

Conclusion: The seaweed pathosystem

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The previous articles emphasize the ecological and economic importance of seaweeds, and the role of disease in the biology of these plants. It is worthwhile in conclusion to provide an overview by comparing terrestrial plant pathology, somewhat familiar to most biologists, with disease in a seaweed ecosystem; first, from a functional perspective, and then in terms of epidemiology and prospective control strategies. I shall use in this comparison the term pathosystem as originally defined by Robinson<sup>1</sup> to mean a component of an ecosystem which involves parasitism. Abiotic disease, discussed by Vadas and North, has been assessed elsewhere (Andrews<sup>2</sup>) and will not be considered further.

Representative diseases or pathogens from either marine or terrestrial pathosystems can be contrasted with respect to the disruption of particular host plant functional processes as tabulated below.

That seaweeds are subject to essentially the same array of pathogens as are their terrestrial counterparts is clear from the table and has been discussed in detail elsewhere (Andrews<sup>2,3</sup>). The degree to which a certain life function may be impaired, however, and the relative importance of a particular category of causal organism involved in such impairment differ in the 2 systems. For example, fungi as a group can cause serious 'damping-off' diseases affecting the critical stage of germination and early growth of terrestrial plants. We have virtually no evidence to date of their comparable involvement with seaweeds. Whereas root rots impair mineral and water uptake by terrestrial plants, this function in seaweeds would unlikely be seriously affected, at least by nonsystemic pathogens, because the entire thallus is bathed in a nutrient medium. Likewise, upward movement of water does

not assume the importance in the sea that it does on land. Although a pathogen might disrupt the primitive conducting elements of certain seaweeds, the effect on the host would probably be slight, and I know of no example remotely analogous to vascular wilts. Seaweeds as cryptogams do not bear fruit, nor do they possess food storage organs comparable to tubers or fleshy roots of phanerogams. However, they typically display a pronounced isomorphic or heteromorphic alteration of generations, and it is likely that the haploid and diploid stages are differentially susceptible to disease, a situation that does not really arise with seed plants. In fact, a bacterial disease unique to the *Conchocelis* phase of *Porphyra* has been described (Nozawa and Nozawa<sup>4</sup>).

If one compares plant disease in undisturbed terrestrial communities (thereby eliminating certain variables peculiar to agroecosystems) with that occurring among seaweeds in the ocean, clearly any unique attributes must originate from either intrinsic differences in the nature of the vegetation or the respective habitats in which it grows. Terrestrial plants, especially angiosperms which have been studied the most thoroughly by pathologists, exhibit various more or less sophisticated responses to the selection pressure of pathogens. These constitute: a) physical defenses, elaborated before or after infection, such as a thick cuticle or epidermal cell walls, callose, cork, tyloses, gums; and b) pre- or post-formed biochemical defense mechanisms, including phenols, phytoalexins, and the hypersensitive reaction (Agrios<sup>5</sup>).

Little is known, on the other hand, about how seaweeds respond to pathogens. Antibiosis, for example, due to production of acids, allyl sulphides, or

Disease as a disruption of normal functions of the plant

Life function affected	Pathosystem	
	Terrestrial	Marine
1. Germination and seedling growth	Damping-off fungi	Viruses
2. Mineral and water uptake	Root rots	-
3. Food translocation	Crown gall	Bacterial galls
	Parasitic seed plants	Parasitic algae
4. Upward movement of water	Vascular wilts	?
5. Photosynthesis	Viruses	Viruses
	Foliar fungi	Pythium red rot of <i>Porphyra</i>
6. Reproduction	Smuts	Viruses
		<i>Petersenia</i> infections of <i>Seirospora</i>
7. Food storage	Brown rot	-
	Bacterial soft rot	
8. Support	Wood decay fungi	Stipe blotch ( <i>Phycomelaina</i> ) of kelps

