LATITUDINAL DIFFERENCES IN PLANT PALATABILITY IN ATLANTIC COAST SALT MARSHES

STEVEN C. PENNINGS,[1,3] ERIN L. SISKA,[1,4] AND MARK D. BERTNESS[2]

[1]*University of Georgia Marine Institute, Sapelo Island, Georgia 31327 USA*
[2]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA*

Abstract. A central hypothesis of biogeography is that consumer–prey interactions are more intense at lower latitudes, leading to increased defenses of prey. Because plants vary in many traits that might affect palatability to herbivores, however, studies of latitudinal variation in single plant traits such as secondary chemistry provide only circumstantial evidence to test this hypothesis. We directly compared the palatability of 10 salt marsh plants from seven northern (Rhode Island and Maine) and eight southern (Georgia and Florida) coastal salt marshes by flying fresh plant material back and forth and allowing 13 species of herbivores direct choices between northern and southern conspecific plants in laboratory assays. In 127 of 149 assays (85%), herbivores showed a significant or marginally significant preference for northern plants. In only one assay did herbivores prefer southern plants. These results occurred regardless of the geographic location of the assay, herbivore species, year, or season of plant collection, although there were hints that latitudinal differences became less pronounced for two plant species late in the growing season. Our results provide the most comprehensive evidence to date for a latitudinal gradient in plant palatability in any community. The proximate plant traits and the ultimate evolutionary factors responsible for this pattern remain to be determined.

Key words: biogeography; chemical defense; herbivory; latitudinal variation; plant defenses; plant–herbivore interactions; salt marsh.

INTRODUCTION

A fundamental paradigm of biogeography is that consumer–prey interactions vary across latitude, with predation and herbivory more intense, and prey defenses better developed, in the tropics than in the temperate zone (MacArthur 1972, Bakus 1974, 1981, Bakus and Green 1974, Green 1977, Vermeij 1978, Jeanne 1979, Bertness et al. 1981, Menge and Lubchenco 1981, Louda 1982, Fawcett 1984, Heck and Wilson 1987, Coley and Aide 1991, Stiven and Gardner 1992, Jablonski 1993, Swihart et al. 1994, Cronin et al. 1997). Despite considerable interest in biogeographic patterns in plant–herbivore interactions (Brower et al. 1972, Gaines and Lubchenco 1982, Krischik and Denno 1983, Hay and Fenical 1988, Horn 1989, Duffy and Hay 1990, Coley and Aide 1991, Steinberg 1992, Steinberg et al. 1995, Coley and Barone 1996, Hay 1996), however, the evidence to date for latitudinal gradients in plant palatability is largely circumstantial or laden with caveats.

Because of the severe logistic constraints inherent in working across large spatial scales, most latitudinal studies have understandably been forced into indirect measurements of plant palatability or compromises of

design. Few studies directly compare the palatability of fresh plants (but see Steinberg et al. 1991, Swihart et al. 1994), instead working with freeze-dried plants or plant extracts, or measuring plant traits that might correlate with palatability (e.g., Levin 1976, Rodriguez 1977, Coley and Aide 1991, Bolser and Hay 1996). Some studies have worked with herbivores from only one geographic region (e.g., Van Alstyne and Paul 1990, Steinberg et al. 1991), raising the concern that herbivores might display preferences based on familiarity rather than on palatability (but see Bolser and Hay 1996, Cronin et al. 1997). Moreover, some studies have utilized only one site in each geographic region (e.g., Cronin et al. 1997), raising the concern that variation within a region might be as large as that observed between regions (Coley and Aide 1991, Bolser and Hay 1996). Finally, because many plant species are not widely distributed, many latitudinal studies compare distantly related plants (e.g., Van Alstyne and Paul 1990, Coley and Aide 1991), raising the concern that phylogenetic constraints unrelated to plant–herbivore interactions might influence the comparisons.

Despite these caveats, most of the limited number of studies available to date are consistent with the general hypothesis that tropical plants are better defended than temperate ones (Hay and Fenical 1988, Coley and Aide 1991, Bolser and Hay 1996). Brown algae and boreal trees, however, show no or the opposite trend (Van Alstyne and Paul 1990, Steinberg 1992, Targett et al. 1992, 1995, Swihart et al. 1994), and several
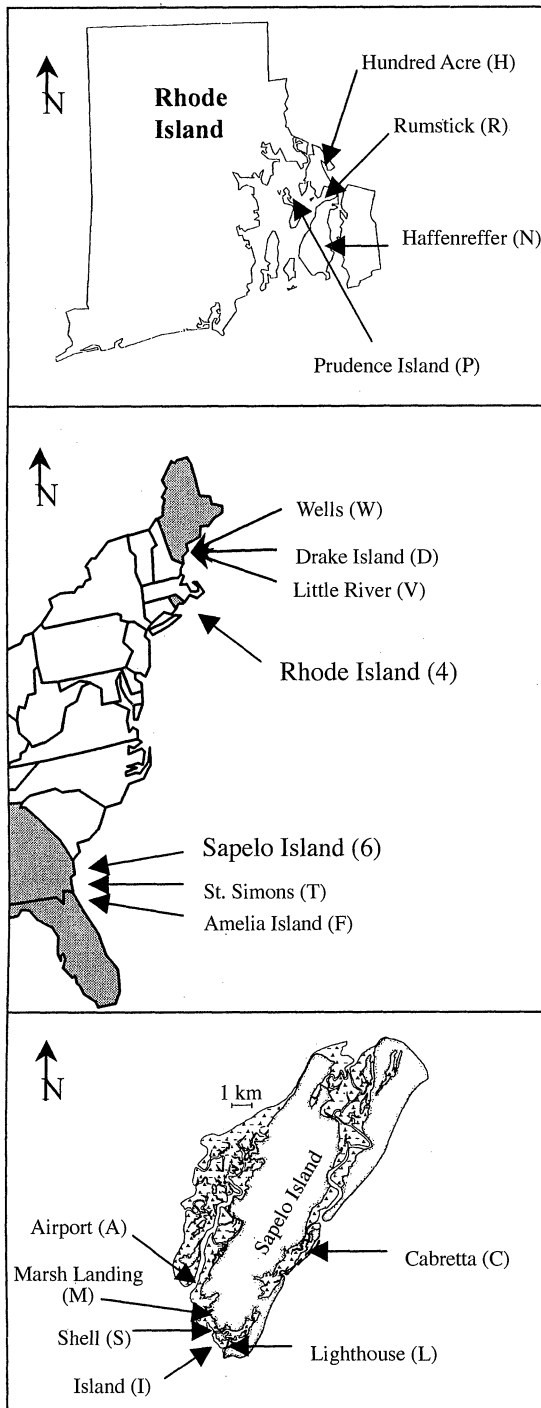
FIG. 1. Map of plant collection sites. Letters in parentheses are used in subsequent figures to indicate collection sites for plants used in each feeding assay.

Coley and Barone 1996). Given the design concerns and sometimes contrary results of the few existing studies, unambiguous data are needed to test the hypothesis that latitudinal trends in plant palatability exist.

Salt marshes along the Atlantic coast of the United States offer an attractive system for examining latitudinal variation in plant palatability. Salt marshes are the dominant intertidal habitat along the East Coast of the United States. The plant community of coastal salt marshes is composed of relatively few species (Chapman 1974), making it logistically possible to study virtually the entire plant community. In addition, most of the individual marsh plant species occur across a wide latitudinal range (Duncan and Duncan 1987, Pennings and Bertness 1999), making it possible to make intraspecific comparisons across latitude. Salt marshes host a diverse assemblage of herbivores that at times can strongly reduce plant biomass and/or mediate plant distributions (Pennings and Bertness 2001).

Our goal was to provide a definitive study of latitudinal variation in plant palatability by working with fresh plants, comparing conspecifics from high- and low-latitude regions, studying the majority of the plant species in the community, using herbivores from both geographic regions, and incorporating replication of sites within each region. Our results document striking latitudinal differences in plant palatability within salt marshes along the East Coast of the United States.

METHODS

Plant collection sites

We collected plants from seven northern (Maine and Rhode Island) and eight southern (Georgia and Florida) sites (Fig. 1, Table 1). The Wells, Drake Island, and Little River sites are located in the Wells National Estuarine Research Reserve (NERR) in southern Maine.

TABLE 1. Collection sites, site abbreviations, and coordinates.

