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Host-specificity of *Endophyton ramosum* (Chlorophyta), the causative agent of green patch disease in *Mazzaella laminarioides* (Rhodophyta)

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The level of host-specificity of *Endophyton ramosum*, the causative agent of green patch disease in *Mazzaella laminarioides*, was experimentally tested in the laboratory. Cross-infection trials demonstrated that the endophyte has the capability of infecting a greater variety of hosts than it does in nature. Furthermore, the pattern of host-specificity does not seem to be related to the life-history phase of the host. This suggestion, however, requires further analysis as indicated by the intraspecific variability in infectivity displayed by *E. ramosum* from different individual hosts. Suggestions that the type of carrageenan present in the host cell walls could determine a given pattern of host-specificity are not supported by this study. In spite of this, *E. ramosum* seems able to discriminate between agarophytes and carrageenophytes. Agar-producing algae were rarely infected and, when the endophyte did penetrate some of them, the development of *E. ramosum* was atypical.

Key words: disease, *Endophyton*, host-specificity, infection, *Mazzaella*

Introduction

In recent studies, various aspects of the biology of intimate relationships established between pigmented endophytic organisms and their algal hosts have been reported (Correa & McLachlan, 1991, 1992, 1994; Correa *et al.*, 1988, 1993, 1994). Most of the in-depth descriptive and experimental information comes from studies of the *Chondrus crispus–Acrochaete operculata* and *A. heteroclada* systems (Correa & McLachlan, 1991, 1992, 1994; Correa *et al.*, 1988). Within this body of knowledge, the phenomenon of host-specificity remains poorly understood, in spite of increasing evidence that some of these associations are pathogenic and, therefore, detrimental to the hosts involved (Correa & McLachlan, 1992, 1994; Correa *et al.*, 1993, 1994).

Pigmented endophytes are considered photosynthate-independent and therefore without a strong, if any, metabolic relationship with their hosts. This notion is supported by studies where a number of these organisms have been isolated from their hosts and cultured successfully in the laboratory (e.g. White & Boney, 1969; 1970; Boney, 1972; Garbary, 1979; Nielsen, 1979). In this context, infection of a macroalga by an algal endophyte is generally considered a casual event where the association itself would not be essential for the existence of the endophyte. The above arguments have been used to explain some observed patterns of poor host-specificity (Iima & Tatewaki, 1987). However, in a number of intimate associations, it is apparent that the infecting alga does not colonize other hosts, even though they coexist with the susceptible species. This is the case for *Acrochaete operculata*, an endophyte that causes severe destruction in *Chondrus crispus*, but is innocuous to *Mastocarpus stellatus* (Correa *et al.*, 1988). In fact, as subsequently demonstrated (Correa & McLachlan, 1991), *A. operculata* proved to be a highly specific endophyte, which developed infections only when in contact with the sporophytic life-history phase of *C. crispus* and *Iridaea cordata*. That study also established, for the first time in this type of association, a close relationship between susceptibility and the type of polysaccharides present in the cell wall of the host.

Most previous reports suggesting some degree of specificity in infections by algal endophytes are based on field observations (reviewed by Goff, 1983). However, although few cross-infection experiments have been performed *in vitro*, some endophytic members of the Rhodophyta (White & Boney, 1969; Boney, 1972; Garbary 1979), Phaeophyta (Apt, 1988) and Chlorophyta (O'Kelly, 1980; Iima & Tatewaki, 1987) have been tested for host-specificity.

On the coast of central and southern Chile, the red alga *Mazzaella laminarioides* hosts at least two endophytic organisms. One, a cyanobacterium (*Pleurocapsa* sp.), causes a deformative disease as the result of galls

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developed by the host in response to the infection (Correa *et al.*, 1993). The other is the filamentous green alga *Endophyton ramosum* Gardner, which causes severe destruction of the thallus (Correa *et al.*, 1994). Initially, this organism was classified as *Endophyton* sp. (Correa *et al.*, 1994) on the basis of minor morphological differences from the only known species, *E. ramosum* (Gardner, 1909). However, information resulting from the in-depth characterization of *E. ramosum* by O'Kelly (1982) and from our current knowledge of the Chilean organism does not warrant, at present, a name other than *E. ramosum* for the endophyte of *M. laminarioides*.

