

## MINIREVIEW

### COMPETITION STUDIES OF MARINE MACROALGAE IN LABORATORY CULTURE

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Competition for space between different species of benthic marine algae or between marine algae and encrusting animals has been primarily examined in the field (e.g. Dayton 1971, 1975, Kooistra et al. 1989, Paine 1990). Few studies have been conducted in laboratory culture, although such an approach can provide several advantages. This paper is intended to review observations from culture studies by ourselves and others on the general topic of macroalgal competition and interaction. By bringing together a diversity of observations from macroalgal culture studies, we hope this brief review will stimulate their greater use to test ecological theory on competition. In particular, we will describe the interactions that occur when fleshy algal crusts, crustose holdfasts, or sporelings of the same or different species grow together. Since these morphologies are restricted to two-dimensional growth, observations in laboratory culture allow for easy macro- and microscopic examination of interaction between individuals (Pentecost 1980) and estimation of competitive success by measurements of areas occupied (Dale 1985).

Culture techniques were first applied to dedicated investigations of competition between species of marine algae by Russell and Fielding (1974) and Fletcher (1975). Russell and Fielding examined interspecific competition among a brown, a red and a green filamentous algal species (*Ectocarpus siliculosus*, *Eythrotrichia carnea* and *Ulothrix flacca*). Fletcher worked with a brown crustose alga (*Ralfsia spongiocarpa*) and two red crusts (*Porphyrodiscus simulans* and *Rhodophyllum elegans*). Both studies reported evidence of interspecific inhibition. Fletcher suggested that the production of antibiotic compounds (allelopathy) by *Ralfsia* enabled it to inhibit the growth of the two red algal crusts. Antibiotic compounds have also been implicated in the inhibition of benthic diatom growth in cultures of crustose germlings of *Chondrus crispus* (Khafji and Boney 1979) and may be involved in the suppression of cyanobacteria by the red crust *Peyssonnelia immersa* (Maggs, unpubl.).

The principal contribution of culture studies to our understanding of macroalgal competition, how-

ever, comes from spore culture studies whose objectives were mainly taxonomic or developmental. Nevertheless, these provide considerable insight into macroalgal intraspecific interactions. Most past work, as well as our own, was conducted on red algae. The examples we will discuss exhibit several life history types, which can be summarized as follows (for further details see West and Hommersand 1981): 1) isomorphic, in which haploid and diploid spores resulting from meiosis and fertilization, respectively, grow into morphologically similar gametophytic and tetrasporophytic thalli that may be entirely crustose or form erect axes from a crustose holdfast (e.g. *Chondrus*, *Gracilaria*); 2) heteromorphic, in which only the haploid, gametophytic phase develops erect axes, and the diploid tetrasporophyte is crustose (e.g. *Gymnogongrus ?patens*, *Phyllophora trillii*); 3) *Rhodophyllum*-type, in which crusts are haploid and diploidized carpogonia divide into tetrasporocytes and regenerative tetrasporangial stalk cells (e.g. *Rhodophyllum elegans*, see Saunders et al. 1989).

The ability of sporelings and crusts of a single species to grow together and form completely coalesced masses has been described in several studies of erect and crustose, fleshy and coralline red algae. We propose here that observations of these phenomena indicate that cooperation, rather than competition, is the most significant feature of intraspecific interactions of this type. We suggest that the benefits of growing as completely coalesced groups of crusts or plants with crustose holdfasts outweigh the costs associated with crowding. The formation of intercellular connections between contiguous individuals is central to the ability to cooperate.

