# PHLOROTANNIN ALLOCATION AMONG TISSUES OF NORTHEASTERN PACIFIC KELPS AND ROCKWEEDS[1]

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**Optimal defense theory (ODT) predicts antiherbivore defensive compounds will be allocated so that the most valuable or most susceptible tissues will be best defended. The growth–differentiation balance hypothesis (GDBH) predicts that defense allocation will be a result of trade-offs between growth and defense. Thus, these two theories predict opposite allocation patterns with respect to "valuable," actively growing meristematic and reproductive tissues. ODT predicts that meristems and reproductive tissues should have higher defense levels than nonmeristematic vegetative tissues; the GDBH predicts the defense levels of meristems and reproductive tissues will be lower than vegetative tissues. We examined allocation patterns of phlorotannins in 21 species of kelps (Order Laminariales) and rockweeds (Order Fucales) from nine sites on the west coast of the United States to determine if allocation patterns better matched the predictions of ODT or the GDBH and to look for differences in allocation patterns among sites. Within-species differences in phlorotannin levels occurred in 10 of the 21 species examined. Meristems of both kelps and rockweeds had higher phlorotannin levels than nonmeristematic vegetative tissues, consistent with ODT. Phlorotannin levels in reproductive tissues of kelps were higher than vegetative tissues, but levels in reproductive tissues of rockweeds were lower than vegetative tissues, indicating that allocation strategies may follow taxonomic lines. Allocation patterns differed among sites in four of the 16 species collected from more than one site. Differences in allocation patterns among sites were usually changes in the ratios of phlorotannins in well-defended compared to poorly defended tissues, rather than changes in which tissues were well defended or poorly defended. We concluded that environmental variability can have large effects on the concentration of phlorotannins in algae but has limited effects on allocation patterns among tissues.**

*Key index words:* **allocation; chemical defenses; Fucales; geographic variation; Laminariales; Phaeophyceae; phlorotannins; spatial variation**

*Abbreviations:* **DM, dry mass; GDBH, growth–differentiation balance hypothesis; ODT, optimal defense theory**

Plants allocate materials and energy among critical functions such as maintenance, growth, reproduction, and defense (Bazazz and Grace 1997 and citations therein). It is widely assumed the total amount of resources available for these functions is limited and all of these functions have significant metabolic costs associated with them. Consequently, over evolutionary time there should be selection for individuals to distribute resources among functions in ways that maximize overall fitness, assuming that allocation strategies are not limited by physiological or other constraints.

Two hypotheses have been proposed to predict resource allocation to defense in plants: optimal defense theory (ODT) and the growth–differentiation balance hypothesis (GDBH). ODT predicts that defenses will be preferentially allocated to tissues with the highest fitness value or tissues most at risk for attack (Rhoades 1979). According to the predictions of this model, meristematic and reproductive tissues, which have a high fitness value, should be better defended than nonmeristematic vegetative tissues. The GDBH predicts trade-offs between growth and defense production (Herms and Matson 1992, Tuomi 1992). According to the predictions of the GDBH, actively growing tissues, such as meristems or reproductive tissues, should produce lower quantities of defenses than nonreproductive vegetative tissues.

Resource allocation patterns may also be affected by environmental variability. Fluctuations in environmental conditions can produce changes in resource pools within plants or affect foraging rates of herbivores (Boggs 1997). Many plants exhibit phenotypic plasticity in resource allocation to defense, such as the production of herbivore-induced defenses (Karban and Baldwin 1997). Most work on resource allocation shifts in response to changing environmental conditions has focused on shifts between major functions such as growth, reproduction, and defense; little is known about shifts among tissues within those functions.

Tissue differentiation in seaweeds is generally less complex than in vascular plants, making seaweeds

an ideal system for testing the predictions of the ODT and GDBH models (Cronin and Hay 1996). Among the seaweeds, the brown algae are particularly useful in this regard. In the kelps (Order Laminariales) and rockweeds (Order Fucales), meristems and reproductive tissues are often distinctly localized; however, they can occur in different areas of the thallus in the two orders (Bold and Wynne 1985). Kelps have an intercalary meristem located at the base of the blade. The meristem in rockweeds is located in the apical portion of the thallus. Many kelps produce reproductive sporophylls off the stipe or reproductive tissues within the blades. In rockweeds, reproduction occurs in apical receptacles.

Another feature of temperate marine kelps and rockweeds that makes them ideal for testing the predictions of the ODT and GDBH models is they all produce phlorotannins or polyphenolic compounds. Phlorotannins are compounds that bind proteins and are ultimately derived from phloroglucinol (Ragan and Glombitza 1986, Steinberg 1992). They have antifeeding activity toward many, though not all (Steinberg and van Altena 1992, Boettcher and Targett 1993), herbivores (Steinberg 1988, Steinberg and van Altena 1992, Winter and Estes 1992, Steinberg et al. 1995, Targett and Arnold 1998). Phlorotannins also have been hypothesized to serve a number of other functions, including protection from pathogens and UV damage (Pavia et al. 1997). Concentrations of phlorotannins in marine brown algae range from undetectable to nearly 20% of an alga's dry mass (Ragan and Glombitza 1986). Phlorotannin concentrations differ greatly among species and among spatial scales, including among tissue types in an individual (Geiselman 1980, Steinberg 1984, 1985, 1989, Johnson and Mann 1986, Tugwell and Branch 1989, Tuomi et al. 1989, Van Alstyne 1989, Pfister 1992, Poore 1994), among sites at scales ranging from tens of meters to hundreds of kilometers (Steinberg 1989, Pavia and Aberg 1996, Van Alstyne et al. 1998), and between global regions (Steinberg 1986, 1992, Van Alstyne and Paul 1990, Steinberg and van Altena 1992, Targett et al. 1992, Steinberg et al. 1995).

Several studies have examined the allocation of defenses in seaweeds in light of the ODT and GDBH models; however, most of these studies have focused on a single species and have not examined the models' predictions across taxonomic groups or a range of habitats that encompass a variety of environmental conditions. The results of these studies have not generated consistent patterns of defense allocation strategies. For example, the brown alga *Dictyota ciliolata* (Cronin and Hay 1996) produces higher concentrations of defensive terpenes in nonmeristematic than meristematic tissues, consistent with the GDBH. In contrast, reproductive tissues of the kelps *Alaria marginata* Postels et Ruprecht (Steinberg 1984), *Ecklonia maxima* (Osbeck) Papenfuss, *Laminaria pallida* Grev. *ex* J. Agardh, and *Macrocystis an-*

*gustifolia* Bory (Tugwell and Branch 1989) and meristematic tissues or young tissues of the brown alga *Zonaria angustata* (Kutzing) Papenfuss (Poore 1994), the kelps *E. maxima,* and *M. angustifolia* (Tugwell and Branch 1989) have higher concentrations of phlorotannins than nonreproductive vegetative tissues, consistent with ODT.

