polysaccharides can vary. In the siphon *Valonia*, the structural polysaccharide is cellulose found in highly ordered microfibrillar forms arranged in strict parallel arrays. Between each layer, the orientation of microfibrils switches by about 90°. In other ulvaphycean forms, the microfibrillar polysaccharides can consist of β-1,3-xylans or β-1,4-mannans or complex heteropolymers. Interestingly, different phases of the life cycles of some species can produce different skeletal wall polysaccharides, yet the given structural wall composition does not necessarily correspond to the ploidy level during the particular life phase.

The matrix polysaccharides surrounding the skeletal fibrillar complex in the Ulvaphyceae consists of an array of xylogalactoarabinans, glucuronoxylorhamnans (e.g. 'ulvan' *sensu* Ray and Lahaye, 1995) and rhamnoxylogalactogalacturonans that are variously sulfated. The functions of the ulvaphycean matrix polysaccharides appear to be similar to matrix mucilages in other seaweeds like brown and red algae. Likewise, in some ulvaphycean forms, significant calcification occurs in the wall complex. In the coral reef alga *Halimeda*, crystals of aragonite encrust the cell wall to create a hard surface.

The Charophyceae is the green algal taxon most closely related to higher plants. Within this group are the stoneworts, *Chara* and *Nitella*, the desmids, filamentous conjugating-forms like *Spirogyra* and the highly advanced *Coleochaete*. The walls of most of the members of this group contain cellulosic skeletal components surrounded by pectin-like matrices. In desmids, the microfibril orientation in the wall layers is similar to that of *Valonia*, except that no period of repetition can be seen in the direction of microfibrils throughout the succession of layers. In the stoneworts, microfibrils form an entangled meshwork that may run in a preferential orientation such as longitudinal, oblique, or transverse with respect to the cell axis. Hydroxyproline-containing glycoproteins have also been found in charophyceaen green algae. In some desmids, an extensive mucilage is released through pores in the cell wall, which in turn, causes the cell to glide. Likewise, these mucilages help the cell to adhere to substrates and may be involved in mineral absorption and in interactions with beneficial bacteria. The mucilage is a glucuronic acid- and fucose-rich polysaccharide (Domozych *et al*., 1993). Perhaps the closest charophycean ancestor to land plants among the green algae is *Coleochaete*. The walls of this algae consist of cellulose and matrix polysaccharides. Recently, a cuticle-like morphology has been identified on the cell surfaces of this alga that is strikingly similar to that found in primitive land plants.

Morphogenesis

Morphogenesis of the green algal wall or covering typically includes components of the endomembrane system, the secretory vesicle network and the cytomotile system and terminates, by extracellular events, upon the plasma membrane surface. In scaly green algae, scales are produced within the Golgi apparatus of the cell. Specific scale types are formed within particular loci of the Golgi cisternae and are packaged within secretory vesicles (Moestrup and Walne, 1979). Interestingly, many different

scale types are formed within the same Golgi cisternae and scales are never seen in peripheral vesicles of Golgi bodies. It is believed that Golgi processing of scales in these organisms entails a mechanism of cisternal progression and maturation as opposed to the more commonly accepted model, the vesicular shuttle mechanism (Domozych, 1991). Secretory vesicles deposit scales onto the cell surface or, in some prasinophytes, the scales are deposited first into a vacuole-like, scale reservoir before being released to the cell surface. In related thecate organisms like *Tetraselmis* or *Scherffelia*, precursors of the theca are also made within the Golgi apparatus, transported via secretory vesicles to the plasma membrane and assembled into the final product upon release to the plasma membrane surface. The scale-like subunits of the theca are believed to be connected via calcium bridges.

The synthesis of at least some of the glycoproteins of volvocalean flagellates occurs within the Golgi apparatus. Secretory vesicles carry these components to the cell surface or possibly to the contractile vacuole where they are ultimately released to the cell surface (Domozych *et al*., 1993). Once on the surface, the glycoproteins 'self-assemble' into the cell wall complex.

