

Biomechanical Properties of Coenocytic Algae (Chlorophyta, Caulerpales)

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ABSTRACT: Coenocytic algae are highly visible components of the seaweed flora in shallow tropical coral and sedimented habitats. Coenocytes are unicellular (acellular) and are able to seal and repair damage to their enclosing membrane, and to possibly regrow lost tissue. There is no documented *in situ* evidence that entire individuals of coenocytic algae are capable of re-attachment once dislodged. These properties suggest that if these organisms are subjected to sufficient physical stress (e.g. hydrodynamic forces), they will break rather than be dislodged from the substratum. Investigation of some biomechanical properties (force to remove, force to break, and strength) of species of *Udotea*, *Halimeda*, and *Penicillus* shows, however, that in more than 95% of cases when these species are so stressed, they detach whole rather than break. This contrasts sharply with the response of most multicellular algae tested, which frequently break within the thallus. Chemical/structural properties of coenocytes that may contribute to these results are the biochemical nature of the cell walls of coenocytes and the presence of a surface layer of calcium carbonate. The potentially rare occurrence of sufficient hydrodynamic forces to dislodge these algae, and the possibly fatal consequences if herbivory damages the thallus, may result in selection for a tough thallus rather than one that breaks.

KEYWORDS: *Udotea*, *Halimeda*, *Penicillus*, coenocyte, biomechanics.

INTRODUCTION

Coenocytic algae are a visibly obvious and ecologically important component of many tropical and subtropical shallow water benthic communities. Research on coenocytes has yielded insights on their biology and ecology, but less is known of their biomechanical properties, and how these shape ecological responses. Here, the biological, chemical, and physical properties of coenocytic algae are reviewed, and the relationship of these properties to known or potential biomechanical properties are examined. Specifically, I focus on species of the order Caulerpales. Based on (few) known properties, I evaluate some predictions against extant data.

What are Coenocytes?

Definition

Coenocytic algae are multinucleate organisms, lacking transverse walls¹; most coenocytes are members of the Chlorophyta, and of the Caulerpales. It is to species of the latter that the comments in this paper are addressed.

Structure

Coenocytes are unicellular except when reproductive structures form, which may be delimited by a transverse wall. While Vroom and Smith² argue

convincingly that a more appropriate term for coenocytic organisms is 'acellular' (organisms lacking cells), this term has not yet come into common usage. Examples of coenocytic algae are species of *Caulerpa* J.V. Lamouroux, *Halimeda* J.V. Lamouroux, *Codium* Stackhouse, and *Penicillus* J.B. de Lamarck, all members of the Chlorophyta and Caulerpales. Closely related structurally to coenocytes are siphonous algae; both types consist of multinucleate cells, but differ in that siphonous algae have some transverse walls. Again, Vroom and Smith² suggest an alternative descriptive term, 'pseudocellular'. Siphonous algae are represented by the Siphonocladales and Cladophorales and genera such as *Cladophora* Kutzing, *Anadyomene* J.V. Lamouroux, and *Dictyosphaeria* Decaisne.

Coenocytes vary in size, but all are macroscopic algae, hence easily visible to the eye. *Caulerpa* 'stolons' may extend for meters over the surface of the substratum whereas, for example, adult individuals of *Penicillus* are much smaller and rarely exceed 15 cm in height above the substratum. Species of *Codium*, while often not exceeding 40 cm in length, can be extensively branched, resulting in individuals of considerable biomass. In judging size of coenocytic algae, their possibly clonal nature must be considered, as some species of coenocytes are joined by subterranean rhizoids, e.g. *Udotea*, *Penicillus*^{3,4,5} and some species of *Halimeda*⁶. Such subsurface rhizoids function to

produce multiple upright individuals (ramets). Since these rhizoids eventually break or disintegrate, the result is separate⁶, but genetically identical, individuals.

It has not been determined experimentally whether such horizontal rhizoids are able to function in regenerating lost ramets of the clone. However, given their demonstrated ability to grow and produce ramets once, it seems at least possible they could do so again if a ramet is lost; however, this may require continued attachment to a 'parent'. *Penicillus*, *Rhipocephalus* Kutzing, and *Udotea* also produce new thalli by such rhizoidal connections⁶, and in *Penicillus* the main form of reproduction is vegetative propagation by rhizoids³.

