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# Chemically mediated interactions between the red alga *Plocamium hamatum* (Rhodophyta) and the octocoral *Sinularia cruciata* (Alcyonacea) *

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**Abstract.** Interactions between the red alga *Plocamium hamatum* J. Agardh (Rhodophyta) and other benthic organisms including the alcyonacean soft coral *Sinularia cruciata* (Tixier-Durivault) were investigated on an inshore fringing reef environment in which *P. hamatum* was the dominant large fleshy alga. Field observations of sessile reef organisms including octocorals and sponges living in close proximity to *P. hamatum* revealed that varying degrees of tissue necrosis were suffered by the invertebrates when in physical contact with the alga. In order to establish whether the chemical constituents of the alga, especially chloromertensene, played a role in this necrosis, manipulative field experiments were carried out in the Pelorus Channel, Palm Island group (18°34′S; 146°29′E), North Queensland, Australia, in November and December 1988. The first experiment involved the relocation of healthy plants and soft corals into contact and non-contact situations on a mesh grid. In all cases of contact between *P. hamatum* and *S. cruciata*, the soft coral suffered tissue necrosis ($n=6, p=0.0022$). The second experiment had the same design, but involved the use of artificial "plants" both uncoated and coated with natural levels of chloromertensene, in contact with *S. cruciata*. In all cases of contact with coated treatments, necrosis was observed in *S. cruciata* ($n=4, p=0.025$). In cases where uncoated artificial fronds were placed in contact with soft corals, *S. cruciata* showed minor abrasion effects, but no appreciable necrosis. Coated treatments were not fouled by epiphytes during the experiment and were not consumed by predators. Uncoated treatments were rapidly reduced in size by predation and any remaining material was biofouled. These experiments thus demonstrated that the deleterious effects observed in soft corals in the field were caused by contact with the alga *P. hamatum*, that these effects were indeed chemically mediated by chloromertensene, and that physical contact without chemical intervention caused no such deleterious effects. This is the first experimental evidence which conclusively demonstrates allelopathy between an alga and other marine organisms and identifies the compound responsible for the observed allelopathic effects.

## Introduction

Tropical marine algae produce an array of secondary metabolites, many of which have been shown to be biologically active (Hay and Fenical 1988, Van Alstyne and Paul 1989). However, the ecological significance of secondary metabolites produced by marine algae has only recently been investigated in studies which have emphasised the specific anti-feedant properties of these compounds in relation to both fish and mesograzers (see review by Hay and Fenical 1988). Other studies have shown that secondary metabolites play roles in anti-fouling (Sieburth and Conover 1965, McLachlan and Craigie 1966, Khfaji and Boney 1979, Phillips and Towers 1982) and gamete attraction (see review by Maier and Müller 1986), and they have been postulated to play a role in competitive interactions including allelopathy (Fletcher 1975, Helleburst 1975, Vadas 1979, Harlin 1987).

Allelopathic interactions [1] are well documented in the terrestrial environment (Rosenthal and Jansen 1979, Fox 1981, Rice 1984). In the marine environment, allelopathy has been experimentally demonstrated in soft corals (Sammarco et al. 1983) and implicated in a number of interactions between invertebrates and other biota, including anemones (Sebens 1976, Bak and Borsboom 1984), sponges (Jackson and Buss 1975, Sullivan et al. 1983, Thompson 1985), ascidians (Bak et al. 1981) and scleractinian corals (Sammarco et al. 1985, De Ruyter van Stevenick et al. 1988). There is, however, no experimental evidence that marine algae exert allelopathic effects on neighbouring organisms.

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[1] "Allelopathy": the reputed baneful influence of one living plant upon another due to a secretion of toxic substances (Webster's Third International Dictionary, see also McNaughton and Wolf 1979)

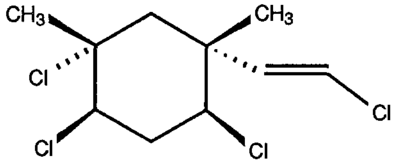

Fig. 1. Structure of the monoterpene chloromertensene

Interactions between the red alga *Plocamium hamatum* J. Agardh (Rhodophyta) and other benthic organisms, especially soft corals, were investigated on an inshore fringing coral reef. *P. hamatum* is the dominant large fleshly alga in that area, and has been shown to produce a number of secondary metabolites (Coll et al. 1988), of which chloromertense, a tetrachlorinated monoterpene (Fig. 1), is the predominant component. The latter compound has been shown to be associated with very low feeding preference, as assessed using herbivorous fish (Hay personal communication).

