Rip stop in marine algae: minimizing the consequences of herbivore damage

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Summary
Structural features of marine macrophytes are generally believed to act as defences against herbivores by reducing the ability of herbivores to consume the plants. Thallus form and calcification in particular have been considered structural defences that act by reducing the probability of consumption of tissue by herbivores. Studies directly measuring the mechanical resistance of a variety of marine algae (tropical and temperate) to herbivores of two important feeding types, rasping herbivores (docoglossan limpets) and a biting herbivore (an herbivorous crab), do not support this hypothesis. I suggest that thallus form and calcification may play a more important role in minimizing the impact of herbivores by reducing the probability of subsequent tissue loss due to herbivore-induced damage. For some algal species, tissue lost subsequent to herbivore damage may greatly exceed loss due to direct consumption by herbivores. I suggest that calcification and thallus properties resulting in preferential tear directions reduce the probability of tissue loss subsequent to herbivore damage rather than prevent herbivores from removing tissue as has been suggested in the past.

Keywords: plant–herbivore interactions; marine algae; calcified algae; structured defences

Introduction
Reviews of marine plant–herbivore interactions have drawn attention to potential causal links between herbivore and plant distributions as well as to correlations between the relative abundance of different marine plant growth forms and other environmental factors (Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982; Hawkins and Hartnoll, 1983). These reviews suggested that plant form, structure and chemistry and the mode of feeding of herbivores, all influence the resistance of plants to herbivores. However, they indicated that not enough empirical data exist to draw general conclusions about the relative importance of these factors in determining plant distributions.

In an effort to construct a generalized approach to examine marine plant–herbivore interactions, Lubchenco and Gaines (1981) formulated a model to determine the potential impact of herbivores on plants. They defined the expected cost of herbivore damage to a plant on the basis of (1) the probability that a plant will be encountered by a herbivore, $P(En)$, (2) the probability that the herbivore will eat a plant given that it is encountered, $P(Ea|En)$ and (3) the expected decline in fitness of the plant, relative to the rest of the population, due to the consumption of tissue by the herbivore, $E\{1-w|EnEa\}$. Thus, the cost of herbivory would be the product

$$P(En) P(Ea|En) E\{1-w|EnEa\}$$

where

$$E\{1-w\} = \sum_{i=1}^{n} P(C_i)(1-w_i)$$

and $P(C_i)$ is the probability of total consumption of the $i$th small part of plant (approximately 0269–7653 © 1993 Chapman & Hall
equal to one bite), $C_i$ is the amount of the $i$th part being consumed and $(1 - w_i)$ is the relative decline in fitness due to the loss of that tissue.

Given this model, the potential antiherbivore defences of plants would include temporally or spatially avoiding herbivores, thus minimizing $P(En)$, as well as direct defences against herbivory, i.e. minimizing either the probability of being eaten when encountered ($P(Eal/En)$) or reducing the amount of tissue consumed ($E\{1-w/EnEa\}$). Structural and chemical defences were considered to act primarily to minimize the probability of a plant being eaten once it is encountered, $P(Eal/En)$, thus reducing the probability of damage. If defences are particularly expensive for the plant or involve a major trade-off in terms of survival or reproduction, one would predict that the defences would be differentially distributed within the plant to minimize the expected fitness decline due to the loss of that tissue, $E\{1-w\}$.

Gaines and Lubchenco (1982) divided marine macrophytes into seven forms: sheets or tubes, filaments, fleshy blades, fleshy branched, erect calcareous, fleshy crusts and calcareous crusts. They found variation in relative abundances of most of these groups with latitude, as well as differences between the east and west coasts of North America at the same latitudes. In most cases these patterns were correlated with herbivore abundance and diversity. On shores with a greater abundance and diversity of herbivores, which have been interpreted as having greater intensity of herbivory, herbivore-resistant plant forms were relatively more abundant (reducing $P(Eal/En)$). These herbivore-resistant plants included the calcified plants, both crustose and erect, fleshy crustose plants and non-calcified branched plants (Gaines and Lubchenco, 1982). These forms are thought to be competitively inferior to those that are more vulnerable to herbivores (Vine, 1974; Wanders, 1977; Steneck, 1982, 1983; but see Padilla, 1982 and Johnson and Mann, 1986a), implying a trade-off between herbivore resistance and competitive ability.

