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PLANT ANIMAL INTERACTIONS

Esther M. Borell · Andrew Foggo · Ross A. Coleman

Induced resistance in intertidal macroalgae modifies feeding behaviour of herbivorous snails

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Abstract Herbivory in terrestrial and marine systems can induce changes in plant chemistry affecting the foraging behaviour of herbivores. A model based on terrestrial plant-herbivore interactions predicts herbivory-induced changes in leaf chemistry to be manifested in (1) increased herbivore mobility, (2) increased feeding dispersal and (3) reduced tissue consumption by herbivores. This study is the first to demonstrate that herbivory-induced changes in the tissue chemistry of the brown seaweed *Ascophyllum nodosum* elicit the same response in the feeding behaviour of the gastropod *Littorina obtusata* as predicted for herbivorous insects, providing good evidence for the model's validity across different ecosystems. The potential benefit of increased feeding dispersal to terrestrial plants as suggested by the model is the prevention of concentrated damage to apical tissues thereby preserving the plant's ability to compete for light; *A. nodosum* does not conform to these predictions. Increased dispersal of feeding damage on *A. nodosum* away from primary frond tissues would reduce the likelihood of frond breakage implying a fitness benefit of induced resistance.

Keywords *Ascophyllum nodosum* · *Littorina obtusata* · Grazing · Herbivore-induced · Defence

Introduction

The ecological rôle of plant secondary metabolites as wound-induced resistance/defence in terrestrial plant-herbivore interactions is well established (Levin 1971) and generally accepted as an effective anti-herbivore mechanism (e.g. Karban and Myers 1989). Macroalgae are similar to terrestrial plants in that they produce a variety of secondary metabolites which have been reported to deter herbivory (e.g. Geiselman and McConnell 1981; Hay and Fenical 1988; Hay 1996; Pavia and Toth 2000). However, plant-herbivore interactions in terrestrial systems have been studied in greater detail and over a much longer period of time than seaweed-herbivore interactions. Thus most, if not all, theory concerning herbivory-induced resistance/defence in plants, and the associated plant-herbivore interactions, is based on ecological evidence drawn from terrestrial plant communities (e.g. Feeny 1976; Coley et al. 1985; Karban and Myers 1989).

Herbivore-induced changes in plant chemistry may be categorized using a number of criteria, but important evolutionary distinctions exist (Karban and Baldwin 1997). Since many "secondary" metabolites have multiple functions (Selmar 1989; Schoenwaelder and Clayton 1998), it is important to distinguish between an induced response which has evolved in response to herbivore pressure, and one that incidentally reduces herbivore performance (Edwards 1989). Following the definition of induced responses in plants given by Karban and Baldwin (1997), an induced response that confers resistance to a plant does not necessarily have to benefit plant fitness, whereas an induced defence will ultimately benefit plant fitness by either decreasing further herbivore damage or increasing plant tolerance to herbivory.

Two influential reviews attempted to identify the adaptive nature of herbivore-induced changes in plant chemistry. Fowler and Lawton (1985) suggested that wound-induced changes in leaf chemistry could be regarded as a defence under the premise that they directly affect herbivore population dynamics, with the consequence that plants should suffer less damage. Edwards and Wratten (1987) objected to this assumption on the grounds of inconclusive evidence. They proposed a model in which increased herbivore mobility and greater dispersal of feeding damage by herbivores constitute the key responses. Thus, changes in leaf chemistry and hence foliage palatability would cause herbivores to be more mobile, moving away from the vicinity of damage to forage for more palatable food at other sites within the plant, thereby

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E. M. Borell · A. Foggo · R. A. Coleman (✉)
Marine Biology and Ecology Research Group, School of Biological Sciences, University of Plymouth,
Plymouth, PL4 8AA, UK
e-mail: racoleman@plymouth.ac.uk
Tel.: +44-1752-232912
Fax: +44-1752-232970

dispersing feeding damage (Edwards and Wratten 1987). Consequently herbivores are hypothesized to spend more time foraging for more palatable food and are predicted to take more meals of smaller sizes, consuming less overall (see Coleman et al. 1996 for the full model). Since this model predicts consequences of induced resistance in terms of movement of grazers, we will refer to the model hereafter as the herbivore-mobility model (HMM).