Field observations of sessile reef organisms, including soft corals, sponges and gorgonians living in close proximity to *P. hamatum*, revealed that wherever contact occurred, the invertebrates suffered varying degrees of tissue necrosis. Accordingly, the possible role of *P. hamatum* and of its chemical constituents, especially chloromertensene, in the observed tissues necrosis was investigated in a series of manipulative field experiments.

## Materials and methods

### Study site and organisms

Field experiments were conducted in the Pelorus Channel between Orpheus Island and Pelorus Island (18°34'S; 146°29'E), in the Palm Island group, 80 km north-west of Townsville in the central region of the Great Barrier Reef, during November and December 1988. This was also the collection site for the algal samples from which chloromertensene was first isolated (Coll et al. 1988). The study area is a fringing coral reef community dominated by soft corals, among which *Sinularia cruciata* (Tixier-Durivault), *S. flexibilis* (Quoy and Gaimard), *S. polydactyla* (Ehrenberg) and *Clavularia inflata* (Schenk) are the major species. *Plocamium hamatum* J. Agardh is the dominant large fleshy alga in this area and was most commonly found growing in rocky crevices or around and between the large soft corals listed above. Herbivorous fishes are also common in the area (Russ 1984).

### Chemical procedures

Details of the isolation and structural elucidation of chloromertensene have been described previously (Coll et al. 1988). In the present study, the purity of chloromertensene was established by $^1$H NMR spectroscopy prior to use.

### Field observations of interactions

After the initial observation in a number of soft coral species of tissue necrosis apparently caused by contact with the red alga *Plocamium hamatum* (Bowden et al. 1989), a field survey was made in the same region to determine the generality of this phenomenon. Studies were carried out using three 20 m × 1 m belt-transects parallel to the depth gradient on the coral reef flat adjacent to the study site. The number of whole *P. hamatum* plants, and the incidence of necrosis whenever *P. hamatum* was in contact with sessile invertebrates was recorded.

### Manipulative field experiments

*Effects of Plocamium hamatum on Sinularia cruciata*

In order to test the effect of *Plocamium hamatum* on *Sinularia cruciata*, healthy intact plants of *P. hamatum* (7 to 10 cm tall) with attached substratum were carefully collected and transferred to three galvanised wire grids (2 m$^2$ in area, of mesh size 250 mm × 50 mm) anchored to the reef. An equal number of colonies of the soft coral *S. cruciata* were collected and relocated to each of the grids. The grids were sited within 5 m of the collection site and at the same depth (3 m). Two treatments were used, one in which *P. hamatum* was placed in direct physical contact with *S. cruciata* ($n = 6$), and one in which *P. hamatum* was placed so that it was unable to make contact with the soft coral under any current conditions, i.e., in close proximity to ($< 5$ cm) but not in direct contact with the coral ($n = 6$). Relocated controls of *P. hamatum* ($n = 6$) and *S. cruciata* ($n = 6$) were attached to the grid so that each individual was at least 30 cm from any other. Other control colonies of *S. cruciata* included those which were labelled and left in their natural environment as field controls either in direct contact with *P. hamatum* ($n = 6$) or not in direct contact with *P. hamatum* ($n = 6$). *S. cruciata* colonies were observed after 24 h, 48 h and 14 d, and tissue necrosis was recorded. Necrosis was considered to have occurred when the tissue darkened and sloughed from the surface of the colony. Further observations were made after 6 wk. The results were analyzed using a two-tailed Fisher exact test (Zar 1984).