Field and laboratory observations of algal species which coexist with *M. laminarioides* have failed to detect either of the infecting organisms or the lesions they cause. In this and several other aspects (see Correa *et al.*, 1994), the infection of *M. laminarioides* by *E. ramosum* appears similar to that of *C. crispus* by *Acrochaete operculata*. Thus, the main purpose of this study was to assess experimentally field observations indicating a high host-specificity of *E. ramosum* in its association with *M. laminarioides*. The factors associated with a given level of host-specificity, based on the *A. operculata–C. crispus* system, were evaluated using the *Endophyton–Mazzaella* system. Finally, the origin of the endophytic isolate as a factor involved in the outcome of the infection was tested.

Table 1. Unialgal isolates of *Endophyton ramosum* used in the *in vitro* infections

Culture code	Date of collection	Locality
M 250891-1[a]	August 1991	Matanzas
M 250891-3[a]	August 1991	Matanzas
M 250891-6[a]	August 1991	Matanzas
M 250891-9[a]	August 1991	Matanzas
M 150492-S[b]	April 1992	Matanzas
M 150492-G[c]	April 1992	Matanzas

[a] Isolates from the same non-fertile frond.
[b] Isolate from a single sporophytic frond.
[c] Isolate from a single gametophytic frond.

Materials and methods

The procedure followed in this study was based on the previous work by Correa & McLachlan (1991). Two sets of experiments were carried out by cross-infecting unialgal isolates of potential hosts with unialgal, clonal isolates of *Endophyton ramosum* (Table 1). Potential hosts included 13 carrageenophytes and 7 agarophytes in the first experiment, and 4 carrageenophytes and 2 agarophytes in the second experiment. Most hosts (Table 2) came from our culture collection maintained in the laboratory (Santiago) and some were the same isolates tested for specificity with *Acrochaete operculata* by Correa

Table 2. Summary of *in vitro* assays with *Endophyton ramosum* isolates M 250891-1, M 250891-3, M 250891-6 and M 250891-9 isolated from a single vegetative frond of *Mazzaella laminarioides*

Host	Host code[a]	Type of infection[b]
Carrageenophytes		
Mazzaella laminarioides (Bory) Fredericq	Ma 280391-S	C
M. laminarioides	Ma 280391-G	C
M. laminarioides	Pe 280691-S	C
M. laminarioides	Pe 280691-G	C
Chondrus crispus Stackhouse	JC 001 PC-S	C
C. crispus	JC 002 PC-G	C
Rhodoglossum californicum (J. Agardh) Abbott	JW 026-G	C
R. californicum	JW 027-G	C
Erythrodermis traillii (Holmes ex Batters) Guiry & Garbary	N. I.-G	C
Phyllophora pseudoceranoides (Gmelin) Newroth & A.R.A. Taylor	P. E. I.-G	C
Ahnfeltiopsis devoniensis (Greville) Silva & De Cew	N. S.-G	C
A. furcellata (C. Agardh) Silva & De Cew	Ma 080192	C
Mastocarpus stellatus (Stackhouse) Guiry	CM 023-G	F
Agarophytes		
Ahnfeltia plicata (Hudson) Fries	N. S.-G	F
A. fastigiata (Postels & Ruprecht) Makienko	B. C.-G	F
Ahnfeltiopsis durvellei (Bory) Silva & De Cew	Ma 080192-G	Sup
Gelidium lingulatum Kützing	Ma 280391-G	Sup
G. latifolium (Greville) Bornet & Thuret	Spain-G	F
Gracilaria chilensis Bird, McLachlan & de Oliveira	Me 240791-G	Sup
G. chilensis	PM 040991-G	Sup
Others		
Nothogenia fastigiata (Bory) Parkinson	Ma 080192	F

[a] Culture collection at the Departamento de Ecología, P. Universidad Católica de Chile, Santiago. S, sporophytic; G, gametophytic.
[b] C, complete, F, failure, Sup, superficial.

& McLachlan (1991). Isolates of *E. ramosum* were obtained as described elsewhere (Correa & McLachlan, 1991; Correa *et al.*, 1994).

Cross-infection experiments were done in 50 × 15 mm glass Petri dishes containing 15 ml of enriched sea water medium SFC (Correa & McLachlan, 1991). Three to six 5 mm apices of the potential host and a 1 ml inoculum of *E. ramosum* were added to each dish. One piece of sporophytic *Chondrus crispus* was also added, as a positive control, to assess infectivity of each inoculum. Although *C. crispus* is not the natural host, during preliminary trials it was demonstrated to be highly susceptible to *E. ramosum*. Each host–endophyte combination was repeated three to six times. Experiments were run for 6–8 weeks at 50 μmol photons $m^{-2} s^{-1}$, 15°C and 16 : 8 or 12 : 12 (light : dark) photoperiod.