For plants, the potential adaptive benefit of a grazing-induced response as predicted by the HMM is based on the assumption that plant fitness in competitive habitats is determined by a plant's ability to successfully compete for light, in order to maximize growth and reproductive output (e.g. Edwards and Wratten 1987). The reduction of a plant's photosynthetic capacity due to the loss or disruption of leaf tissue as a result of herbivory is therefore predicted to have negative consequences for plant fitness. Since not all plant parts have equal value in terms of promotion of fitness (e.g. Tuomi et al. 1989; Van Alstyne et al. 1999), and given a certain cost of producing secondary metabolites as predicted by optimal defence theory (Rhoades 1979), the allocation of defensive compounds should vary among tissue types (Coley et al. 1985; Herms and Mattson 1992; Pavia et al. 2002). Accordingly, the HM model suggests a defence to be particularly pronounced in young leaves and the growing apical tissues of older leaves, since these are most involved in the competition for light.

Although the HMM was originally devised to apply to all plants in competitive habitats, and is supported by evidence from deciduous woody and herbaceous plant species (Green and Ryan 1972, 1973; Edwards et al. 1986, 1992; Silkstone 1987; Barker et al. 1995), it has never been tested for plant-herbivore interactions in marine systems. Good theories should enable predictions of plant-herbivore interactions across different ecosystems, and it is therefore appropriate to test the validity of the HMM for plant defences in marine systems. To our knowledge this study is the first to investigate the applicability of the HMM of plant resistance/defence in marine intertidal habitats.

We experimentally tested key predictions of the HMM using the fucoid alga *Ascophyllum nodosum* (L.) Le Jol. and the grazing gastropod *Littorina obtusata* (L.) as model organisms. *L. obtusata* exhibits a strong feeding preference for *A. nodosum* (Watson and Norton 1987; Vermeij 1992) and has been demonstrated to elicit a wound-induced response in *A. nodosum* giving elevated concentrations of tissue phlorotannins, which have been correlated with subsequent reduction in *L. obtusata* feeding rates (Pavia and Toth 2000). Although mobility of *L. obtusata*, relative to the size of their food plant, is limited compared to larger herbivores such as fish and urchins, *L. obtusata* cannot be thought of as a static herbivore, and we therefore did not test for the effect of an induced response on growth and fitness parameters (Barker 1992; Coleman et al. 1996).

We tested the following hypotheses derived from the HMM: (a) *L. obtusata* on herbivore-induced tissue will be more mobile than *L. obtusata* on non-induced tissue (this effect should be more pronounced on tissues from growing apices than on more basal tissues); (b) grazing damage will be more dispersed on herbivore-induced tissue than on non-induced tissue resulting in smaller meal sizes; ©) *L. obtusata* on herbivore-induced plant tissue will consume less than those on non-induced tissue. A common criticism of many studies investigating plant wound-induced responses to herbivory is that conclusions are often drawn from experiments that apply mechanical rather than real damage (e.g. Haukioja and Neuvonen 1985; Van Alstyne 1988; Barker et al. 1995); mechanical damage often fails to adequately mimic actual herbivory (Baldwin 1990). This study therefore includes two damage treatments constituting natural and simulated herbivory, and tests the above hypotheses for both of these treatments.