*Effects of chloromertensene on Sinularia cruciata*

In order to determine whether the necrotic effects of the alga on the soft coral tissue were chemically induced, fronds of synthetic aquarium "plants" (dried and dyed colonies of the bryozoan *Sertularia argentea*, supplied by Aquafern, England), were coated with a solution of chloromertensene dissolved in diethyl ether. The diethyl ether evaporates leaving the chloromertensene adhering to the fronds. The final concentration of chloromertensene on the "plants" was 2%. This is approximately the average concentration of chloromertensene recorded in natural populations of *Plocamium hamatum* which varies between 0 and 5% of the freeze-dried weight of the alga (Wright 1989). Other specimens were coated with diethyl ether only to act as controls. Lipid-soluble metabolites such as chloromertensene have been shown to adhere to surfaces after the diethyl ether evaporates, and only slowly diffuse into aqueous media such as seawater (McConnell et al. 1982, Targett et al. 1986, Hay et al. 1987, Paul et al. 1987). Four replicates of coated and control "plants" were attached as previously described to grids in the field so that they were in contact with *Sinularia cruciata*. The *S. cruciata* colonies were examined for tissue necrosis or other deleterious effects after 24 h, 48 h and 14 d. Further observations were made after 6 wk. The results were analyzed using a two-tailed Fischer exact test (Zar 1984).

## Results

### Field observations of interactions

Field observation of a number of soft coral species [*Sinularia cruciata* ($n = 14$), *S. flexibilis* ($n = 12$), *S. polydactyla* ($n = 4$), and *Clavularia* sp. ($n = 2$)], a sponge [*Dictyoce-*