Site	State†	Latitude	Longitude
Northern sites			
Hundred Acre (H)	RI	41°45'	71°18'
Rumstick (R)	RI	41°45'	71°17'
Haffenreffer (N)	RI	41°40'	71°15'
Prudence Island (P)	RI	41°38'	71°20'
Drake Island (D)	ME	43°15'	69°50'
Little River (V)	ME	43°15'	69°50'
Wells (W)	ME	43°15'	69°50'
Southern sites			
Airport (A)	GA	31°25'	81°15'
Shell (S)	GA	31°25'	81°15'
Island (I)	GA	31°25'	81°15'
Lighthouse (L)	GA	31°25'	81°15'
Cabretta (C)	GA	31°25'	81°15'
Marsh Landing (M)	GA	31°25'	81°15'
St. Simons Island (T)	GA	31°15'	81°20'
Amelia Island (F)	FL	30°40'	81°30'

† RI = Rhode Island, ME = Maine, GA = Georgia, FL = Florida.

studies suggest important regional differences in plant palatability unrelated to latitude (Steinberg 1989, 1992, Coley and Aide 1991, Targett et al. 1992, 1995, Bryant et al. 1994, Steinberg et al. 1995, Bolser and Hay 1996,

TABLE 2. Plant species studied and typical habitats in which each occurs.

Species	Common name	Habitat
Asteraceae		
Aster tenuifolius	Saltmarsh aster	High marsh
Baccharis halimifolia	Silverling, groundsel tree	Marsh terrestrial border
Iva frutescens	Marsh-elder	Marsh terrestrial border
Solidago sempervirens	Seaside goldenrod	High marsh, marsh terrestrial border
Poaceae		
Distichlis spicata	Salt or spike grass	High marsh, disturbed or high-salinity areas
Spartina alterniflora	Smooth cordgrass	Low marsh dominant
Spartina patens	Marshhay, salthay	High marsh (north); marsh terrestrial border (south)
Chenopodiaceae		
Salicornia europaea	Glasswort, samphire	High marsh, disturbed or high-salinity areas
Salicornia virginica	Woody glasswort, pickleweed	High marsh, cobble beaches (north); high marsh, high-salinity areas (south)
Plumbaginaceae		
Limonium carolinianum	Sea lavender	High marsh

Notes: For the purposes of this table, the marsh is divided into three elevational zones: low marsh, high marsh, and marsh terrestrial border. Taxonomy is based on Radford et al. (1964).

The Prudence Island site is located in the Narragansett Bay NERR in Rhode Island (RI). The Rumstick site is a small embayment of Smith Cove in Barrington, RI. The Hundred Acre site is a public recreation area on Narragansett Bay near Barrington, RI. The Haffenreffer site faces Mount Hope Bay from the Brown University research area within the Haffenreffer Anthropological Museum grounds in Bristol, RI. Marsh Landing, Airport, Shell, Lighthouse, and Island sites are located within the Sapelo Island NERR on Sapelo Island, Georgia (GA). The Cabretta site is located outside the NERR on Sapelo Island, GA. The St. Simons Island, GA, and Amelia Island, Florida, sites are marshes adjacent to causeways accessing these barrier islands.

Plants and herbivores

We worked with most marsh plant species common at both northern and southern sites (Table 2). These 10 species represented a majority of the species and >75% of the total marsh plant biomass in both geographic locations (S. C. Pennings, E. L. Siska, M. D. Bertness, *personal observation*). Thirteen species of common consumers, including crabs, beetles (both adults and larvae), grasshoppers, and moth larvae were collected for feeding trials (Table 3). Consumers ranged in feeding behavior from specialist herbivores (e.g., *Ophraella*) to moderately generalized herbivores (e.g., all the Orthoptera) to omnivores (e.g., *Armases*). We tried to collect all common herbivores present at each geographic region (excluding deer and leaf-mining, galling, and sapsucking insects due to logistic problems) with the goal of maximizing the number of species that would feed on each plant species. Herbivore species were easier to

find in the south than in the north, so more assays were ultimately conducted in GA than in RI.

Feeding trials

To ensure that our results did not vary depending on the geographic origin of the consumers, we conducted feeding trials in both Rhode Island (RI) and Georgia (GA), using local consumers. To ensure that results did not vary over the growing season, or between years, we ran feeding trials two or three times during the growing season for two years (June and September 1997; June, July and September 1998). We will refer to June trials as "early," July trials as "middle," and September trials as "late." To ensure that our results were not biased by collecting plants from any particular site, we collected different species of plants from a total of seven to eight sites within each geographic region. Each individual assay compared plants from one northern site vs. one southern site, but we often repeated trials with a given plant species by using different combinations of northern and southern collection sites.

Southern plant material was collected in the morning, and flown to Providence, RI, in a chilled cooler. Northern plants were simultaneously collected by an assistant and held in a similar cooler. In each case, plant material was collected from multiple plants spaced widely over each site. Experiments were set up ~12 h after plants were collected, using northern herbivores collected during the previous 72 h and held with ad lib food. Northern plants were subsequently flown to GA following the same protocol for feeding assays with southern herbivores.

TABLE 3. Herbivores used as consumers, herbivore abbreviations used in figures, location (North or South) in which assays with each herbivore were conducted, and plant species evaluated in palatability assays by each herbivore.

Species	Abbreviation	Location	Plants tested	References
Decapoda				
Armases cinereum (Grapsidae)	AC	S	All	Abele (1992), Niem (1996), Pennings et al. (1998)
Orthoptera				
Conocephalus sp., probably *spartinae* (Tettigoniidae)	CS	N	*Distichlis, Spartina alterniflora, S. patens*	Bertness et al. (1987), Bertness and Shumway (1992)
Orchelimum fidicinum (Tettigoniidae)	OF	S	*Distichlis, Spartina alterniflora, S. patens*	Smalley (1960)
Orphulella pelidna (Acrididae)	OP	S	*Distichlis, Spartina alterniflora, S. patens*	Blatchley (1920), Davis and Gray (1966), Otte (1981)
Paroxya claviliger (Acrididae)	PC	S	*Distichlis, Iva, Solidago*	Blatchley (1920), Helfer (1953), Davis and Gray (1966)
Melanoplus sp., probably *sanguinipes* (Acrididae)	MS	N	*Solidago*	
Coleoptera				
Erynephala maritima (Chrysomelidae) adults	EM	N	*Salicornia europaea, S. virginica*	Rand (1999)
Erynephala maritima (Chrysomelidae) larvae	EL	N	*Salicornia europaea, S. virginica*	
Microrophora vattata (Chrysomelidae)	MV	N	*Solidago*	
Ophraella notulata (Chrysomelidae) adults	ON	N, S	*Iva*	Futuyma (1990), Futuyma and McCafferty (1990), Futuyma et al. (1993), Funk et al. (1995)
Ophraella notulata (Chrysomelidae) larvae	OL	N	*Iva*	
Paria aterrima (Chrysomelidae)	PA	S	*Iva*	Wilcox (1957)
Trirhabda baccharidis (Chrysomelidae)	TB	S	*Baccharis*	Boldt (1989)
Lepidoptera				
Simyra henrici (Noctuidae)	SH	N	*Spartina alterniflora*	Rockburne and La-Fontaine (1976), Rings et al. (1992)
Spargonothis spp.	SP	S	*Salicornia europaea, S. virginica*	

Note: References point to selected papers on the taxonomy and/or ecology of each consumer.

Individual consumers were offered a choice between an undamaged leaf (or photosynthetic stem in the case of *Salicornia* spp.) from a northern plant and one from a conspecific southern plant. Each feeding trial began with up to 24 replicates, depending on the availability of consumers. Consumers were housed individually within appropriate chambers (crabs in 1000 mL glass jars with a water dish, grasshoppers in screen cages, beetles and moth larvae in petri dishes). Individual replicates were checked twice a day and were terminated when substantial feeding (~30%) on at least one leaf had occurred. Occasional replicates in which neither diet was eaten after a period of 72 h or in which both diets were completely consumed provided no information on relative palatability of northern vs. southern plants and were omitted.

In most assays, consumption was measured as square millimeters of leaf area consumed. This estimate of consumption would have been biased if leaves from different geographic regions differed in thickness or density. Casual observation suggested that such geographic differences in leaf mass/area existed for about half of the plant species studied, but that they were modest and inconsistent between species, with southern leaves more robust for some species (e.g., *Spartina alterniflora*), and northern leaves more robust for others (e.g., *Iva frutescens*). Given that differences in consumption were often large and were consistent between species, we did not attempt to correct for differences in leaf mass per area. In a few cases, however, consumption was measured as change in leaf biomass, and these assays produced results qualitatively similar to assays measuring leaf area consumed. For assays measuring biomass consumed, an equal number of additional replicates were run without consumers to estimate mass change in the absence of herbivory; and

mass changes in the presence of herbivores were adjusted by the minor mass changes of paired no-herbivore controls. Differences in consumption were compared between geographic locations using paired t tests, or, when assumptions of normality were not met, with Wilcoxon signed-ranks tests.