Materials and methods

Induced changes of tissue phlorotannins

Sampling and experiments were performed during the summer of 2003. For the induction experiment, undamaged *Ascophyllum* plants of similar size (constituting three to four primary shoots approximately 30 cm in length), and individuals of *L. obtusata* of similar shell size (approximately 5–6 mm from the apex to the lowest point of the body whorl) were collected from a sheltered rocky shore in south-west England (50°21.4′N, 04°07.6′W). Due to logistical constraints, herbivore-induction and bioassays were carried out in two trials of identical design with four replicates per treatment for each trial. Test plants were kept in a culture room with 16/8 h light/dark at 14°C, similar to the temperature of the seawater at that time. Transparent plastic aquaria (4 l, n =12) containing *Ascophyllum* plants were set up and plants were randomly assigned to one of the following three treatments:

1. Herbivory using *L. obtusata* as model herbivore.
2. Simulated herbivory using a bastard file (Baldwin 1990; Coleman et al. 1996).
3. Control, no additional physical damage.

Ascophyllum plants were hand cleaned of epibiota and holdfast dwelling invertebrates avoiding superficial damage to the plant's tissue in order to prevent incidental phlorotannin synthesis (Jormalainen et al. 2003). The seawater in the aquaria was aerated continuously and exchanged every 2 days. For each replicate in treatment 1, snails (n =3) were placed onto haphazardly selected parts of primary and annual shoots of similar length (circa 20 cm) comprising approximately the same amount of tissue estimated by the number of shoots, and were confined to these areas using netting (mesh size 0.7 mm). Induced damage by simulated herbivory in treatment 2 was carried out using a bastard file as the shape and arrangement of the file's teeth physically resemble the radulae of *L. obtusata* (Steneck and Watling 1982; Baldwin 1990). Radula movement was mimicked by filing in the forward direction only. The damage was inflicted by bending the shoot over a finger and carefully filing off tissue using the middle part of the file. Tissue was removed daily; the amount removed and patterns of damage were similar to *L. obtusata* feeding (preliminary observations). Each trial was run over a period of 2 weeks (Pavia and Toth 2000). Phlorotannins were quantified colometrically following a technique based on the Folin-Ciocalteu method (Van Alstyne 1995). Differences in phlorotannin content were tested by ANOVA with post-hoc separation of significant factors using SNK tests. Prior to statistical analyses, the data were tested for homogeneity of variances using Cochran's C-test, and if necessary $\ln(x+1)$ transformed to stabilise variances (Underwood 1997). All analyses were carried out using WinGMAV5 (EICC, University of Sydney, Australia).

Bioassay approach

Bioassays were performed using uplighting only in order to eliminate possible shadow responses in *L. obtusata* (Gutierrez and Womersley 2001). All experiments were run over 100 min so that phlorotannin leaching (Deal et al. 2003) and autogenic changes in the plant, e.g. water loss (Peterson and Renaud 1989; Karban and Baldwin 1997) were minimized. Individuals of *L. obtusata* of similar size as used for herbivore-induction were collected from the same shore and starved for 24 h prior to the initiation of each experiment (Cronin and Hay 1996; Granado and Caballero 2001). All bioassays were carried out at room temperature.

Wound-induced effects on herbivore mobility

Ascophyllum plants (size as above) were placed onto plastic trays (36×29 cm, 8 cm deep) containing seawater (depth approximately 0.5 cm). One individual *L. obtusata* was placed on the middle part of each plant and was allowed to forage freely for 100 min. An A4-sized acetate grid (1-cm^2 cells) was placed over the tray and secured with adhesive tape. The grid was divided into three parts: top, middle and bottom, corresponding to the annual shoots and apical tissue, the middle primary shoots and the stipes, respectively. The coordinates of the snails on the seaweed were recorded at 20-min intervals, and distances between these locations were measured as straight lines between each set of coordinates. The length of time that each snail spent on different plant parts was expressed as the number of sightings per plant part.

