



Tissue-specific induction of resistance to herbivores in a brown seaweed: the importance of direct grazing versus waterborne signals from grazed neighbors

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Received 15 October 2001; received in revised form 1 February 2002; accepted 11 March 2002

Abstract

In theory, plants could induce resistance to herbivores after being directly grazed or after sensing cues from the grazing of neighboring plants (i.e., the “talking trees” effect). Despite an extensive literature on induced defenses in plants, the relative importance of direct attack versus cues from neighbors in mediating induction is not well understood; this is especially true for seaweeds, where few investigations of induction due to attacks on neighbors have been conducted. We measured changes in resistance to grazing for stipes and blades of the brown seaweed *Sargassum filipendula* (Phaeophyta; Fucales) when it was directly grazed by amphipods or when it received potential waterborne cues from the grazing of neighboring plants, relative to plants that experienced neither direct grazing nor cues from grazed neighbors. After 25 days of these treatments in outdoor tanks, the amphipod *Ampithoe longimana* consumed top stipes from control plants 2.8 times more rapidly than top stipes from directly grazed plants, but did not differentiate between top blades in the same comparison. The amphipod did not discriminate between plants with grazed neighbors and plants with control neighbors when feeding on either stipes or blades. Thus, induction of resistance in *S. filipendula* was tissue-specific and occurred as a result of direct grazing, but not due to the grazing of neighboring plants.

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Keywords: Amphipod; *Ampithoe longimana*; Induction, interplant communication; *Sargassum filipendula*; Seaweed defense

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1. Introduction

A variety of plant structures and metabolites is effective at deterring grazers (Hay and Fenical 1988; Hay, 1996; Hartley and Jones, 1997), but these defenses can be expensive to produce and maintain (Zangerl et al., 1997; Baldwin, 1998). As a consequence where herbivory is patchy and unpredictable, plants should, therefore, benefit from possessing defenses that are rapidly induced when needed rather than being permanently expressed (Harvell and Tollrian, 1999). It is now well established that many plants induce defenses in response to herbivory (Karban and Baldwin, 1997). If chemicals released from grazers or grazed neighbors provided a reliable warning of imminent herbivory, then these signals could also be used as cues to boost resistance. Numerous studies have reported defensive responses of terrestrial plants to grazing of their neighbors (the so-called “talking trees” phenomenon), but most of these studies are laboratory-based, compromised by pseudoreplication, or subject to alternative interpretations (Baldwin and Schultz, 1983; Rhodes, 1983; Fowler and Lawton, 1985; reviewed by Karban and Baldwin, 1997; but see Dicke and Bruin, 2001). Consequently, little is known about the prevalence of the “talking trees” effect and its importance as a plant defensive strategy relative to induction in response to direct grazing. There is, therefore, a need for studies that simultaneously assess the relative importance of both cues for induction.

In coastal marine systems, grazing on seaweeds can be intense (see examples in Lawrence, 1975; Lubchenco and Gaines, 1981; Hay, 1992), but is often variable in time and space (Lubchenco and Cubitt, 1980; Hay et al., 1983; Hay, 1984). Seaweeds possess an array of constitutive chemical deterrents to herbivory (see reviews of Hay and Fenical, 1988; Paul et al., 2001), and some species also increase concentrations of defensive compounds in response to grazing on their tissues, and these increases can further enhance their resistance to herbivores (Van Alstyne, 1988; Cronin and Hay, 1996; Pavia and Toth, 2000). Induction of reduced palatability (Renaud et al., 1990) or of increased levels of secondary metabolites (Hammerstrom et al., 1998) can occur in as little as one day. Such a rapid response to attack should allow seaweeds to reduce their susceptibility on a time scale that is ecologically meaningful for numerous types of marine herbivores. However, given that grazing by large herbivores such as fishes or sea urchins can destroy entire plants in seconds to hours, rather than days, it has been hypothesized that seaweeds will be defended constitutively against these herbivores, and that it is the small, insect-like mesograzers of marine systems (e.g., amphipods, isopods, and snails) that are most likely to induce defenses in seaweeds (Hay, 1996). Induced defenses could be effective against these consumers because they remove smaller amounts of tissue over extended periods of time (giving the plant time to respond) and because mesograzers are more intimately associated with their host plants, allow changes in the chemistry of an individual plant to have a greater impact on both plant and herbivore fitness.