#### *Sporeling Coalescence*

The most detailed observations to date on sporeling coalescence are of the red alga *Chondrus crispus* (Gigartiniaceae), which has an isomorphic life history involving the formation of erect fronds from basal discs of sporelings of both phases. The coalescence of basal discs of sporelings of each phase has been described by several authors including Rosenvinge (1931), Tveter and Mathieson (1976), Chen and Taylor (1976) and Tveter-Gallagher and Mathieson (1980). Based on light (Tveter and Mathieson 1976)

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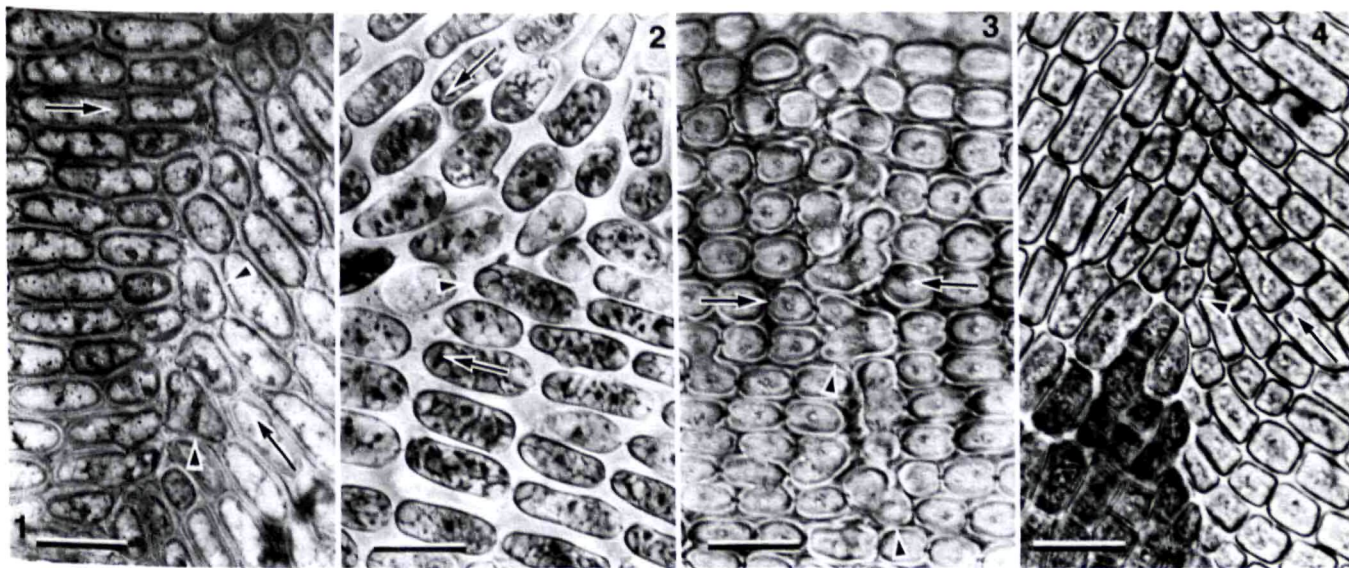


PLATE II. FIGS. 1–4. Secondary pit connections and cell fusions formed between cells of two crustose algal individuals when crust margins come into contact. Arrows show direction of growth of each individual; arrowheads indicate cell fusions or secondary pit connections between cells of different thalli. Scale bars = 20  $\mu$ m. FIG. 1. *Gymnogongrus ?patens*. Secondary pit connections between cells of two genetically identical diploid crusts grown from spores of a single cystocarp. Many secondary pit connections occur between cells within a thallus and result in multinucleate cells. FIG. 2. *Phyllophora trillii*. Secondary pit connections between cells of genetically different sibling basal discs grown from meiotic tetraspores of a single parent. FIG. 3. *Gloiosiphonia capillaris*. Abundant cell fusions formed along the line of junction between two genetically identical crusts derived from mitotic bispores. FIG. 4. *Rhodophysemma elegans*. Cell fusions between two genetically different crusts grown from meiotic tetraspores.

