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HERBIVORE GRAZING INCREASES POLYPHENOLIC DEFENSES IN THE INTERTIDAL BROWN ALGA *FUCUS DISTICHUS*[1]

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Abstract. Although predator-induced defenses have been reported for several species of terrestrial vascular plants, they have not been previously described in aquatic or non-vascular plants. In this study, field manipulations were used to demonstrate the presence of inducible chemical defense production in the intertidal brown alga *Fucus distichus*. When experimentally damaged, *Fucus* increased its concentrations of polyphenolic compounds by ≈20% over uninjured control plants within 2 wk. These increases occurred in the area where the plant was injured and within adjacent undamaged branches. The increase in concentrations of polyphenolic compounds in clipped plants in these experiments corresponded well with differences in phenolic levels in naturally grazed and ungrazed algae.

Herbivorous snails (*Littorina sitkana*) showed a preference for clipped plants immediately after they were wounded. However, over a 2-wk period the snails shifted their preference towards the uninjured control plants, corresponding with the increase in polyphenolic levels within the experimentally damaged plants. *L. sitkana* spent less time feeding on clipped plants, and these plants lost ≈50% less tissue (by surface area) to grazers than did uninjured algae. The presence of induced defenses in algae causes plant quality to vary spatially and temporally. This may result in variation in intra- and interspecific food preferences of herbivores, and ultimately may affect benthic algal community structure.

Key words: behavior; chemical defenses; Fucus; herbivory; induced defenses; intertidal; Littorina; plant defenses; plant–herbivore interactions; polyphenolic compounds; seaweeds.

INTRODUCTION

Herbivory is an important factor in determining the structure of benthic algal assemblages in marine communities. Grazing by herbivorous fishes, echinoderms, and molluscs has been shown to play a role in determining the diversity, abundance, and species composition of algae in both intertidal and subtidal communities (see reviews by Lubchenco and Gaines 1981 and Hawkins and Hartnoll 1985). Grazers may also affect plant fitness, not by decreasing survivorship, but by influencing growth rate and reproductive output.

Food preferences of herbivores are important in mediating the effects of herbivores on the distribution and abundance of marine algae (Vadas 1977, Lubchenco 1978). Preferences can be influenced by a number of physical and chemical characteristics of the potential prey (Vadas 1977, Paul and Hay 1986), which, in some cases, are thought to have evolved in response to selection pressures imposed by herbivory. Physical features that may affect herbivore choice include an alga's size and shape (Littler and Littler 1980, Hay 1981, Steneck and Watling 1982), toughness (Watson and Norton 1985*a, b*), degree of calcification (Paul and Hay 1986), cuticle production (Gaines 1985), and produc-

tion of protuberances. An alga's chemical composition may affect herbivore choice because it determines the nutritive value of the plant and because some chemicals deter feeding (Geiselman 1980, Geiselman and McConnell 1981, McConnell et al. 1982, Steinberg 1984, 1985, Paul and Hay 1986, Paul and Van Alstyne 1987).

Marine algae produce a variety of secondary metabolites whose primary function appears to be herbivore deterrence (Norris and Fenical 1982, Faulkner 1984). These compounds are thought to reduce digestibility or plant nutritional qualities, affect nervous system or cardiac functions, or be otherwise toxic or unpalatable to herbivores. No algal secondary metabolites have yet been reported to function as feeding stimulants.

It is assumed that there is a cost in the production of defensive compounds that is reflected in decreases in the growth rate, reproductive output, or competitive ability of the organisms producing them (McKey 1979, Coley et al. 1985, Coley 1986, Harvell 1986). For a particular defense to be favored by natural selection, it should not require a greater investment of a plant's resources than would otherwise be lost to herbivory. A plant producing too many defenses would be at a competitive disadvantage relative to those producing fewer defenses because of its low growth rate or reproductive output. This could be especially critical in communities where space is limiting or where success depends upon spore availability when new patches open

TABLE 1. Densities of herbivores that were observed to feed on *Fucus distichus* from the main beach and Pole Island Draw study sites. Data are means ± 1 SE of *n* replicate measurements taken with a 10 × 10 cm quadrat in May 1986.