The sequence of events, from spore settlement to the complete colonization of the natural host, has been described elsewhere (Correa *et al.*, 1994). At the end of the experiment, the outcome of the infection was classified as (a) failure, (b) superficial and (c) complete. Using a stereoscopic microscope (Nikon SMZ 1B) at maximum magnification under combined dark and bright field illumination, penetrating germlings 3 or 4 cells in size could easily be detected. When doubts arose, hand-cut sections of the tissue were observed by standard bright field microscopy. To ensure that superficial infections were not confused with germlings resting on the surface of the thalli, all samples were brushed and then sonicated at 50 kc s^{-1} for 30 s before making the final observations. Failure indicates that *E. ramosum* was unable to invade to any extent the potential hosts. Superficial infections included those where *E. ramosum* broke through the outer cell wall and into the cortex of the hosts. In these cases no further development of the endophyte occurred and infections occupied significantly less than 5% of the total thallus surface. Complete infections were those where penetration into the medulla was extensive and the endophyte replaced large areas of the host cortex (usually > 50%). This category comprised only hosts which displayed an infection pattern similar to the one described for infected, wild *Mazzaella laminarioides* (see Correa *et al.*, 1994).

Results

Spores of all *Endophyton ramosum* isolates settled and germinated similarly on susceptible and non-susceptible hosts as well as on the glass of the culture dishes. Spore-generated plants developed as masses of filaments adhering loosely to the substratum when germination occurred on non-susceptible hosts and glass. Usually, however, these plants became detached when gentle agitation of the culture dishes or brushing of the thalli was applied. In susceptible hosts, on the other hand, spores settled and in 1–2 weeks there was clear microscopic evidence of host invasion. These invasive germlings could not be removed by combined brushing and sonication; the infections persisted and the infective alga spread into the host.

Infection of *Mazzaella laminarioides* (Figs 1, 2) and *Chondrus crispus* (Figs 3, 4) was complete (Table 2). All thalli of *M. laminarioides* were almost entirely colonized by *E. ramosum* (Fig. 1) and, at the end of the experiment, the infection was so severe that tissue became softened and apices ceased growth. In these fronds, most of the cortex had been replaced by endophytic filaments (Fig. 2). Similar development of the infection occurred in *C. crispus*, where *E. ramosum* colonized large areas of the fronds (Fig. 3). In both *M. laminarioides* and *C. crispus*, it was clear that the endophyte could enter the host through the intact cortex and through the cut surface at the base of the fragments (Fig. 3). Colonization of the medulla was particularly massive in sporophytic thalli of *C. crispus* (Fig. 4). No differences in the infection pattern were detected between *M. laminarioides* from Matanzas and Pelancura.

Some differences arose, however, when isolates M 150492-S and M 150492-G, obtained from sporophytic and gametophytic *M. laminarioides* respectively, were assayed with *M. laminarioides* and *C. crispus* (Table 3). The former isolate infected similarly the two life-history phases of *C. crispus* and the sporophytic phase of *M. laminarioides*. *E. ramosum* M 150492-G, on the other hand, developed fully when in contact with *M. laminarioides*, regardless of the host's life-history phase, whereas only few scattered lesions developed in *C. crispus*. Colonization of *C. crispus* by M 150492-G, although patchy (Fig. 5), affected the cortex and medulla (Fig. 6) of the host.

Infection of the other carrageenophytes (excluding *Mastocarpus stellatus*) was also complete (Table 2) and the lesions were remarkably similar to those affecting wild *Mazzaella laminarioides*. For example, at the end of the experiment with *Rhodoglossum californicum*, endophytic cells appeared scattered among host cortical cells (Fig. 7) and invasive filaments had penetrated the medulla (Fig. 8).

Susceptibility to infection was variable in agarophytes and depended on the host species involved and the endophytic isolate assayed (Tables 2, 3). Only *Gracilaria chilensis*, *Gelidium lingulatum* and *Ahnfeltiopsis durvillei* were colonized, and only by some isolates of *E. ramosum* (Table 2, Figs 9, 10). Infection of agarophytic thalli was characterized by the development of nodules of endophytic cells, which modified their normal elongate shape and became spherical. Density of these nodules was very low (< 10 per thallus) and in most cases they were restricted to the cortical tissue (Fig. 10), near the base of the fragment.