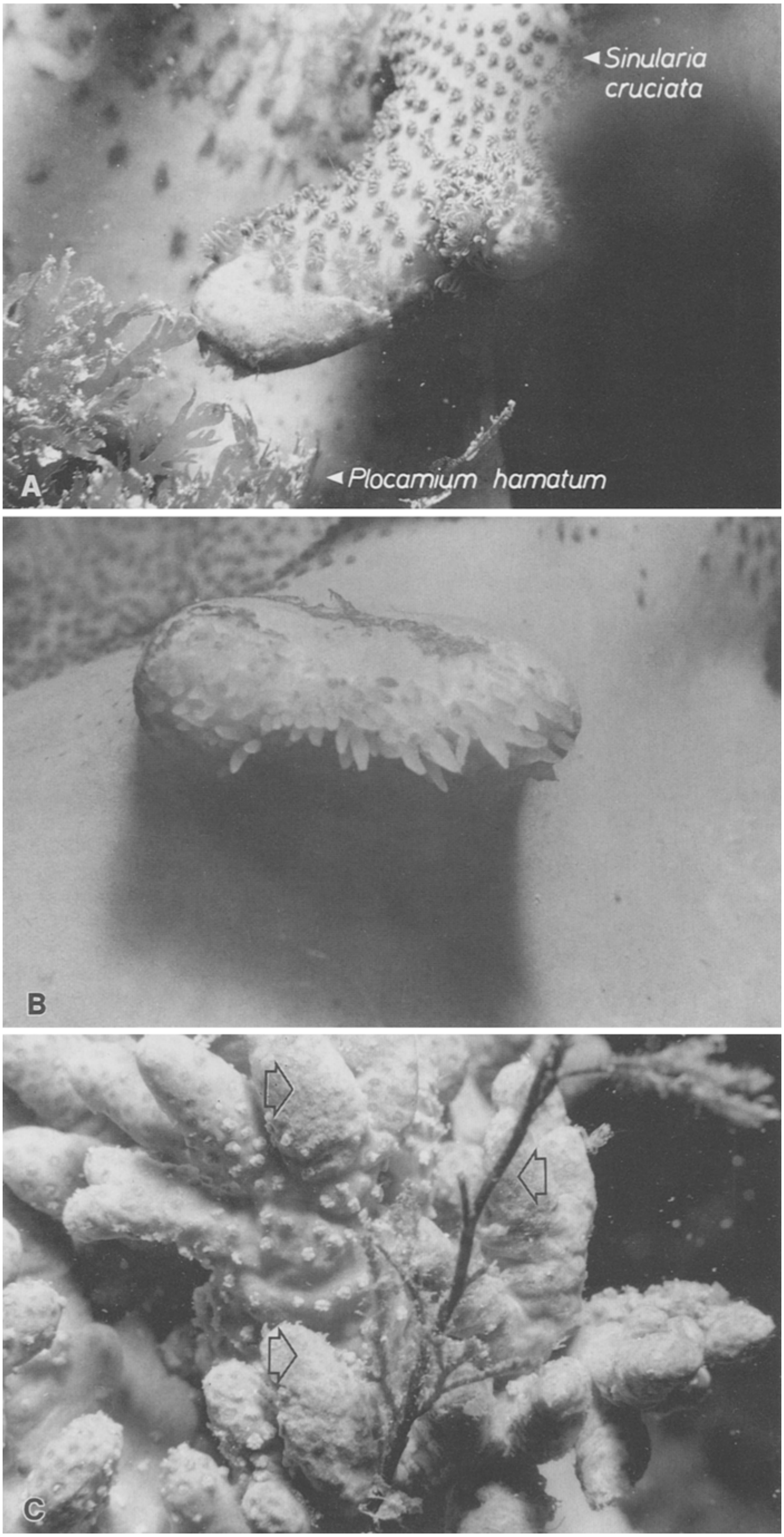

**Fig. 2.** *Sinularia cruciata*. (A) Polyp withdrawal and tissue necrosis in lobe of colony after 48 h contact with *Plocamium hamatum*; (B) exposure of spicules of colony resulting from tissue necrosis after prolonged contact with *P. hamatum*; (C) Tissue necrosis (arrowed) in parts of colony after 48 h contact with Aquafern® coated with chloromertensene

*ratida* sp. ($n=1$)] and a gorgonian [*Isis* sp. ($n=5$)] revealed that the invertebrates suffered tissue necrosis whenever they were in contact with *Plocamium hamatum*. Similar association of the soft coral species and *S. cruciata* and *S. flexibilis* with the green alga *Chlorodesmis fastigata* (C. Agardh) (Ducker ($n=9$), did not result in contact-necrosis.

## Manipulative experiments

### *Effects of Plocamium hamatum on Sinularia cruciata*

Tissue necrosis was recorded in *all* cases where *Plocamium hamatum* was in contact with *Sinularia cruciata* ($p=0.0022$, $\alpha=0.05$). The initial response of *S. cruciata* to contact with *P. hamatum* was polyp withdrawal, followed by thinning of the surface mucus layer after 24 h. After 48 h, tissue hardening and darkening was evident which eventually resulted in tissue death in all treatments in which *S. cruciata* was in contact with the alga (Fig. 2A). After 6 wk, necrosis in some *S. cruciata* colonies had occurred to such an extent that spicules were exposed (e.g. Fig. 2B). Spicule exposure was only observed when larger *P. hamatum* plants were in contact with *S. cruciata* colonies. None of the relocated colonies of *S. cruciata* which were out of direct contact with *P. hamatum* (5 or 30 cm separation) suffered any type of tissue necrosis ($p=0.0022$, $\alpha=0.05$). In two cases, *P. hamatum* plants which were originally out of direct contact with *S. cruciata* (> 5 cm) grew into contact with the coral after about 6 wk and caused necrosis. Control colonies were unchanged throughout the course of the experiment.

### *Effects of chloromertensene on Sinularia cruciata*

In all cases, portions of colonies of *Sinularia cruciata* in contact with the aquarium "plants" coated with chloromertensene showed tissue necrosis (Fig. 2C) after 48 h ($p=0.025$ $\alpha=0.05$). No tissue necrosis was induced by the controls treated only with diethyl ether ($p=0.025$ $\alpha=0.05$), although mucus loss occurred in some areas of the soft coral in contact with the "plants", probably due to abrasion. The severity of tissue necrosis in *S. cruciata* in direct contact with the aquarium "plants" coated with chloromertensene was greater after 14 d than after 48 h, although it was less severe than that caused by contact with *Plocamium hamatum* for the same period. After 48 h, two of the four untreated control "plants" had decreased in size, apparently due to grazing, and the remainder had become epiphytized by algae and small sessile invertebrates. After two weeks, all the "plant" controls had either entirely disappeared, or consisted only of the lower parts of the thicker central axis. By contrast, all "plants" coated with chloromertensene were intact after 2 wk, with few epiphytes present. From field observations, the only commonly occurring fouling organism of *P. hamatum* is the foraminiferan *Calcarina sponglera* (Carpenter) Linné.