Hawkins and Hartnoll (1983) noted similar patterns and also attributed herbivore resistance to the same algal morphologies. Other researchers have erected hypotheses predicting, among other factors, algal resistance to herbivores based on morphology (Littler and Littler, 1980; Steneck and Watling, 1982). These ideas have been synthesized into a general view of algal morphology suggesting that plant form and calcification act primarily to increase the mechanical resistance of algae to herbivore damage (Littler and Littler, 1980; Johansen, 1981; Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982; Steneck and Watling, 1982; Hawkins and Hartnoll, 1983; Littler et al., 1983). Mechanical tests with two important types of herbivores, however, do not support these hypotheses. The mechanical resistances of a variety of marine algae have been measured. These include both temperate and tropical algae and several different herbivores of two important feeding types, rasping herbivores (docoglossan limpets, Padilla, 1985, 1987, 1989a) and biting herbivores (herbivorous crabs, Padilla, 1987; D.K. Padilla, in preparation). In all cases the results were inconsistent with these models. Neither the degree of calcification nor the form of the plant increased mechanical resistance to tissue loss by rasping or biting type herbivores. These results imply that, at least for two important types of herbivores, calcification and plant form are not acting as simple mechanical defences resisting plant tissue loss to herbivores (i.e. not minimizing $P(Eal/En)$). Alternative explanations for the observed correlations between patterns of distribution of particular plant forms and herbivory must be considered.

Extension of the model

Here, I propose that another major component be added to the above equation regarding the total impact of herbivores on plants they consume. This is the probability of subsequent tissue
loss due to herbivore damage and its concomitant change in fitness. Adding this component to the equation of Lubchenco and Gaines (1981) yields

\[
\text{Expected total impact of herbivore damage} = P(En) \cdot P(Ea|En) \cdot E\{1-w|EnEa\} + P(Sl|EnEa) \cdot E\{1-w'|EnEaSl\}
\]

where \(P(Sl)\) is the probability of the subsequent loss of a unit of plant tissue due to the damage and \(E\{1-w'\}\) is the expected change in fitness (either increase or decrease) due to this additional tissue loss. The fitness decrement due to tissue lost secondarily may be very different from that due to direct consumption by a herbivore.

**Support from the literature**

For some algal species in certain environments, subsequent tissue loss may greatly exceed primary loss to herbivores (Black, 1976; Koehl and Wainwright, 1977; Santelices et al., 1980; Johnson and Mann, 1986b). Black (1976) found that of the *Egregia laevigata* (Phaeophyta) plants washed on the shore in southern California, 122 of 129 broken rachises and 58 of 86 broken stipes were attributable to herbivore damage. Koehl and Wainwright (1977) examined the large kelp, *Nereocystis*, that had washed ashore at two sites, Tatoosh Island, Washington, an exposed coastal area and Friday Harbor Laboratories on San Juan Island, Washington, a protected area. They found that 43–51% of the plants cast ashore had broken at an urchin bite mark. On the Chilean coast, Santelices et al. (1980) found that 33 of 37 broken stipes in *Lessonia nigrecens* had limpet scars, whereas only 51 of 160 whole stipes examined had limpet scars. Johnson and Mann (1986b) found that although the snail *Lacuna vincta* ate only 0.05% of the available biomass of *Laminaria longicurris*, subsequent tissue loss due to herbivore damage cost these plants 27.3% in lamina area increase and 28.3% in standing biomass as compared to ungrazed plants. These examples clearly illustrate that subsequent tissue loss due to herbivore damage may have strong effects on fitness and needs to be assessed when measuring the impact of herbivory.