	Herbivore density (no./m²)	
Herbivore species	Main Beach	Pole Island Draw
Littorina sitkana	200 ± 163 (*n* = 3)	4120 ± 591 (*n* = 10)
Littorina scutulata	167 ± 33 (*n* = 3)	570 ± 130 (*n* = 10)
Siphonaria thersites	0 ± 0 (*n* = 3)	40 ± 22 (*n* = 10)
Idotea wosnesenskii	0 ± 0 (*n* = 3)	0 ± 0 (*n* = 10)

up. On the other hand, a plant producing too few defenses would suffer high tissue losses or death because it would be a more preferred food relative to better defended plants.

The problems of allocation to defenses are further complicated by spatial or temporal variations in herbivore grazing rates. If grazing pressure is constant and predictable then prey should maintain uniform levels of defenses (Harvell 1986). However, grazing pressure is seldom constant and only occasionally predictable in marine communities (Lubchenco and Cubit 1980, Cubit 1984). Changes in grazing activity can be brought about by seasonal or even day-to-day variation in weather or water conditions. Movement of herbivores will also cause both spatial and temporal changes in herbivore pressure. Ideally, defenses against predation should vary with changes in predation rates. Many terrestrial plants use damage by herbivores as a cue to increase concentrations of herbivore-deterrent compounds within their tissues (see reviews by Harbone 1986 and Havel 1986). This type of strategy should be effective only if initial attacks by predators are good predictors of future attacks (Harvell 1986). Herbivore-induced chemical defenses have not previously been reported in marine or nonvascular plants.

In this study, I show that *Fucus distichus*, (=*F. gardneri*), a temperate intertidal brown alga, is capable of using physical damage similar to damage caused by herbivores as a cue to increase its production of defensive compounds. I further demonstrate that this increase makes these plants less susceptible to future attacks and hence decreases tissue loss from herbivores by affecting the foraging behavior of the grazers.

Natural history and study sites

Fucus distichus ssp. *edentatus* (de la Pyl.) Pow. is an abundant brown alga on sheltered rocky shores of northwestern North America (Abbott and Hollenberg 1976). It often forms extensive beds in the mid to high intertidal, harboring large numbers of herbivorous gastropods and crustaceans (200–5000 grazers/m⁻²; K.

Van Alstyne, *personal observation*). *Fucus*, like other brown algae, produces large quantities of phenolic compounds (Ragan 1976, Ragan and Glombitza 1986) that effectively deter feeding by several marine herbivores (Geiselman 1980, Geiselman and McConnell 1981, Steinberg 1985). These compounds are primarily polymers of phloroglucinol linked by aryl–aryl, ether–ether, or aryl–ether bonds (Ragan and Glombitza 1986). They bind to both plant and animal proteins, reducing the nutritive value of the plant as well as inactivating herbivore digestive enzymes (Swain 1979). Interspecific differences in phenolic levels in brown algae are negatively correlated with gastropod (Steinberg 1985) and sea urchin (Anderson and Velimirov 1982) food preferences. Both *F. distichus* and *F. spiralis* are low-preference foods for *Littorina sitkana*, the herbivorous gastropod investigated in this study, and *Littorina scutulata* (Van Alstyne 1988).

All of the work done in this study took place on Tatoosh Island, Washington, USA. Collections of *F. distichus* were made on the main beach of the island. This site is a sheltered beach composed mainly of large cobbles and boulders. *F. distichus* grows in an extensive bed here harboring several herbivorous molluscs. Only the gastropods *Littorina sitkana*, *Littorina scutulata*, and *Siphonaria thersites*, and the isopod *Idotea wosnesenskii* have been observed to graze on *F. distichus* on Tatoosh Island. *L. sitkana* was the most abundant herbivore at all sites and appeared to be the major source of damage to *F. distichus*. *L. scutulata* was common and did some damage to *F. distichus*, whereas *S. thersites* and *I. wosnesenskii* were rare and probably had little impact on the algae. Herbivore densities on the main beach were generally low (Table 1), and many plants showed no sign of herbivore-produced damage. The second study site, Pole Island Draw, was used primarily for transplant experiments. The draw is sheltered from most wave action. The substrate here is mostly bedrock with a few large boulders. Densities of all herbivores were much higher in Pole Island Draw than at the main beach site. All of the *F. distichus* here were grazed, many back to the midrib.