RESULTS

Overall, 127 of 149 trials (85%) resulted in a significant (120 trials) or marginally significant (seven trials with $P \leq 0.06$) preference for northern over southern plants. Only one trial resulted in a significant preference for southern plants. Results did not vary depending on whether assays were conducted using northern or southern herbivores (83% vs. 86% significant or marginally significant, $P = 0.79$, Fisher's exact test). Overall, there was a larger proportion of significant or marginally significant tests early vs. late in the season (93% vs. 80%, respectively, $P = 0.03$, Fisher's exact test); this pattern was largely driven by results with *Iva* and *Distichlis*, and was only significant for *Iva*. Given the weakness of this seasonal pattern, and the possibility of obtaining occasional spurious results when conducting large numbers of tests, we view this as an interesting trend requiring further examination rather than as a clearly established pattern. Results for specific plants and herbivores are expanded on below.

Aster tenuifolius.—Six of seven (86%) trials conducted in GA using the marsh crab *Armases cinereum* as the herbivore resulted in a significant preference for northern over southern plants (Fig. 2 top left). We were unable to collect a common northern herbivore that would readily eat *Aster*, so no reciprocal tests were performed.

Baccharis halimifolia.—Both feeding trials conducted in GA using the beetle *Trirhabda baccharidis* as the herbivore resulted in a significant preference for northern over southern plants (Fig. 2 top right). We were unable to collect a common northern herbivore that would readily eat *Baccharis*.

Limonium carolinianum.—Five of nine (56%) trials conducted in GA using the marsh crab *Armases cinereum* as the herbivore resulted in a significant preference for northern over southern plants (Fig. 2 bottom). Two additional trials were marginally significant ($P \leq 0.06$). We were unable to collect a common northern herbivore that would readily eat *Limonium*.

Iva frutescens.—Eight of 12 (67%) trials conducted in RI (using larvae and adults of the beetle *Ophraella notulata* as herbivores) resulted in a significant preference for northern over southern plants (Fig. 3 top). The three nonsignificant and the one contrary (significant preference for southern plants) results all occurred late in the growing season, and only in assays with adult beetles. All 15 trials conducted in GA (using four different herbivores) resulted in a significant preference for northern over southern plants (Fig. 3 bottom). Combining RI and GA trials, 15 of 15 trials conducted early in the growing season indicated a preference for northern plants, vs. only 8 of 12 (67%) trials conducted late ($P = 0.03$, Fisher's exact test).

Solidago sempervirens.—Seven of nine (78%) trials conducted in RI (using two different herbivores) resulted in a significant preference for northern over southern plants (Fig. 4 top). One additional trial was marginally significant ($P = 0.06$). Four of eight (50%) trials conducted in GA (using two different herbivores) resulted in a significant preference for northern over southern plants (Fig. 4 bottom).

Distichlis spicata.—One of two (50%) trials conducted in RI using the grasshopper *Conocephalus* sp. as the herbivore resulted in a significant preference for northern over southern plants (Fig. 5 top). Eleven of 19 (58%) trials conducted in GA (using three different herbivores) resulted in a significant preference for northern over southern plants (Fig. 5 bottom). Two additional trials were marginally significant ($P = 0.06$). Combining RI and GA assays, nine of 10 (90%) trials conducted early in the growing season indicated a preference for northern plants, vs. only four of eight (50%) trials conducted late (middle-of-season trials dropped, $P = 0.12$, Fisher's exact test).

Spartina alterniflora.—All four trials conducted in RI (using two different herbivores) resulted in a significant preference for northern over southern plants (Fig. 6 top). Fifteen of 17 (88%) trials conducted in GA (using three different herbivores) resulted in a significant preference for northern over southern plants (Fig. 6 bottom). One additional trial was marginally significant ($P = 0.06$).

Spartina patens.—Both trials conducted in RI using the grasshopper *Conocephalus* sp. as the herbivore resulted in a significant preference for northern over southern plants (Fig. 7 top). Thirteen of 15 (87%) trials conducted in GA (using three different herbivores) resulted in a significant preference for northern over southern plants (Fig. 7 bottom). One additional trial was marginally significant ($P = 0.06$).

Salicornia europaea.—All six trials conducted in RI (using adults and larvae of the beetle *Erynephala maritima*) resulted in a significant preference for northern over southern plants (Fig. 8 top). Eleven of 12 (92%) trials conducted in GA (using two different herbivores) resulted in a significant preference for northern over southern plants (Fig. 8 bottom).

Salicornia virginica.—The one trial conducted in RI and eight of nine (89%) trials conducted in GA (using one northern and two southern herbivores, respectively) resulted in a significant preference for northern over southern plants (Fig. 9).

DISCUSSION

Our results document a striking pattern for northeastern salt marsh plants to be more palatable than southeastern conspecifics. This pattern held true across virtually the entire plant and herbivore community, be-