For a given plant, the relative importance of these two components, direct tissue loss to herbivores and subsequent loss, will be a function of several factors, both intrinsic and extrinsic in nature. Important extrinsic factors include the degree of water motion or wave exposure that a plant experiences and the relative size of the herbivore (or herbivore’s bite mark) to the size of the plant as well as the way in which the herbivore damages the plant (rasping vs biting, tearing from the edge vs excavating centre of blades). The importance of the relative size of the herbivore to the plant may vary as a function of the physical environment (Fig. 1A). In low water motion conditions, the probability of loss may be low independent of the type or amount of damage. In high water motion conditions, however, even small amounts of damage may have a large impact on total loss due to a much greater probability of subsequent loss.

I would also like to suggest that intrinsic factors such as thallus form and calcification play a more important role in reducing this subsequent tissue loss (reduce \(P(Sl|EaEn)\)) in some environments than in preventing herbivores from removing tissue (reducing \(P(Ea|En)\)) as has been suggested in the past.

Plants that are crustose, branched and/or calcified may be less susceptible to subsequent tissue loss than are other algal forms (Table 1). In moving water, plants are exposed to forces such as drag, which deform or strain the thalli (Vogel, 1981; Denny, 1988). The stresses imposed on thalli (tensile and shear stress) can lead to material or structural failure. Crustose plants, being adherent to the substrate across one entire side of the thallus, do not experience these forces. Although branched plants are subject to such stresses, failure at one branch does not affect the vulnerability of the rest of the plant and may reduce the total amount of stress on the holdfast by
Figure 1. The relative importance of subsequent tissue loss (SL) to direct loss (DL) to herbivore consumption on the total impact of herbivores on algae as a function of both water motion and the size of the herbivore (or its damage) relative to the size of the plant. The vertical axis is the relative amount of subsequent tissue loss to direct loss (SL/DL). The horizontal axes are water motion (increasing from low to high) and the size of the herbivore (or the size of its bite marks) relative to the size of the plant. (A) A typical bladed alga. (B) An algal crust.
reducing the drag experienced by the entire plant. By being calcified, plants could increase their breaking strength, thus reducing the probability of failure. In addition, calcification may act to stop or slow crack or tear propagation that would lead to failure.

Thus, subsequent tissue loss in algae could be minimized in several ways: (1) by having large breaking strengths, (2) by preventing tissue damage from subsequently weakening the structure of the plant or (3) by promoting crack propagation in directions that minimize tissue loss. Although tissue is still lost to herbivores, the total impact of herbivory is reduced. Subsequent tissue loss may be a more accurate description of the impact of herbivory if it far exceeds the losses due to direct consumption by herbivores ($E(l-w') > E(l-w)$; Black, 1976, Johnson and Mann, 1986b). I conducted experiments designed to test some of these ideas.

### Experimental support

#### Methods

This research was conducted at the Smithsonian Tropical Research Institute marine laboratory at Punta Galeta (9°24'21"N, 79°52'18"W) on the Caribbean coast of the Republic of Panama. A variety of algae were collected from shallow, algal reefs, the Galeta Lab reef and similar reefs to the west at Isla Margarita. The floral and faunal diversity of these sites have been described elsewhere (Cubit and Williams, 1983; Hay, 1984).