METHODS

Comparisons of phenolic compounds in grazed and ungrazed plants

Phenolic concentrations were measured in naturally grazed and ungrazed *Fucus distichus* collected from the main beach on Tatoosh Island in May 1985. Twenty grazed plants were collected from areas where herbivore densities were relatively high. Grazed algae were considered to be those in which at least 10% of the plant's surface area had been removed by herbivores. Because wave action in this area is low, physical damage due to abrasion was unlikely to be the cause of tissue loss in these plants. Sixty ungrazed plants were collected from areas on the beach where few herbivores

were present. Only plants that showed no signs of her-
bivore-produced damage were used for these assays.
All the plants used in this study were young, nonre-
productive, and ranged from 10 to 15 cm long. Because
F. distichus recruits throughout the year (Thom 1983),
similar-sized plants are likely to be about the same age.

Phenolic compounds from *F. distichus* were extract-
ed as soon as possible after collecting the plants, usually
within 24–48 h. One 0.25–0.50 g piece of each algal
midrib was weighed and placed in 15 mL of 70% meth-
anol. Each piece was ground in methanol for 2–4 min
using a Virtis "45" homogenizer, then filtered through
a Whatmann GF/A Glass Microfibre filter. The filtrate
was stored at −10°C prior to analysis for phenolic con-
centrations. Another similar-sized piece of midrib tis-
sue from each plant was weighed and dried for 48 h at
60° to obtain a dry mass : wet mass ratio.

Phenolic compounds were quantified using a Folin-
Denis analysis for total phenols according to Swain
and Goldstein (1964). This assay measures amounts
of hydroxylated aromatic groups, but does not distin-
guish between different phenolic compounds. The pres-
ence of phloroglucinol polymers was verified using pro-
ton nuclear magnetic resonance spectroscopy (K. Van
Alstyne and V. J. Paul, *personal observation*) and Lindt's
Reagent (Ragan and Craigie 1978), a vanillin stain spe-
cific to phloroglucinol derivatives. A standard curve
for the Folin-Denis analyses was derived using phloro-
glucinol dihydrate. Phenolic concentrations in grazed
and uninjured algae were compared using a Mann-
Whitney *U* test (Sokal and Rohlf 1981).

Clipping experiments

In order to assess the changes in defensive chemistry
that occur when *F. distichus* is injured, I performed a
series of experiments in which previously uninjured *F.
distichus* were wounded by clipping away ≈10% of the
plant's vegetative surface area. Damage to experimen-
tal plants was done in a way that mimicked injury by
herbivores; tissue was removed from the wings of non-
reproductive algae, avoiding injury to the midrib and
apices. Plants damaged in this way survive to grow and
reproduce and show no obvious signs of stress. Five
to 10 clipped and 12 to 27 control plants were left in
the field for 2 wk. They were then collected, and phe-
nolic levels were analyzed in a single piece of the re-
maining midrib tissue at the site of injury in the clipped
plants and in the midribs of the control plants using
the methods described above. These experiments were
repeated four times between May 1985 and May 1986.
All of the clipping experiments took place on the main
beach of Tatoosh Island.

In two of these trials, phenolic concentrations were
measured at two or three locations (depending upon
the size of the plant) along the midrib of the clipped
plants to determine whether the change in defensive
compounds was a general response throughout the en-
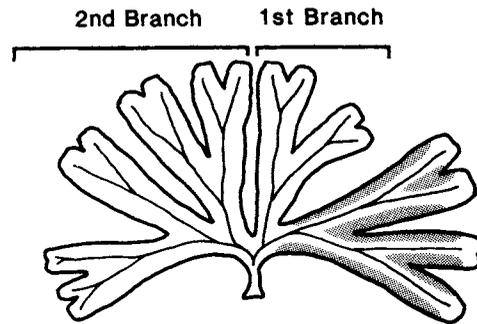tire thallus or only a localized response to the injury.

FIG. 1. Design of clipping experiment for looking at with-
in-plant variation in defenses. The shaded area denotes tissue
removed by clipping. Phenolic levels were later measured at
one and two branches from the clipped branch.