and electron microscope (Tveter-Gallagher and Mathieson 1980) observations, coalescence in *Chondrus* has been characterized as exhibiting the following features: vertical and horizontal alignment of cells, cuticular continuity, and formation of secondary pit connections between cells of confluent individual sporelings. Once two or more sporelings have coalesced, they may become indistinguishable. Occasionally, however, a furrow is left along the junction between individuals due to cellular damage during coalescence. The degree of damage appears to be related to the stage of development of the sporelings at the time of coalescence, with less damage occurring in younger plants (Tveter-Gallagher and Mathieson 1980). Similar coalescence of sporelings also has been reported in the red algae *Mastocarpus* (as *Gigartina*) *stellatus* (Petrocelidaceae) (Tveter and Mathieson 1976, Rueness 1978) and *Gracilaria verrucosa* (Gracilariaceae) (Jones 1956).

The formation of secondary pit connections between basal discs of coalesced red algal sporelings and confluent crusts is probably far more commonplace than appreciated in the literature. Primary pit connections linking kindred cells are characteristic of the Florideophycidae (see Pueschel and Cole 1982). Secondary pit connections are found in a great diversity of red algae from many florideophycan orders. In most species, secondary pit connections develop by the unequal division of an intercalary cell to produce a nucleate conjuncture cell that fuses with a neighboring cell. This results in a uninucleate and a binucleate cell linked by a secondary

pit connection (Goff and Coleman 1986, Pueschel 1988). Both nuclei persist in binucleate cells but, as far as we know, there is no evidence as to whether one or both nuclei participate in cellular control. Meristematic dividing cells do not normally become binucleate or multinucleate. Some parasitic red algae form secondary pit connections with host cells (Goff and Coleman 1985).

As yet, very little is known about what effect, if any, genetic similarity and ploidy level have upon coalescence and formation of secondary pit connections. We have examined several members of the Phyllophoraceae with a view to detecting the effect of genetic relationships on the formation of secondary pit connections between individuals. Secondary pit connections were observed between the following genetically identical individuals grown from mitospores: tetrasporophytic crusts of *Gymnogongrus ?patens* derived from a single cystocarp (Plate II, Fig. 1); gametophytic basal discs of clonal *Gymnogongrus devoniensis*. The cells linked by secondary pit connections between individual holdfast discs of *Gymnogongrus* spp. gametophytes (Plate II, Fig. 1) are homokaryotic, containing genetically identical nuclei. Secondary pit connections were also formed between genetically different, although sibling, gametophytic discs of *Phyllophora trillii* grown from meiotic tetraspores (see Maggs 1989); these resulted in heterokaryotic cells (Plate II, Fig. 2). This raises the possibility that coalescence between genetically different individuals could result in chimeric multiaxial axes with filaments of two genotypes. If co-