Aster
tenuifolius
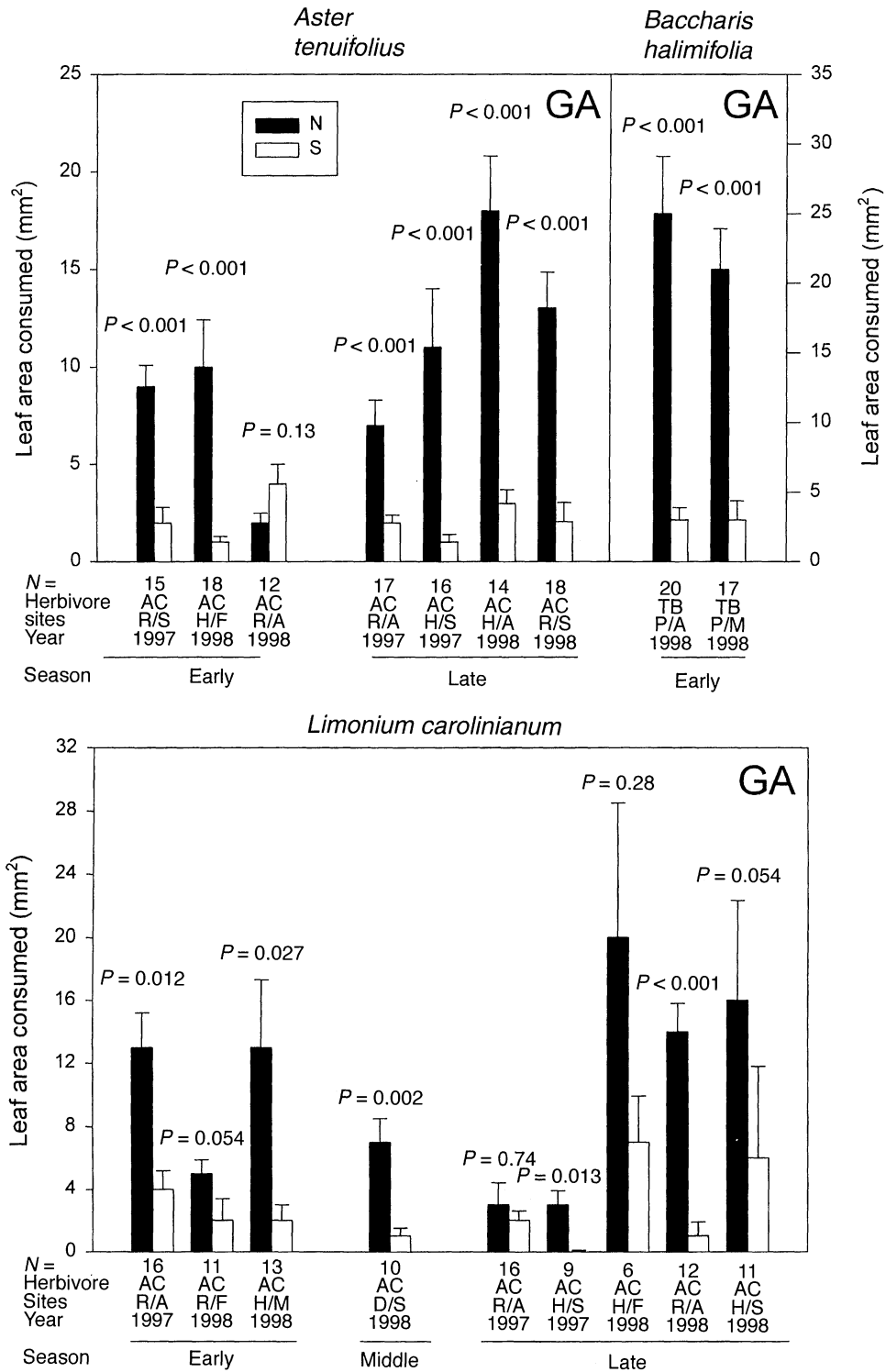
Baccharis
halimifolia

Limonium carolinianum

FIG. 2.   For *Aster tenuifolius*, *Baccharis halimifolia*, and *Limonium carolinianum*, consumption of northern vs. southern leaves in paired feeding trials conducted in GA. Data are means ±1 SE; sample sizes, herbivore species, collection sites, and timing of trial are indicated below paired bars. See Fig. 1 and Table 3 for abbreviations.
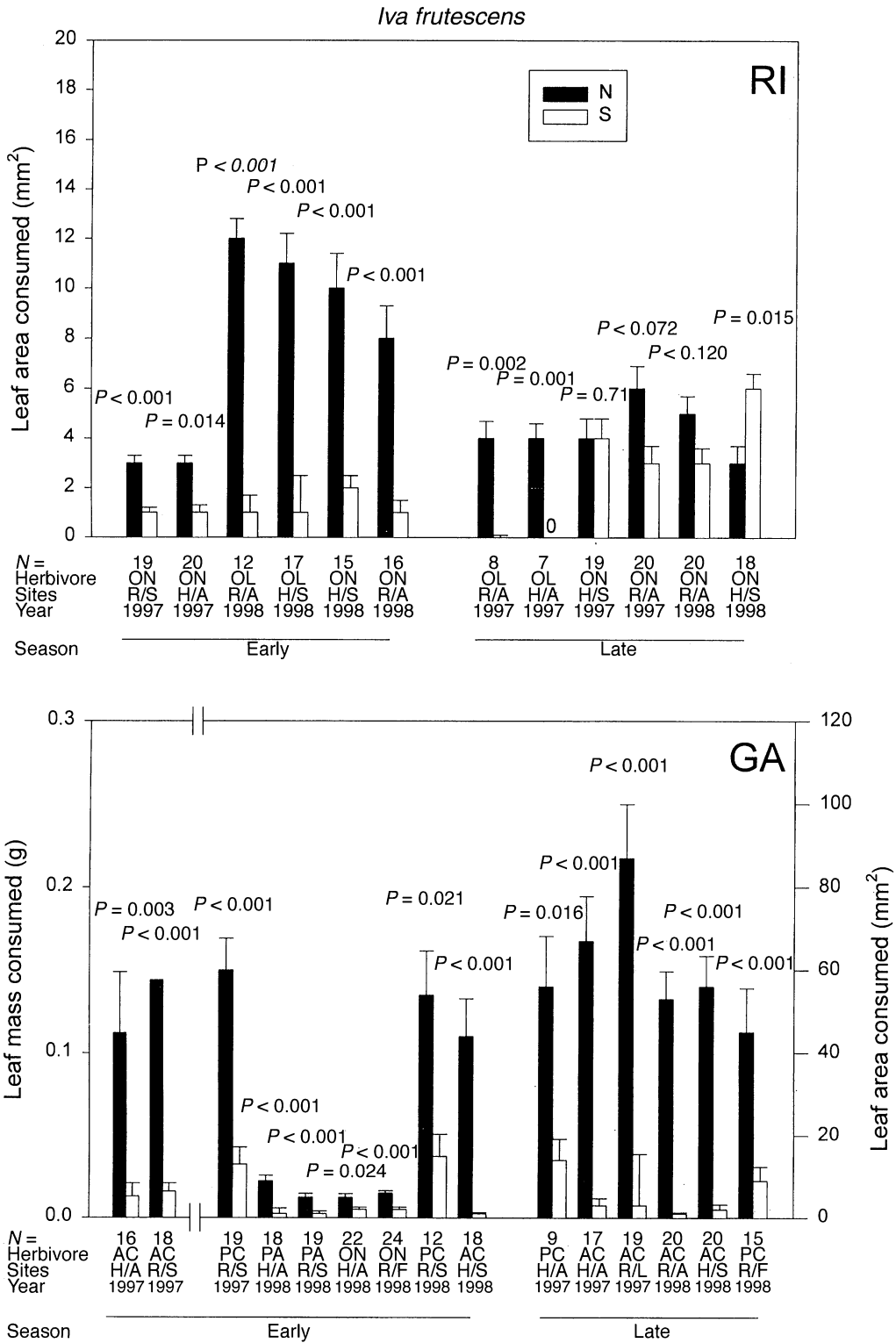
FIG. 3. For *Iva frutescens*, consumption of northern vs. southern leaves in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.
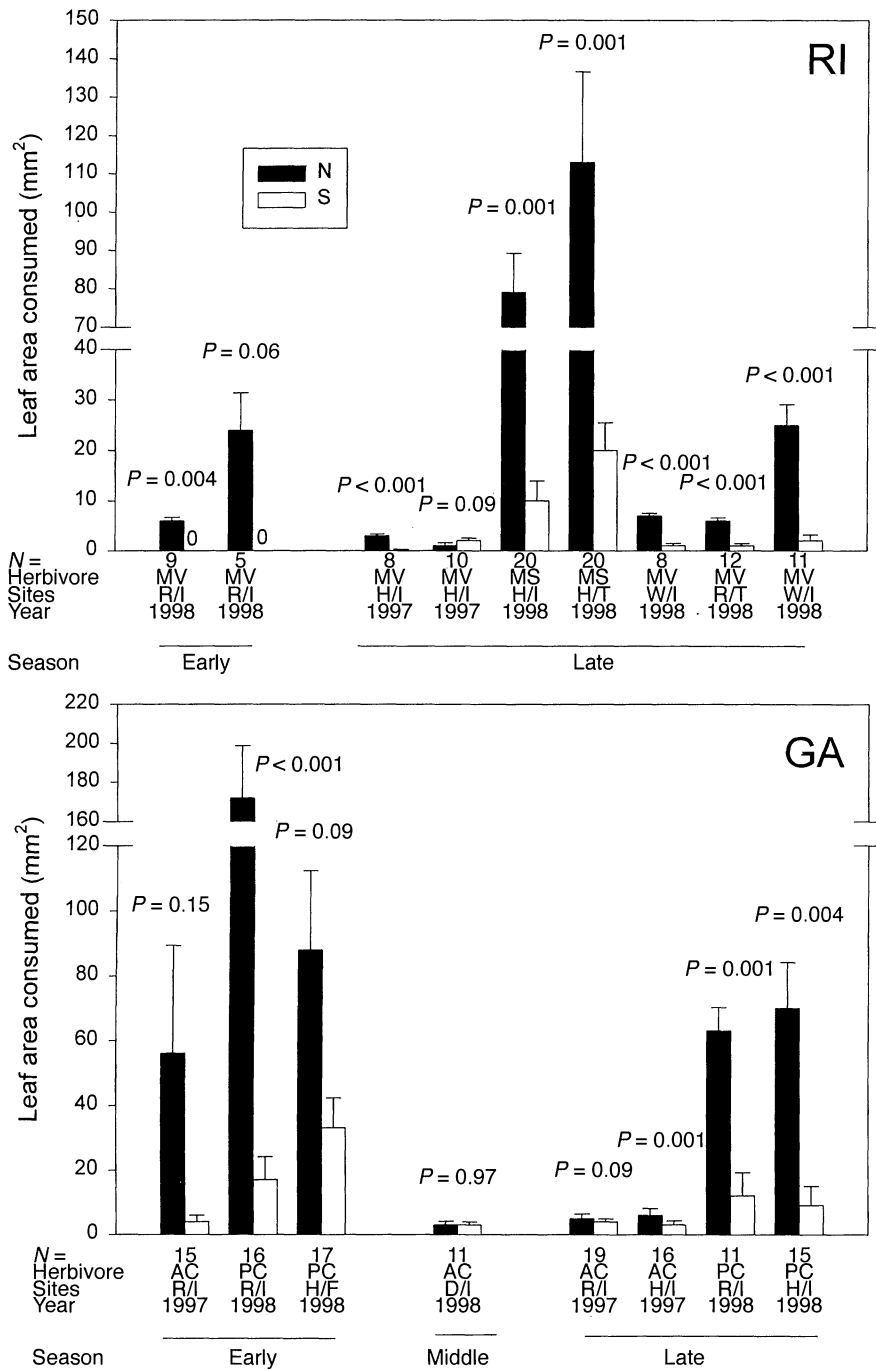
Solidago sempervirens

FIG. 4. For *Solidago sempervirens*, consumption of northern vs. southern leaves in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.