The plants were clipped as described above; however,
phenolic concentrations were measured in midrib tis-
sue at the site of injury and in midrib tissue one and
two branches away from the injury (Fig. 1) in the clipped
plants.

Transplant experiments

A second series of experiments was done to assess
the effects of changes in algal defensive chemistry on
the foraging behavior of the herbivorous gastropod *Lit-
torina sitkana,* the primary consumer of *F. distichus*
(K. Van Alstyne, *personal observation*). In these ex-
periments, clipped and uninjured *F. distichus* were
transplanted from the beach, an area where grazer den-
sities were low, to Pole Island Draw, an area with high
littorine densities.

Holes ≈5 cm in diameter and 3 cm deep were chis-
eled into the rock substrate and then cleared of debris
and dust. Fast-drying marine cement was poured into
the depressions in the rock (Fig. 2). As the cement
began to set, one end of a McMahon 1/A stainless steel
fishing swivel with a 2.5-cm steel nail through one end
was pushed into the drying cement. Swivels were set
up in three arrays of 20 pairs. *F. distichus* was trans-
planted by first pulling the plants, along with their hold-
fasts, from the substrate. If this is done carefully, the
entire holdfast can be removed without causing any
visible damage to the alga. Part of the rock substrate
often came off with the plant. A 1–1.5 cm piece of
surgical tubing (3 mm [⅛-in.] inside diameter, 8 mm
[⁵⁄₁₆-in.] outside diameter) was slit lengthwise and
wrapped around the stipe of the alga, immediately above
the holdfast (Fig. 3). The tubing formed a skirt around
the stipe and protected it from abrasion. A 10 mm
diameter cotter ring (obtainable at boating supply stores)
was placed inside a number 3 aluminum bird band
(Gey Band and Tag Company, Norristown, PA) that
was tightened around the stipe to hold the surgical
tubing in place. The ring was then attached to the end
of the stainless steel swivel that had been imbedded at
the transplant site. *F. distichus* transplanted using this
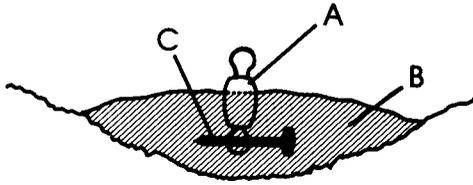procedure had an average loss rate of 0.27%/d (3 out

FIG. 2. Stainless steel fishing swivel (A) cemented on the rock substrate. One end of the fishing swivel was embedded in the cement (B) and anchored with 2.5-cm steel nail (C).

of 130 transplanted plants were lost). Because the plants were moved during a low tide they did not receive longer than normal emersion. As a result, none of the algae appeared stressed in any way. Transplanted *F. distichus* continued to increase in length and several plants became reproductive after being moved. None of the algae developed red patches on the thallus or softened tissue that are characteristic of stressed *Fucus* (Schonbeck and Norton 1980). Phenolic concentrations were measured in 10 uninjured transplanted and 10 uninjured control plants to insure that there was no change in amounts of these compounds caused by transplanting the algae.

In the first set of experiments, which took place in May 1986, plants were clipped and then were immediately transplanted in 19 pairs (2–3 cm apart) with undamaged control plants. Paired comparisons were used because of the high spatial heterogeneity in herbivore density. By transplanting the plants immediately after clipping there is insufficient time for the production of additional phenolic compounds; therefore the levels of defensive compounds in the control and clipped algae should be the same. A second set of nine plants from the main beach was clipped and then transplanted 2 wk after injury, a procedure that allows the clipped plants time to increase their concentrations of defensive compounds prior to being offered to the herbivores. On the day following transplanting, the number of *L. sitkana* foraging on each plant was counted at the next two low tides. The number of snails grazing on *F. distichus* were later normalized by plant surface area and compared using a Wilcoxon Signed Ranks test for paired comparisons (Sokal and Rohlf 1981).

Another set of 20 clipped *F. distichus* and 20 control plants had been transplanted in September 1985 in order to compare the relative amounts of tissue loss by clipped and uninjured plants over a 2-wk period. After 2 wk plants were removed and photocopied onto acetate transparencies from which surface area measurements were made using a LI-COR 3000 Surface Area meter. The portions of the plant that had been removed by grazers was drawn in on the acetate using a black pen and the area of the "ungrazed" plant was measured. The surface area removed by grazers was calculated as the final value minus the initial value and compared using a sign test. One week after these plants

were transplanted I counted the number of *L. sitkana* grazing on each plant at 1–2 h intervals throughout the day. *L. sitkana* counts were normalized by plant size and compared using a Wilcoxon Signed Ranks test for paired comparisons.