Other characteristics of the ecology and physiology of seaweeds suggest that they could induce resistance due to cues received from the grazing of neighboring plants. Seaweeds often form dense monospecific stands where individuals are in close physical contact (Dayton, 1985; Schiel and Foster, 1986) and water movement is reduced (Eckman et al., 1989; Komatsu and Murakami, 1994), potentially facilitating the transmission of chemical signals between neighboring plants. Some seaweeds are able to sense waterborne cues

such as the concentration of inorganic carbon (Pearson et al., 1998). The fact that two genera of freshwater phytoplankton and a diverse array of aquatic animals can alter their behavior or morphology in response to consumer-related waterborne cues is a further indication that chemical signals can be transmitted, detected, and responded to in aquatic environments (Tollrian and Harvell, 1999). However, despite the potential for the phenomenon to occur, the response of seaweeds to herbivore-induced waterborne cues has been detected in only one seaweed, the brown alga *Ascophyllum nodosum* (Toth and Pavia, 2000).

In this paper, we search for a “talking trees” effect in the fucalean brown seaweed *Sargassum filipendula* C. Agardh, 1824. We ask if *S. filipendula* can decrease its palatability to herbivores in response to direct grazing or to grazing of neighboring plants. By simultaneously assessing the effects of direct attack and of induction due to attacks on neighbors, we can compare the strengths of the two types of potential cues for induction. Because induction can be tissue-specific in seaweeds (Hammerstrom et al., 1998), we assayed changes in palatability of recently emerged blades and stipes, the two major tissue types in *S. filipendula*.

2. Methods

Induction experiments were run in outdoor mesocosms at the University of North Carolina at Chapel Hill’s Institute of Marine Sciences in Morehead City, NC. Forty pairs of 11-l tanks were staggered so that one tank in each pair was above and to the side of the other (Fig. 1). Filtered seawater from nearby Bogue Sound was pumped at ~ 0.06 l/s into the upper tank, which contained either a *S. filipendula* plant inoculated with herbivorous amphipods or a control plant that was not inoculated. The water from this upper tank flowed via a pipe fitted with a 200- μ m mesh bag filter (to prevent amphipod movement

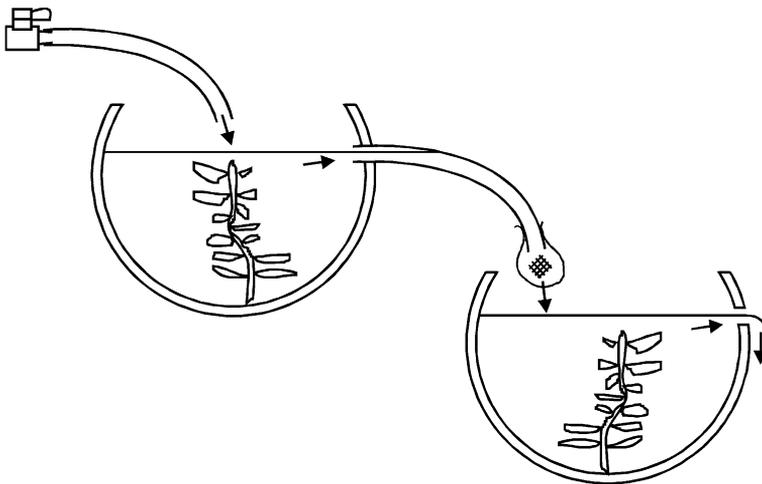


Fig. 1. Profile diagram of experimental setup.

among tanks) into the lower tank. The lower tanks each contained a *S. filipendula* plant that was devoid of amphipods. Plants in the lower tanks were not grazed directly, but were exposed to seawater flowing over plants that either had or had not been grazed by amphipods. All tanks were covered with a layer of burlap, which lowered light levels to those typically found in the natural habitat at the plant collection site.

On 13 November 1998, *S. filipendula* plants were collected from the shallow subtidal at Radio Island Jetty, near Beaufort, NC (34°42'N, 76°41'W), and held overnight in water tables with flowing seawater. The next day, two 200–300-mm-long individual ramets were collected from an individual plant, cleaned of amphipods using a dilute solution of insecticide (following Duffy and Hay, 2000), and cable-tied at the base to a small PVC pipe that served to anchor the plant in place. The two ramets from each individual were placed singly into adjacent treatment and control tanks. At the start of the experiment, half of the upper tanks ($n = 20$) each received 10 *Ampithoe longimana* to serve as grazers whose feeding might produce induction signals. Because there appeared to be minimal grazing by day 10 of the experiment, we added five *A. marcuzzii* to each of these same tanks at this time. Both of these gammarid amphipods are known consumers of *S. filipendula* (Duffy, 1990; Duffy and Hay, 1991). No amphipods were added to the remaining 20 upper tanks, which served as controls. Every 2 days, each tank was stirred briefly to reduce the buildup of detritus on the plants.