tween seasons and years, using both northern and southern herbivores. Overall, 127 out of 149 trials indicated a significant or marginally significant ($P \leq 0.06$) preference for northern plants. In most cases, preferences were very strong, with herbivores typically eating several times more of the northern plant than of the southern plant. In addition, most nonsignificant tests showed a trend toward preferring the northern plant, and only one trial indicated a significant preference for a southern plant. We believe that these results are the most comprehensive evidence to date for latitudinal patterns of plant palatability in any community.
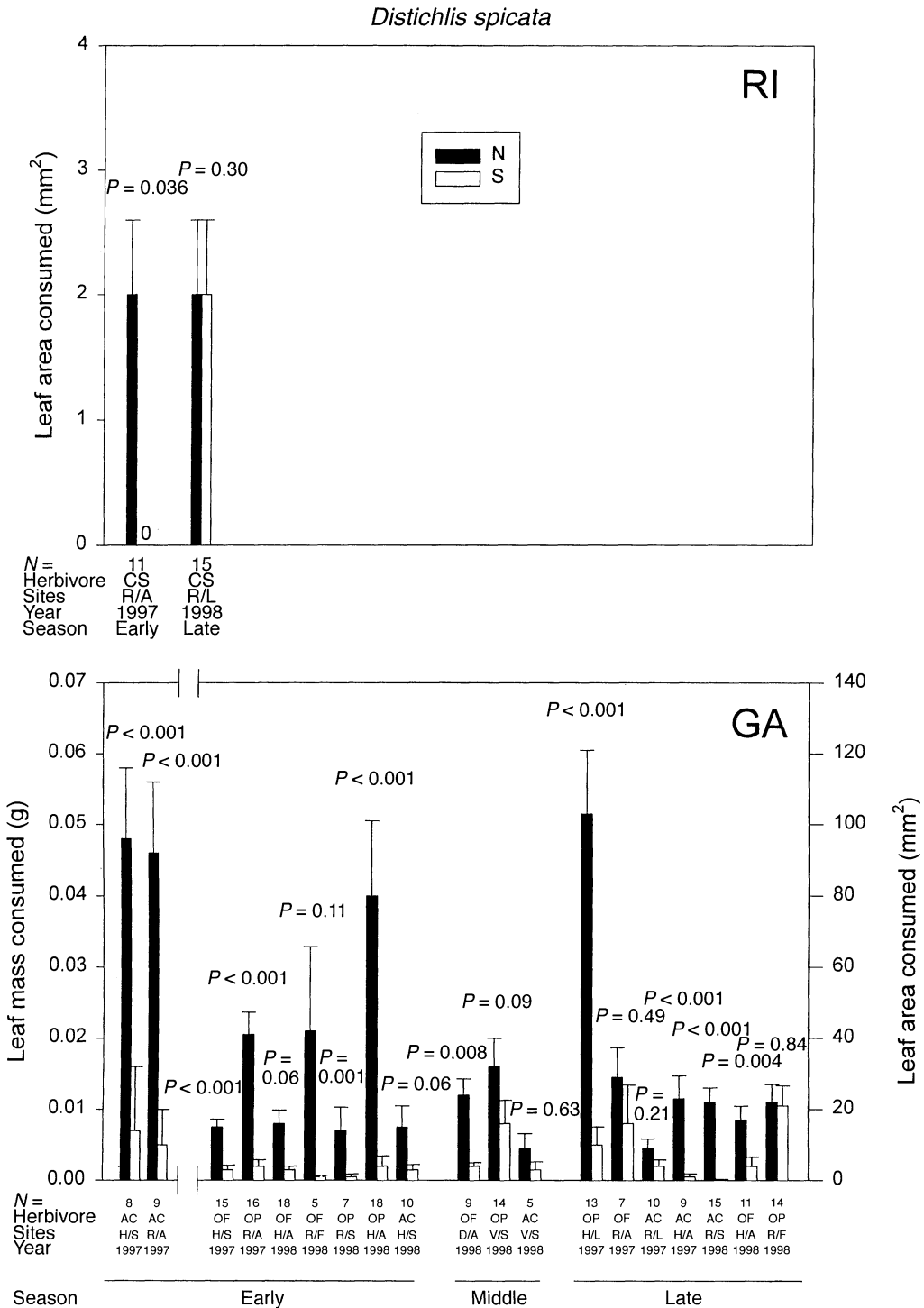
FIG. 5. For *Distichlis spicata*, consumption of northern vs. southern leaves in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.

Strength of our test

To ensure that our results were representative of the entire community rather than being based on only a few, perhaps idiosyncratic, species, we attempted to work with as many species of plants and herbivores as was feasible. We were very successful at achieving this goal with plants; we worked with all 10 species that occur in common in northeastern and southeastern coastal salt marshes, and these represent the majority of the species and biomass present at each site (S. C.
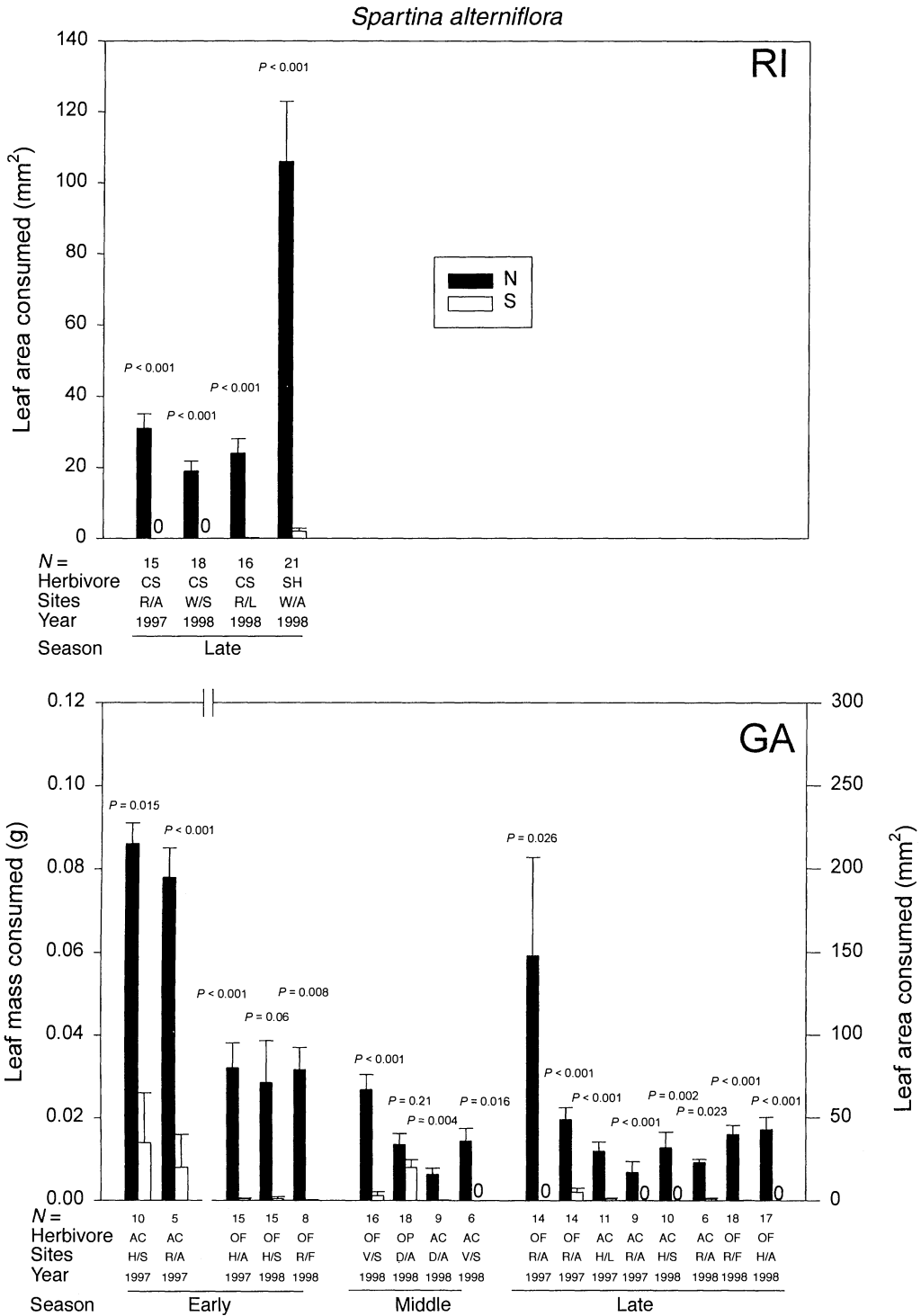
FIG. 6. For *Spartina alterniflora*, consumption of northern vs. southern leaves in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.

Pennings, E. L. Siska, M. D. Bertness, *personal observation*). In the case of the herbivores, we were forced to exclude deer and mining, galling, and sap-sucking insects as being logistically problematic, thus, our results strictly apply only to leaf-chewing invertebrates.