We tested the hypothesis that snails on herbivore-induced algal tissue would be more mobile by examining the distance moved and frequency of moves by snails as well as looking to see whether the time spent on different parts of the plant were independent of treatment. Total distance moved was calculated as the sum of all translocation vectors for each individual snail; these were analysed by ANOVA and post-hoc SNK tests which allowed us to check for between trial variation. Prior to ANOVA, data were tested for homogeneity of variance using Cochran's test, and if necessary ln(x+1) transformed (Underwood 1997). The total number of moves, regardless of distance of each move, was tested by χ^2 using a null hypothesis of no treatment effects. Our expected frequencies of moves were derived from the total number of moves averaged amongst treatments. Time spent in each area of the frond was measured by the number of sightings in each part of the alga for each replicate of each treatment. We used a log-likelihood (G) test with William's correction (Sokal and Rohlf 1995) to test whether time spent in each part of the plant was independent of treatment.

Wound-induced effects on feeding dispersal and meal size

Middle parts of undamaged primary shoots of *A. nodosum* of similar length (circa 10 cm) from each treatment were placed into 14-cm petri dishes half-filled with seawater. Middle parts of the primary shoots were chosen since *L. obtusata* has been shown to have a feeding preference for these tissues (Pavia 1999), and has been observed to predominantly graze on these parts under natural conditions (Watson and Norton 1987). One snail was placed into each dish and was allowed to forage freely for 100 min. Induced effects on differences in meal-sizes taken by *L. obtusata* were assessed by counting the number of feeding scars, and the size of each feeding scar was measured using an acetate grid of 1-mm^2 cells under a dissection microscope. Analysis of the number and size of feeding scars was performed by ANOVA.

Wound-induced effects on tissue consumption

Undamaged segments of similar length (10 cm) from the middle of a primary shoot (see previous section) from plants of each treatment were removed using scissors. Since herbivore-induced changes in tissue chemistry in *A. nodosum* are systemic (Toth and Pavia 2000), snails were unlikely to be influenced by additional visual or olfactory cues associated with either treatment 1 or 2. Each segment of algal tissue was placed in a 14-cm petri dish lined with filter paper that was kept moist throughout the experiment preventing shoot desiccation and dehydration of the snail (Kogan 1986; Coleman et al. 1996). One individual of *L. obtusata* was placed onto each segment and allowed to forage freely for 100 min. Changes in weight (measured to 10^{-4} g) of each tissue sample were recorded at 0 and 100 min, using an electronic balance (Satorius 1702, Goettingen, Germany). The effect of treatment on amount of tissue consumed was analysed by ANOVA.

Results

Induced changes of tissue phlorotannins

Phlorotannin concentrations in the tissues of *A. nodosum* in both trials varied significantly with treatment (Table 1). SNK tests revealed that phlorotannin concentrations in herbivore-induced plants were significantly higher than in plants subjected to simulated herbivory and control treatment with no substantial difference between the latter two treatments. At the end of the 2-week induction period the mean phlorotannin content (dry mass) was 6.8±1.18% (mean ± SE, n =8) in herbivore-induced plants, 3.2±0.08% (mean ± SE, n =8) in plants subjected to simulated herbivory and 3.2±0.42% (mean ± SE, n =8) in control plants.

Wound-induced effects on herbivore mobility

There was no effect of trial: each trial was consistent in the total number of moves made by snails (Table 2). Snails feeding on plants subjected to prior herbivory moved (expressed as sum of 1-cm^2 units) significantly more than snails feeding on either plants exposed to simulated herbivory or control plants (Table 2; grazing =9.63±1.3, simulated herbivory =11.13±2.4, control =20.75±5.1; mean ± SD, n =8). The total number of translocations by snails on plants exposed to the three treatments was significantly different from our null hypothesis of 1:1:1 (χ^2 =6.28, 2 df, P <0.05). Snails on herbivore-induced plant tissue moved 40 times, those on plants exposed to simulated herbivory 24 times and on control plants 24

Table 1 ANOVA of phlorotannin content of *Ascophyllum nodosum* after 2-weeks exposure to three different herbivore damage treatments: herbivory, simulated herbivory and no treatment (control). Variances were homogeneous after ln (x+1) transformation, Cochran's C =0.50, not significant

Source of variation	*df*	MS	*F*	*P*
Damage	2	1.186	4.8	<0.05
Residual	21	0.247		

times. Time spent on different parts of the plant was dependent on treatment (G_{adj} =24.16, 4 *df*, P<0.001). Most snails on herbivore-induced algae spent most of their time at the area of the frond designated top, whereas for the other two treatments most animals did not move out of the middle area (Fig. 1). For plants exposed to simulated herbivory, the snails that moved were more frequently on the stipe and for control plants the pattern was reversed.