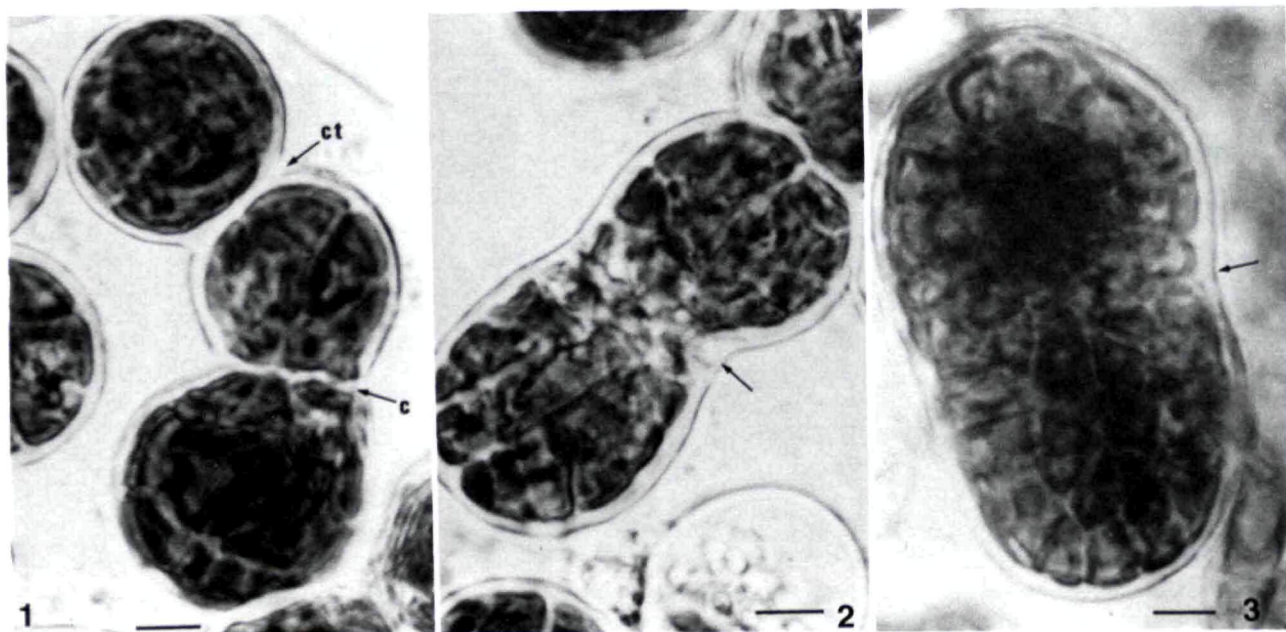


PLATE III. FIGS. 1-3. Sporeling coalescence sequence between germinating gametophytes produced from sibling tetraspores of *Chondrus crispus*. Coalescence is occurring at an early developmental stage. Sporelings have been stained with neutral red. FIG. 1. Initiation of coalescence between three sporelings. Note that the top two sporelings are still clearly separated by cuticular material (ct) after adherence whereas at a slightly later stage, the cuticular material and side indentation are much reduced as coalescence (c) is initiated between the middle and bottom sporelings. Scale bar = 25  $\mu$ m. FIG. 2. Intermediate stage in coalescence. Note the nearly complete coalescence of cells and the small cuticular indentation (arrow) that remains at the junction between the original sporelings. Scale bar = 25  $\mu$ m. FIG. 3. Final stage in coalescence, in which the original sporelings have completely coalesced at the junction between them (arrow) and are no longer distinguishable (i.e. they appear as a single cell mass). Scale bar = 30  $\mu$ m.

alescence occurred between haploid and diploid holdfasts, such a chimera could provide an additional mechanism for mixed-phase reproduction in single thalli besides those described by van der Meer and Todd (1977) and Oliveira and Plastino (1984). However, when diploid crusts and haploid basal discs of *Gymnogongrus ?patens* were grown together, secondary pit connections were not formed between individuals of different ploidy. Instead, the thallus margins grew under or over each other. These observations suggest that incompatibility mechanisms may discriminate between individuals of different ploidy although not between siblings of the same ploidy.

Intraspecific coalescence between sporelings of similar and different ploidy level has been investigated by us in *Chondrus crispus* and *Gracilaria* species using pigmentation markers to distinguish dissimilar individuals. In *Chondrus crispus*, coalescence was examined between green-pigmented gametophytic sporelings produced from tetraspores of a green mutant and red-pigmented gametophytic or tetrasporophytic sporelings, produced from tetraspores and carpospores, respectively, of red, wild-type plants. Our results for coalescence between sporelings of the same ploidy level were similar to those of Tveter and Mathieson (1976), whether the sporelings were produced by sibling spores (i.e. came from the same parent) or not. The typical sequence of coalescence for sibling sporelings coalescing at an early devel-

opmental stage is illustrated in Plate III, Figures 1-3. The net result in such cases is complete coalescence of the original sporelings; that is, secondary pit connections are produced between their cells, and they become virtually indistinguishable (Plate III, Fig. 3). Similar results were obtained for red and green-pigmented (i.e. non-sibling) sporeling coalescence, when coalescence occurred at an early developmental stage (Cheney, unpubl).