The goal of this study was to test the predictions of ODT and the GDBH by examining allocation patterns of phlorotannins in a large number of brown algal species across sites where environmental conditions are likely to vary. We collected 21 species of kelps and rockweeds from nine sites along the west coast of the United States and measured phlorotannin concentrations in meristems, reproductive tissues, and nonmeristematic vegetative tissues. The specific questions addressed in this study were: (1) Do patterns of phlorotannin concentrations among tissues follow the predictions of either the ODT or the GDBH? (2) Do allocation patterns of phlorotannins across tissues vary among populations (sites)? (3) Do allocation patterns follow taxonomic lines; for example, are they different in the kelps and rockweeds?

## MATERIALS AND METHODS

*Collection sites.* Kelps and rockweeds were collected over a 2-week period from nine sites, ranging from southern California to northern Washington, U.S.A. These sites included (1) the intertidal zone and a shallow *Macrocystis pyrifera* (Linnaeus) C. Agardh bed at depths from 2 to 10 m at Catalina Island, California (33°23′ N, 118°21′ W); (2) an intertidal cobble beach at San Simeon, California (35°39′ N, 121°13′ W); (3) a kelp bed at 3–5 m depth off Lover's Point (36°38′ N, 121°56′ W) near Pacific Grove, California; (4) a wave-exposed intertidal promontory at Pigeon Point (37°12′ N, 122°24′ W) ~10 km north of Davenport, California; (5) an exposed rocky shore at Mouda Point (41°08′ N, 124°10′ W) ~25 km north of Eureka, California; (6) an exposed rocky shore at Boiler Bay (44°50′ N, 124°04′ W) ~5 km north of Depoe Bay, Oregon; (7) the intertidal zone of Tatoosh Island, Washington (48°23′ N, 124°44′ W); (8) a kelp bed at 5–8 m depth near the site of the former Cantilever Pier and off the floating dock of the Friday Harbor Laboratories (48°32′ N, 123°02′ W) on San Juan Island; and (9) a moderately wave-exposed intertidal site at Cattle Point (48°27′ N, 122°58′ W) at the southern tip of San Juan Island. A map of these sites and a more detailed description of them can be found in a previous publication (Van Alstyne et al. in press).

After collection, the algae were wrapped in damp paper towels and placed on ice for overnight mailing to Ohio, where they were stored at 6° C for no more than 1 day before they were extracted. In controlled experiments at the Friday Harbor Laboratories, we found that phlorotannin levels did not decrease for 3–4 days if the algae were kept cool and damp.

*Measurement of phlorotannins.* We sampled ~1 g of tissue from each of several areas of kelps: reproductive tissues; meristems; and vegetative tissues ⅓ up the blade, ⅔ up the blade, and at the distal ends of the blade (Van Alstyne et al. in press). In rockweeds, samples were taken from the meristem, reproductive tissues, and a nonreproductive, nonmeristematic vegetative portion of the blade. If 1 g of tissue was not available we used as much tissue as possible. Phlorotannin concentrations were measured as described by Van Alstyne and coworkers (in press) with a modified (Van Alstyne 1995) Folin–Ciocalteu method (Folin and Ciocalteu 1927). This assay is nearly identical to the Folin–Denis assay, which is routinely used to quantify levels of phenolic compounds in brown algae (Ragan and Glombitza 1986, Van Alstyne 1995,
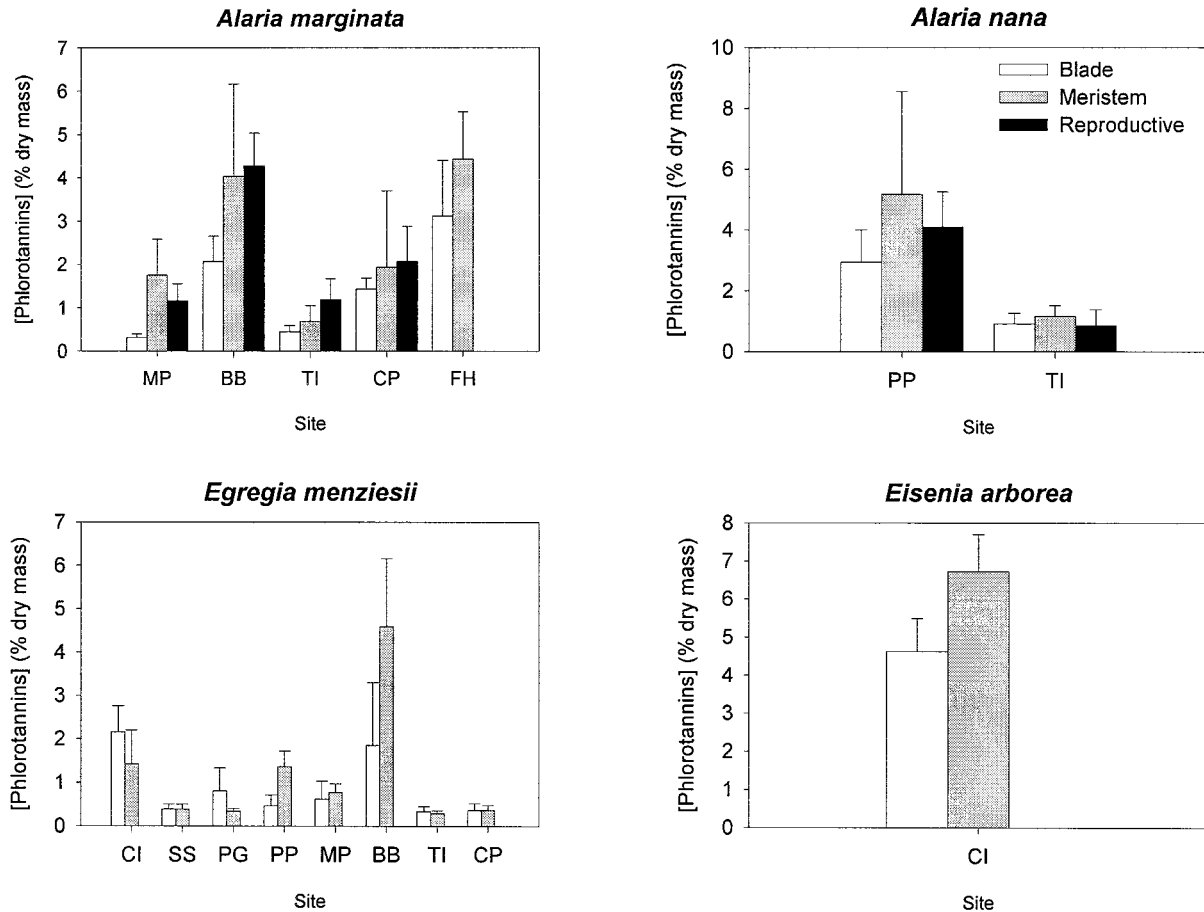
FIG. 1. Order Laminariales, Family Alariaceae. Phlorotannin concentrations (% dry mass ± 1 SD) of vegetative blades (white bars), meristematic tissues (gray bars), and vegetative and reproductive tissues (black bars). *Alaria marginata* (two-way analysis of variance: tissue $F = 5.32$, $P = 0.030$; site $F = 32.95$, $P < 0.001$; interaction $F = 1.86$, $P = 0.178$; $N = 4–5$); *Alaria nana* Schrader (two-way analysis of variance: tissue $F = 15.62$, $P < 0.001$; site $F = 58.94$, $P < 0.001$; interaction $F = 1.72$, $P = 0.133$; $N = 5–9$); *Egregia menziesii* (Turner) Areschoug (two-way analysis of variance: tissue $F = 0.01$, $P = 0.937$; site $F = 9.13$, $P < 0.001$; interaction $F = 1.49$, $P = 0.194$; $N = 2–8$); and *Eisenia arborea* Areschoug (one-way analysis of variance: tissue $F = 18.84$, $P = 0.001$; $N = 6$). BB, Boiler Bay, Oregon; CI, Catalina Island, California; CP, Cattle Point, San Juan Island, Washington; FH, Friday Harbor, San Juan Island, Washington; MP, Mouda Point, California; PG, Pacific Grove, California; PP, Pigeon Point, California; SS, San Simeon, California; TI, Tatosh Island, Washington.