Desmids exhibit distinct cellular symmetry and have been important specimens in understanding how cell wall morphogenesis occurs. This determines the morphogenesis of the cell. During the cell cycle of the desmid, *Micrasterias*, four types of secretory vesicles are produced in the Golgi apparatus and are associated with wall and extracellular matrix production: (1) 200-nm dark vesicles carrying pectin-like primary wall precursors, (2) flat vesicles containing membrane particles that may represent hexagonal arrays of cellulose synthetase rosettes for secondary wall production, (3) large vesicles carrying mucilage, and (4) 300-nm pore vesicles responsible for the secretion of the plugs necessary for the production of wall pores. Cytoplasmic streaming carries these vesicle populations to and around the cell periphery and it is unknown how particular vesicles are removed from the streaming channels and fused at particular sites of the plasma membrane. Wall development and whole cell morphogenesis is apparently regulated by calcium. Membrane calcium channels are found in distinct zones of the desmid cell periphery but may not be the focal points of wall vesicle fusion and, ultimately, cellular morphogenesis (Holzinger *et al*., 1995).

Cellulose biosynthesis in plants, including the algae, is typically associated with cellulose synthetase positioned on the plasma membrane in terminal complexes. Rosette-like, globule-like, or hexagonal terminal complexes have been found in the Charophyceae, while in the Chlorophyceae and Ulvaphyceae, the terminal complexes are found in linear arrays. From the terminal complexes, cellulose microfibrils are synthesized and movement of these terminal complexes across the plasma membrane yields specific orientations of the cellulose microfibril network in the wall. It has been suggested that subplasma membrane microtubules may be involved in controlling the terminal complex position and movement, and in turn, the orientation of the microfibrillar network. However, at least in some marine green algae like *Chaetomorpha* or *Boergesenia*, there may be no link between cortical microtubule arrangement and microfibrillar orientation (Kimura and Mizuta, 1995).

Red Algae

The red algae (Rhodophyta) represent a diverse assemblage of unicellular to macroscopic morphological types and consist of over 10 000 described species. Members of this group are allied by the absence of motile cells in their life histories, the presence of chlorophyll *a* and phycobilin accessory pigments, the presence of floridean starch as their primary food reserve, and chloroplasts with non-aggregated thylakoids and no external endoplasmic reticulum. Red algae are the commonly encountered biota of the 'seaweed' and coral-based ecosystems of the oceans (Cole and Sheath, 1990). The cell walls of red algae constitute a diverse assortment of both structural and matrix polysaccharides, various glycoproteins, and in some cases, mineralized components.

Composition and structure

The red algal cell is typically surrounded by a cell wall consisting of rigid structural glycans embedded in various matrix polymers of a more flexible nature (Craigie, 1990). Among the structural glycans, cellulose can constitute up to 12% of the cell wall. In addition, structural β-1,4-mannans and β-1,3-linked or β-1,4-linked xylans can be found in various red algae. Both cellulose and β-1,3-xylans are microfibrillar in nature but usually do not appear together in the same phase of the life cycle of the alga. The microfibrillar components of red algae are found in layers that lie parallel to the cell surface. The microfibrils do not exhibit any preferential orientation within each layer.

The matrix components of the red algal cell wall are both diverse and complex. Among primitive forms, e.g. *Porphyridium*, *Rhodella* and *Batrachospermum*, a high molecular weight mucilage is present and contains significant amounts of xylose, glucuronic acid, glucose and galactose. Varying amounts of sulfation and methylation of these sugars have also been noted. These mucilages are produced during the light segment of the photoperiod and can be solubilized into the growth medium during the dark phase. Experimental analysis of isolated matrices from these primitive forms shows that these polysaccharides can form gels, but are of a weaker strength than agars (Geresh and Arad, 1991).

The most common of matrix components of red algae are the sulfated galactans, including the agars and

carrageenans. These polysaccharides are found in diverse forms of red seaweeds. Their backbone is repeating galactose and 3,6-anhydrogalactose residues linked β-1,4 and α-1,3 respectively. This underlying structure is often masked by other sugars and sulfate. Sulfation levels vary from 20–38% in carrageenans to 20% in agaropectin to about 2% in agarose (these last two materials are subcomponents of agar). Carrageenans are found in many diverse red algae but have been most thoroughly examined in the economically important order of red seaweeds, the Gigartinales. Based on sulfation patterns, carrageenans are grouped into several families including kappa, beta and lambda. In most cases, different types of carrageenans can be found in the same alga. Agar is another type of sulfated galactan that belongs to the supergroup of 'agarocolloids' found in at least eight orders of red algae. Structurally, carrageenans are arranged in right-handed helices while agar exists in a left-handed helix. Gelation of these polysaccharides may result from transformation from random coils into distinct double helices (e.g. upon cooling heated solutions) or by cations facilitating side-by-side aggregations of the double helix into three-dimensional gels. Environmental factors including temperature and nitrogen availability can affect the composition of these matrix materials and their gel strength. Some of the matrix polysaccharides have significant commercial applications in the pharmaceutical and food industries. Agars and carrageenans collected from red seaweeds are used as stabilizers, binders, gelling agents and texturizers in food products and as key components of matrices in the medical and dental fields (Renn, 1997).