While species of *Caulerpa* are unicellular like other coenocytes, many have internal elaborations (trabeculae), branched cell wall extensions that can span the diameter of the cell. The function of trabeculae is unknown, but it is assumed that they provide some structural rigidity. Trabeculae may also prevent a rapid collapse of the stolon if it is punctured, thus reducing loss of cytoplasm.

Holdfast morphology is generally similar for coenocytic algae growing in sediments, often consisting of a cylindrical plug of filaments, and incorporating many of the calcium carbonate grains that make up the sediment. The same species growing on rock have a different holdfast morphology, often one that follows the contours of the hard substratum. The relationship between holdfast morphology and biomechanical function, and the variability of holdfast morphology within and between species of coenocytes has been little studied.

Calcium carbonate is a common cell wall component in many coenocytes. Individuals of *Halimeda* are relatively heavily calcified, especially in the older (above ground) basal portions, whereas genera such as *Penicillus* and *Udotea* are less calcified. Few, if any data exist indicating a relationship between the thickness of calcium carbonate and environmental factors such as wave exposure or herbivore intensity. Padilla⁷ investigated the biomechanical consequences of calcification and found that calcified tropical algae (a coenocyte and two multicellular species) were significantly stronger than similar non-calcified algae. In a biomechanical context calcification thus acts to strengthen the thallus against tensile forces, in addition to having other possible functions such as influencing the effectiveness of herbivory^{4,7,8}

Habitat

As indicated by the genera named, coenocytic algae are most common in tropical and subtropical waters, and much less so in cold temperate seas. For example, there are two species of *Codium* on the Pacific shores of Canada, in contrast to some 109 species worldwide⁹.

The depth at which coenocytes grow, and the substratum on which they reside, varies greatly. Depth ranges from the mid- to low-intertidal to shallow subtidal, and to some 130m¹⁰ for *Halimeda*, to 200m for a species of *Codium*, *C. mamillosum* Harvey (personal collection) in Hawaii. In warmer waters coenocytes are predominantly subtidal, whereas the few temperate species of *Codium* are commonly found in the mid- to low-intertidal zone. In tropical areas, coenocytes can be found growing on (usually) dead coral, and on the interspersed sediments, though different species often predominate on one substratum. In temperate waters, *Codium* is restricted to rocky or other hard substrata.

Wave exposure varies among habitats of coenocytic algae. There are, however, only subjective measures of wave exposure available for such habitats. Species of *Penicillus*, *Udotea*, and *Halimeda* are found in seaward sediments fringing many mangrove habitats (relatively wave sheltered sites), as well as intermixed with seagrasses on the shoreward side of reefs. Species of *Halimeda* and *Udotea* can also be found on the seaward face of some reefs, where wave exposure is more intense.

Thallus morphology and orientation of coenocytes is known to vary with the direction of the incoming waves³. In shallow water habitats, both the stipe and capitulum of *Penicillus dumetosus* (J.V. Lamouroux) Blainville and *P. pyriformes* A. Gepp & E.S. Gepp are flattened perpendicular to the direction of incoming waves. In deeper water and where wave direction is more variable, such flattening is absent. These authors³ note a similar phenomena in some species of *Avrainvillea* Decaisne, *Udotea*, and *Halimeda*. Such flattening may minimize destructive torsion (rotational) forces on wave exposed species, and encourage bending which reduces drag forces on these thalli.

Structural Differences Between Coenocytic and Multicellular Algae, and their Biomechanical Implications

The most obvious structural difference between coenocytic and non-coenocytic algae is the multicellular nature of the latter. Much less obvious is whether this and other structural differences might lead to biomechanical differences. Biomechanical properties of interest here include strength (force to break per unit area, N m⁻²), removal force (force required to remove an organism from the substratum, N), and break force (force required to break an organism, N). Ecological consequences related to biomechanical properties include location of the break, whether an organism breaks before it is detached from the substratum, and consequences of removal and breaking. Secondary properties of interest are questions about the relationship between morphological and biomechanical properties, for

example between blade surface area and holdfast volume, between blade surface area and force to remove, and between removal force and holdfast volume. One might expect, for example, that as blade surface area increases (resulting in increased drag) that holdfast volume and attachment tenacity will increase to compensate.