Targett and Arnold 1998). The Folin–Ciocalteu assay also quantifies nonphenolic hydroxylated aromatic compounds; however, nonphenolic compounds are thought to make up less than 5% of the total Folin–Ciocalteu-reactive compounds in marine brown algae (Van Alstyne 1995, Targett and Arnold 1998). Dry to wet mass ratios for each sample were determined after dividing each sample in half. One half was weighed, placed in a drying oven at 60° C for 48 h, then reweighed; the other half was used to conduct the Folin–Ciocalteu analysis. Phloroglucinol dihydrate was used as a standard.

*Statistical analyses.* In kelps, a composite vegetative phenolic level was calculated by taking the average of the phenolic levels of the vegetative ⅓, vegetative ⅔, and distal ends for each individual. Two-way analyses of variance were performed on angularly transformed phenolic levels to determine whether phenolic levels differed among tissues (meristem, reproductive tissues, or composite vegetative average in kelps and vegetative value in rockweeds) or among sites for each species. When species were only collected from a single site, one-way analyses of variance were used to determine whether there were tissue-specific differences in phenolic levels. Significant ($\alpha = 0.05$) tissue by site interaction effects were used as an indicator of site-specific differences in allocation strategies. Two-sample *t*-tests were used to test for differences in phlorotannin concentrations between tissues within sites when significant tissue by site interactions occurred.

RESULTS

Phlorotannin concentrations differed among tissues in eight kelp species (*Alaria marginata, A. nana, Eisenia arborea, Agarum fimbriatum, Laminaria complanata, L. farlowii, L. setchellii,* and *L. sinclairii,* Figs. 1–4). The seven species not showing differences in phlorotannin levels among tissues (*Egregia menziesii, Costaria costata, Cymthere triplicata, Hedophyllum sessile, Laminaria groenlandica, Lessoniopsis littoralis,* and *Macrocystis pyrifera*) usually had vegetative phlorotannin levels that were less than 2% dry mass (DM). When phlorotannin levels varied among tissues, levels in meristems were higher than levels in nonmeristematic vegetative tissues. Levels in reproductive tissues of *A. marginata* were significantly higher than concentrations in vegetative tissues (Fig. 1; Tukey's test, $P = 0.019$) but were not significantly different from levels in meristems (Tukey's test, $P = 0.389$). In *A. nana,* phlorotannin levels in meristems were significantly higher than in nonmeristematic vege-
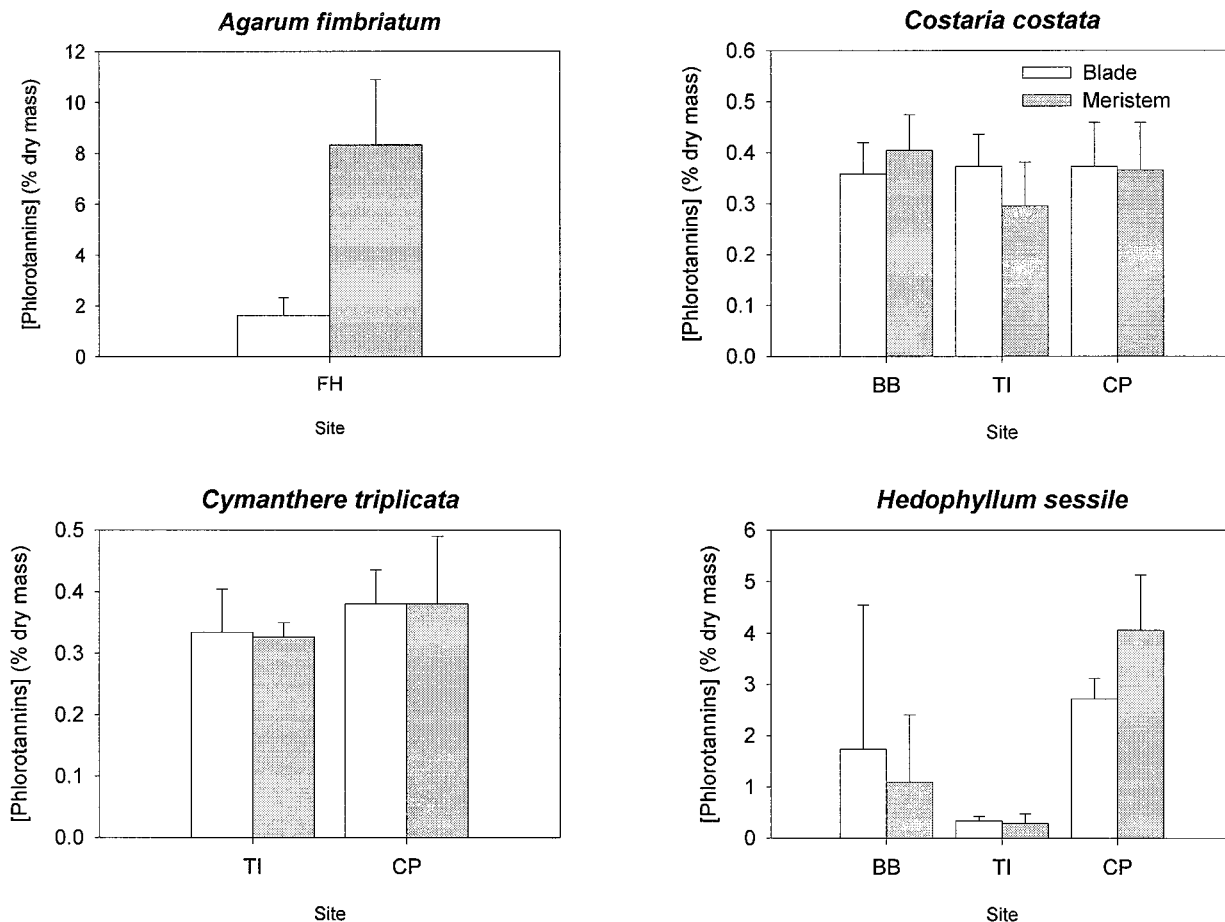
FIG. 2.   Order Laminariales, Family Laminariaceae. Phlorotannin concentrations (% dry mass ± 1 SD) of vegetative blades (white bars) and meristematic tissues (gray bars). *Agarum fimbriatum* (Harvey) (one-way analysis of variance: tissue $F = 43.34$, $P < 0.001$; $N = 5$); *Costaria costatum* (C. Agardh) Saunders (two-way analysis of variance: tissue $F = 0.23$, $P = 0.794$; site $F = 0.69$, $P = 0.414$; interaction $F = 0.50$, $P = 0.614$; $N = 5$); *Cymanthere triplicata* (Postels et Ruprecht) J. Agardh (two-way analysis of variance: tissue $F = 0.40$, $P = 0.534$; site $F = 0.70$, $P = 0.413$; interaction $F = 0.19$, $P = 0.673$; $N = 4$–5); and *Hedophyllum sessile* (two-way analysis of variance: tissue $F = 0.60$, $P = 0.446$; site $F = 20.90$, $P < 0.001$; interaction $F = 1.25$, $P = 0.307$; $N = 5$–6). Site abbreviations as in Figure 1.

tative tissues (Fig. 1; Tukey's test, $P = 0.041$); levels in reproductive tissues were not (Tukey's test, $P = 0.567$).