Nevertheless, we were able to work with 13 species of consumers from a variety of taxa and dietary strategies, ranging from specialists to generalists, and including both larval and adult forms of two species. These consumers represented all the leaf-chewing invertebrates
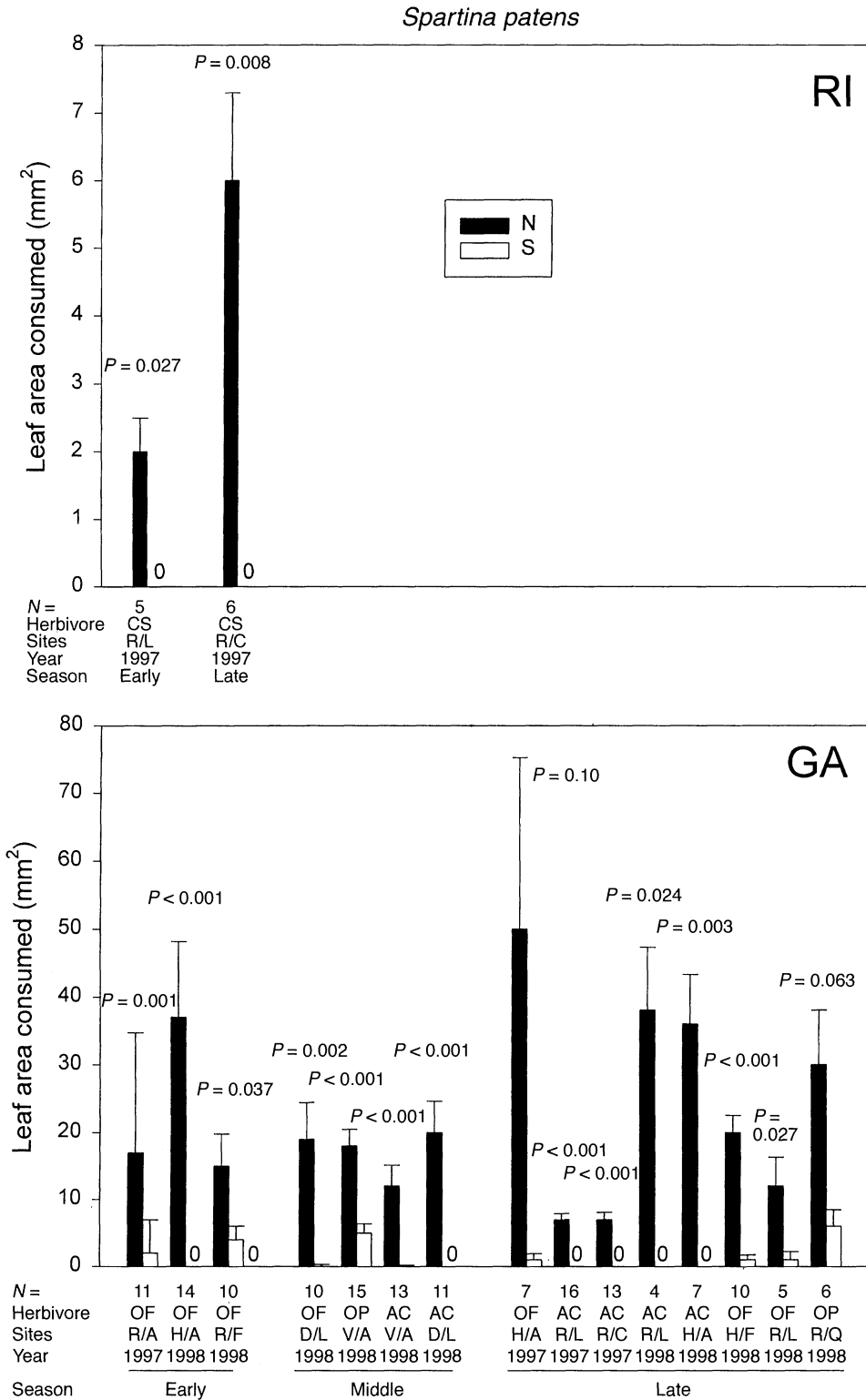
FIG. 7. For *Spartina patens*, consumption of northern vs. southern leaves in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.
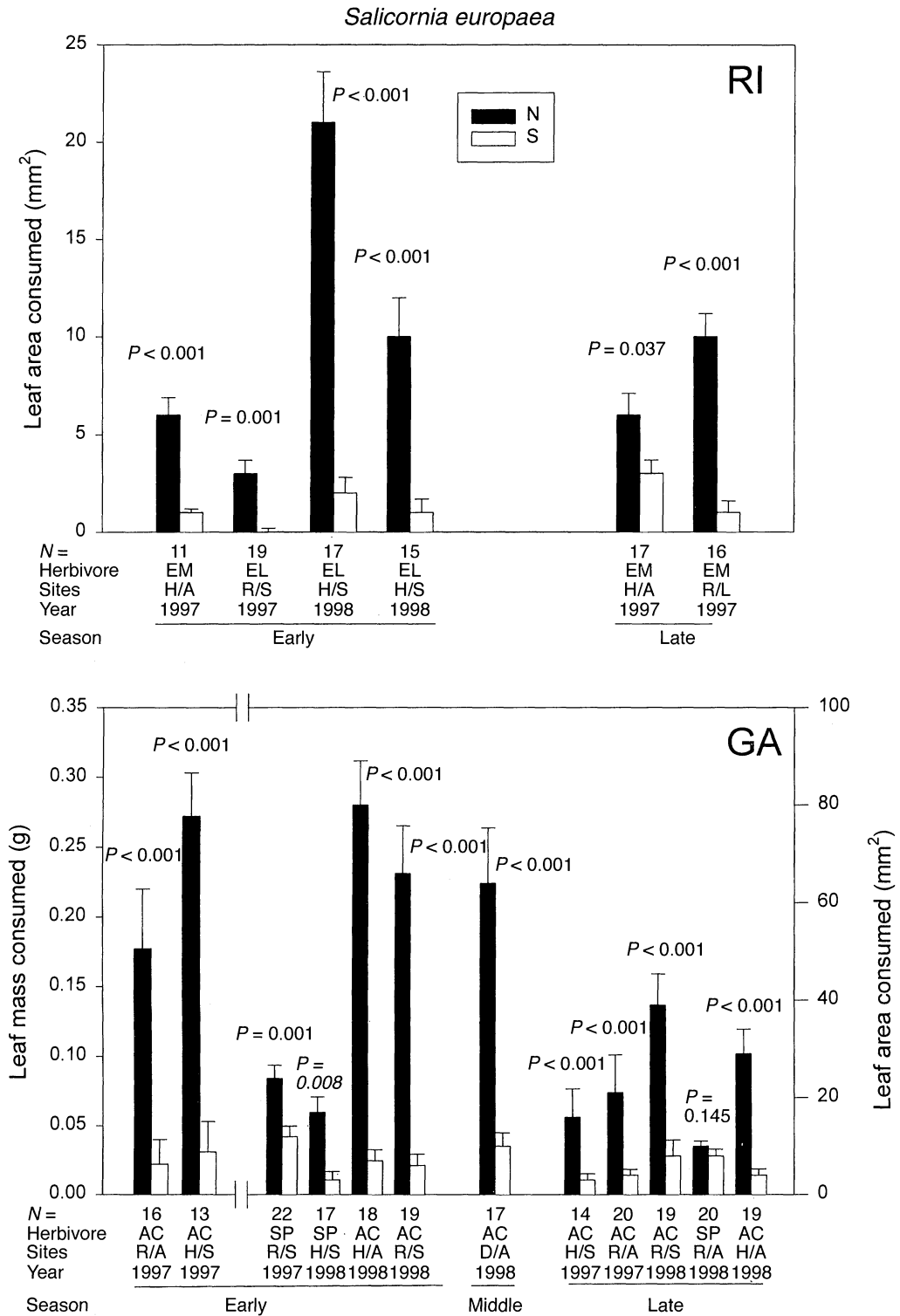
FIG. 8. For *Salicornia europaea*, consumption of northern vs. southern stems in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.
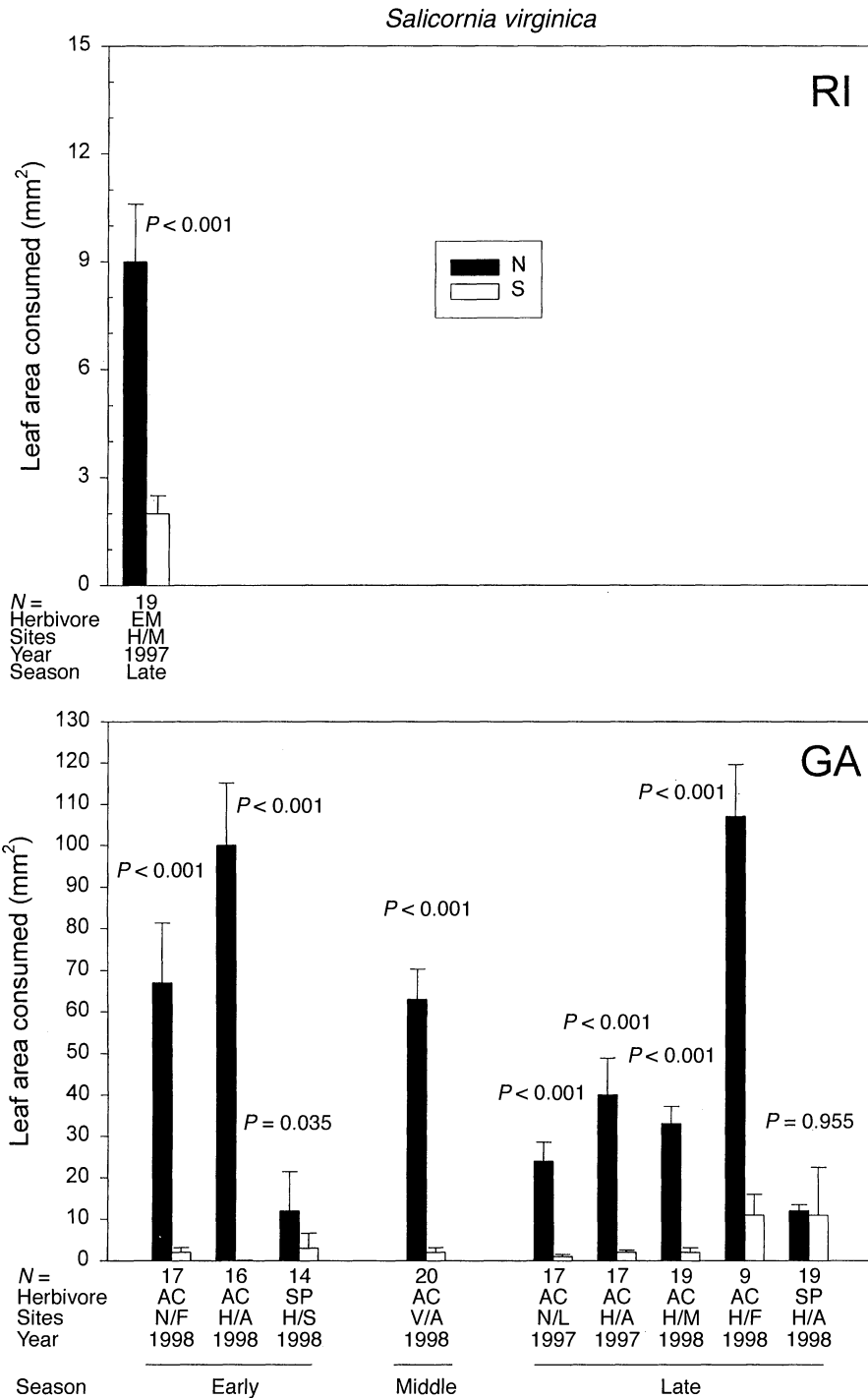
Salicornia virginica