Cell wall composition is a biochemical character that may have biomechanical consequences; however, this possible relationship has not been examined. Biochemical analyses indicate that many coenocytes have walls not based on cellulose fibrils (unlike many other green algae), but rather consist of polymers of xylose, e.g. *Caulerpa*¹¹, or mannose, e.g. *Codium*¹², within a matrix of hemicellulose (a viscous polymer). Mannan and xylose polymers also occur within the walls of some Rhodophyta (e.g. *Porphyra* C. Agardh), thus are not unique to these green algae. *Udotea*, *Penicillus*, and *Halimeda* have a cell wall composed mainly of xylan, with little or no cellulose¹³. Many multicellular algae have sulfated polysaccharides, e.g. alginates, agar, or carageenan, as a cell wall constituent intercalated between the individual cells; coenocytic algae apparently lack these constituents.

If tearing occurs in a stipe or blade, it probably occurs differently in multicellular algae vs. coenocytes. In a coenocyte, a tear must propagate into the cell wall, hence the construction and composition of the cell wall as a whole is critical. If a complete fracture occurs this subjects the entire cell (= organism) to a potential loss of cytoplasm. Is the coenocyte wall a single homogeneous material, and hence with similar biomechanical properties throughout, or is it a composite material, e.g. layers of material each with different properties (such as moduli of elasticity, and strength)? In a coenocyte such as *Codium*, there is evidence for mannan microfibrils bound to a protein component. In other algae containing mannan, e.g. *Dasycladus* C. Agardh, the mannan microfibrils appear to run vertically in the inner wall, and transversely in the outer wall¹⁴. Such structures suggest composites but their biomechanical characteristics are as yet unknown.

Contrasting with coenocytes, multicellular algae may break either through cells, or along a common fracture zone through the wall but between cells¹⁵ (Fig. 5.34¹⁵). Mackie & Preston¹² and Vincent¹⁵ point out that "... fracture of plant materials ... has been mostly very poorly studied ..."; little appears to have been added that is relevant to algae since this time. If present, does the layer of sulfated polysaccharides serve as a fracture conduit in multicellular algae? Biedka et al.¹⁶ studied fractures in *Pterygophora* Ruprecht, a kelp, and noted that longitudinal tears shattered individual cells, whereas transverse tears most likely progressed

between columns of radially oriented cells (but nevertheless resulting in many cells being torn open). The role, if any, of the sulfated polysaccharide layer in directing tearing remains unclear.

Another factor influencing tearing in multicellular algae is the brittleness of their tissue. As a result, if a flaw occurs, and if this flaw exceeds a critical length, little additional stress is required to propagate such a fracture^{16,17}. Thus, in this case, the multicellular structure does not deter fracture. However, few such data are available for algae in general. There is much research to be done, as investigations on fractures, and fracture propagation, in algae are even less common than for vascular plants.

Within coenocytic algae, differences in construction may affect their biomechanical properties. Here it is useful to distinguish between two types of coenocyte morphologies, the essentially tubular morphology of, e.g. species of *Caulerpa*, vs. the interwoven-siphon (= IS) construction of most other coenocytes, e.g. species of *Codium*, *Halimeda*, *Udotea*, and *Penicillus*. There are no biomechanical data available for the former type, so further discussion is restricted to the IS construction. Biomechanically, the IS type is similar to a rope constructed of many separate fibers – a construction which increases the force-to-break well beyond that of the individual fibers. Is the acellular but rope-like structure of many coenocytes more or less stronger than a cellular construction? It makes sense that, at a minimum, the 'rope' structure confers a degree of safety, in that the breaking of one or a few fibers is not likely to be critical to the biomechanical integrity of the alga.

If Coenocytic Alga Break, What are the Consequences?

For coenocytic algae, the consequences of breaking could theoretically result in extensive loss of cytoplasm, and this topic is reviewed by Ram & Babar¹⁸. The ability for coenocytic algae to heal wounds is well documented^{19,20,21,22}. In general, a gelatinous plug forms within seconds^{1,23} of wounding, and is subsequently elaborated, with a new wall completed within 2 – 6 days. Thus, given the rapidity of the healing process, cytoplasmic loss is usually minimal. Other methods of survival and propagation may remain to be discovered, as recently Kim et al.²⁴ report that subprotoplast formation occurs after wounding in *Bryopsis* J.V. Lamouroux, and Chang et al.²⁵ report formation of gametangium-like propagation buds in *Codium edule* P.C. Silva. Responses to, and consequences of, breaking may differ in coenocytes with a *Caulerpa*-like morphology vs. those with an IS construction. Again, the IS construction may minimize loss of vital cellular materials, if the break occurs in only a few siphons.