RESULTS

Differences in naturally grazed and ungrazed algae

In May 1985, *Fucus distichus* that were grazed by herbivores had significantly ($P < .001$) higher levels of phenolic compounds than did ungrazed plants. Mean phenolic concentrations (as percent of dry mass ± 1 SE) in ungrazed plants were 9.64 ± 0.27% whereas those in grazed plants were 12.34 ± 0.54%. These values are significantly different ($P \leq .0001$) using a Mann-Whitney U test (Sokal and Rohlf 1981). The observed differences in phenolic levels might reflect between-site local selection for better defended plants in areas in which grazing pressures are higher, between-site differences in phenolics for reasons unrelated to herbivore densities, or the presence of herbivore-induced polyphenolic production.

Induction experiments

When *F. distichus* was damaged by clipping, there was a significant difference in phenolic concentrations in control and clipped plants 2 wk later during the May 1985, June 1985, and September 1985 experiments (Table 2). In these trials, the clipped plants had ≈20% higher concentrations of defensive compounds. However, in the fourth trial there was only an 8% difference, which was not statistically significant. Analysis of the data from these four experiments using a two-way ANOVA shows that there are significant differences due to both date and clipping (Table 3), with no significant interaction effects between the two factors. When phenolic concentrations were measured in May and June
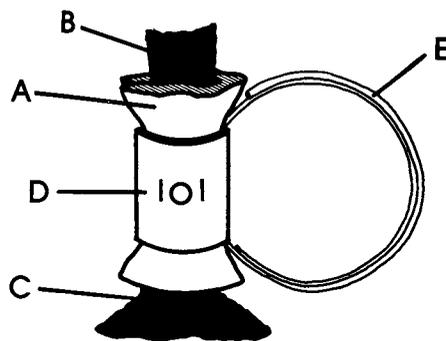

FIG. 3. Apparatus used to transplant *Fucus distichus* between sites. A small piece of rubber surgical tubing (A) was wrapped around the stipe of the attached plant (B) immediately above the holdfast (C) and secured with an aluminum bird band (D). A cotter ring (E) ran under the bird band and was attached to the free end of the fishing swivel shown in Fig. 2.

TABLE 2. Phenolic concentrations ($\bar{X} \pm 1$ SE) of n clipped and uninjured *Fucus distichus*. Measurements from clipped plants were from the midrib at the site of injury. Measurements from control plants were also made from midrib tissue.

Date	Phenolic concentrations (% dry mass)†		% in-crease
	Clipped plants	Uninjured plants	
May 1985	9.84 ± 0.49 ($n = 5$)	7.89 ± 0.44† ($n = 12$)	25
July 1985	11.93 ± 0.57 ($n = 8$)	10.15 ± 0.32** ($n = 27$)	18
Sept 1985	10.90 ± 0.54 ($n = 11$)	9.05 ± 0.37† ($n = 12$)	20
May 1986	9.38 ± 0.41 ($n = 10$)	8.65 ± 0.32 ($n = 17$)	8

† $P < .025$; ** $P < .01$; Mann-Whitney U test comparing clipped vs. unclipped plants.

1986 at different locations within the clipped plants there was no significant difference within individual plants (Table 4).

Responses by herbivores

The results of the Folin-Denis analysis for total phenolics in plants that were and were not transplanted show that there was no significant difference ($P = .473$ using a Mann-Whitney U test) between phenolic levels of clipped control ($\bar{X} \pm 1$ SE: 6.82 ± 0.63%) and transplanted plants ($\bar{X} \pm 1$ SE: 7.19 ± 0.78%). Thus, transplanting algae does not appear to stress the plants in ways that would affect concentrations of these defensive compounds.