Breaking strengths were measured with a mini-tensometer. Each end of the plant was placed in a padded grip that could be tightened, so the plant did not slip when placed in tension, but was not damaged. Plants which were particularly difficult to hold were attached to the grips with a cyanoacrylate adhesive. The padding on the grips was made of hot-melt glue (Thermogrip Inc.). The two sides of the grip were matched by placing a piece of sheet teflon between them, closing the grip tightly and placing it in very hot water until the two sides had conformed to a smooth surface. Small pieces of sheet silicon were placed in the back portions of the grip so that the grip placed an even force across the thallus irrespective of thallus shape or size. Trials in which algae broke at the grip were not counted. One grip was fixed to a force transducer mounted at one end of the mini-tensometer. The other was fixed to a slide which moved along a threaded rod. The rod was rotated with a small hand crank at one end. A linearly variable differential transformer (LVDT) was also attached to the moveable slide. Thus, once a plant was placed in the grips, the crank was turned placing the plant in tension. The plant was strained at a constant rate, with the deflection and forces required simultaneously recorded on a chart recorder. All plants were submerged until used and kept moist during the trials.
The cross-sectional area of the plant at the point of breakage was determined in one of two ways. For large plants the height and width of the cross-section were measured with an ocular micrometer under a dissecting microscope at the highest power that was possible to see the entire surface. Plants that were smaller or quite thin were sectioned with a freezing microtome. The section was then measured for height and width with the ocular micrometer of a compound or dissecting microscope. Cross-sectional shapes were considered to be either rectangles or ellipses, with the area determined appropriately for each. Each area was measured three times. In all cases this error was less than <3%.

To acquire herbivore damaged plants, I presented undamaged plants to a stoplight parrotfish (Sparisoma viride) which was kept in an aquarium with flow-through sea water. Therefore, the same individual herbivore bit all of the plants tested to control for possible differences in bite shape, size or biting technique. The point along the thallus at which breakage occurred was determined to test whether breakage occurred preferentially at the point of damage.

Finally, the loss rates of damaged and undamaged plants in the field were measured. Plants were exposed to the same captive parrotfish. These damaged plants were paired by visual assessment with undamaged plants of approximately the same size and shape. Pairs of plants were placed in Plexiglas holders and attached with biosponge, a polymer adhesive, which attached the plants to the Plexiglas and padded but did not damage them. These were then attached with plastic cable ties to a 1 m² piece of plastic mesh attached to the reef surface with steel spikes, near the wave exposed reef edge. Plants were measured, photographed and placed out as the tide was rising on days of heavy wave action. To minimize the probability of herbivores grazing the experimental plants, plants were left out only while the water was high and removed as the water began to recede. The extreme water motion during this time prevented herbivores from feeding on the reef edge during high water. Hence, any plant tissue loss could be attributed to wave and current stress rather than to herbivores. The plants were measured and photographed again after removal and tissue loss was determined by the change in height of the plant.

Results

Six non-calcified algae (Acanthophora spicifera, Laurencia papillosa, Dictyota bayteresii, Caulerpa racemosa, Caulera serrulteridies and Anadyomene stellata), three calcified algae (Padina jamacensi, Halimeda opuntia and Amphiroa hancockii) and an angiosperm, the sea grass Thalassia testudinum, were compared. Calcified algae were significantly stronger than non-calcified species (one-way analysis of variance, $p < 0.01$; Student–Newman–Kuels test, $p < 0.05$; Zar, 1974). The breaking strength of the sea grass was within the range of that of the calcified algae (Fig. 2).

Three non-calcified plants (Dictyota, Acanthophora and the sea grass Thalassia) and the three calcified plants were also tested to determine if herbivore damage was the site of failure. The calcified plants were less likely to break at the point of damage than were the non-calcified species (Fig. 3). All individuals of the two non-calcified algae and of the seagrass broke at the point of herbivore damage. For the calcified algae, most broke at points other than the place of damage. These differences are significant (Mann-Whitney Test, $p < 0.05$; Zar, 1974).

The field experiments on loss rates supported these results as well (Table 1). The sea grass and three species of calcified algae were tested. However, it was not possible to obtain data for non-calcified algae due to difficulty with the holding apparatus (non-calcified algae either came free from the holder or tore at the place of attachment). There was no significant increase in the loss of tissue following herbivore damage for the calcified plants (Mann-Whitney Test, $p > 0.8$; Zar,
1974). This was not the case for the seagrass ($p < 0.01$). Seven of eight seagrasses lost height while only one of 14 calcified plants lost height. No controls lost tissue (Table 1).