Proteins and glycoproteins are minor components of the red algal cell wall. They have been shown to be important in cell adhesion, for physical protection of the algal surface, and as antifouling agents through sloughing off of the outer cuticular layers. The wall-based glycoproteins of red algae are devoid of arabinose–hydroxyproline linkages typically found in higher plant extensins. Many red algae possess a distinct cuticle or an outer layer of wall that can be removed from the cell wall proper. The cuticle consists of various amounts of protein and carbohydrate, including mannans, and can be complexed with sulfate or bromine.

Calcification

Many species of red algae produce calcium carbonate-encrusted surfaces and are important components of coral reefs and other marine ecosystems. Two types of calcium carbonate can be deposited in these red algae: in coralline red algae (Corallinales) the rhombohedric calcite is deposited, while in other orders, e.g. Nemaliales, the orthorhombic aragonite is deposited. The calcification process requires photosynthesis which raises the pH near the surface of the alga. This serves as the chemical basis for carbonate deposition. Calcium carbonate deposition is ordered and is believed to occur around a network of organic fibres in the cell wall. While little is known of this process, it is thought that glucuronic acid-rich alginate may be a key component of the process.

Brown Algae

The brown algae (Phaeophyta) are similar to golden algae in that they possess chlorophylls *a* and *c* and fucoxanthin and β-1,3-glucans as their food reserve. In fact, many evolutionary biologists suggest that they should be grouped with the golden algae into the large group, the Chromophyta. The vast majority of brown algae are marine and form complex multicellular thalli that are familiar to us as rocky shore seaweeds (e.g. *Fucus*) and kelps (e.g. *Macrocystis* and *Laminaria*) (Sze, 1998).

Structure and composition

The cell walls of brown algae consist of a fibrillar framework enmeshed in complete matrices (Kloareg and Quatrano, 1988). The structural fibrils of the wall are made of cellulose. Like red algae, the cellulose microfibrils are contained in layers parallel to the cell surface, although they do not exhibit any preferential orientation within each layer.

The major matrix component of the brown algal cell wall is alginate, which may constitute up to 45% of the dry weight of the alga. This polysaccharide primarily consists of two sugar acids, mannuronic acid and guluronic acid, and is arranged in specific blocks of units which can be linked to form a macromolecule with a total molecular weight of 800 000. Introduction of calcium ions into alginate solutions leads to the formation of insoluble gels, whereas alginate gels formed from complexing with sodium or magnesium, lead to water-soluble gels. *In vivo*, the calcium-based alginate gels embed the cellulose microfibrils. It has recently been shown that phenolic compounds may also play key roles in the alginate–wall complex (Schoenwaelder and Clayton, 1998). The gel-like nature of alginates is believed to be significant in prevention of desiccation and other protective roles such as maintenance of rigidity and ion regulation. Alginates are economically significant. They are extracted from various brown algae and are utilized as thickeners and stabilizing agents in pastry/cake icings, frozen foods, salad dressing, pharmaceutical tablets and dental impression media (Renn, 1997). Several other matrix polysaccharides can be found in brown algae including the fucoidans and ascophyllans.

Morphogenesis

The development of the brown algal cell wall has been well studied during the postfertilization period in the zygote of

Fucus. Alginates were the first main wall component detected in 15 minutes after fertilization. This was followed by cellulose production 30 minutes postfertilization and fucoidan production 45 minutes after fertilization. After 4 hours, the zygote wall has stable structure and consists of 60% alginate, 20% cellulose, 20% fucans. During the developmental process, the sugar composition of alginate is relatively stable whereas significant qualitative changes occur in fucoidan composition. Cellulose synthesis occurs in terminal complexes upon the plasma membrane surface. These complexes are arranged in linear arrays or in distinct pentads.

Golden Algae

The golden algae consists of a diverse assemblage of organisms that have chlorophylls *a*, *c*1, *c*2 and fucoxanthin, β-1,3-linked glucans as their food reserve, and three membranes in the chloroplast envelope. Taxonomic groupings within this group are both complex and variable (Sandgren *et al*., 1995; Sze, 1998). A multitude of morphological types exists within the golden algae and similar diversity is seen in their cell walls and related extracellular coverings.