FIG. 9. For *Salicornia virginica*, consumption of northern vs. southern stems in paired feeding trials conducted in RI (top) or GA (bottom). All other details are as in Fig. 2.

that were common at our study sites. Thus, we are confident that our results represent a community-wide pattern of leaf palatability to chewing herbivores. Whether similar results would hold with phloem-feeders such as aphids is less obvious.

Constraints of previous tests

Because of the severe logistic problems inherent in working across large distances, many studies of geographic variation in plant palatability have not directly

assessed the palatability of fresh plant material, but instead have worked with freeze-dried plants, plant extracts, or have measured plant traits that might correlate with palatability. This approach is potentially vulnerable to two criticisms. First, since plants are likely to vary in a wide number of factors that affect palatability, including toughness, nitrogen content, and the type and concentration of secondary metabolites, studies that measure a limited selection of plant traits may obtain an incomplete understanding of variation in palatability. For example, latitudinal patterns in alkaloid production (Levin 1976) may not predict latitudinal patterns in palatability since different alkaloid compounds may differ in palatability, and since plants that do not produce alkaloids may produce other types of unpalatable compounds, or may be unpalatable for other reasons (e.g., they might be tough or low in nutrients). Second, even if differences in plant traits are clearly demonstrated, it does not necessarily follow that these differences are large enough to affect feeding behavior of herbivores. For example, marine invertebrate herbivores from Australasia are tolerant of very high concentrations of algal phenolics and do not discriminate between seaweeds based on differences in phenolic content (Steinberg and van Altena 1992, Steinberg et al. 1995), and many marine herbivores do not appear to discriminate among plants based on nitrogen content (Horn 1989, Bolser and Hay 1996, Pennings et al. 1998). Using freeze-dried, ground plant tissues is probably the closest approximation to using living plants, but traits such as toughness, water content, and the presence of volatile primary and secondary metabolites are still likely to differ from fresh plant material (Bolser and Hay 1996). Using plant extracts represents a further approximation to fresh plant material (e.g., results with plant extracts explained only 60% of Bolser and Hay's [1996] results with freeze-dried plants).

Geographic studies that utilize consumers from only one geographic region (e.g., Van Alstyne and Paul 1990, Steinberg et al. 1991) are potentially vulnerable to the criticism that consumers might prefer or avoid foods based on novelty rather than on intrinsic palatability. This criticism is probably more of a concern when comparing distantly related plants, which are likely to differ qualitatively, than when comparing (as did Steinberg et al. 1991) congeners or conspecifics that are likely to primarily differ quantitatively (e.g., in the concentration rather than the types of secondary metabolites, or in leaf toughness rather than in the presence or absence of mineral defenses). Although high- and low-latitude herbivores may differ in sensitivity to particular chemical defenses (Cronin et al. 1997), the limited results available to date suggest that they display similar rank preferences for high- vs. low-latitude plants (Bolser and Hay 1996; see *Results* in this paper). Nevertheless, this equivalence should be tested, rather than assumed.

Proximate and ultimate causes of variation in plant palatability

Given our demonstration of latitudinal differences in plant palatability, we can raise two further lines of inquiry. First, which plant traits differ across latitude to generate differences in palatability? A variety of plant traits including toughness, nitrogen and mineral content, and secondary metabolites may affect palatability to consumers (Pennings and Paul 1992, Pennings et al. 1998), and any of these might differ across latitude. Geographic variation in these traits in salt marsh plants is a subject of ongoing study by our group. Preliminary results suggest that no single factor explains geographic variation in palatability for all the plant species. Rather, different traits appear to vary geographically in different plant species, and geographic variation in palatability may be explained by one or several traits in any given species (E. L. Siska, S. C. Pennings, M. D. Hanisak, *unpublished manuscript*).

Second, why do latitudinal differences in plant traits exist? A variety of factors including herbivore pressure, climate, shading, desiccation, and nutrient availability may affect plant traits that mediate palatability (Clausen et al. 1948, Coley et al. 1985, Bryant et al. 1989, Karban and Myers 1989, Renaud et al. 1990, Tuomi et al. 1991, Cronin and Hay 1996), and any of these might cause variation across latitude. Two lines of observational evidence suggest that herbivore pressure does vary across latitude in salt marshes on the Atlantic coast of the United States. First, we conducted more assays using southern than northern herbivores because we found it easier to collect herbivores for our assays at southern sites. In fact, for three plant species, we were able to collect suitable herbivores only at southern sites, and performed no assays using northern herbivores. To the extent that our ability to collect herbivores reflects herbivore abundance, this suggests greater herbivore pressure at southern sites. Second, qualitative observations suggest that herbivore damage is more severe at southern sites than at northern sites, particularly for the grasses *Distichlis spicata*, *Spartina alterniflora*, and *S. patens*, and the shrub *Baccharis halimifolia* (S. C. Pennings, E. L. Siska, M. D. Bertness, *personal observation*). On the other hand, the shrub *Iva frutescens* appears to suffer greater herbivore damage at our northern sites (S. C. Pennings, E. L. Siska, M. D. Bertness, *personal observation*). Because observations of herbivore damage confound geographic variation in potential herbivore pressure with geographic variation in plant palatability, experiments using plants of standardized palatability will be necessary to unambiguously demonstrate latitudinal variation in herbivore pressure. Such a demonstration, of course, would not preclude other factors also selecting for geographic variation in plant palatability.

LITERATURE CITED

Abele, L. G. 1992. A review of the Grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. Smithsonian Contributions to Zoology Number 527, 1–60.

Bakus, G. J. 1974. Toxicity in holothurians: a geographical pattern. Biotropica **6**:229–236.

Bakus, G. J. 1981. Chemical defense mechanism on the Great Barrier Reef, Australia. Science **211**:497–499.

Bakus, G. J., and G. Green. 1974. Toxicity in sponges and holothurians: a geographical perspective. Science **185**:951–953.

Bertness, M. D., S. D. Garrity, and S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical–temperate comparison. Evolution **35**:995–1007.

Bertness, M. D., and S. W. Shumway. 1992. Consumer driven pollen limitation of seed production in marsh grasses. American Journal of Botany **79**:288–293.

Bertness, M. D., C. Wise, and A. M. Ellison. 1987. Consumer pressure and seed set in a salt marsh perennial plant community. Oecologia **71**:190–200.

Blatchley, W. S. 1920. Orthoptera of Northeastern America. The Nature Publishing Company, Indianapolis, Indiana, USA.