When sibling sporelings coalesced after each was already well developed, they remained as distinct entities with clear marginal distinctions or furrows separating them (Plate I, Fig. 2). Similar marginal furrows also occurred in the few cases of coalescence we observed between sporelings of different ploidy level (i.e. between green gametophytic and red tetrasporophytic basal discs), regardless of whether the sporelings coalesced early or late in development (Plate I, Fig. 3). Interestingly, the area of the red, tetrasporophytic basal disc was always greater than that of the green, gametophytic disc, which it partially surrounded. Whether this was caused by the culture conditions (e.g. irradiance levels) or reflected inherent ploidy differences is unknown. Unfortunately, it was not determined whether secondary pit connections were produced by plants either within or between ploidy levels in cases where individual sporelings remained distinct. Our results for coalescence between sporelings of the same ploidy level were thus similar to those of Tveter and Mathieson



(1976), whether the spores were similar in genotype (i.e. came from the same parent) or not.

Similar sporeling coalescence experiments have been conducted with *Gracilaria*, both within and between different species (Cheney, unpubl., Duke and Cheney, unpubl.). That is, we examined coalescence between green- and red-pigmented gametophytic sporelings produced from tetraspores of green mutant (NMG; van der Meer 1986) and red, wild-type *Gracilaria tikvahiae* plants, as well as between green-pigmented gametophytic *G. tikvahiae* sporelings from NMG and red-pigmented *G. chilensis* sporelings produced from tetraspores of a red, wild-type plant. In both types of co-culture experiments (i.e. intra- and interspecific), sporeling coalescence was achieved, and red and green, bicolored cell masses were produced (Plate I, Figs. 4, 5). Whether the red and green sporelings were of the same or different species apparently did not affect their capability to coalesce and even to form secondary pit connections (Plate I, Fig. 5), as long as coalescence occurred at an early developmental stage. One or both cell types within the bicolored cell mass subsequently produced upright fronds that were always of the same pigmentation as the cells that produced them. Although both red- and green-pigmented fronds were produced from a single bicolored cell mass, individual chimeric fronds were not observed. The ability for sporelings of two non-interfertile species (i.e. *G. tikvahiae* and *G. chilensis*, Cheney and Bradley, unpubl.) to coalesce came as a surprise to us, and raises some interesting questions about self-self recognition. How commonplace this phenomenon is within the genus *Gracilaria* or other algae needs to be examined.

#### Somatic Cell Fusions

Cell fusion differs from the situation described above in that there is a direct contact between the cytoplasm of the cells involved without the formation of a conjuctor cell. Direct cell fusions occur between cells of the same thallus in a number of species including members of the Kallymeniaceae (Codomier 1973, Hansen 1977), Corallinaceae (Cabiocch 1970), and in *Rhodophyllum* spp. (?Palmariaceae; Saunders et al. 1989). As far as we can determine, naturally-occurring fusions between cells of different individuals have previously been reported only for one member of the Corallinaceae (Afonso-Carrillo 1985). Probably the best known example of somatic cell fusion is the work by Waaland and colleagues describing the induced fusion between vegetative cells of male and female strains of the red alga *Griffithsia tenuis* (Ceramiaceae) (e.g. Waaland 1978). However, we have observed uninduced cell fusions between cells of adjacent crusts in mitotically reproducing clonal cultures (see Maggs 1988) of bisporangial *Gloiosiphonia capillaris* and tetrasporangial *Plagiospora gracilis* (both *Gloiosiphoniaceae*) and of bisporangial *Rhodophyllum elegans*. During protoplast fusion, nuclei may fuse to form a

genomic hybrid that has a single nucleus per cell, but in these uninduced fusions, the nuclei of both cells persist and usually remain in their original positions. There is no evidence as to whether the cytoplasm and other organelles of the originally separate cells mix or remain separate. The frequency of fused cells along the junction between crusts was greater than that between filaments of the same crust (Plate II, Fig. 3). Since the cultures were all clones, the fused cells were homokaryons. Cell fusions were also observed between individuals in tetrasporangial cultures of *R. elegans* (Plate II, Fig. 4). These meiotically derived crusts (Saunders et al. 1989) are genetically different, and fused cells of different individuals are therefore heterokaryons.