**Discussion**

The general model of Lubchenco and Gaines (1981), which assesses the impact of herbivores on plants, includes the probabilities that a plant is encountered and subsequently eaten by a herbivore. Chemical, structural and nutritional attributes of a plant may influence the probability of tissue consumption by the herbivore. The decline in fitness of a grazed plant relative to undamaged plants depends on which tissues are eaten (e.g. holdfasts, meristems, reproductive tissues), the season of damage (e.g. early growth, reproductive times) and the ontogenetic stage of the plant at the time of damage (e.g. sporeling, mature plant, post-reproductive plant). I suggest that the decline in fitness potential should include the probability of subsequent tissue loss following damage to the thallus by herbivores as well as tissues lost directly to herbivory.

Algae may possess many different types of mechanisms for reducing tissue loss subsequent to herbivore damage (Table 2). Calcification may make plants stronger, more resistant to breakage and more resistant to tearing or crack propagation (Gordon, 1968). Cracks or tears in materials generally cause them to break when tensional forces are placed on them (Wainwright et al., 1976).

Discontinuities and weak interfaces in the material can prevent crack propagation (Wainwright

![Figure 2. Breaking strengths (MN/m²) of calcified and non-calcified algae and the seagrass Thalassia. Bars represent averages and the lines represent standard errors. Sample sizes are above the bars.](image-url)
Rip stop in algae

et al., 1976; Gordon, 1968) by forcing the crack to move around them, thus dispersing energy and preventing propagation. Calcification in marine plants could have such a crack-stopping capacity. In this way, a calcified plant damaged by herbivores (or sustaining any type of damage) would be less susceptible to subsequent tissue loss than would a similarly damaged non-calcified plant.

A similar argument may be developed for overall plant morphology. Sheet-like plants are generally considered to be the most susceptible to herbivores. If a herbivore damages a sheet-like alga, the resulting crack or tear can propagate across the entire thallus, resulting in great tissue loss. The presence of a mid-rib or other types of ribbing, structural fibres in a thallus, cell wall alignment or other tissue or cell wall properties could also minimize the propagation of cracks across the thallus or cause a preferential tear direction along the thallus. Cracks parallel to the direction of tension reduce the probability of tearing and reduce the amount of tissue that would be lost (Padilla, 1989b). Thus, the location of damage will determine how much and what tissue will be lost. Although the amount of tissue actually consumed by the herbivore may be quite small, the loss of tissue due to the damage may be quite large.

Branched plants are considered more resistant to herbivores than sheet-like forms (Littler and Littler, 1980; Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982; Steneck and Watling, 1982). Although a plant of this morphology may have equal or less mechanical resistance to the herbivore than a sheet, a thallus divided into branches ensures that damage to any single branch will not affect the other branches. For an encrusting plant the negative consequences of herbivory will be limited to the amount of tissue actually consumed by the herbivore. The thallus is

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![Percent Broken At Damage](image)

**Figure 3.** Percent of damaged plants which broke at the point of damage when placed in tension. Sample sizes are above the bars.
Table 2. (A) Algal form and the potential for subsequent loss. (B) Mechanisms for reducing tissue loss subsequent to herbivore damage

<table>
<thead>
<tr>
<th>Algal form group</th>
<th>Potential for subsequent loss</th>
<th>(B) Mechanisms for reducing subsequent loss</th>
</tr>
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<tbody>
<tr>
<td>Sheet/tube</td>
<td>High</td>
<td>Increasing breaking strength</td>
</tr>
<tr>
<td>Filament</td>
<td>Low</td>
<td>Calcification</td>
</tr>
<tr>
<td>Blade</td>
<td>High</td>
<td>Structural fibres</td>
</tr>
<tr>
<td>Branched</td>
<td>Low-med</td>
<td>Material properties of thallus</td>
</tr>
<tr>
<td>Crust</td>
<td>None</td>
<td>Crack/tear strength</td>
</tr>
</tbody>
</table>

completely attached to the substratum on one side, and therefore is not subject to tensional or shear stresses due to drag induced by water motion (Fig. 1B). No tissue will be lost due to tearing, only to direct consumption by the herbivore. Thus, many algal traits including calcification, dividing the thallus or being crustose, could reduce the probability or amount of tissue lost due to the mechanical stresses of water motion following any type of damage that a plant might experience, whether imposed by herbivores or other sources (e.g. abrasion, rocks, logs, etc.).