The transplant experiments from May 1986 demonstrate that initially, clipped algae are preferred over uninjured control plants (Table 5). Snail densities were 65% higher on the clipped plants a day after the plants were clipped and transplanted. However, the snails switched their preference from clipped plants to uninjured plants over the 2-wk period. When plants were transplanted 2 wk after being clipped there were over twice as many snails feeding on undamaged plants. This switch is well-correlated with the increase in defensive compound concentrations of the clipped plants after 2 wk. Tissue losses to herbivores were also less in the clipped algae, which lost about half as much photosynthetic surface area to grazers as did the undamaged control plants (Table 6).

Observations of snails feeding throughout the day 1

TABLE 4. Phenolic concentrations ($\bar{X} \pm 1$ SE) within n clipped plants. Measurements were made 2 wk following clipping. Concentrations at the site of injury and one and two branches away are not significantly different ($P > .05$ using a one-way ANOVA on arcsin $\sqrt{p}$ transformed data).

Location within plant*	Phenolic concentrations (% dry mass)	
	May 1985	July 1985
Site of injury	9.84 ± 0.49 ($n = 5$)	11.93 ± 0.57 ($n = 8$)
One branch away from injury	10.05 ± 0.87 ($n = 5$)	11.19 ± 0.63 ($n = 8$)
Two branches away from injury	8.50 ± 0.98 ($n = 3$)	11.08 ± 0.95 ($n = 2$)

* See Fig. 1 for depiction of these locations.

wk after the algae were transplanted showed that *Littorina sitkana* encountered clipped and uninjured algae at approximately the same rate but moved off the plants at different rates (Fig. 4). *L. sitkana* were attached to the rock substrate while the tide was in but began to forage soon after it receded. Initially, the snail densities on the clipped and undamaged plants were the same, however at low tide the densities of *L. sitkana* were significantly less on the clipped plants. As the snails moved off the plants onto the rock substrate prior to the incoming tide, the densities on clipped and undamaged plants no longer showed a significant difference.

DISCUSSION

In these experiments, I have demonstrated that marine algae can use physical damage, such as that which might be produced by herbivory, as a cue for the production of additional defensive chemicals that can reduce future losses to grazers. This causes both spatial and temporal changes in polyphenolic concentrations within and between individual plants. This type of variation in defense composition may cause both intra- and interspecific food preferences to change over small distances or time intervals. If predation pressure is severe enough to affect prey survivorship, differences in preferences could have an effect on community organization.

Intraspecific variations in defenses have been reported from many aquatic organisms. Chemical defenses in algae vary spatially, ranging in scale from between-population to within-plant differences (Gaines 1985, Paul and Van Alstyne 1987). This variation oc-

TABLE 3. Two-way analysis of variance for *Fucus distichus* clipping experiments.

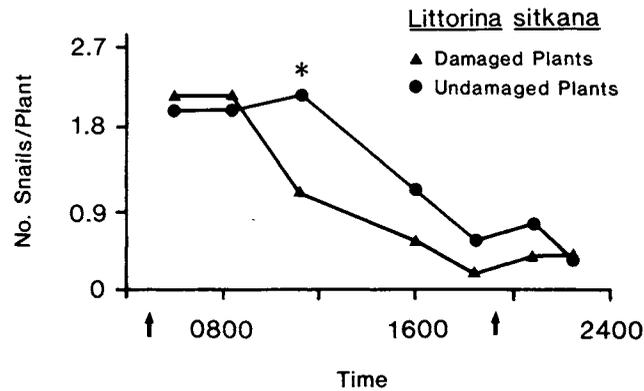| Source	df	SS	MS	F	P
Date	3	68.539	22.846	9.809	<.001
Clipping	1	41.634	41.634	17.880	<.001
Time × clipping	3	14.218	4.739	2.035	NS
Error	94	218.906	2.329		
Total	101	343.297			

FIG. 4. Number of *Littorina sitkana* on clipped and uninjured algae throughout a tidal cycle. Herbivore numbers were normalized by plant surface area. Arrows mark the time of the high tides. Significantly different ($P < .05$ using a Wilcoxon Signed Ranks test) densities are marked with an asterisk.

curs both in the compounds present and in their amounts. Daily (Paul and Van Alstyne 1987) and seasonal (Ragan and Jensen 1978, Geiselman 1980) variation in algal chemical defenses have also been reported. Few cases of variation in secondary metabolite production in marine animals have yet been documented, although predator-induced morphological defenses have been reported in bryozoa (Harvell 1984, 1985, 1986), barnacles (Lively 1986a, b), rotifers (Gilbert and Stemberger 1984, Stemberger and Gilbert 1984), and a tropical brown alga (Lewis et al. 1987).