In contrast to the somatic cell fusions described above, efforts to fuse spores of *Gracilaria* have proven unsuccessful (Duke and Cheney, unpubl.). Even with polyethylene glycol (PEG), which has been used for fusing protoplasts (Cheney 1990), we were unable to fuse spores of any ploidy or strain. This failure appears to be due to the presence of cell wall material, since wall-less protoplasts of *Gracilaria tikvahiae* and *G. chilensis* have been successfully fused (Cheney 1990). *Chondrus crispus* spores did not fuse either, even in the presence of PEG, but PEG promoted spore adherence and thus the formation of coalesced sporelings.

#### Ecological and Evolutionary Implications

Much of the information presented here is preliminary but it points to the overwhelming conclusion that coalescence and intercellular contact between individuals are far more widespread in red algae with crustose thalli or sporeling stages than is generally recognized. Except for the studies of Jones (1956), Tveter and Mathieson (1976) and Tveter-Gallagher and Mathieson (1980), these phenomena have received little attention to date. However, their ecological and evolutionary consequences could be significant.

We propose that such coalescence and intercellular contact should be viewed as a mechanism for uniting separate individuals into a single "super-organism." There is continuity of the plasma membrane between cells linked by pit connections, both primary and secondary, and effective ionic communication occurs via pit connections (Bauman and Jones 1986). Two individual sporelings or crusts joined by secondary pit connections might, therefore, be expected to be under the same metabolic controls and to behave as a single organism. In other words, these phenomena suggest that intraspecific cooperation is occurring rather than competition. Cooperation may be defined as "a dynamic ecological state of organisms living in aggregation characterized by sufficient mutual benefit to outweigh disadvantages associated with crowding" and is usually restricted to cases when there is a risk of fitness loss if others do not participate (see Buss 1981). We



think that intraspecific cooperation occurs both among crustose algae and those that produce upright fronds from basal discs.

In the crustose algae we examined, the fusion zone between individuals shows an enhanced frequency of cell fusions and secondary pit connections, which could increase mechanical resistance to damage. In addition, a continuous coverage of the substratum without gaps between individuals will reduce the ability of competing algae to gain a foothold.

For species that form erect axes, there is good evidence that cooperation between coalesced individuals is occurring. A tendency for erect axes to form at the junction between different holdfast discs has been observed in several red algae including *Mastocarpus stellatus* (Rueness 1978) and *Ahnfeltia plicata* (Ahnfeltiaceae) (Maggs and Pueschel 1989). Likewise, reproductive sorus development appears to be stimulated at the junction between *Ahnfeltia fastigiata* crusts (Maggs et al. 1989). Earlier initiation and faster growth of uprights are promoted by coalescence of sporelings in *Gracilaria verrucosa* (Jones 1956), *Chondrus crispus* and *Mastocarpus stellatus* (Tveter and Mathieson 1976). Jones (1956) pointed out that *G. verrucosa* grows in habitats subject to sand inundation, so that the rapid formation and growth of fronds would be particularly advantageous. The mechanism of such enhanced shoot formation is unclear, but growth hormones have been suggested as a possible cause in other reports of increased algal growth due to crowding (Mshigeni 1974). It is also likely that increased erect axis development in plants with coalesced holdfasts is related to the cessation of lateral growth of holdfast tissue. Jones (1956) and Tveter and Mathieson (1976) suggested that the total number of fronds formed by a coalesced group of holdfasts was reduced relative to the same number of uncoalesced basal discs, possibly because the first-formed fronds suppress growth of others. Removal of the initial fronds of a coalesced sporeling group of *Chondrus crispus* stimulated the development of new fronds both from the same basal disc and from adjacent discs. The existence of metabolic interaction between individuals in a coalesced group could be investigated further with species showing photoperiodic requirements. It would be very interesting to determine whether the physiological results of photoperiodic stimuli could be transmitted between fronds of different individuals via coalesced holdfasts.