## Discussion

The high species diversity and population densities on coral reefs suggest that space can be a limiting resource for benthic reef organisms (Glynn 1973, Porter 1974, Jackson 1977, Sheppard 1980, Benayahu and Loya 1981). There is evidence that a number of mechanisms have evolved which enable particular species to compete successfully for space (see reviews by Sheppard 1982 and Samarco and Coll 1988), one of which is allelopathy (Sammarco and Coll 1988). Macroalgae are generally considered important competitors for space on reefs, often being among the first organisms to occupy available space, and some species have been shown to limit the settlement of coral larvae (Dart 1972, Birkeland 1977), or to kill juvenile corals by overgrowing them (Potts 1977, Bak and Engel 1979, Sammarco 1980, 1982, Van Moorsel 1985), or by entrapping sediment (Sammarco 1980). Overgrowth of larger coral colonies by algae has also been observed (Connell 1973, Glynn 1973, Dahl 1974, Coll et al. 1987) and demonstrated experimentally (Potts 1977, Sammarco 1982, Lewis 1986). Competitive interactions between microscopic planktonic algae have been described for a number of species (see review by Fogg 1966 and Hellebust 1975), and the concept of a "chemical claw" mechanism of interspecific competition between macroscopic marine algae was proposed as early as 1948 by Walker and Smith. This mechanism was invoked to explain the effect of the exudates from *Ascophyllum nodosum* (L.) Le Jol. on zoospores of *Laminaria cloustoni* Edmonst. Fletcher (1975) observed that growth of the crustose red algae *Porphyrodiscus simulans* Batt. and *Rhodophysema elegans* (Croun frat. ex J. Ag.) Dixon was inhibited in culture by ectocrines of *Ralfsia spongiocarpa* Batt., a species known to liberate considerable quantities of tannins into tide pools (Conover and Sieburth 1966). Khfaji and Boney (1979) demonstrated that diatom growth was inhibited in the vicinity of *Chondrus crispus* Stackh. germlings grown in culture. Algal secondary metabolites have been shown to be exuded into the water column by a number of algae (Carlson and Carlson 1984, Gschwend et al. 1985); however, there is no direct evidence to date that secondary metabolites are released from algae involved in these interspecific interactions, or that these algal secondary metabolites are the cause of the observed deleterious effects in these competitive situations.

In the present study, manipulative field experiments showed that contact between the alga *Plocamium hamatum* and the soft coral *Sinularia cruciata* was necessary for tissue necrosis to occur, and that the necrosis was largely caused by the major secondary metabolite produced by the alga, chloromertensene. Although the observed necrosis in *S. cruciata* caused by chloromertensene coated on artificial fronds was less severe than that caused by *P. hamatum*, this was not unexpected, as the living alga continued to synthesise the compounds (Wright 1989). After prolonged (6 wk) exposure to *P. hamatum*, spicules of *S. cruciata* were visible, and secondary algal infection of the dead tissue was observed, indicating a loss of the normal resistance of the soft coral to algal infection (Coll et al. 1987). Our experiments show that chloromertensene is not released into the water column in sufficient quantities to effect organisms in close proximity, and that contact is necessary for necrosis to occur ($p < 0.0025$). Chloromertensene may be localised in cytoplasmic vesicles in the surface cells of the alga (e.g. Young et al. 1980), which may be excised or burst when the surface cells are abraded.

It appears that chloromertensene may also function as an antifouling agent. In the experiment involving coated "plant" fronds, it was found that after 48 h a number of the uncoated controls became colonized by epiphytes and grazed by fish, while the treatment coated with chloromertensene were not colonised by epiphytes and remained intact. After 14 d the "plant" controls had been completely consumed, while the coated "plants" were still intact. It is not known whether the fish were avoiding the coated "plants" in our experiment due to the absence of epiphytes as a food source, or due to presence of chloromertensene as a feeding deterrent, although other investigators have shown that chloromertensene is a feeding deterrent (Hay personal communication).

Studies of other macroalgae associated with soft corals, including *Chlorodesmis fastigata*, an alga known to produce secondary metabolites (Wells and Barrow 1979, Paul and Fenical 1985), have not shown any comparable contact-induced allelopathic interaction between the alga and associated biota, suggesting that the allelopathic effects observed in *Plocamium hamatum* may be species-specific for a particular environmental niche. This is consistent with the hypothesis of Whittaker and Feeney (1971) that chemical defenses play an important role in niche differentiation and control of community structure in numerous ecosystems.

Chloromertensene thus appears to play a multifunctional role in the success of the red alga *Plocamium hamatum*. It plays an allelopathic role in the red alga *P. hamatum* by preventing overgrowth by the locally dominant soft corals, and appears to act as an antifouling and antifeedant agent, further ensuring its prolific growth.

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