The xylan-producer *Nothogenia fastigiata* was not susceptible to any isolate. In some of the non-susceptible hosts, including *Ahnfeltia plicata*, *A. fastigiata* and *Gelidium latifolium*, *E. ramosum* isolates failed even in the initial penetration of host thalli. Other non-susceptible hosts, such as *Mastocarpus stellatus*, *Ahnfeltiopsis durvillei* and

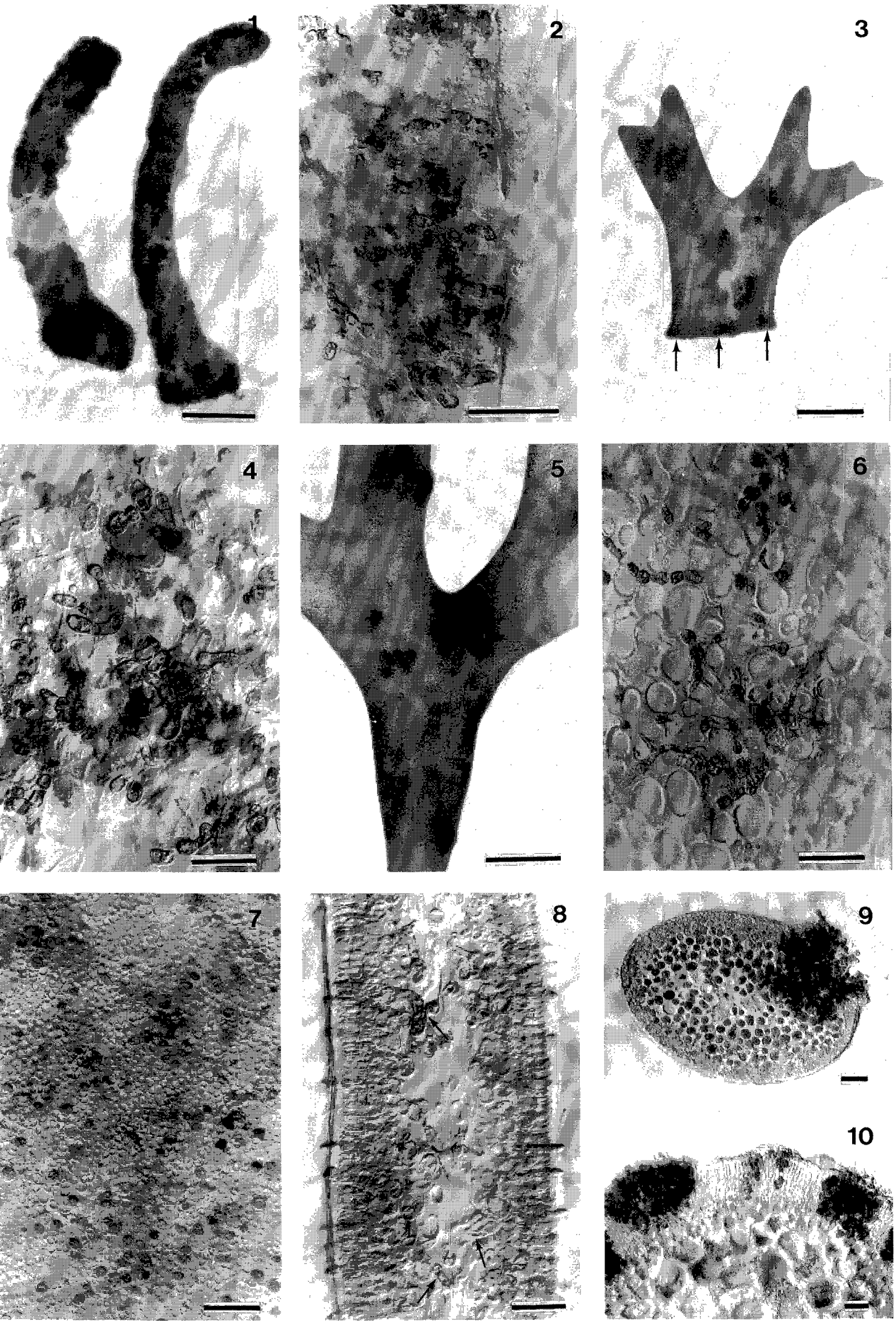

Table 3. Summary of the infections of selected hosts by *Endophyton ramosum* isolated from reproductive *Mazzaella laminarioides*