Besides enhancing the colonization by and establishment of a group of plants, sporeling coalescence also contributes to longevity by forming a large basal holdfast. In plants such as *Chondrus crispus*, the holdfast system is perennial and provides a stable, resilient and long-lived source of new fronds (Taylor et al. 1981). The capability of such a holdfast to persist and propagate new fronds vegetatively over a long time period offers a significant competitive advantage over plants without such a system. Cheney (1978)

has suggested that coalesced sporelings may be more resistant to grazing. Coalesced holdfast systems could potentially be of evolutionary significance in acting as a mechanism analagous to a seed pool in vascular plants (see Templeton and Levin 1979). As a result of sporeling coalescence, such perennial holdfasts could act as a buffer against elimination by "storing" different genotypes for future frond production. The incorporation of less-competitive basal discs into the coalesced super-organism, rather than their destruction by overgrowth, will also tend to maintain genetic diversity. Jones (1956) confirmed that sporeling coalescence actually occurs in the field, and Cheney (unpubl.) has observed gametophytic and sporophytic *Chondrus* axes arising from the same, presumably coalesced, holdfast. Sporeling coalescence may be promoted in *Chondrus* by the release of spores in a sticky, mucilaginous plug. The development of a turf of young axes from a coalesced holdfast provides the benefits of a turf lifestyle such as resistance to desiccation, grazing and mechanical damage (Hay 1981, Carpenter 1990).

Clearly, much more information is needed on many of the aspects of intraspecific interaction we have mentioned. These include the recognition of relatedness as measured by formation of secondary pit connections or cell fusions and the performance of coalesced versus solitary individuals in interspecific competition or under environmental stress. We have no evidence of the costs involved in intraspecific cooperation but suggest that these could include greater competition for nutrients and shading effects. We feel, however, that the apparent regulation of total frond numbers by a coalesced holdfast group may be significant in minimizing detrimental effects of cooperation.

Finally, although we have emphasized the red algae in this mini-review, we do not believe that the phenomena we have described are unique to the red algae. Recently Aberg (1989) reported that holdfasts from different individuals of the brown seaweed *Ascophyllum nodosum* can fuse so that what appears to be a single holdfast originates from more than one zygote; Paine (1990) has observed apparent cytoplasmic continuity between haptera of adjacent *Postelsia palmaeformis* plants. We expect that coalescence and close cellular contact might also occur in crustose brown algae such as *Ralfsia*. The ability of the coenocytic green alga *Codium* to overgrow and exclude other intertidal algae in the field (Santelices et al. 1981) might be due in part to coalescence of individuals. The occurrence and significance of coalescence needs to be examined further in all groups of macroalgae.

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**Question (Paine):** Performance could be measured, at the least, as thallus mortality, reproductive output or growth rate. If laboratory generated plants were outplanted to a variety of natural (field) conditions, what differences in these factors would you expect to observe in homokaryotic versus heterokaryotic plants?

**Answer:** We have no evidence as to the significance, even in culture, of the formation of heterokaryotic cells and chimeric fronds. Until there is some understanding of the role of multiple nuclei, including those of different genotypes, no theoretical prediction can be made.

**Question (Carpenter):** Within an algal species, is there evidence for more frequent sporeling or holdfast coalescence in particular physical or biological environments, such as across a desiccation gradient or in environments with high versus low grazer abundance, that would give genotypes that coalesce a physiological or deterrent advantage?

**Answer:** It is notable that red algae with extensive crustose holdfasts, such as *Chondrus crispus*, *Ahnfeltia plicata* and *Mastocarpus stellatus*, are among the most characteristic species in habitats subject to both severe grazing and mechanical disturbance. It seems likely that their success is related partly to their formation of coalesced holdfast groups because extensive holdfasts are important in these environments, and coalescence leads to a rapid increase in holdfast area.