Wound-induced effects on feeding dispersal

The effect of treatment on both the area of shoot tissue consumed and the number of feeding scars did not vary between trials. While treatment had a significant effect on the number of feeding scars (Table 3; grazing =4.00±0.63, simulated herbivory 1.5±0.27, control 1.3±0.16; mean ± SD, n =8) there was no significant variation in the total area of shoot tissue consumed (Table 3). There was no significant difference between the number of feeding scars on shoots of simulated herbivory and control treatments. Shoots from both treatments exhibited more concentrated feeding damage, with larger but fewer feeding scars compared to shoots from plants that had been subjected to grazing by snails.

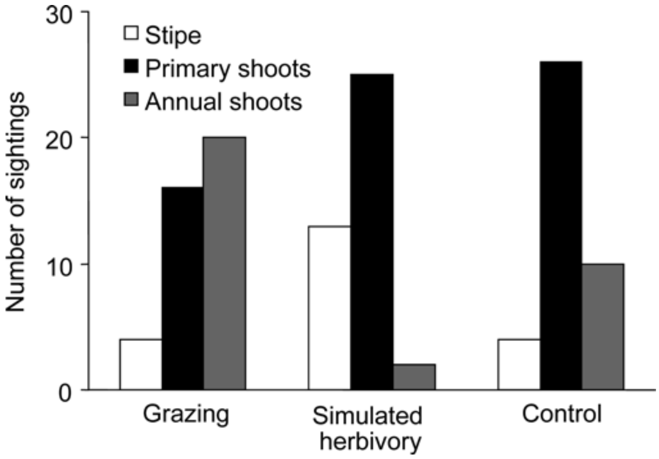

Fig. 1 Total number of times *Littorina obtusata* was sighted on different parts (stipe, primary shoots, annual shoots) of *Ascophyllum nodosum* plants (~30 cm) recorded at 20-min intervals over 100 min after 2-weeks exposure to the treatments: grazing, simulated herbivory and no treatment (control)

Table 2 ANOVA of the effect of herbivore damage treatments (as in Table 1) on the total mobility of *Littorina obtusata* in two repeat trials. Variances were homogeneous after ln (x +1) transformation, Cochran's C =0.35, not significant

Source of variation	*df*	MS	*F*	*P*
Damage	2	1.270	3.67	<0.05
Trial	1	1.194	3.45	>0.07
Damage × trial	2	0.020	0.06	>0.94
Residual	18	0.346		

Wound-induced effects on tissue consumption

Analysis of variance showed a significant trial by treatment variation, i.e. the effect of treatment varied with trial (Table 3, Fig. 2). Investigation of the post-hoc tests showed that this was due to reduced consumption of tissue from plants exposed to simulated herbivory in trial 1 compared to trial 2. SNK tests showed the following significant differences: trial 1 grazing < simulated herbivory < control and trial 2 grazing < simulated herbivory = control. Thus in all cases prior herbivory resulted in a significant reduction of material consumed (Fig. 2).

Discussion

The responses of *A. nodosum* to grazing by *L. obtusata*-were consistent with the findings of Pavia and Toth (2000); real herbivory caused a substantial increase in tissue phlorotannin concentrations, whilst simulated herbivory failed to elicit an induced response. The bioassay results support all three hypotheses concerning the effects of changes in plant chemistry on herbivores; marine plants and their associated grazers may indeed conform to the predictions made by the HMM.