Interpopulation variation in defensive compound concentrations and predator-induced chemical defenses are also common in terrestrial plants (Denno and McClure 1983, Harbone 1986, Havel 1986). Havel (1986), in a recent review of the literature on consumer-induced defenses, reports 43 examples of herbivore-induced defenses in terrestrial plants. In 33 of these examples, the compounds that increase subsequent to herbivore attacks are known. Thirteen of these 33 compounds are phenolic metabolites. This high representation of phenolics among induced compounds is prob-

ably a reflection of the ease with which total phenolic levels can be measured. If simple assays were available for measuring other types of secondary compounds, the proportion of species in which herbivore-induced increases in phenolic compounds have been reported might be much lower.

Damage-induced changes in plant chemistry appeared to account for most of the interpopulation variation that I observed. The spatial variation in phenolic concentrations that I observed between the grazed and ungrazed populations of *F. distichus* could have resulted from either (1) the presence of induced defenses, (2) localized selection for higher concentrations of defensive compounds in areas of high grazing intensity, or (3) between-site differences in phenolic concentrations that were unrelated to herbivore density. The results of the clipping experiments indicate that the first hypothesis is the most probable since the increases in phenolic concentrations due to clipping the plants corresponded well with the increased levels seen in the populations of grazed algae. This does not entirely rule out the possibility that localized selection or differences caused by other factors may also operate in causing between-site variation within these plants.

Increases in polyphenolic concentrations brought

TABLE 5. Numbers of *Littorina sitkana* ($\bar{X} \pm 1$ SE) foraging on *n Fucus distichus* that had been transplanted to a site where herbivores were abundant, either immediately or 15 d after being clipped.

Time of transplant (days following clipping)	Number of foraging snails per plant‡	
	Clipped plants	Uninjured plants
1	1.30 ± 0.19 (n = 19)	0.80 ± 0.16*** (n = 18)
15	2.71 ± 0.05 (n = 9)	5.72 ± 0.09† (n = 9)

† $P < .025$; *** $P < .001$; Wilcoxon Signed Ranks tests for paired comparisons of clipped vs. uninjured plants within each transplant time.

‡ Snails were counted on each plant 1 d after the plants were transplanted. These values were normalized by plant surface area.

TABLE 6. Tissue surface area (SA) loss to herbivores ($\bar{X} \pm 1$ SE) in *n* clipped and injured *Fucus distichus*. Plants were transplanted to an area of high herbivore density in pairs of one clipped and one uninjured plant immediately after damage to clipped plants. Surface areas were measured 2 wk after transplanting.

Measure	Clipped	Uninjured
Absolute SA removed (cm²/d)	0.42 ± 0.08 (n = 18)	0.76 ± 0.14* (n = 18)
Proportion SA removed (%/d)	0.58 ± 0.10 (n = 18)	0.97 ± 0.18* (n = 18)

* $P < .05$; Wilcoxon Signed Ranks tests for paired comparisons.

about by damage to *F. distichus* were ≈20% above background phenolic levels, which fluctuated seasonally. Seasonal variation in polyphenol levels has been well documented in *Fucus vesiculosus* (Ragan and Jensen 1978, Geiselman 1980). Geiselman (1980) suggests that polyphenolic levels are highest at the time of peak grazing intensity. Although temporal changes in polyphenolic compounds have not been documented in *Fucus distichus* on the northeast Pacific coast, it is likely that regular seasonal variation also occurs. During the year in which the clipping experiments were done there was considerable temporal variability in phenolic concentrations between experiments. These levels were highest in midsummer (July) and lower in the spring (May) and autumn (September). Both *Littorina sitkana* and *L. scutulata* are inactive during periods of heavy rainfall but more active in foggy weather (K. Van Alstyne, *personal observation*). The Washington coast receives most of its rainfall during the winter and very little in summer months, with intermediate amounts occurring in the spring and fall (Anonymous 1983). Coastal fogs occur primarily in the summer (Dayton 1971, Thomson 1981, Paine 1984). Thus, littorine activity should be highest in summer. The polyphenolic levels that were measured in this study were higher in midsummer than in the spring or fall, which corresponds with the expected levels of grazer activity.