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## A COMPARISON OF AIR AND WATER AS ENVIRONMENTS FOR PHOTOSYNTHESIS BY THE INTERTIDAL ALGA *FUCUS SPIRALIS* (PHAEOPHYTA)<sup>1</sup>

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### ABSTRACT

The response of photosynthesis and respiration of the intertidal brown alga *Fucus spiralis* L. to light and temperature at ambient and elevated concentrations of inorganic carbon was investigated. The light-saturated rate of photosynthesis was greater in air at 15°C and 20°C, but greater in water at 10°C. Light compensation point and  $I_k$  was about 50% lower under submerged relative to emerged conditions, whereas the initial slope of photosynthesis versus irradiance was higher, except at 20°C. Under both submerged and emerged conditions light-saturated photosynthesis was limited to a similar degree (78% and 65%, respectively) by the availability of inorganic carbon at naturally occurring concentrations. In air, slight desiccation at tissue water contents of about 96% to 92% caused a stimulation in the rate of net photosynthesis to 110–148% of fully hydrated fronds. At lower water contents the rate of net photosynthesis declined linearly with decreasing water content and became zero at a water content of about 15%. Dark respiration declined linearly with tissue water content and remained positive to a water content of 8%. Upon reimmersion the fronds showed a complete recovery within 35 min following desiccation to a water content of 20–30%. Thus *F. spiralis* seems to be very tolerant to desiccation. Since *F. spiralis* photosynthesizes effectively in air, even at a higher rate than in water as long as it has not lost a large proportion of its water in desiccation, the alternating exposure to air may be beneficial by increasing the daily carbon gain compared to a fully submerged situation.

**Key index words:** desiccation; *Fucus spiralis*; inorganic carbon; light; photosynthesis; respiration; temperature

**Intertidal algae experience continual alternation between two different environments, air and water,**

as the tide level changes. When in water, the algae grow and photosynthesize in an environment with a relatively low availability of light because of reflection at the water surface and attenuation within the water column. Although the total dissolved inorganic carbon (DIC) concentration is higher in aerated seawater, 2.3 mM compared to about 15  $\mu$ M in air, the majority of DIC is bicarbonate ( $\text{HCO}_3^-$ ) and the concentration of free  $\text{CO}_2$  is similar to that in air. The rate of supply of  $\text{CO}_2$  to plants underwater is lower than in air because of an approximately  $10^4$  times lower diffusion coefficient. Thus, even for species able to use bicarbonate in photosynthesis the availability of inorganic carbon is restricted in water compared to air (Sand-Jensen and Gordon 1984, Holbrook et al. 1988).

If a species can survive desiccation it may benefit from the greater availability of  $\text{CO}_2$  in air to increase its production. Oates (1985, 1986) showed that production in air for two saccate algae, which experience little desiccation because they retain a reservoir of seawater within their thallus, is likely to be important in their daily carbon balance.

The goal of the present study was to compare the response of photosynthesis and respiration of an intertidal alga, *Fucus spiralis* L. to light and temperature at ambient DIC and to elevated concentrations of DIC. *F. spiralis* has no source of water when emerged and thus has to tolerate desiccation. The effect of desiccation on photosynthesis and respiration were evaluated.

### MATERIALS AND METHODS

Thalli of *F. spiralis* were collected in May and June during low tide from the upper intertidal zone, just below the mean height of neap tides, at the Hind Rock, St. Andrews. For experiments, apical pieces of thalli 2–3 cm long were randomly selected from the plants and kept in the laboratory for 12–24 h in aerated natural seawater (salinity app. 34‰) at 15°C, which was approximately the ambient temperature. They received about 200  $\mu$ mol photons  $\text{m}^{-2} \text{s}^{-1}$  (PAR) from fluorescent tubes for 16 h out of

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