Host	Host code[a]	Endophyte[b] M 150492-S	Endophyte[b] M 150492-G
Mazzaella laminarioides	Ma 280391-S	Complete	Complete
M. laminarioides	Ma 280391-G	Superficial	Complete
Chondrus crispus	JC 001 PC-G	Complete	Superficial
C. crispus	JC 002 PC-S	Complete	Superficial
Gelidium lingulatum	Ma 280391-G	Failure	Superficial
Gracilaria chilensis	Me 240791-G	Failure	Superficial

[a] S, sporophytic thalli; G, gametophytic thalli.
[b] S and G, the life-history phase of the frond used to obtain the isolate.

N. fastigiata, allowed penetration but infective germlings did not grow larger than a few cells (e.g. in *A. durvillei*). In some cases, such infections then degenerated leaving a scar as the only indication of the infection (e.g. in *M. stellatus* and *N. fastigiata*).

Discussion

Our results demonstrated that *Endophyton ramosum*, whose infections cause a degradative disease in *Mazzaella laminarioides*, has some degree of host-specificity. In spite of the extremely narrow host-range displayed in nature, this species is able to infect a higher diversity of algal hosts in laboratory trials. For example, species such as *Ahnfeltiopsis durvillei* and *Gelidium lingulatum*, which occur just below *M. laminarioides* in the intertidal zone (Santelices, 1988) but have never been found infected by *E. ramosum* (Correa, personal observation), developed superficial infections in our *in vitro* assays. On the other hand, hosts never naturally exposed to *E. ramosum*, such as *Chondrus crispus*, *Rhodoglossum californicum*, *Erythrodermis traillii*, *Phyllophora pseudoceranoides* and *Ahnfeltiopsis devoniensis*, were susceptible to the endophyte, and infection of both cortex and medulla was similar to that in *M. laminarioides*. The factors which determine this broader host range in laboratory infection trials remain to be elucidated. It is possible that conditions present *in vitro* increase contact between infecting spores and hosts which, in their natural habitat, occur at some distance from the carrier host *M. laminarioides*. Thus, the 'artificial' contact would create an unnatural situation, facilitating the infection of the tested hosts. However, it is clear that this is not the key issue when the outcome of the experiments with *Nothogenia fastigiata* is considered. In nature, this species coexists with *M. laminarioides* in such a way that it is common to find patches of *N. fastigiata* scattered among or under the fronds of *M. laminarioides* (Correa, personal observation). In spite of this coexistence in the field, we have not detected *Endophyton ramosum* in fronds of wild *N. fastigiata*, which is consistent with the failure of our *in vitro* cross infections.

The pattern of specificity displayed by *E. ramosum* was not related to the life-history phase of the hosts. Both sporophytic and gametophytic thalli of *M. laminarioides* were susceptible to the endophyte and this is in agreement with the susceptibility of the two phases to infections by *E. ramosum* reported for wild populations of the host (Correa *et al.*, 1994; Correa & Sánchez. 1996). The two life-history phases of *Chondrus crispus* were also susceptible. This differs significantly from the pattern of specificity displayed by *Acrochaete operculata* (Correa & McLachlan, 1991), which infected only the sporophytic phase of *C. crispus* and *Iridaea cordata*. The first suggestion that sporophytic and gametophytic stages of a single species could be differentially susceptible to infections came from Andrews *et al.* (1979). However, observations of field-collected material (Saito *et al.*, 1977; Goff & Coleman, 1984) and of laboratory experiments with parasitic (Nonomura, 1979; Goff & Coleman, 1984; Zuccarello & West, 1994*a*) and epiphytic (Gonzalez & Goff, 1989) algae indicate no correlation between susceptibility to infection and life-history phase of the host. This is further supported by the results of infections by the pigmented green algal endophytes *Blastophysa rhizopus* (Iima & Tatewaki, 1987) and *Acrochaete heteroclada* (Correa & McLachlan, 1991), where no differences in sporophytic and gametophytic susceptibility were detected. Thus, the available evidence suggests that differential susceptibility to infections of different life-history phases of algal hosts may be rare, and its occurrence could be indicative of associations where the pair of symbionts has a much longer evolutionary history of living together.