Phenolic levels differed among sites in five (*Alaria marginata, A. nana, Egregia menziesii, Hedophyllum sessile,* and *Laminaria sinclairii*) of the 13 species sampled at more than one site (two-way analysis of variance, site effect, $P < 0.05$). Tissue by site interaction effects were only significant ($P < 0.05$) in 3 kelp species, *H. sessile* (C. Agardh) Setchell (Fig. 2), *L. setchelli* Silva, and *L. sinclairii* (Harvey) Farlow, Anderson, et Eaton (Fig. 3). In *H. sessile,* phenolic levels did not differ significantly ($\alpha = 0.05$) among tissues at Boiler Bay or Tatoosh Island; however, at Cattle Point, meristems had significantly higher phlorotannin concentrations than vegetative tissues (Fig. 2; two-sample *t*-test, F = 7.12, $P = 0.028$). In *L. setchellii* (Fig. 3), phlorotannin levels in meristems were significantly higher than in vegetative blades at San Simeon (two-sample *t*-test, F = 11.78, $P = 0.009$), Pigeon Point (two-sample *t*-test, F = 33.90,

$P < 0.001$), Mouda Point (two-sample *t*-test, F = 38.21, $P < 0.001$), and Boiler Bay (two-sample *t*-test, F = 12.24, $P = 0.008$), but not Tatoosh Island, where meristematic phlorotannin levels tended to be less than levels in nonmeristematic blades (two-sample *t*-test, F = 1.27, $P = 0.303$). In *L. sinclairii,* meristematic phlorotannin levels were twice as high as vegetative levels at San Simeon and Pigeon Point but were 4.5 times higher at Mouda Point (Fig. 3).

In the Fucales, phlorotannin concentrations differed significantly between tissues in *Fucus gardneri* Silva and *Pelvetia compressa* (J. Agardh) DeToni (Fig. 5). In *F. gardneri* and *P. compressa,* reproductive tissues had significantly lower phlorotannin levels than vegetative blade tissues (Tukey's test, $P = 0.020$ and $P = 0.029$, respectively). Meristems of *F. gardneri* and *Hesperophycus harveyanus* (Decaisne) Setchell et Gardner had higher phlorotannin concentrations than vegetative blade tissues, but the differences were not significant (Tukey's tests, $P = 0.072$, and one-way ANOVA, F = 6.03, $P = 0.091$, respectively).
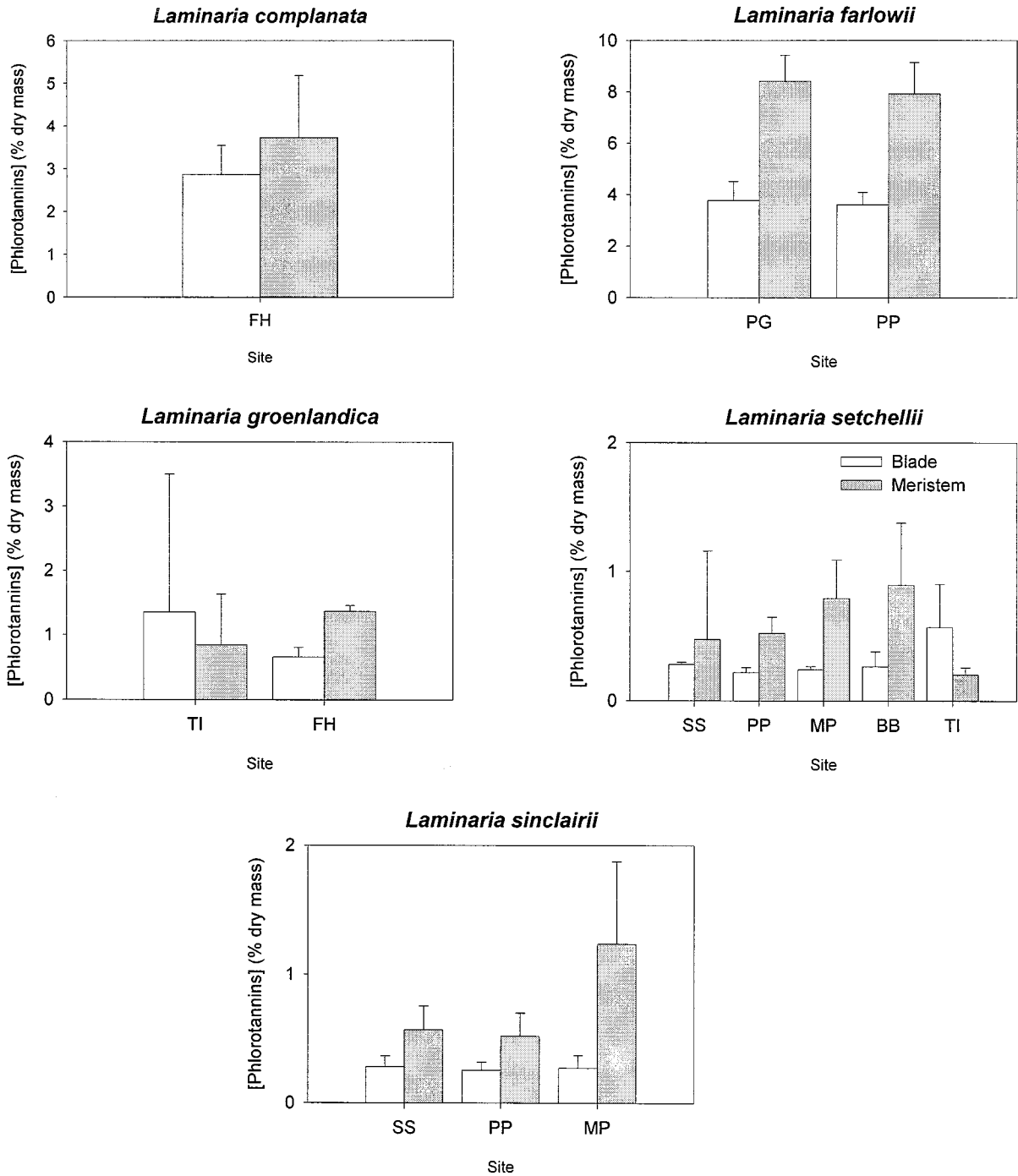
FIG. 3.   Order Laminariales, Family Laminariaceae, *Laminaria*. Phlorotannin concentrations (% dry mass ± 1 SD) of vegetative blades (white bars) and meristematic tissues (gray bars). *Laminaria complanta* (Setchell et Gardner) Setchell (one-way analysis of variance: tissue $F = 32.17$, $P < 0.001$; $N = 5$); *Laminaria farlowii* Setchell (two-way analysis of variance: tissue $F = 169.58$, $P < 0.001$; site $F = 0.35$, $P = 0.562$; interaction $F = 1.63$, $P = 0.220$; $N = 5$–6); *Laminaria groenlandica* Rosenvinge (two-way analysis of variance: tissue $F = 0.84$, $P = 0.374$; site $F = 0.35$, $P = 0.562$; interaction $F = 1.63$, $P = 0.220$; $N = 4$–5); *Laminaria setchellii* (two-way analysis of variance: tissue $F = 16.42$, $P < 0.001$; site $F = 1.21$, $P = 0.324$; interaction $F = 4.53$, $P = 0.004$; $N = 5$–6); and *Laminaria sinclairii* (two-way analysis of variance: tissue $F = 40.78$, $P < 0.001$; site $F = 3.39$, $P = 0.049$; interaction $F = 7.27$, $P = 0.003$; $N = 3$–6). Site abbreviations as in Figure 1.

