



Inducible defenses against herbivory and fouling in seaweeds



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ABSTRACT

Secondary metabolites play an important ecological role as a defense mechanism in seaweeds. Chemical defenses are well known to change in response to herbivory, but other driving factors, either biotic or abiotic, are often neglected. Epibiosis may not only reduce seaweed fitness, but also increase attractiveness to consumers, and thus defense production should also be triggered by epibionts. In this study, three Southwestern Atlantic seaweeds, *Gracilaria cearensis*, *Pterocladia capillacea* (Rhodophyceae) and *Codium decorticatum* (Chlorophyceae) were investigated in laboratory bioassays designed to test whether the action of herbivory or simulated epibiosis influences chemical defenses. Crossed induction experiments were also performed in order to assess whether herbivore induction influences antifouling chemical defense, as well as whether epibiont induction would affect defense against herbivores. The effect of laboratory conditions on seaweeds in the absence of field stimuli was also investigated by comparing consumption of artificial food with extracts from acclimatized and non-acclimatized seaweeds (i.e., natural defense levels). Only the green seaweed *C. decorticatum* exhibited inducible antifouling defenses triggered by simulated epibiosis, but not by herbivores. In the other seaweeds there was no induction either by herbivory or simulated epibiosis. Acclimatization did not affect *C. decorticatum* defenses. However, non-acclimatized *G. cearensis* artificial foods were preferred over acclimatized ones, while extracts from acclimatized *P. capillacea* increased herbivore consumption, highlighting the need to acclimatize seaweeds before the main induction experiments. This is the first report of inducible defenses due to simulated fouling in seaweeds.

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1. Introduction

Herbivory is known as a major biological factor capable of generating a significant impact on seaweed beds and, consequently, assumed to be an important selective force driving algal chemical defense production. For a long time scientists speculate about the existence of a relationship between defense production – in particular chemical defenses – and herbivory pressure (Wright et al., 2004). This relationship seems to explain observations of variation in amounts of secondary compounds produced by seaweeds and how they act against herbivores in marine tropical and temperate ecosystems (e.g. Cronin et al., 1997).

In fact, today and likely during most of the evolutionary history, a wide array of secondary metabolites from seaweeds constitute the most relevant defense strategy against herbivores, such as fish, sea urchins, and gastropods, among others (Pereira and Da Gama, 2008). However, the amount of these algal chemicals is not an absolute or inexorable characteristic of a given species, as the concentration of defensive chemicals may vary in response to environmental conditions, as abiotic (e.g. Sudatti et al., 2011) or even in response to biological factors, typically, herbivory (e.g. Ank et al., 2013).

Some mesoherbivores can spend long periods feeding (and sometimes living) in the same thallus, which allows sufficient time for a chemical counterattack to be launched, and some herbivores are deterred only by high amounts of seaweed chemical defenses (see Hay, 1996 for a revision). When feeding in the same branch, a herbivore can induce defense production on this thallus part, which then becomes less palatable. Acting in this manner, the herbivore spends more time looking for food than feeding, and as a consequence, pieces ingested are smaller and damage as well as defense production occur in multiple locations in the plant. In fact, previously herbivore-induced brown seaweeds (*Ascophyllum nodosum*) had more herbivore movements than algae that had not been induced, and therefore feeding by the gastropod *Littorina obtusata* was significantly higher in the latter case (Borell et al., 2004). Similarly, grazing by the amphipod *Ampithoe longimana* induced increased concentrations of chemical defenses (dictyol E) in the brown alga *Dictyota menstrualis*, making this alga less susceptible to further herbivore attack (Cronin and Hay, 1996a).

After the first example of induced responses in a seaweed species, which was published in the late 1980s (Van Alstyne, 1988), the number of studies has increased progressively, mainly in the end of the last decade (e.g. Jormalainen and Honkanen, 2008). Although interest in the topic continues unabated (e.g. Flöthe and Molis, 2013), and sometimes the existence of induced defenses in seaweeds is unequivocal, the

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knowledge on this subject is still contradictory and fragmented, and certain questions remain unanswered, as defense induction was confirmed in a few green and brown algae, but not among red algae (Toth and Pavia, 2007; Jormalainen and Honkanen, 2008).

However, besides acting as mediators in the interaction with herbivores, secondary metabolites seem to reinforce seaweed protection against other harmful biological factors, such as pathogenic bacteria and fungi, or fouling organisms such as algal spores and invertebrate larvae growing as epibionts on algal thalli (Da Gama et al., 2014), and thus increase the ecological benefits of producing defenses (Amsler, 2008). Epibiosis has been demonstrated to reduce growth and reproduction of seaweed hosts (Orth and Montfrans, 1984; Brawley, 1992; Williams and Seed, 1992), increase drag and consequently losses due to detachment during storms (Brawley, 1992; Williams and Seed, 1992; Dixon et al., 1981), cause depletion of nutrients (Buschmann and Gómez, 1993), stimulate consumption (e.g., Da Gama et al., 2008a, 2008b) and consequently increase biomass loss of fouled seaweeds (Bernstein and Jung, 1979), promote tissue damage by mechanical anchoring and thallus penetration (González and Goff, 1989), thus epibiosis can affect negatively the fitness of host in different ways.