Less well documented is the ability of a newly healed

coenocyte to regenerate lost parts, e.g. photosynthetic and reproductive structures. Colombo and De Carli²⁶ investigated regeneration in *Udotea petiolata* Boergeson in culture, and report that regrowth began within 2 months after wounding, in all parts of the thallus (blades and stipe), and resulted in regrown parts similar to those formed by normal morphogenesis. They also noted that polarity was retained in cut sections, e.g. blades regenerated from the distal portion, and rhizoids from the opposite end.

The above short review makes it clear that there is much we do not know about biomechanical traits of coenocytic algae. Based on available data, however, some predictions can be made. First, given that the healing process in coenocytes is apparently rapid, and that complete removal of a thallus from the substratum (rather than breaking) most likely leads to mortality, it seems advantageous that when such algae are exposed to sufficient force, coenocytes will behave as most multicellular algae, and break somewhere within the thallus. This would result in maintaining space, rapid healing and, potentially, regrowth. The biomechanical mechanism whereby a break occurs, thus preventing complete detachment, is that holdfast tenacity must be greater than the force required to break some part of the thallus. Second, since wave-exposed coenocytic

algae are subjected to greater drag forces than those in wave-sheltered sites, and since calcium carbonate has been shown to make the thallus less likely to break, algae in more wave exposed habitats are predicted to have a thicker layer of calcium carbonate.

Known Biomechanical Properties of Multicellular and Coenocytic Algae

Table 1 summarizes biomechanical properties relevant to this review. These data were obtained from replicates of individual algae that were of average size within their population. As a result, these data will differ for individuals smaller and larger (though strength may not). Based on these data, strength of some multicellular algae (e.g. *Mastocarpus papillatus* (C.Agardh) Kutzing; Rhodophyta) is two orders of magnitude below that of the coenocytic algae tested to date. The maximum strength of multicellular algae (e.g. *Hedophyllum sessile* (C. Agardh) Setchell; Phaeophyceae) is the same as that of the strongest coenocyte tested to date. The force to break for multicellular algae (e.g. *Mazzaella splendens* Setchell & N.L. Gardner) Fredericq) is considerably larger than for the coenocytic species. For coenocytes, the force to dislodge an individual is always less than the force to break, whereas this situation is frequently reversed for multicellular

Table 1. Summary of biomechanical characteristics of some coenocytic and multicellular algae.

Algae	Variables						
	Surface Area (M ²)	Strength (MN/m ²)	Force to Break (N)	Force to Dislodge or Break (N)	Location of Break	Velocity to Remove (m/s)	
Coenocyticalgae							
<i>Halimeda incrassata</i>	0.0026	1.0 (0.2)	12.3 (1.8)	7.1 (1.7)*	At genicula; No break if tested at stipe	7.3	
<i>Udotea flabellum</i>	0.0049	3.5 (0.8)	22.1 (3.4)	12.7 (3.0)	Removed without breaking	15.5	
<i>Penicillus capitatus</i>	0.0003	7.0 (1.6)	8.1 (0.9)	5.0 (0.6)	Removed without breaking	15.8	
<i>Penicillus pyriforme</i>	0.0004	4.5 (0.5)	6.6 (0.9)	4.9 (0.4)	Removed without breaking	13.4	
Multicellular algae							
<i>Alaria marginata</i> **	0.075	3.5 (0.7)	26 (2)	26 (2)	45% HF/Stipe 55% Blade	18	
<i>Hedophyllum sessile</i> **	0.22	0.07 (0.02)	101 (8)	101 (8)	60% HF 30% Stipe	10	
<i>Egregia menziesii</i> **		1.7 (1.1)	92 (7.2)	92 (7.2)	52% HF/Stipe 48% Blade	NA	
<i>Mastocarpus papillatus</i> ***	0.0015	6.7 (2.8)	Stipe 2.2 (1.17) narrow base of stipe	3 (0.4)	3 (0.4)	88% broke at narrow base of stipe	65
<i>Mazzaella linearis</i> **	0.015	4.6 (0.11)	15 (1.2)	15 (1.2)	88% HF/Stipe	23	
<i>Mazzaella splendens</i> **	0.015	7.2 (0.7)	9.8 (0.8)	9.8 (0.8)	63% HF/Stipe 31% Stipe	26	

* Clamp placed at stipe, as individual discs broke at forces too low to measure.