There was a significant tissue by site interaction effect in *F. gardneri* (Fig. 5). Phlorotannin levels differed among tissues at Boiler Bay (one-way ANOVA, $F = 6.72$, $P = 0.012$), Tatoosh Island (one-way AN-OVA, $F = 48.12$, $P < 0.001$), and Cattle Point (one-way ANOVA, $F = 10.93$, $P = 0.002$), but not at Pigeon Point (one-way ANOVA, $F = 2.93$, $P = 0.105$). Phlorotannin levels in meristems were significantly
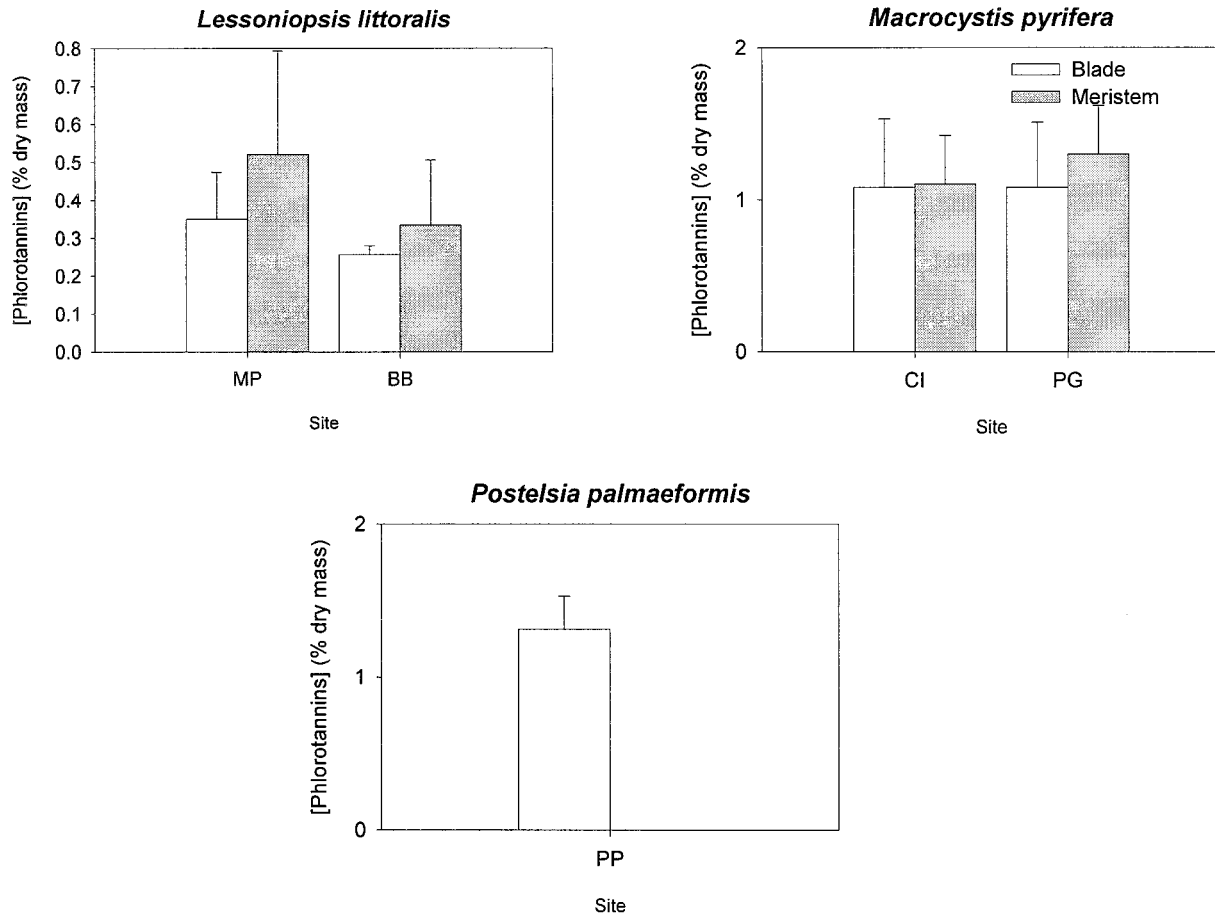
FIG. 4. Order Laminariales, Family Lessoniaceae. Phlorotannin concentrations (% dry mass ± 1 SD) of vegetative blades (white bars) and meristematic tissues (gray bars). *Lessoniopsis littoralis* (Tilden) Reinke (two-way analysis of variance: tissue $F = 3.26$, $P = 0.090$; site $F = 3.06$, $P = 0.099$; interaction $F = 0.37$, $P = 0.553$; $N = 4–5$); *Macrocystis pyrifera* (two-way analysis of variance: tissue $F = 1.10$, $P = 0.309$; site $F = 2.02$, $P = 0.172$; interaction $F = 0.60$, $P = 0.449$; $N = 5–6$); and *Postelsia palmaeformis* Ruprecht ($N = 5–6$). Site abbreviations as in Figure 1.

higher than in vegetative blades at Tatoosh Island (Tukey's test, $P < 0.001$). Levels in reproductive tissues were significantly lower than in vegetative blades at Cattle Point (Tukey's test, $P = 0.008$). Phlorotannin levels in meristems were significantly higher than in reproductive tissues at Boiler Bay (Tukey's test, $P = 0.018$), Tatoosh Island (Tukey's test, $P < 0.001$), and Cattle Point (Tukey's test, $P = 0.003$).