Epibiosis also interacts with herbivory, since palatable epibionts may offer an additional attractiveness to consumers, i.e., a fouled seaweed may exert more attraction to consumers than an epibiont-free alga (Pereira et al., 2003; Da Gama et al., 2008a). This aspect seems to be surprisingly common in the marine environment, in spite of the reasonable assumption that the disadvantages to the host organism promoted the evolution of antifouling chemical defenses or the evolution of compounds that can deter simultaneously consumers and epibionts – i.e., exert multiple ecological functions (Wahl and Hay, 1995; Schmitt et al., 1995). Many seaweeds exhibit mechanisms to cope with epibiosis, including the production of antifouling compounds (Da Gama et al., 2014). For instance, the crude extract of the red seaweed *Laurencia dendroidea* (= *L. obtusa*) was able to inhibit the settlement of a wide spectrum of fouling organisms in field assays (Da Gama et al., 2002, 2003). The cortical cells of *Laurencia* species possess special organelles, the *corps en cerise*, which has been implicated in the production, storage and release of antifouling compounds to the thallus surface (Paradas et al., 2010). Other red seaweeds also exhibit special structures, such as gland cells in *Delisea pulchra* (Dworjanyn et al., 1999) and mevalonosomes in *Plocamium brasiliense* (Paradas et al., 2015), involved in antifouling defense production and release. However, antifouling chemical defense in other seaweed groups, such as green algae, remains elusive (Da Gama et al., 2008b).

In the present work, the relationship between epibiosis, herbivory and inducible chemical defense was investigated in the seaweeds *Codium decortiatum* (Chlorophyceae), *Gracilaria cearensis*, and *Pterocladia capillacea* (Rhodophyceae) through experimental manipulations in the laboratory. We addressed the following questions: (1) How chemical defenses change in the absence of field stimuli? (2) Are chemical defenses activated or induced by herbivory and/or epibiosis? (3) Do herbivore-induced defenses inhibit epibiosis, or epibiont-induced defenses inhibit herbivory?

2. Materials and methods

2.1. Sampling sites and organisms

Induced defense in 3 species of seaweeds was tested in a set of 6 bioassay experiments conducted in the Marine Aquaria Laboratory of the Department of Marine Biology of the Universidade Federal Fluminense (UFF) in the city of Niterói (Rio de Janeiro state, Brazil). The red seaweeds *G. cearensis* and *P. capillacea* were collected by free diving in the intertidal zone of Rasa (22°73'40"S, 41°95'79"W) and Forno (22°46'40"S, 41°52'57"W) beaches, respectively, in the city of Armação dos Búzios, while the green seaweed *C. decortiatum* was collected subtidally from Itaipu beach in Niterói city (22°97'43"S, 43°04'78"W).

Both sites are located in Rio de Janeiro State, SE Brazilian coast (SW Atlantic) (Fig. 7).

Chemical defenses were evaluated through antifouling and anti-herbivory experiments according to the protocols proposed by Da Gama et al. (2003) and Hay et al. (1994) using *Perna perna* mussels and *Elasmopus brasiliensis* amphipods, respectively, as test organisms. Amphipods were also used as herbivore inducers, while fouling induction was promoted by simulated epibionts (see below for details). Juvenile brown mussel (*Perna perna*) specimens used in antifouling assays were collected from the intertidal zone of Itaipu beach 2 h before the experiments. The community of amphipods dominated by *E. brasiliensis* (used to induce defense production and in further herbivory bioassays, see Weidner et al., 2004) was collected from Boa Viagem beach, Guanabara Bay, Niterói (22°90'91"S, 43°13'07"W), where they occur associated with the common green seaweed *Ulva fasciata* and bryozoans. After transfer to the laboratory, herbivores were kept with *U. fasciata* as a food and shelter source until needed.

2.2. Experimental set-up

In 3 closed water systems (ca. 1500 l each, one per seaweed species), seawater was continuously aerated and filtered through a system comprised of layers of sand, plankton mesh, activated carbon and a water-pumped protein skimmer. Water was kept at constant temperature (ca. 20 °C), pH (8.5 ± 0.5; pH-MV-TEMP-analyser), and salinity (35 ± 1; Salinometer 5–10 No. 147, Shibuya Optical).

Seawater was equally distributed by aquarium hoses (effective diameter = 0.4 cm) to the experimental units (EUs), and through them drained again to the filtering and reservoir system, exchanging the total water volume at approximately every hour. The EUs comprised independent, rectangular transparent plastic aquaria (12 × 18 × 11 cm, volume = 2 l), each with an in- and out-flow at opposite sides (Fig. 1). Treatments were always pairwise, and all EU pairs were randomly arranged under daylight fluorescent lamps (40 W, Agrolux), irradiating macroalgae at a mean quantum flux density (Li-185 B, Li-Cor) of 100 ± 10 μmol m⁻² s⁻¹ in a 12:12 h light:dark cycle.

For each macroalgal species, paired experiments were performed consisting of an acclimatization phase to allow adjustment to laboratory conditions and, possibly, relaxation or recovery of defense levels (14 days - d), then an induction phase with either herbivores (7 d) or epibiont mimics as inducers (7 d), and finally, bioassays to assess induction of chemical defenses against herbivory and fouling. Algal biomass (wet weight, ww) was recorded before/after acclimatization, and before/after control and treatment conditions (induction phase). Increase



Fig. 1. Rectangular transparent plastic aquaria (12 × 18 × 11 cm, volume = 2 l) used as experimental units, EU.

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