Boldt, P. E. 1989. Biology and host specificity of *Trirhabda baccharidis* (Coleoptera: Chrysomelidae) on *Baccharis* (Asteraceae: Asteraea). Environmental Entomology **18**:78–84.

Bolser, R. C., and M. E. Hay. 1996. Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. Ecology **77**:2269–2286.

Brower, L. P., P. B. McEvoy, K. L. Williamson, and M. A. Flannery. 1972. Variation in cardiac glycoside content of monarch butterflies from natural populations in eastern North America. Science **177**:426–429.

Bryant, J. P., P. J. Kuropat, S. M. Cooper, K. Frisby, and N. Owen-Smith. 1989. Resource availability hypothesis of plant antiherbivore defense tested in a South African savanna ecosystem. Nature **340**:227–229.

Bryant, J. P., R. K. Swihart, P. B. Reichardt, and L. Newton. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. Oikos **70**:385–395.

Chapman, V. J. 1974. Salt marshes and salt deserts of the world. Interscience Press, New York, New York, USA.

Clausen, J., D. D. Keck, and W. M. Heisey. 1948. Experimental studies on the nature of species. I. Environmental responses of climatic races of *Achillea*. Carnegie Institution of Washington Publication, **581**.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 *in* P. W. Price, editor. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York, New York, USA.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics **27**:305–335.

Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science **230**: 895–899.

Cronin, G. V., and M. E. Hay. 1996. Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology **77**:1531–1543.

Cronin, G., V. J. Paul, M. E. Hay, and W. Fenical. 1997. Are tropical herbivores more resistant than temperate herbivores to seaweed chemical defenses? Diterpenoid metabolites from *Dictyota acutiloba* as feeding deterrents for tropical versus temperate fishes and urchins. Journal of Chemical Ecology **23**:289–302.

Davis, L. V., and I. E. Gray. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. Ecological Monographs **36**:275–295.

Duffy, J. E., and M. E. Hay. 1990. Seaweed adaptations to herbivory. Bioscience **40**:368–375.

Duncan, W. H., and M. B. Duncan. 1987. Seaside plants of the Gulf and Atlantic coasts. Smithsonian Institution Press, Washington, D.C., USA.

Fawcett, M. H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. Ecology **65**:1214–1230.

Funk, D. J., D. J. Futuyma, G. Orti, and A. Meyer. 1995. A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. Evolution **49**:1008–1017.

Futuyma, D. J. 1990. Observations on the taxonomy and natural history of *Ophraella* Wilcox (Coleoptera: Chrysomelidae), with a description of a new species. Journal of the New York Entomological Society **98**:163–186.

Futuyma, D. J., C. Herrmann, S. Milstein, and M. C. Keese. 1993. Apparent transgenerational effects of host plant in the leaf beetle *Ophraella notulata* (Coleoptera: Chrysomelidae). Oecologia **96**:365–372.

Futuyma, D. J., and S. S. McCafferty. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera, Chrysomelidae). Evolution **44**:1885–1905.

Gaines, S. D., and J. Lubchenco. 1982. A unified approach to marine plant–herbivore interactions. II. Biogeography. Annual Review of Ecology and Systematics **13**:111–138.

Green, G. 1977. Ecology of toxicity in marine sponges. Marine Biology **40**:207–215.

Hay, M. E. 1996. Marine chemical ecology: what's known and what's next? Journal of Experimental Marine Biology and Ecology **200**:103–134.

Hay, M. E., and W. Fenical. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. Annual Review of Ecology and Systematics **19**:111–145.

Heck, K. L., Jr., and K. A. Wilson. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. Journal of Experimental Marine Biology and Ecology **107**:87–100.

Helfer, J. R. 1953. The grasshoppers, cockroaches and their allies. Wm. C. Brown, Dubuque, Iowa, USA.

Horn, M. H. 1989. Biology of marine herbivorous fishes. Oceanography and Marine Biology an Annual Review **27**: 167–272.

Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. Nature **364**:142–144.

Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. Ecology **60**:1211–1224.

Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics 20:331–346.

Krischik, V. A., and R. F. Denno. 1983. Individual, population, and geographic patterns in plant defense. Pages 463–512 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Levin, D. A. 1976. Alkaloid-bearing plants: an ecographical perspective. American Naturalist 110:261–284.

Louda, S. M. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs 52:25–41.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York, New York, USA.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecological Monographs 51:429–450.

Niem, V. H. 1996. Phylogenetic relationships among American species of *Sesarma* (subgenus *Armases*) (Brachyura, Grapsidae). Crustaceana 69:332–348.

Otte, D. 1981. The North American grasshoppers. Volume I. Harvard University Press, Cambridge, Massachusetts, USA.

Pennings, S. C., and M. D. Bertness. 1999. Using latitudinal variation to examine effects of climate on coastal salt-marsh pattern and process. Current Topics in Wetland Biogeochemistry 3:100–111.

Pennings, S. C., and M. D. Bertness. 2001. Salt marsh communities. *In* M. D. Bertness and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

Pennings, S. C., T. H. Carefoot, E. L. Siska, M. E. Chase, and T. A. Page. 1998. Feeding preferences of a generalist salt marsh crab: relative importance of multiple plant traits. Ecology 79:1968–1979.

Pennings, S. C., and V. J. Paul. 1992. Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. Ecology 73:1606–1619.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1964. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, South Carolina, USA.

Rand, T. A. 1999. Effects of environmental context on the susceptibility of *Atriplex patula* to attack by herbivorous beetles. Oecologia 121:39–46.

Renaud, P. E., M. E. Hay, and T. M. Schmitt. 1990. Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. Oecologia 82:217–226.

Rings, R. W., E. H. Metzler, F. J. Arnold, and D. H. Harris. 1992. The owlet moths of Ohio. Order Lepidoptera family Noctuidae. Ohio Biological Survey Bulletin New Series Volume 9, Number 2. College of Biological Sciences, Ohio State University, Columbus, Ohio, USA.

Rockburne, E. W., and J. D. LaFontaine. 1976. The cutworm moths of Ontario and Quebec. Canada Department of Ag-

riculture, Publication 1593. Printing and Publishing Supply and Services Canada, Ontario, Ottawa, Canada.

Rodriguez, E. 1977. Ecogeographic distribution of secondary constituents in *Parthenium ciferae* (Compositae). Biochemical Systematics and Ecology 5:207–218.

Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. Ecology 41:785–790.

Steinberg, P. D. 1989. Biogeographical variation in brown algal polyphenolics and other secondary metabolites: comparison between temperate Australasia and North America. Oecologia 78:373–382.

Steinberg, P. D. 1992. Geographic variation in the interaction between marine herbivores and brown algal secondary metabolites. Pages 51–92 *in* V. J. Paul, editor. Ecological roles of marine natural products, Comstock Publishing Associates, Ithaca, New York, USA.

Steinberg, P. D., K. Edyvane, R. de Nys, R. Birdsey, and I. A. van Altena. 1991. Lack of avoidance of phenolic-rich brown algae by tropical herbivorous fishes. Marine Biology 109:335–343.

Steinberg, P. D., J. A. Estes, and F. C. Winter. 1995. Evolutionary consequences of food chain length in kelp forest communities. Proceedings of the National Academy of Sciences (USA) 92:8145–8148.

Steinberg, P. D., and I. van Altena. 1992. Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecological Monographs 62:189–222.

Stiven, A. E., and S. A. Gardner. 1992. Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality. Journal of Experimental Marine Biology and Ecology 160:81–102.

Swihart, R. K., J. P. Bryant, and L. Newton. 1994. Latitudinal patterns in consumption of woody plants by snowshoe hares in the eastern United States. Oikos 70:427–434.

Targett, N. M., A. E. Boettcher, T. E. Targett, and N. H. Vrolijk. 1995. Tropical marine herbivore assimilation of phenolic-rich plants. Oecologia 103:170–179.

Targett, N. M., L. D. Coen, A. A. Boettcher, and C. E. Tanner. 1992. Biogeographic comparisons of marine algal polyphenolics: evidence against a latitudinal trend. Oecologia 89:464–470.

Tuomi, J., F. Torbjörn, and P. Niemelä. 1991. Carbon allocation, phenotypic plasticity, and induced defenses. Pages 85–104 *in* D. W. Tallamy and M. J. Raupp, editors. Phytochemical induction by herbivores. John Wiley and Sons, New York, New York, USA.

Vermeij, G. J. 1978. Biogeography and adaptation. Harvard University Press, Cambridge, Massachusetts, USA.

Van Alstyne, K. L., and V. J. Paul. 1990. The biogeography of polyphenolic compounds in marine macroalgae: temperate brown algal defenses deter feeding by tropical herbivorous fishes. Oecologia 84:158–163.

Wilcox, J. A. 1957. A revision of the North America species of *Paria* Lec. (Coleoptera: Chrysomelidae). New York State Museum and Science Service Bulletin No. 365. Albany, New York, New York, USA.