polyphenols, is a common phenomenon in the ocean (Sieburth<sup>6</sup>) and presumably accounts to a large extent for algal defense. Are pathogens sloughed off by the copious secretion of mucilage (Khailov and Burlakova<sup>7</sup>) characteristic of many seaweeds? Epiphytism and encrustations (discussed by Vadas and North) are much more common in the ocean than on land. This poses the problem of shading to the marine host, and seaweeds apparently confront it by growing rapidly or producing mucilage and antibiotics. Once evolved, these mechanisms could also be effective against pathogens. It seems logical to propose that seaweeds may rely more than terrestrial plants on a pre-formed chemical mode of resistance in view of their anatomical simplicity and pronounced secretory activity. This raises the fundamental question as to whether the response to pathogens by plants of widely divergent taxa is basically the same or different. There are certainly marked differences in the animal kingdom. Channeling of energy (resources) by seaweeds into biomass instead of sophisticated defense mechanisms (i.e. *r* vs *K* selection discussed by Vadas) would be consistent with the general evolutionary strategy in the open oceans which, according to Parsons<sup>8</sup>, is to be large or numerous. We do not yet have sufficient information about seaweed pathology to provide a definitive answer.

From the preceding contributions, it is apparent that the etiology of seaweed disease corresponds to that of terrestrial plants. The relative importance of factors influencing epidemiology, however, is quite different in the 2 pathosystems. On land the predominant media of pathogen dispersal are air, water, insects and plant debris, each having varying roles, depending on the nature of the inoculum. Rapid transport of aerial inocula is common and occasionally may occur over distances of hundreds or thousands of km. In oceans, water is presumably the medium in which agents of disease dissemination are carried, yet little is known regarding pathogen mobility or vectors. The significance of aerosol dispersal remains to be established. It may be of considerable importance, particularly on a local scale.

Long distance transport of the ascomycete *Lindra thalassiae* from islands in the West Indies into the Sargasso Sea Gyre is a classic example of inoculum dispersal in the marine environment. According to Kohlmeyer<sup>9</sup>, infected leaves and rhizomes of *Thalassia testudinum* drift into the Sargasso Sea under the influence of oceanic currents, where the pathogen infects air bladders of the floating seaweed *Sargassum*. The host tends to collect in large parallel bands; it is likely that local mixing of inoculum and *Sargassum* is mediated by counter-rotating eddies known as Langmuir Circulation.

In overview, while we can expect marine and terrestrial sources or reservoirs of inocula to be similar, the

mode and rate of pathogen dispersal and survival en route are likely to be quite different.

Not enough epidemiological data are available to ascribe a particular seaweed disease to the 'simple interest' or 'compound interest' categories used by Van Der Plank<sup>10</sup> for assessment of epidemics in terrestrial pathosystems. Eventual application of these or analogous aquatic models on disease dynamics will be valuable for defining optimal control strategies in particular situations. Generalizations can nevertheless be made regarding approaches which should be emphasized. The history of agriculture points to the fact that concentration of a single plant species, even without attendant genetic homogeneity, favors epidemics. Intentional selection for reduced intraspecific diversity (i.e. for varietal and age uniformity) has accentuated vulnerability to disease. As in terrestrial agriculture, aquatic monocultures both in the ocean (discussed by Wheeler et al. and Kazama) and in raceways on land (Ryther<sup>11</sup>, Prince<sup>12</sup>) have been fraught by significant pest problems. As in terrestrial agriculture, they generally require substantial inputs of energy and resources to maintain productivity.

Cultivation of heterogeneous stocks of several seaweed species as intercrops in a biologically and structurally diversified mariculture should be feasible, economical and effective. Such production would emphasize avoidance of disease and eradication of inoculum through sanitation, use of certified stock, appropriate selection of planting date, spatial distribution, geographical location and site. An aqueous medium poses certain unique problems for the use of chemicals, but does not preclude their judicious use when and where situations warrant application. It would seem that pesticides could be employed advantageously in raceways which are accessible and easily manipulated. Initially, certain seaweed crops in the ocean could be treated selectively as necessary at low tide. Eventually, selective systemic chemicals could be deployed, perhaps in granular form, as protectants or therapeutants.