** Bamfield Marine Sciences Centre Fall Program Class (2000).

*** Carrington.³⁰

species. Note, however, that the coenocytic species tested to date all were anchored in sediments, whereas multicellular species tested all grew on rocky substrata.

Known Correlations Between Morphological and Biomechanical Properties

Given the multitude of morphological features that could potentially affect biomechanical properties, one might expect correlations between some of them, e.g. between blade surface area and dislodgment force. As blade surface area increases, and thus presents a greater surface area for the generation of drag, so might such features as holdfast volume increase (or surface of attachment to the substratum), and similarly the force required to remove an individual from the substratum. In a review of published data (predominantly for multicellular algae), Thomsen and Wernberg²⁷ concluded that the only consistently significant and positive correlation was between force to break and area of the thallus. Anderson et al.⁵ reached a similar conclusion for coenocytic algae, and concluded that the only consistently positive correlation among the coenocytes tested was between blade surface area (= BSA) and force to remove, and often between BSA and holdfast volume.

CONCLUSIONS AND DISCUSSION

What conclusions can be made about biomechanical properties of coenocytic algae, comparative properties with multicellular algae, and future research directions related to this topic? Despite similarities, one outstanding difference is that coenocytic algae dislodge from the substratum before breaking, whereas multicellular algae tend to break in some part of the thallus, and thus leave behind a holdfast, or the holdfast and parts of the stipe and blade. The ecological consequences of these differences need to be explored by manipulative experiments, but some could be explored in the context of known reproductive and regenerative capacities.

For coenocytic algae it is suggested that, given sufficient applied force, they would break rather than be dislodged in their entirety. The evidence to date indicates that in more than 90% of cases whole thallus dislodgment occurs in coenocytic algae growing in sediments. This is a surprising result and, given the likely consequences (death), one that does not make immediate sense from an evolutionary perspective. Possibilities that need to be explored are first, whether re-attachment of a dislodged thallus is more likely than supposed and, two, if regrowth from connecting rhizoids occurs, and whether this compensates for lost ramets.

In the case of *Halimeda*, evidence indicates that

pieces of the thallus are able to re-attach and regenerate a new thallus. This ability arises in part from the tendency of the *Halimeda* thallus to fragment into the constituent calcified discs, due to biomechanically weak sites in the uncalcified genicula. Additionally, Walters & Smith²⁸ report that fish grazing produces fragments from mid-segment of *Halimeda*, and that reattachment structures rapidly grew from these fragments. No such weak points exist in the coenocytic genera tested to date, *Udotea* and *Penicillus*, hence an entire individual would need to re-attach. There are no field data on the ability of species of these latter two genera to regrow (once completely detached) from connecting rhizoids, and it is similarly not generally known how common such rhizoidal connections are (Anderson et al.⁵ report that about 10-15% of thalli had such connections; and see previous discussion). Hillis-Colinvaux⁶ reports that rhizoidal connections were present in some species of *Halimeda*, but Anderson et al.⁵ failed to find such connections in *Halimeda incrassata* (J. Ellis) J.V. Lamouroux (note: this species was identified in error as *H. gracilis*; thanks to Dr. Heroen Verbruggen for calling this to our attention).

Another possibility that could account for the apparent contradiction inherent in whole plant detachment of these coenocytes is that so few individuals suffer this fate that it is ecologically unimportant. The approximate forces required for detachment can be calculated for these algae⁵, and translated into the corresponding water velocities required to generate such forces. In general, young individuals (with correspondingly less surface area to generate drag) are highly unlikely ever to encounter water velocities sufficient to remove them through this factor alone⁵. Larger thalli are more likely to encounter such forces, but it would still require hydrodynamic forces that would only be generated by a major storm⁵. In the absence of any data on water velocities encountered (but see some speculative data in Collades-Vides et al.²⁹), but knowing that such velocities are in any case uncommon, factors other than hydrodynamic ones may be more relevant in shaping morphology and biomechanical properties of coenocytes. For example, herbivory (prevalent in many tropical habitats), which results in parts of the thallus being sheared away, might result in an adaptive response for rapid healing, a tougher cell wall to prevent penetration, and for calcification to deter herbivory and strengthen the thallus. All of the latter would result in a thallus more likely to be removed in its entirety, rather than breaking.

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