Our results indicate that *L. obtusata* spent a significant proportion of the total feeding time on primary and annual shoots, and the number of moves was highest on plants that had been previously subjected to grazing. This is in good agreement with previous experimental (Pavia 1999) and observational (Watson and Norton 1987) evidence of the feeding preferences of *L. obtusata*. The effect of treatments upon the distribution pattern of *L. obtusata* was less clear; some individuals were frequently sighted on the stipes of *A. nodosum*, despite their reportedly low preference for these tissues (Pavia 1999). This may be attributable to a number of factors, amongst them interplant variation in phlorotannin concentrations, and differ-

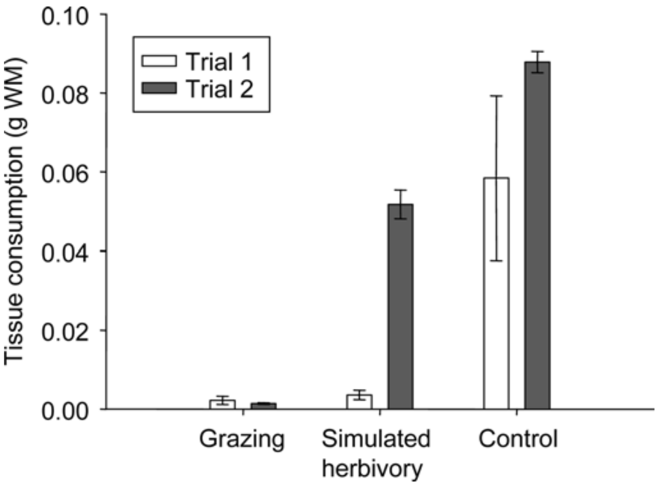

Fig. 2 Mean (± SE, n =8) tissue consumption (g WM) from segments of primary shoots of *Ascophyllum nodosum* by *Littorina obtusata* after 2-weeks exposure to the treatments: grazing, simulated herbivory and no treatment (control)

Table 3 ANOVA of the effect of herbivore damage treatments on number of feeding scars, the area of tissue consumed and the mass of tissue consumed in two repeat trials. Variances were homogeneous after ln (x +1) transformation, Cochran's C =0.38, 0.48 and 0.44 (all non-significant) for each of the three parameters measured

Source of variation	*df*	Feeding scars			Area of tissue consumed			Amount of tissue consumed		
		MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Damage	2	2.839	12.31	<0.001	42.792	1.09	>0.35	28.755	54.71	<0.001
Trial	1	0.001	0.01	>0.94	51.042	1.3	>0.25	8.450	16.08	<0.001
Damage × trial	2	0.176	0.76	>0.48	3.792	0.1	>0.90	4.462	8.49	<0.005
Residual	18	0.230			39.264			0.525		

ent morphological and physiognomical characteristics of the tissues.

Feeding damage on *Ascophyllum* plants caused by *L. obtusata* was significantly more dispersed on herbivore-induced tissue than on non-induced tissues, with feeding scars on herbivore-induced tissues being significantly smaller and more dispersed than those on control plants and plants subjected to simulated herbivory. This evidence clearly supports the underlying paradigm of the HM-model in which a response to an induced defence is manifested in an increased dispersion of feeding damage as herbivores move away from the vicinity of damage to forage for more palatable food at other sites on the plant.