On 7 December (day 23), we used *A. longimana* to assay the palatability of blades and stipes from upper portions of directly grazed plants and their controls and the palatability of upper blades from the two sets of downstream plants. On December 9 (day 25), the palatability of the upper stipes from downstream plants was assayed in a similar manner. Individual *A. longimana* was simultaneously offered a choice between preweighed (~ 30 mg blotted wet mass; ± 1 mg) pieces of tissue taken from plants grazed by amphipods and their ungrazed controls (or plants downstream from each of these plants). We used upper portions because the meristem is apical in *S. filipendula*, making these upper portions the youngest and the ones most likely to have been produced during the treatment conditions described above.

S. filipendula tissues used in the feeding assays were placed on either side of a glass rod crossing the bottom of each assay dish. Amphipods could easily move back and forth over this rod, but could not move the algal pieces across it, thus enabling subsequent identification of the treatment and control tissue. An identical dish with pieces from the same plants was maintained without an amphipod to act as a control for autogenic changes in plant mass. Replicates were stopped after the amphipods had eaten at least half of one plant piece, or when 2–3 days had elapsed. Plant pieces were reweighed, and the change in mass of each piece was scaled to account for autogenic mass changes in the controls using the formula $T_i(C_f/C_i) - T_f$, where T_i and T_f represent the initial and final masses, respectively, of tissue subject to grazing and C_i and C_f represent, respectively, the initial and final masses of the control tissue. Replicates were dropped if the amphipod died during the assay or if the maximum mass of plant eaten in either treatment was ≤ 3 mg. Paired *t*-tests were performed on the amount of plant eaten.

Inspections of defaunated plants at the beginning of the experiment revealed very few herbivorous amphipods, but to verify that amphipod densities were higher on the amphipod-addition plants and that negligible numbers of grazers were present on down-

stream plants, we removed grazers from all plants at the conclusion of the experiment. This was done by dunking plants twice in freshwater for 5 s and collecting the juvenile and adult animals that vacated the plant, a method which efficiently removes nearly all

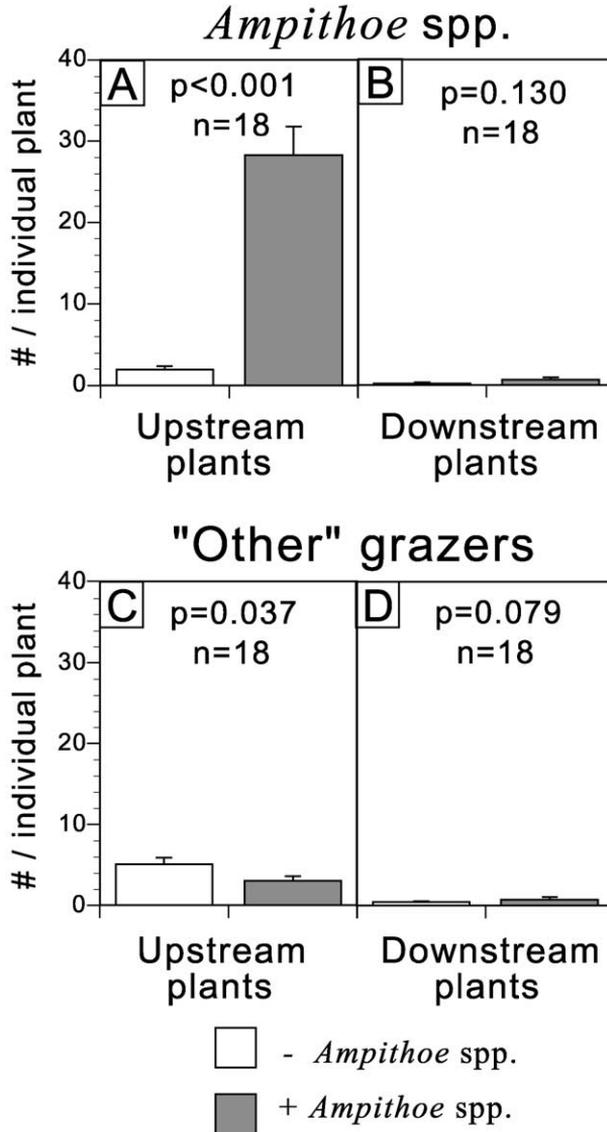


Fig. 2. Average number of herbivores per individual *S. filipendula* at the end of the experiment. (A) and (C) represent the number of *Ampithoe* spp. amphipods and other grazers (respectively) on upstream plants. (B) and (D) represent the number of *Ampithoe* spp. and other grazers (respectively) on downstream plants. Analyses were by two-tailed, unpaired *t*-test. Bars indicate +1 S.E.

amphipods (Holmlund et al., 1990). The blotted mass of each downstream plant was also recorded (± 0.1 g).