For marine plants, protection from subsequent tissue loss will be important even if they possess other types of antiherbivore defences. Frequently, antiherbivore chemicals in plants are hydrophobic, therefore, herbivores must taste the plant, thereby damaging it, for these chemicals to be effective (Norris and Fenical, 1982; Hay and Fenical, 1988). Also, for some antiherbivore chemicals, their effective quantities increase once damage has occurred (Paul and Van Alstyne, 1988; Van Alstyne, 1988). In addition, the nutritional qualities of the plant may be most easily assessed from taste, again imposing damage on the plants. Hence, even if the plant has alternative defences against a herbivore, protecting the thallus from subsequent tissue loss due to damage could be very important. This could explain why plants such as *Halimeda*, which have potent antiherbivore chemicals, are also calcified (Paul and Fenical, 1983; Paul and Hay, 1986).

I suggest that calcification and overall form in marine plants could be mechanisms that minimize the probability of subsequent tissue loss following damage, including damage caused by herbivores. Calcification strengthens and prevents tearing where an alga has been damaged (Padilla, 1987). Small amounts of damage (small enough to be caused by invertebrate herbivores) considerably reduce the work to fracture for the stipes of a kelp, *Pterygophora californica* (Biedka et al., 1987). Biedka et al. (1987) also concluded that stipe breakage was an important source of mortality for this species. Clearly more experiments are needed to test the generality of these results, particularly for plants of different thallus form.

These results may also be relevant to the evolutionary maintenance of calcification in marine plants. Several different hypotheses have been proposed to account for the evolution and/or maintenance of algal calcification. Calcification may be a by-product of photosynthesis in calcium saturated water (Borowitzka, 1982). Calcification may be a means of detoxification (Simkiss, 1977; Brasier, 1986). Calcification may be a major structural deterrent to herbivores (Johansen, 1981; Steneck and Watling, 1982; Steneck, 1982, 1983; Hawkins and Hartnoll, 1983). Calcifi-
cation could be selected for or maintained for protection against herbivores which are not capable of eating calcium carbonate or for protection from abrasion along the thallus edge. It could also be important in influencing the wear rates of the feeding apparatus of an herbivore and therefore affect feeding efficiencies of herbivores (D.K. Padilla, in preparation) or affect digestive efficiencies in animals with acidic digestive systems.

Why do not all algae calcify? What would be the selective disadvantages of calcification? One disadvantage would occur if calcification slowed growth rates. Some calcified algae grow slowly (1–2 cm per year, Johansen, 1981), however, some heavily calcified algae in the tropics grow very rapidly (1–2 cm per week, D.K. Padilla, personal observation). Also, temperate calcified crustose algae grow faster than non-calcified crustose species (M. Dethier and R. Steneck, personal communication). Therefore, growth rate may depend on the type of calcification (Borowitzka, 1982) and local environmental conditions. Also, calcification makes plants more susceptible to desiccation (Dromgoole, 1980; Johansen, 1981), and may make them more susceptible to certain types of herbivores (Padilla, 1985, 1989b; D.K. Padilla in preparation).

Whether calcification and thallus form (1) acted as direct defences against herbivory or (2) were acting primarily to minimize subsequent loss, the general patterns of distribution of marine plants and herbivores that would be observed are similar. Therefore, does knowing the exact mechanism matter? At the ecosystem level the answer is yes, if one wishes to know where energy is flowing (e.g. directly into herbivores or into detritus-based food webs). At the level of plant community organization the consequences of damage would probably not affect the distribution, but could affect the abundance of the plants. At the population level the answer again would be yes, particularly regarding the potential for selection on and effectiveness of, antiherbivore defences. A plant whose form or structure minimizes subsequent tissue loss could suffer tissue loss directly to herbivores, but have a lower total fitness reduction than plants of other forms.

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