Qualitative changes in polyphenolic compounds may also occur when defenses are induced. Because concentrations of compounds were quantified using a general assay for polyphenolics, it is not known specifically which metabolites were increasing when the plant was wounded. Ragan and Craigie (1978) have separated at least six phloroglucinol-containing compounds from *Fucus vesiculosus*. Phloroglucinol polymers are more polar than most algal secondary metabolites. Thus, they tend to be more difficult to isolate and identify than other defensive compounds. In general, ecologists have avoided working with individual phenolic compounds because of the difficulties involved in isolating them and because of the availability of general assays such as the Folin-Denis analysis. Hence, little is known about the variation and action of individual metabolites. In *F. distichus*, the 20% increase in defensive compounds that occurs when the plant is clipped could result from a 20% increase in all phenolic compounds, a greater increase in one or more individual compounds, or the de novo synthesis of new metabolites. Further work is needed to identify the specific activities of individual metabolites and to quantify temporal changes in their abundances.

The benefits to be gained by producing inducible defenses may not be limited to herbivore deterrence. Fucoid algae release polyphenolic compounds into seawater (Craigie and McLachlan 1964, Sieburth 1969, Sieburth and Jensen 1969, Carlson and Carlson 1984). These types of compounds have been shown to inhibit growth of bacteria and epiphytes (Conover and Sie-

burth 1964, McLachlan and Craigie 1966). Thus, damaged plants with higher levels of these compounds may be less susceptible to invasion by pathogens and other algae than are wounded plants that do not increase concentrations of phenolic compounds. Phenolic compounds may also aid in wound healing through their protein-binding properties. However, if the sole reason for increasing the use of these compounds were to heal wounds, phenolic levels would not be expected to increase across the entire thallus of the injured plant.

The induction of chemical-defense production by marine plants may also affect foraging strategies of herbivores and the risks associated with foraging. Because the induction of antiherbivore compounds causes plant nutritional quality to vary in time and space, herbivores should not feed continuously on a single plant but should move in search of better food as the quality of the alga they are feeding on declines. Snails moving to a new area may be susceptible to higher levels of predation, desiccation, or wave exposure (Behrens 1972). *L. sitkana* that do not find crevices in which to hide during the high tide can be carried up to 2 m away by tidal water movement (K. Van Alstyne, *personal observation*). Because these snails often occupy habitats that are near sandy beaches, they are in danger of becoming buried in sand if they are washed off rock substrates. Thus, induced defenses in algae may affect herbivores not only by decreasing the quality of the food but also by increasing the risks associated with foraging.

How does a signal to induce chemical defense production get transported from a wound to distant tissues in a "nonvascular" plant? Marine algae either lack vascular systems or, like *Fucus*, have a series of tracheal cells that may form a primitive transport system (Moss 1983, Diouris and Floc'h 1984). In addition, waterborne cues, similar to the air-borne cues found to induce defenses in terrestrial plants (Baldwin and Schultz 1983), could operate in inducing defenses in algae. If cues cannot be sent to different parts of the plant internally, then they might be transported externally, either in air or water. If this mechanism is operating in *Fucus*, then it should produce interplant induction of chemical defenses. Because the plants in the clipping experiments were only a few centimetres apart, defenses should have been induced in control plants if this mechanism were operating. Therefore, it is unlikely that air-borne or water-borne cues induce increased phenolic production within individual plants.

Consumer-induced defenses are a common phenomenon in marine, freshwater, and terrestrial predator-prey systems (Havel 1986). Little is known about the importance of induced defenses in structuring populations and communities. However, they may affect differential survival and reproduction of the prey (Harvell 1986), decrease predator fitness, and cause variation in preferences by generalist consumers for different plant species. Shifts in preferences could

conceivably cause local extinctions of more poorly defended species, thereby driving changes in the diversity and structure of the community. Clearly, much more needs to be known about the mechanisms underlying defense induction and the effects of induced defenses on the dynamics of predator–prey interactions.

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