As predicted, *L. obtusata* consumed significantly less tissue from herbivore-induced plants than from non-induced plants. Our results show that the amount of tissue consumed from plants exposed to simulated herbivory varied significantly between trials, but consumption of induced tissue in both trials was substantially lower than consumption of tissue from control plants. It is unlikely that the low consumption rate from plants of simulated herbivory treatment relative to control plants was related to tissue phlorotannins, since mean concentrations of phlorotannins in both treatments did not differ significantly. Although the assays were standardized using middle parts from primary shoots only, intra-plant differences in chemical (Pavia et al. 2003) or morphological characteristics of the tissues could have affected the consumption rate of *L. obtusata*. Furthermore, under natural conditions *L. obtusata* preferentially feeds during the high tide (McQuaid 1996), whilst the *Ascophyllum* shoots in the bioassay were only kept moist from beneath. This combined with the experimental conditions, e.g. handling the snails, temperature, humidity (Petraitis 1992; Petraitis and Sayigh 1987), may have inhibited feeding in trial 1. Despite this discrepancy however the results of both trials clearly indicate that tissue consumption by *L. obtusata* was significantly higher in control tissues than in herbivore-induced tissues. In our study snails consumed more non-induced tissue than in other reported work (e.g. Pavia and Toth 2000); this is probably due to differences in temperature or body size of *L. obtusata* between the studies which may have affected consumption rate (Petraitis 1992).

The total area of shoot tissue consumed in the feeding dispersal experiment did not vary significantly between induced and non-induced tissues. However, the combined results from the feeding experiment on tissue consumption and the observed variation in size and distribution of feeding damage support the predictions from the HMM that the number of meals taken on induced tissues should be greater than those taken on non-induced tissues, with the overall amount of tissue consumed being less on induced than on non-induced plants. Our results indicate that feeding scars on induced tissues may have been more superficial than those on non-induced tissues, with consequent differences occurring in weight of tissue consumed, but not area. Phlorotannins in brown seaweeds are stored in physodes, which are particularly abundant in epidermal tissue (Ragan and Glombitza 1986). Herbivores are therefore likely to detect "unpalatable" concentrations of these compounds soon after they start feeding and subsequently move away from that site foraging for more palatable tissue, thereby dispersing their feeding damage over the plant.

The plant-herbivore system we studied departs from the assumptions of the HMM regarding the potential adaptive benefit of an induced defence being particularly pronounced on young leaves and the growing apical tissues of older parts of the plant. Induced responses within different tissue parts of *A. nodosum* following grazing damage have been shown to be highest in the stipe, intermediate in annual shoots and lowest in the reproductive tissue (Pavia et al. 2002). This suggests that damage to meristematic tissue may have less dramatic consequences on the fitness of *A. nodosum* than damage to basal tissue. Thus the potential adaptive benefit of an induced response for the fitness of *A. nodosum* is likely to depend upon factors other than the successful competition for light, despite the organism living in a highly competitive habitat characteristic of rocky shore assemblages.

In a demographic sense, perennial fucoids such as *A. nodosum* are similar to long-lived, slow-growing woody plants, with high elasticity for survivorship and low elasticity for fecundity (Franco and Silvertown 1996). Similarly to most plants with multiple meristems, *A. nodosum* grows indeterminately continuously, increasing its fecundity and reproductive value (Åberg 1992). Since such plants commonly feature low adult mortality, their fitness depends less upon fast development and high fecundity. They therefore have a lesser need for high levels of defences in reproductive or young growing tissues. For long-lived species such as *A. nodosum*, grazing damage inflicted to primary shoots has more dramatic consequences on the plant's fitness in terms of growth rates, than damage to meristematic tissue, i.e. annual shoots (Pavia et al. 2002). Although the stipe of *A. nodosum* constitutes the tissue of highest fitness value and contains the highest concentrations of phlorotannins in respect to other tissues, the effect of an induced response on *L. obtusata* in our mobility bioassay would have been unlikely, since the stipe is the least preferred food of *L. obtusata* and snails would therefore spend the least time feeding on this tissue.

Grazing damage by *L. obtusata* can affect the demography of shoots and plants of *A. nodosum* as feeding scars of *L. obtusata* increase the chances of frond breakage (Viejo and Åberg 2003). Thus dispersed feeding damage as a result of an induced response in *A. nodosum* is likely to benefit the plant by reduced chance of breakage of fronds from primary shoots, which would exert a greater effect on plant fitness by decreasing survivorship.

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