Suggestions that the type of carrageenan could be an important factor in determining a particular pattern of specificity are not supported by the present study. All carrageenophytes, with the exception of *Mastocarpus stellatus*, were equally susceptible to *E. ramosum*, regard-

Figs 1–10. Infection of various host species of red alga by the green endophyte *Endophyton ramosum*. **Figs 1, 2.** Sporophytic *Mazzaella laminarioides* infected by isolate M 150492-S. **Fig. 1.** Whole thalli. **Fig. 2.** Cross-section through the cortex, almost completely replaced by the endophyte. **Figs 3–6.** Sporophytic *Chondrus crispus*. **Fig. 3.** General view of thallus infected by isolate M 150492-S. Dark band at the base of the fragment (arrows) indicates penetration through the cut region. **Fig. 4.** Colonization of the medulla by isolate M 150492-S. **Fig. 5.** General view of thallus infected by isolate M 150492-G. **Fig. 6.** Medullary tissue infected by isolate M 150492-G. **Figs 7, 8.** Gametophytic *Rhodoglossum californicum* infected by isolate M 250891-1. **Fig. 7.** Surface view of the frond. **Fig. 8.** Endophytic filaments have colonized both sides of the frond, and the medulla (arrows). **Fig. 9.** Gametophytic *Gelidium lingulatum* infected with isolate M 150492-G. **Fig. 10.** Gametophytic *Gracilaria chilensis* infected with isolate M 150492-G. Scale bars represent: Figs 1 and 5, 1 mm; Figs 2, 4, 6, 7 and 8, 40 μm; Fig. 3, 1·5 mm; Figs 9 and 10, 50 μm.

less of the carrageenan type they produced (see Craigie, 1990, for a review of carrageenans). In the case of *Acrochaete operculata*, on the other hand, the pattern of specificity appeared to be determined by the presence of lambda carrageenan in the cell wall of the algae used in the assays (Correa & McLachlan, 1991). This conclusion was reached after cross-infection experiments where lambda carrageenan-producer hosts, belonging to two different genera (*Chondrus* and *Iridaea*), developed the same type of lesions whereas plants of the same species producing lambda and kappa carrageenans displayed a remarkably different susceptibility (Correa & McLachlan, 1991). The failure of *E. ramosum* to infect *M. stellatus* is difficult to explain with our present knowledge. Fronds of *M. stellatus* in eastern Canada were consistently free of endophytic algae (Correa, 1990), with the exception of the generalist epi/endophyte *A. heteroclada* (Correa & McLachlan, 1991). The occurrence of some type of non-specific host response to infections may play a role in preventing infections in *M. stellatus*, as suggested by the presence of dark brown-reddish amorphous material surrounding the invasive filaments of the endophytes in wild infected fronds (Correa, 1990).

Although it is clear that *E. ramosum* does not discriminate among different carrageenan-producing species nor between different host life-history phases within the carrageenophytes, it discriminates against agar-producing hosts. This view is supported by observations where *E. ramosum* developed as in its natural host only when in contact with carrageenophytic species. In the few instances in which agarophytes were infected, only the cortex was involved and the density of the infection was low and far less severe than in carrageenophytes. Furthermore, it seems interesting that only Chilean agarophytes were affected. At present, it still remains to be elucidated whether this carrageenophyte/agarophyte difference is due to the chemical nature of the cell wall polysaccharides (Craigie, 1990) or to the physical properties determined by these bio-polymers (see Kloareg & Quatrano, 1988).

Integrity of the host thallus does not have a significant impact on the outcome of the infection by *E. ramosum*. Thus, if a susceptible host (e.g. *Chondrus crispus*) was inoculated, *E. ramosum* gained access through both the intact cortex and the cut surface left when cutting the fragment, where the inner tissues were exposed. In contrast, when a non-susceptible species (e.g. *Nothogenia fastigiata*) was assayed, the endophyte was unable to penetrate even through the open areas of the thallus. These responses agree with those reported for *Acrochaete operculata* (Correa & McLachlan, 1991), whose endophytic habit is not determined by openings or wounds in the host thallus. In other endophytic associations, however, infecting organisms require open wounds (Goff, 1976, 1982; Goff & Cole, 1976) or weakened points (White & Boney, 1969) to penetrate into a given algal host. Similarly, artificial wounds in hosts inoculated with *Blastophysa rhizopus* enhanced infectivity of the endophyte (Iima & Tatewaki, 1987).