3. Results

At the end of the 25-day experimental period, average densities of *Ampithoe* species were 14 times higher on inoculated plants than on controls (Fig. 2A), and other herbivores were rare on both (Fig. 2C). *Ampithoe* spp. readily grazed *S. filipendula*, reducing the blotted wet mass of inoculated plants to $58 \pm 12\%$ (mean ± 1 S.E.) of the mass of controls ($p < 0.02$, unpaired *t*-test, $n = 18$). Virtually no herbivores were present on either treatment of the

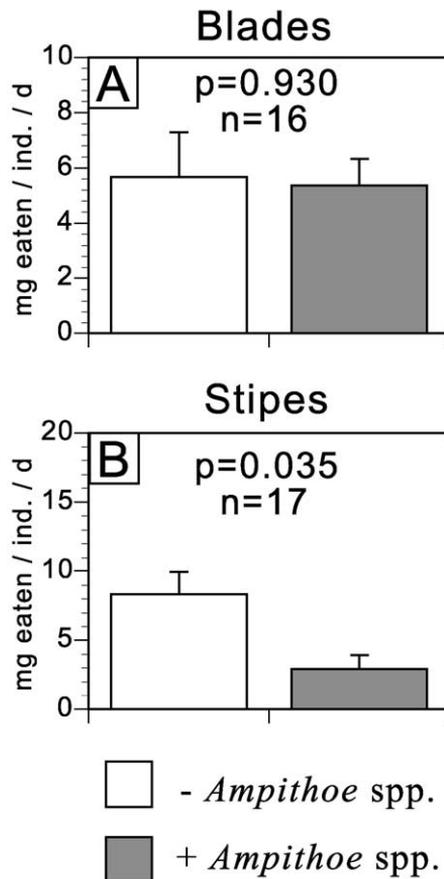


Fig. 3. Average feeding rates by the amphipod *A. longimana* offered a choice between *S. filipendula* tissues from plants grazed by amphipods or ungrazed controls; (A) top blades consumed and (B) top stipes consumed. Bars indicate +1 S.E.

downstream plants (Fig. 2B and D). Thus, if differences in palatability were detected between downstream plant treatments, it should be in response to a waterborne grazing cue and not to direct grazing on the plants.

In the assays designed to measure the strength of induction due to direct grazing (i.e., the contrast of upstream plants with and without addition of *Ampithoe* spp.), *A. longimana* did not differentiate between blades from these treatments (Fig. 3A). *A. longimana* did, however, strongly prefer stipes from the ungrazed as opposed to the previously grazed plants. They consumed 181% more stipe from the control plants than from the grazed plants (Fig. 3B). In the assays designed to measure the strength of induction due to grazing of upstream neighbors, *A. longimana* did not discriminate between tissues of plants that were downstream from grazed versus ungrazed neighbors ($p=0.73$ and 0.88 for contrasts between blades and between stipes, respectively; Fig. 4).