As society embarks upon an age of extensive mariculture, it would be wise to pause and reflect upon the attributes and shortcomings of terrestrial agriculture. Delay in developing mariculture is to some extent fortunate in that, consequently, agroecosystems on land will serve as the testing ground for new concepts (a current example of which is integrated pest management) which, if valid, can be exploited as aquatic technology advances. We may also learn much from the approach in fisheries and game management wherein the goal is to attain stable production without undue energy input. Our best option in the final analysis may be one of sophisticated management in the broadest sense for a moderate (relatively lower productivity/biomass) but stable and efficient harvest.

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## SPECIALIA

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### Sesquiterpenes based on the cadalane skeleton from the brown alga *Dilophus fasciola*<sup>1</sup>

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**Summary.** From the brown alga *Dilophus fasciola* (Dictyotaceae) the new sesquiterpene ether 4,10-epoxymurolane has been isolated, along with known sesquiterpenes based on the cadalane skeleton, and its structure determined by spectroscopic methods.

The algal family Dictyotaceae is a rich source of terpenoids and other metabolites<sup>2</sup>. In a recent paper<sup>3</sup> we reported the isolation of a compound of mixed biogenesis, namely geranylgeranyl glycerol, from the more polar fractions of the chloroform extract of *Dilophus fasciola* (Roth) Howe, a brown alga belonging to this family. An investigation of the less polar fractions of the same extract has now led to the isolation of 5 sesquiterpenoids based on the cadalane skeleton, the hydrocarbons 1–3, the alcohol 4 and the novel cyclic ether 5.

**Material and methods.** *D. fasciola* (2.5 kg fresh weight) was collected near Catania, Sicily, during the spring of 1977. The chloroform extract of the freeze-dried alga was subjected to a gross fractionation on silica gel using increasing concentrations of ether in hexane as the eluent. From the early fractions of the hexane eluent, a hydrocarbon mixture was obtained, wherefrom isolation of individual components in pure form required extensive use of chromatography over AgNO<sub>3</sub> impregnated silica gel. Later eluates, which emerged from the column with 10% ether, on further chromatography over silica gel using benzene as eluent, gave the alcohol 4 and the ether 5, and in addition 2 further oxygenated sesquiterpenoids currently under investigation. Aromatization was performed by heating at 250 °C for 3 h the pertinent compound (100 mg) with 10% Pd/C (100 mg). The crude product was chromatographed on silica gel (hexane as eluent) to give cadalene, identified by comparison of physical properties (UV, IR and NMR) with those of a reference sample. Partial aromatization of 1-epibicyclosesquiphellandrene was carried out with trifluoroacetic acid in the condition described by Andersen et al.<sup>4</sup>.

**Results and discussion.** For all the isolated compounds the cadalane skeleton was established by dehydrogenation to cadalene. Compound 1 (0.1% dry weight of the alga) C<sub>15</sub>H<sub>22</sub>, and compound 2 (0.02%), C<sub>15</sub>H<sub>24</sub>, were identified, respectively as (1S-trans)-(-)-calamenene and  $\delta$ -cadinene by comparison of their physical data ([ $\alpha$ ]<sub>D</sub>, MS, UV, IR and NMR) with those reported in the literature<sup>4,5</sup>. The 3rd hydrocarbon (0.25%), C<sub>15</sub>H<sub>24</sub>, [ $\alpha$ ]<sub>D</sub> = +4.1° (c 1 in EtOH), was a conjugated diene that had spectral properties which matched those reported for 1-epibicyclosesquiphellandrene<sup>6</sup>. However, since the OR of this compound, recently isolated from *Ocimum basilicum*<sup>6</sup>, has not been recorded, the possibility that the algal metabolite could be its enantiomer was taken into consideration but definitely ruled out in view of the formation of (1S-trans)-(-)-calamenene by partial aromatization of 3.