In addition to the possible role that host polysaccharides may play in determining specificity, our study suggests that variability in infectivity within *E. ramosum* could be responsible for the differences in the patterns of infection, since isolates of the same species, obtained from different individual host fronds and at different times, varied in their specificity patterns. Both spatial and temporal intraspecific variability in infectivity has been reported in pathogens of terrestrial plants, phenomena resulting from genetic heterogeneity of both host and pathogens (see Burdon & Leather, 1990; Zuccarello & West, 1994*b*). No equivalent information is available for algal pathosystems, although epidemiological studies of green patch disease in Matanzas are showing a high degree of heterogeneity in host susceptibility, which is expressed as a patchy distribution of the infected individuals (Correa & Sánchez, 1996). High intraclonal variation in a number of algal characters has also been reported (Santelices & Varela, 1993), which may result in intraspecific differences in infectivity by the endophytes, as well as intraspecific differences in host susceptibility to infections by foreign organisms. In this context, information on genetic variability in host resistance and pathogen infectivity/virulence, similar to that reported for terrestrial pathosystems, may be crucial for understanding the spatial and temporal persistence of both *Mazzaella* and *E. ramosum* in wild populations of the host in central and southern Chile.

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References

ANDREWS, J.H., VADAS, R.L., WHEELER, W.N., NEUSHUL, M., WOESSNER, J., KOHLMEYER, J., DODDS, J.A., KAZAMA, F.Y. & NORTH, W.J. (1979). Pathology of seaweeds: current status and future prospects. *Experientia*, **35**: 429–450.

APT, K.E. (1988). Etiology and development of hyperplasia induced by *Streblonema* sp. (Phaeophyta) on members of the Laminariales (Phaeophyta). *J. Phycol.*, **24**: 28–34.

BONEY, A.D. (1972) *In vitro* growth of the endophyte *Acrochaetium bonnemaisoniae* (Batt.) J. et G. Feld. *Nova Hedwigia*, **23**: 173–186.

BURDON, J.J. & LEATHER, S.R. (1990). *Pests, Pathogens and Plant Communities*. Blackwell Scientific Publications, Oxford.

CORREA, J.A. (1990). *Pigmented Algal Endophytes of Chondrus crispus Stackhouse: Host-specificity, Fine Structure and Effects on Host Performance in Infections by Acrochaete operculata Correa et Nielsen and A. heteroclada Correa et Nielsen*. PhD dissertation, Dalhousie University, Canada.

CORREA, J.A. & MCLACHLAN, J. (1991). Endophytic algae of *Chondrus crispus* (Rhodophyta). III. Host-specificity. *J. Phycol.*, **27**: 448–459.

CORREA, J.A. & MCLACHLAN, J. (1992). Endophytic algae of *Chondrus crispus* (Rhodophyta). IV. Detrimental effects on the host following infections by *Acrochaete operculata* and *A. heteroclada* (Chlorophyta). *Mar. Ecol. Progr. Ser.*, **81**: 73–87.

CORREA, J.A. & MCLACHLAN, J. (1994). Endophytic algae of *Chondrus crispus*

Stackhouse (Rhodophyta). V. Fine structure of the infection by *Acrochaete operculata* (Chlorophyta). *Eur. J. Phycol.*, **29**: 33–47.

CORREA, J.A. & SÁNCHEZ, P. (1996). Ecological aspects of algal infectious diseases. *Hydrobiologia*, in press.

CORREA, J.A. NIELSEN, R. & GRUND, D.W. (1988). Endophytic algae of *Chondrus crispus* (Rhodophyta). II. *Acrochaete heteroclada* sp. nov., *A. operculata* sp. nov., and *Phaeophila dendroides* (Chlorophyta). *J. Phycol.*, **24**: 528–539.

CORREA, J.A., FLORES, V. & SÁNCHEZ, P.A. (1993). Deformative disease in *Iridaea laminarioides* (Rhodophyta): gall development associated with an endophytic cyanobacterium. *J. Phycol.*, **29**: 853–860.

CORREA, J.A., FLORES, V. & GARRIDO, J. (1994). Green patch disease in *Iridaea laminarioides* (Rhodophyta), caused by *Endophyton* sp. (Chlorophyta). *Dis. Aquat. Org.*, **19**: 203–213.

CRAIGIE, J.S. (1990). Cells walls. In *The Biology of the Red Algae* (Cole, K.M. & Sheath, R.G., editors), 221–257. Cambridge University Press, Cambridge.