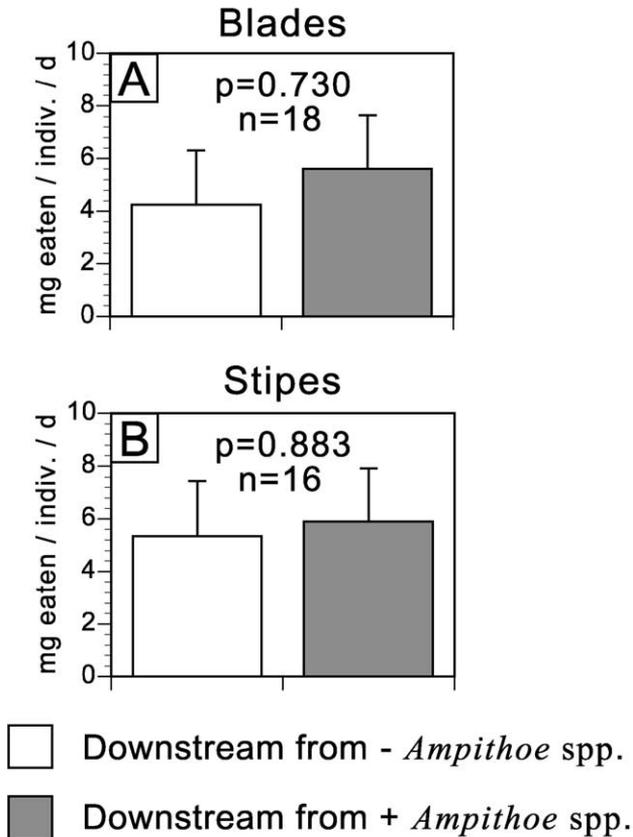


Fig. 4. Feeding rates by the amphipod *A. longimana* offered a choice between *S. filipendula* tissues from plants downstream of grazed or ungrazed plants; (A) top blades consumed and (B) top stipes consumed. Bars indicate +1 S.E.

4. Discussion

Stipes of *S. filipendula* subjected to direct grazing induced greater resistance to the amphipod *A. longimana* than did stipes of ungrazed controls; in contrast, blades of this alga did not induce resistance (Fig. 3). Thus, *S. filipendula* can be added to the short list of seaweeds known to be capable of induced resistance (Lewis et al., 1987; Van Alstyne, 1988; Renaud et al., 1990; Cronin and Hay, 1996; Pavia and Toth, 2000), but in this case, the induction is tissue-specific. Differential induction of resistance as a function of tissue type has not previously been evaluated for seaweeds (but see Hammerstrom et al., 1998 for example of tissue-specific induction of phlorotannins that presumably serve as chemical deterrents), so it is not possible to determine if this is common or unusual for marine macrophytes. Because grazing on stipes can cause loss of distal tissue when water motion causes stipes to fail at grazing scars (Koehl and Wainwright, 1977), differential defense of stipes could well be adaptive.

In contrast to the direct effects of grazing, we did not detect a “talking trees” effect in *S. filipendula*. Palatability of *S. filipendula* tissues was not reduced by grazing on upstream neighbors (Fig. 4). As pointed out by Karban and Baldwin (1997), there are few unequivocal demonstrations of the “talking trees” phenomenon. Many studies that purportedly address the effect employed pseudoreplicated designs, failed to exclude alternative hypotheses, or were conducted in laboratories under unnatural conditions (Fowler and Lawton, 1985; Karban and Baldwin, 1997; but see Dicke and Bruin, 2001). Our experiment addressed these limitations with the exception that our rates of flow and, thus, rates of dissolution of chemical signals were likely much lower than would occur in most field situations. We probably maximized our chances of finding an effect generated by grazed neighbors, yet we did not detect any effect. A relatively high number of independent replicates ($n = 16–18$) gave our experiment sufficient power to detect differences in palatability between the directly grazed (inoculated) plants and their controls (Fig. 3); thus, our design should have had the power to detect comparable changes in palatability of plants downstream from grazed neighbors. Because the plants were in separate containers, replicates were independent and interactions between individual plants could be ruled out as a confounding influence. In our outdoor tanks, the plants were subject to natural fluctuations in water temperature, salinity, turbidity, nutrients, and light, and the herbivore densities on grazed plants approximated those found naturally on *S. filipendula* in early summer (Duffy, 1989, 1990). Thus, our result constitutes strong evidence against waterborne induction of chemical defenses in this seaweed.

It is possible that higher levels of grazing over longer time periods could have eventually induced resistance in downstream plants, but this seems unlikely for several reasons. First, amphipod grazing over the 25-day duration of this experiment significantly reduces plant mass (Duffy, 1990; Duffy and Hay, 2000; see Results), which suggests that induction should operate during this time scale in order to be advantageous to the plant. Second, the reduction in palatability of directly grazed stipes (Fig. 3) indicates that induction of *S. filipendula* resistance occurs within this experimental time scale. Finally, other studies have detected induction of resistance in seaweeds within this timeframe using ecologically realistic grazer densities or simulated damage (e.g., Van Alstyne, 1988; Cronin and Hay, 1996; Pavia and Toth, 2000).