### DISCUSSION

The phlorotannin allocation patterns exhibited by northeastern Pacific kelps and rockweeds support the ODT model in some cases and the GDBH in others. The relative differences in meristem and nonmeristematic vegetative tissue phlorotannin concentrations followed patterns that would be predicted by the ODT in both the Fucales and Laminariales. Meristems, actively growing tissues that presumably have a high fitness value, had higher phlorotannin concentrations than nonmeristematic tissues. These data are consistent with trends reported for

kelps from South Africa (Tugwell and Branch 1989), *Zonaria angustata* from Australia (Poore 1994), and tropical *Halimeda* spp. (Hay et al. 1988, Paul and Van Alstyne 1988). The brown alga *Dictyota ciliolata* is the only seaweed in which defense levels were higher in nonmeristematic than meristematic tissues (Cronin and Hay 1996). Cronin and Hay (1996) attribute differences between *Dictyota* and other seaweeds to *Dictyota*'s lack of vascular tissue. Kelps and rockweeds contain primitive vascular systems that may be able to transport defensive compounds within the thallus; siphonous green algae, such as *Halimeda*, have the potential to transport materials via their siphons. Both *Dictyota* and *Zonaria* lack transport systems; yet, *Dictyota* has higher levels of terpenes in nonmeristematic tissues (Cronin and Hay 1994) and *Zonaria* has higher numbers of phlorotannin-containing physodes in the meristems (Poore 1996). This suggests that differences in allocation patterns between *Dictyota* and other seaweeds are not solely due to the presence or absence of a transport system.
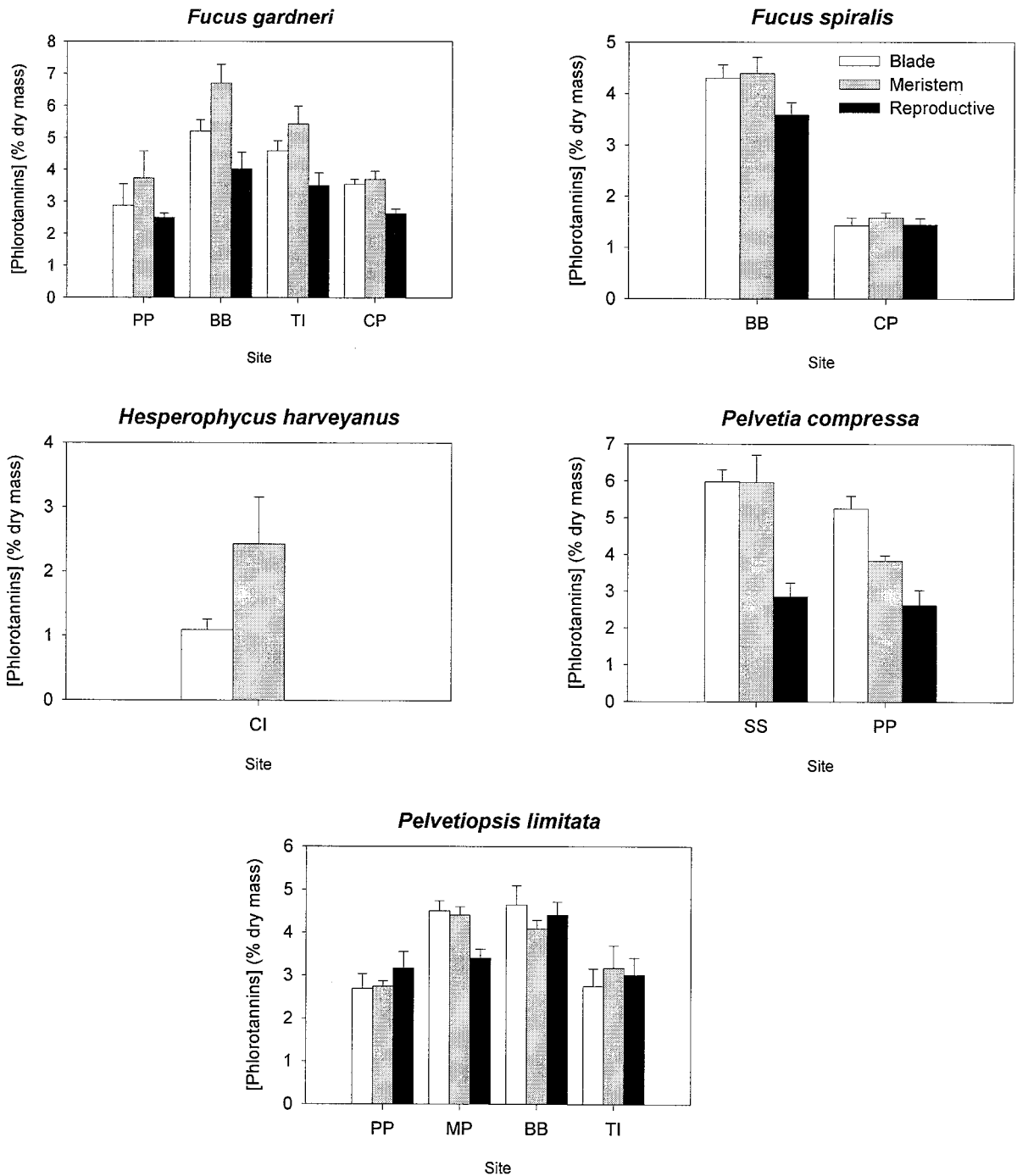
FIG. 5. Order Fucales. Phlorotannin concentrations (% dry mass $\pm$ 1 SD) of vegetative blades (white bars), meristematic tissues (gray bars), and vegetative and reproductive tissues (black bars). *Fucus gardneri* (two-way analysis of variance: tissue $F = 4.93$, $P = 0.012$; site $F = 4.98$, $P = 0.005$; interaction $F = 3.45$, $P = 0.007$; $N = 4$–5); *Fucus spiralis* Linnaeus (two-way analysis of variance: tissue $F = 2.46$, $P = 0.107$; site $F = 268.82$, $P < 0.001$; interaction $F = 1.33$, $P = 0.284$; $N = 5$); *Hesperophycus harveyanus* (one-way analysis of variance: tissue $F = 6.03$, $P = 0.091$; $N = 5$); *Pelvetia compressa* (two-way analysis of variance: tissue $F = 4.33$, $P = 0.026$; site $F = 0.08$, $P = 0.775$; interaction $F = 0.685$, $P = 0.515$; $N = 5$); and *Pelvetiopsis limitata* Gardner (two-way analysis of variance: tissue $F = 0.72$, $P = 0.491$; site $F = 15.61$, $P < 0.001$; interaction $F = 1.25$, $P = 0.300$; $N = 5$). Site abbreviations as in Figure 1.

The trends presented by comparisons of phloro-tannin allocation to reproductive versus nonmeriste-matic vegetative tissues are less clear. Reproductive tissues of the kelp *Alaria marginata* at some locations contain higher phlorotannin concentrations than vegetative tissues, supporting ODT. Reproductive tissues of the rockweeds *Pelvetia compressa* and *Fucus gardneri* at some locations contain lower phlorotannin concentrations than vegetative tissues, supporting the GDBH. These data suggest that allocation

strategies differ between the orders Fucales and Laminariales, although a larger number of species would need to be examined to unequivocally determine this.