GARBARY, D. (1979). A revised species concept for endophytic and endozoic members of the Acrochaetiaceae (Rhodophyta). *Bot. Not.*, **132**: 451–455.

GARDNER, N.L. (1909). New Chlorophyceae from California. *Univ. Calif. Publ. Bot.*, **3**: 371–375.

GOFF, L.J. (1976). The biology of *Harveyella mirabilis* (Cryptonemiales, Rhodophyceae). V. Host responses to parasite infection. *J. Phycol.*, **12**: 313–328.

GOFF, L.J. (1983). Marine algal interactions: epibiosis, endobiosis, parasitism and disease. In *Proceedings of the Joint China–US Phycology Symposium* (Tseng, C.K., editor), 221–274. Science Press, Beijing.

GOFF, L.J. & COLE, K. (1976). The biology of *Harveyella mirabilis* (Cryptonemiales, Rhodophyceae). III. Spore germination and subsequent development within the host *Odonthalia floccosa* (Ceramiales, Rhodophyceae). *Can. J. Bot.*, **54**: 268–280.

GOFF, L.J. & COLEMAN, A.W. (1984). Transfer of nuclei from a parasite to its host. *Proc. Natl. Acad. Sci. U.S.A.*, **81**: 5420–5424.

GONZALEZ, M.A. & GOFF, L.J. (1989) The red algal epiphytes *Microcladia coulteri* and *M. californica* (Rhodophyceae, Ceramiaceae). II. Basiphyte specificity. *J. Phycol.*, **25**: 558–567.

IIMA, M. & TATEWAKI, M. (1987). On the life history and host-specificity of *Blastophysa rhizopus* (Codiales, Chaetosiphonaceae), an endophytic green alga from Muroran in laboratory cultures. *Jpn. J. Phycol.* (Sôrui), **35**: 241–250.

KLOAREG, B. & QUATRANO, R.S. (1988). Structure of the cell walls of marine algae and ecophysiological functions of the matrix polysaccharides. *Oceanogr. Mar. Biol. Annu. Rev.*, **26**: 259–315.

NIELSEN, R. (1979). Culture studies on the type species of *Acrochaete, Bolbocoleon* and *Entocladia* (Chaetophoraceae, Chlorophyceae). *Bot. Not.*, **132**: 441–449.

NONOMURA, A.M. (1979). Development of *Janczewskia morimotoi* (Ceramiales) on its host *Laurencia nipponica* (Ceramiales, Rhodophyceae). *J. Phycol.*, **15**: 154–162.

O'KELLY, C.J. (1980). Host-specificity and the mechanisms of speciation and dispersal in the endophytic algal genus *Endophyton* Gardner (Chlorophyta). *J. Phycol.*, **16** (Suppl.): 31.

O'KELLY, C.J. (1982). Observations on marine Chaetophoraceae (Chlorophyta). III. The structure, reproduction and life history of *Endophyton ramosum*. *Phycologia*, **21**: 247–257.

SAITO, Y., YONETA, T. & YOSHIKAWA, M. (1977). The relationships of parasite and host in the red algae *Janczewskia tokidae* and *Laurencia nipponica*. *Bull. Jpn. Soc. Phycol.*, **25**: 311–317.

SANTELICES, B. (1988). *Algas marinas de Chile. Distribución, Ecología, Utilización y Diversidad.* Ediciones Universidad Católica de Chile, Santiago.

SANTELICES, B. & VARELA, D. (1993). Intraclonal variation in the red alga *Gracilaria chilensis*. *Mar. Biol.*, **116**: 543–552.

WHITE, E.B. & BONEY, A.D. (1969). Experiments with some endophytic and endozoic *Acrochaetium* species. *J. Exp. Mar. Biol. Ecol.*, **3**: 246–274.

WHITE, E.B. & BONEY, A.D. (1970). *In situ* and *in vitro* studies on some endophytic and endozoic *Acrochaetium* species. *Nova Hedwigia*, **19**: 841–881.

ZUCCARELLO, G.C. & WEST, J.A. (1994*a*). Host specificity in the red algal parasites *Bostrychiocolax australis* and *Dawsoniocolax bostrychiae* (Choreocolacaceae, Rhodophyta). *J. Phycol.*, **30**: 462–473.

ZUCCARELLO, G.C. & WEST, J.A. (1994*b*). Genus and race specificity in the red algal parasite *Leachiella pacifica* (Choreocolacaceae, Rhodophyta). *Phycologia*, **33**: 213–218.