In contrast to our experimental results with *S. filipendula*, Toth and Pavia (2000) detected induction of chemical resistance in the knotted wrack *A. nodosum* in response to waterborne cues of grazed neighbors. There are several potential explanations for these distinct results. First, *S. filipendula* might not have the physiological mechanisms to sense and respond to waterborne cues, as *Sargassum* and *Ascophyllum* come from separate families of seaweeds within the order Fucales (Sargassaceae and Fucaeeae, respectively). Second, *A. nodosum* more commonly occurs in dense monospecific stands than does *S. filipendula* (although dense stands of *S. filipendula* occur in some areas), potentially making among-neighbor signals more likely to be received among *A. nodosum* than among *S. filipendula* plants. Third, *S. filipendula* is most abundant in warm-temperate and tropical regions where the predominant herbivores are large fishes, while *A. nodosum* is most abundant on cold-temperate shores where the predominant herbivores are sea urchins and mesograzers rather than fishes (Vermeij, 1978; Gaines and Lubchenco, 1982). When large herbivorous fishes encounter palatable brown seaweeds in tropical areas, they consume these rapidly (Hay, 1984) and can remove months of accumulated growth in only hours (Lewis, 1986). In such cases, seaweeds will need to be constitutively defended against fishes because they will not have time to induce defenses metabolically. In temperate areas, mesograzers can significantly impact seaweed abundance and species composition (Tegner and Dayton, 1987; Duffy and Hay, 2000), but they do this over days, weeks, or months—providing an opportunity for seaweeds to respond by inducing defenses over ecologically appropriate scales of time. Additionally, because mesograzers are more intimately associated with their host plants than are larger herbivores (Hay et al., 1987; Poore and Steinberg, 1999), they are more likely to be sensitive to the induced responses of individual plants and, thus, more likely to select for induced defenses (Hay, 1996). These combined differences may make it more likely for induced defenses to occur in response to mesograzers than in response to larger herbivores and to occur in temperate than in tropical marine communities.

To date, induced chemical resistance to marine herbivores has been documented only in temperate systems and only in response to attack by mesograzers (Van Alstyne, 1988; Cronin and Hay, 1996; Pavia and Toth, 2000) or slowly feeding sea urchins (Renaud et al., 1990). Induction of chemical defenses among tropical seaweeds has been investigated, and there are patterns of compound distribution that suggest induction in herbivore-rich habitats, but direct tests have failed to demonstrate induction (Paul, 1992) even though activation of preformed defenses can occur (Paul and Van Alstyne, 1992; Cetrulo and Hay, 2000). In contrast to these patterns, induction of morphological escapes from herbivores is known for seaweeds in tropical systems (Steneck and Adey, 1976; Lewis et al., 1987).

Finally, it is possible that in North Carolina, the presence of herbivores on nearby plants is not a good predictor of imminent attack, in which case there may be no selective advantage in recognizing and responding to waterborne grazing cues. This might be the case for seaweeds attacked by tube-building amphipods, like the *Ampithoe* spp. used here, which are sometimes patchily distributed on seaweeds (Cronin and Hay, 1996) and have restricted mobility that may keep them on a reduced number of hosts during their lifetime (Duffy and Hay, 1994; Poore and Steinberg, 1999). Furthermore, induction due to direct grazing could occur very quickly (Hammerstrom et al., 1998), thus reducing the advantage of perceiving advanced warning from neighboring plants.

A more general question concerns whether induction from direct grazing is more important than induction due to grazing of neighboring plants in the defense strategies of seaweeds. Though induction in response to both types of cues has been documented in *A. nodosum*, a test of its relative importance was not conducted (Pavia and Toth, 2000; Toth and Pavia, 2000). Van Alstyne (1988) and Cronin and Hay (1996) briefly discussed the possibility of induction in response to waterborne cues from grazed neighboring plants in their seaweeds (*Fucus distichus* and *Dictyota menstrualis*, respectively), but both studies considered the effect unimportant because directly grazed plants were more deterrent than control plants that were only 2–30 cm away. Both sets of experiments were designed to measure induction by direct grazing only, and neither included the contrast required to measure induction due to grazing of neighbors (this contrast would be their “controls” versus true controls that were not exposed to water from grazed plants). As such, their experiments assessed the relative magnitude of each type of cue, but not their absolute effects (see Figs. 3 and 4). Nevertheless, for the three seaweed species for which relevant data exist, induction due to direct grazing was stronger than induction due to grazing of neighboring plants (Van Alstyne, 1988; Cronin and Hay, 1996; this study).

Acknowledgements

Support was provided by NSF grant OCE #95-29784 to MH and by a New Zealand Science and Technology Post-Doctoral Fellowship (1997, UNC701) to RBT. Preparation of the final manuscript also benefited from support of the Teasley endowment to Georgia Tech. An anonymous reviewer provided comments to improve the manuscript. [RW]

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