Synurophyte members of the golden algae (class: Synurophyceae) are unicellular or colonial flagellates characterized by an elaborate covering of diversely shaped siliceous scales (Sandgren *et al*., 1995). The scales are arranged in an imbricate style and held in place by a protein-like adhesive. The scales are produced within a network of silica deposition vesicles (SDVs) emanating from the surface of the chloroplast. The production of scales has been shown to be sensitive to silica levels in the growth medium and cytoskeletal disrupting agents (i.e. poisons that affect microtubules and microfilaments).

The prymnesiophytes or coccolithophorids (class: Prymnesiophyceae) are important marine phytoplankton which sometimes bloom to create a phenomenon known as the white tide. They are covered by a series of scales called the coccosphere which contains 10–100 coccolith scales ranging in size from 5 to 50 μm. Each coccolith consists of an organic base plate surrounded by a rim of calcium carbonate crystals. An organic coat of acidic polysaccharides surrounds the coccoliths. The formation of the coccolith includes a special coccolith vesicle (CV) which is situated near the nuclear envelope and is connected to a series of branched tubules (Marsh, 1996). Polysaccharides are delivered to the CV by a series of Golgi-derived vesicles.

In the chrysophyceae proper (class: Chrysophyceae), the walls or coverings can either be scale- or lorica-like. They are usually mineralized with silica, iron, manganese or various calcareous structures. Likewise, a distinctive resting stage, the statocysts, can be formed by members of this group. The statocyst wall is complexed with silica and formed within a distinct SDV. Proteinaceous plugs are found in some pores of the silica covering (Sze, 1998). In the xanthophycean or tribophyceaean members of this group, the wall is believed to be cellulosic with a pectin matrix.

Diatoms (class: Bacillarophyceae) are the most extensively studied group of golden algae. These organisms are especially important as primary producers in marine and freshwater ecosystems and as biofouling agents. Diatoms are unicellular or filamentous microorganisms that are distinguished by their cell wall or frustule. The frustule consists of two large overlapping parts, a hypovalve and an epivalve, and a series of girdle bands inserted between the valves. Based on general frustule structure, diatoms can be classified into two large groups: centric diatoms (radially symmetric about an axis passing through the centre of the cell) and pennate diatoms (bipolar and usually elongate forms that have an axis of symmetry along the length of the cell). Many pennate diatoms have a distinct slit running the length of the cell called the raphe. This structure is the focal point of mucilage extrusion which results in gliding motility. The frustule consists of various forms of silica or amorphous hydrated silicium dioxide along with an organic matrix of protein and polysaccharides. Two classes of proteins have been found associated with the frustule (Kroger *et al*., 1997); an EDTA-soluble group known as the frustulins and a hydrofluoric acid-extractable group known as HEPs (hydrofluoric acid-extracted proteins).

The formation of the elaborate components of the frustule has long fascinated scientists. Frustule biogenesis is associated with cell division. During and after cytokinesis, one daughter cell receives the parental epivalve and must make a corresponding hypovalve while the other daughter cell receives the parental hypovalve and makes a corresponding epivalve. The formation of the new valves occurs within the specialized membranous compartment, the SDV, commonly seen in many of the Chrysophyta. Soluble silicate is removed by the diatom from its medium and transported to the SDV. Here, it is condensed into an insoluble silica form with the aid of a protein- and/or polysaccharide-based organic matrix. The intricate assembly of a species-specific frustule shape occurs within the developing SDV, ultimately leading to the release of this wall component to the cell surface (Pickett-Heaps *et al*., 1990). The daughter cell that receives the original epivalve of the parent cell is the same size as the parent cell. However, the daughter cell that has the parental hypovalve produces a smaller epivalve and is smaller than the parent cell. As cell division continues, the average cell size of the diatom population may progressively decrease until sexual reproduction restores cell size to maximum.

The diatom cell wall is also often associated with a variety of extracellular polymeric substances (EPSs) that take the form of stalks, tubes, apical pads or films. These materials are associated with the frustule or more often are outside the frustule. The functions of the EPSs include adhesion to surfaces, increased surface area for

associations with bacteria, and metal chelation (Hoagland *et al*., 1996). One of the more obvious functions of the EPS can be seen in motile diatoms. Out of the central groove-like raphe, a cable-like material is released which, upon interactions with the growth medium, causes a propulsion of cells forward (e.g. 'gliding'). The EPSs consist of various molecules ranging from acidic and sulfated polysaccharides to proteoglycans to chitin fibrils. Synthesis of these materials has been demonstrated in the Golgi apparatus and upon the plasma membrane.

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