The lack of strong support for either the ODT or GDBH may reflect several assumptions made in formulating these models. The models assume (1) phlorotannins function primarily as antiherbivore defenses, (2) reproductive and meristematic tissues have a high fitness value, and (3) phlorotannin concentrations at a single point in time are indicative of long-term allocation patterns.

Phlorotannins have been hypothesized to have functions other than antiherbivore defense. They have been shown to increase in response to UV light (Pavia et al. 1997), chelate metal ions (Ragan and Glombitza 1986), and decrease growth rates of phytoplankton and fouling organisms (Craigie and McLachlan 1964, McLachlan and Craigie 1964, 1966, Conover and Sieburth 1966, Sieburth and Conover 1966, but see Jennings and Steinberg 1997 and Steinberg et al. 1997). Phlorotannin levels did not differ between tissues in many species examined in the present study. Kelps lacking among-tissue differences were species in which phlorotannin concentrations were usually below 2% DM. At these low levels, phlorotannins may not be functioning as defenses. Phlorotannins have been shown to deter feeding by herbivores at 2% DM and higher, and increasing concentrations from 2% to 5%–6% resulted in significant decreases in feeding rates (Geiselman and McConnell 1981, Steinberg 1988, Winter and Estes 1992); however, it is not known if phlorotannins are effective deterrents at concentrations less than 2% DM. If low concentrations of phlorotannins are ineffective at deterring grazing or if the primary function of phlorotannins is not herbivore deterrence, then allocation patterns would not be expected to follow predictions based on ODT or the GDBH.

Optimal defense theory predicts that tissues that are relatively more valuable to the plant or are more susceptible to grazing will have higher concentrations of defensive compounds (Rhoades 1979). In this study, it was assumed that meristems and reproductive tissues would have a higher value to the algae than nonreproductive tissues. Tissues other than those examined in this study may also have a high fitness value. For example, tissue loss following grazing may be more extensive than losses due directly to herbivores (Padilla 1993). Protection of tissues that prevent subsequent loss, such as stipes, holdfasts, and midribs, may be more beneficial to the long-term fitness of algae than allocating compounds to meristems and reproductive tissues. Stipes and holdfasts of kelps frequently, although not always, have higher concentrations of phlorotannins than blade tissues (Tugwell and Branch 1989, Hammerstrom et al. 1998, Van Alstyne et al., unpubl.); however, phlorotannin concentrations in midribs

are generally a half to a third of concentrations in adjacent blade tissues (Van Alstyne, unpubl.). Patterns of allocation would also be expected to differ from those described here if the primary function of phlorotannins is not herbivore deterrence or if the value of tissues is measured with respect to functions not considered here.

Phlorotannin concentrations in brown algal tissues are not static. They can change in response to environmental conditions such grazing pressure (Van Alstyne 1988, Peckol et al. 1996, Hammerstrom et al. 1998), nitrogen levels (Ilvessalo and Tuomi 1989, Yates and Peckol 1993, Arnold et al. 1995, Peckol et al. 1996), and salinity (Pedersen 1984). Phlorotannins may also be exuded from tissues, although exudation rates are thought to be relatively small in unstressed plants (Jennings and Steinberg 1997). Turnover rates of phlorotannins have been estimated at 120 days in *Lobophora variegata* and *Sargassum pteropleuron* to 260 days in *Fucus distichus* (Arnold and Targett 1998). It is not currently known if significant movement of phlorotannins occurs among tissues in brown algae over time.

Our results provided limited evidence of site-to-site differences in allocation strategies among tissues. Significant site by tissue interaction effects occurred only in *Hedophyllum sessile, Laminaria setchellii, L. sinclairii,* and *Fucus gardneri*. In most cases, the differences were in shifts of the ratios of compounds among tissues, but not in which tissues had the highest phlorotannin concentrations. For example, in *L. sinclairii,* meristems always had higher concentrations of phlorotannins than vegetative blades; however, at Mouda Point the ratios of meristem phlorotannin levels to blade phlorotannin levels were much higher than they were at San Simeon or Pigeon Point (Fig. 2). Only in a few cases (e.g. *L. setchellii* at Tatoosh Island or *H. sessile* at Cattle Point, Fig. 2) did we find more extreme differences in allocation patterns. This pattern and the fact that the most species showed no site-to-site differences in allocation patterns suggests allocation patterns are not strongly affected by environmental variation. Environmental conditions may affect the total amount of phlorotannins stored by the alga (Pederson 1984, Van Alstyne 1988, Ivassalo and Tuomi 1989, Yates and Peckol 1993, Peckol et al. 1996, Pavia et al. 1997, Hammerstrom et al. 1998, Van Alstyne et al. in press), but they appear to have little effect on which tissues will have the highest phlorotannin levels relative to other tissues.

Arnold, T. M., Tanner, C. E. & Hatch, W. I. 1995. Phenotypic variation in polyphenolic content of the tropical brown alga *Lobophora variegata* as a function of nitrogen availability. *Mar. Ecol. Prog. Ser.* 123:177–83.

Arnold, T. M. & Targett, N. M. 1998. Quantifying *in situ* rates of phlorotannin synthesis and polymerization in marine brown algae. *J. Chem. Ecol.* 24:577–95.

Bazazz, F. A. & Grace, J. 1997. *Plant Resource Allocation.* Academic Press, San Diego, 303 pp.

Boettcher, A. A. & N. M. Targett. 1993. Role of polyphenolic molecular size in reduction of assimilation efficiency of *Xiphister mucosus. Ecology* 74:891–903.

Boggs, C. L. 1997. Resource allocation in variable environments: comparing insects and plants. *In* Bazazz, F. A. & Grace, J. [Eds.] *Plant Resource Allocation.* Academic Press, San Diego, pp. 73–92.

Bold, H. C. & Wynne, M. J. 1985. *Introduction to the Algae.* Prentice-Hall, Englewood Cliffs, New Jersey, 720 pp.

Conover, J. T. & Sieburth, J. McN. 1966. Effects of tannins excreted from Phaeophyta on planktonic animal survival in tide pools. *Proc. Int. Seaweed Symp.* 5:99–100.

Craigie, J. S. & McLachlan, J. 1964. Excretion of colored ultraviolet-absorbing substances by marine algae. *Can. J. Bot.* 42:23–33.

Cronin, G. & Hay, M. E. 1996. Within-plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth–differentiation balance hypothesis. *Oecologia* 105:361–8.

Folin, O. & Ciocalteu, V. 1927. On tyrosine and tryptophane determinations in proteins. *J. Biol. Chem.* 73:627–50.

Geiselman, J. A. 1980. Ecology of chemical defenses of algae against the herbivorous snail, *Littorina littorea,* in the New England rocky intertidal community. Ph.D. dissertation, Massachusetts Institute of Technology/Woods Hole Oceanographic Institute, Cambridge/Woods Hole, 209 pp.

Geiselman, J. A. & McConnell, O. J. 1981. Polyphenols in brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defenses against the marine herbivorous snail, *Littorina littorea. J. Chem. Ecol.* 7:1115–33.

Hammerstrom, K., Dethier, M. N. & Duggins, D. O. 1998. Rapid phlorotannin induction and relaxation in five Washington kelps. *Mar. Ecol. Prog. Ser.* 165:293–305.

Hay, M. E., Paul, V. J., Lewis, S. M., Gustafson, K., Tucker, J. & Trindell, R. N. 1988. Can tropical seaweeds reduce herbivory by growing at night? Diel patterns of growth, nitrogen content, herbivory, and chemical versus morphological defenses. *Oecologia* 75:233–45.

Herms, D. A. & Mattson, W. J. 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67:283–335.

Ilvessalo, H. & Tuomi, J. 1989. Nutrient availability and accumulation of phenolic compounds in the brown alga *Fucus vesiculosus. Mar. Biol* 101:115–9.

Jennings, J. G. & Steinberg, P. D. 1997. Phlorotannins versus other factors affecting epiphyte abundance on the kelp *Ecklonia radiata. Oecologia* 109:461–73.

Johnson, C. R. & Mann, K. H. 1986. The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J. Exp. Mar. Biol. Ecol.* 97:231–67.

Karban, R. & Baldwin, I. T. 1997. *Induced Responses to Herbivory.* University of Chicago Press, Chicago, 319 pp.

McLachlan, J. & Craigie, J. S. 1964. Algal inhibition by yellow ultraviolet-absorbing substances from *Fucus vesiculosus. Can. J. Bot.* 42:460–1.

——— 1966. Antialgal activity of some simple phenols. *J. Phycol.* 2:133–5.

Padilla, D. K. 1993. Rip stop in marine algae: minimizing the consequences of herbivore damage. *Evol. Ecol.* 7:634–44.

Paul, V. J. & Van Alstyne, K. L. 1988. Chemical defense and chemical variation in some tropical Pacific species of *Halimeda* (Halimedaceae; Chlorophyta). *Coral Reefs* 6:263–9.

Pavia, H. & Aberg, P. 1996. Spatial variation in polyphenolic content of *Ascophyllum nodosum* (Fucales, Phaeophyta). *Hydrobiologia* 326/327:199–203.

Pavia, H., Cervin, G., Lindgren, A. & Aberg, P. 1997. Effects of UV-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophylum nodosum. Mar. Ecol. Prog. Ser.* 157:139–46.

Peckol, P., Krane, J. M. & Yates, J. L. 1996. Interactive effects of inducible defense and resource availability on phlorotannins in the North Atlantic brown alga *Fucus vesiculosus. Mar. Ecol. Prog. Ser.* 138:209–17.

Pedersen, A. 1984. Studies on phenol content and heavy metal uptake in fucoids. *Hydrobiologia* 116/117:498–504.

Pfister, C. A. 1992. Costs of reproduction in an intertidal kelp: patterns of allocation and life history consequences. *Ecology* 73:1586–96.

Poore, A. G. B. 1994. Selective herbivory by amphipods inhabiting the brown alga *Zonaria angustata. Mar. Ecol. Prog. Ser.* 107:113–23.

Ragan, M. A. & Glombitza, K. W. 1986. Phlorotanins, brown algal polyphenols. *In* Round, F. E. & Chapman, D. J. [Eds.] *Progress in Phycological Research,* vol. 4. Biopress, Bristol, pp. 129–241.

Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. *In* Rosenthal, G. A. & Janzen, D. H. [Eds.] *Herbivores: Their Interaction with Secondary Plant Metabolites.* Academic Press, New York, pp. 1–55.

Sieburth, J. McN. & Conover, J. T. 1966. *Sargassum* tannin, an antibiotic which retards fouling. *Nature* 208:52–3.

Steinberg, P. D. 1984. Algal chemical defenses against herbivores: allocation of phenolic compounds in the kelp *Alaria marginata. Science* 223:405–7.

——— 1985. Feeding preferences of *Tegula funebralis* and chemical defenses of marine brown algae. *Ecol. Monogr.* 55:333–49.

——— 1986. Chemical defenses and the susceptibility of tropical brown algae to herbivores. *Oecologia* 69:628–30.

——— 1988. The effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *J. Exp. Mar. Biol. Ecol.* 120:221–37.

——— 1989. Biogeographical variation in brown algal polyphenolics and other secondary metabolites: comparison between temperate Australasia and North America. *Oecologia* 78:374–83.

——— 1992. Geographical variation in the interaction between marine herbivores and brown algal secondary metabolites. *In* Paul, V. J. [Ed.] *Ecological Roles of Marine Natural Products.* Cornell University Press, Ithaca, pp. 51–92.

Steinberg, P. D., deNys, R. & Kjelleberg, S. 1997. Chemical inhibition of epibiota by Australian seaweeds. *Biofouling* 10:1–18.

Steinberg, P. D., Estes, J. A. & Winter, F. C. 1995. Evolutionary consequences of food chain length in kelp forest communities. *Proc. Natl. Acad. Sci. USA* 92:8145–8.

Steinberg, P. D. & van Altena, I. 1992. Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australia. *Ecol. Monogr.* 62:189–222.

Targett, N. M. & Arnold, T. M. 1998. Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. *J. Phycol.* 34:195–205.

Targett, N. M., Cohen, L. D., Boettcher, A. A. & Tanner, C. E. 1992. Biogeographic comparisons of marine algal phenolics: evidence against a latitudinal trend. *Oecologia* 89:464–70.

Tugwell, S. & Branch, G. M. 1989. Differential polyphenolic distribution among tissues in the kelps *Ecklonia maxima, Laminaria pallida,* and *Macrocystis angustifolia* in relation to plant-defence theory. *J. Exp. Mar. Biol. Ecol.* 129:219–30.

Tuomi, J. 1992. Toward integration of plant defence theories. *Trends Ecol. Evol.* 7:365–7.

Tuomi, J., Niemela, P., Siren, S. & Jormalainen, V. 1989. Within-plant variation in phenolic content and toughness of the brown alga *Fucus vesiculosus. Bot. Mar.* 32:505–9.

Van Alstyne, K. L. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus. Ecology* 69: 655–63.
——— 1989. Adventitious branching as an herbivore induced defense in the intertidal brown alga *Fucus distichus. Mar. Ecol. Prog. Ser.* 56:169–76.
——— 1995. A comparison of three methods for quantifying brown algal polyphenolic compounds. *J. Chem. Ecol.* 21:45–58.
Van Alstyne, K. L., McCarthy, J. J. III, Hustead, C. L. & Duggins, D. O. Geographic variation in polyphenolic levels of northeastern Pacific kelps and rockweeds. *Mar. Biol.* (in press).

Van Alstyne, K. L. & Paul, V. J. 1990. The biogeography of polyphenolic compounds in marine macroalgae: temperate brown algal defenses deter feeding by tropical herbivorous fishes. *Oecologia* 84:158–63.
Winter, F. C. & Estes, J. A. 1992. Experimental evidence for the effects of polyphenolic compounds from *Dictyoneurum californicum* Ruprecht (Phaeophyta: Laminariales) on feeding rate and growth in the red abalone *Haliotus rufescens* Swainson. *J. Exp. Mar. Biol. Ecol.* 155:263–77.
Yates, J. L. & Peckol, P. 1993. Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus. Ecology* 74:1757–66.