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## LATITUDINAL VARIATION IN PALATABILITY OF SALT-MARSH PLANTS: WHICH TRAITS ARE RESPONSIBLE?

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**Abstract.** Biogeographic theory predicts that intense consumer–prey interactions at low latitudes should select for increased defenses of prey relative to high latitudes. In salt marshes on the Atlantic coast of the United States, a community-wide pattern exists in which 10 species of low-latitude plants are less palatable to a diverse suite of herbivores than are high-latitude conspecifics. Examination of proximate plant traits (toughness, palatability of polar and nonpolar extracts, nitrogen content) of high- and low-latitude conspecifics of nine plant species suggested that all these proximate traits had the potential to contribute to latitudinal differences in palatability of some plant species. Southern plants were tougher than northern plants (five species), had less palatable polar extracts (four species), and had lower N content (six species). Experimental evidence linking traits to latitudinal differences in palatability was strongest for polar extracts and lacking for N content. For one plant species, none of the traits we studied correlated with latitudinal variation in palatability. Because palatability differences may change when moving from fresh plants to freeze-dried plants to plant traits, studies of latitudinal variation in freeze-dried plants or plant traits are likely to under- or overestimate latitudinal variation in palatability of fresh plants. This study has begun to identify the proximate plant traits responsible for latitudinal variation in plant palatability in Atlantic coast salt marshes, but the ultimate evolutionary factors responsible for variation in these traits remain to be determined.

**Key words:** Atlantic coast (USA) salt-marsh plants; biogeographic theory; chemical defense; herbivory; latitude and plant variation; palatability, affected by multiple plant traits; palatability, plant variation across latitude; plant chemical defenses, latitudinal variation; plant–herbivore interactions.

### INTRODUCTION

Biogeographic theory predicts that increased consumer pressure at low latitudes should select for increased defenses of prey relative to high latitudes (MacArthur 1972, Bakus 1974, 1981, Bakus and Green 1974, Green 1977, Vermeij 1978, Jeanne 1979, Bertness et al. 1981, Gaines and Lubchenco 1982, Louda 1982, Fawcett 1984, Heck and Wilson 1987, Coley and Aide 1991, Stiven and Gardner 1992, Jablonski 1993, Cronin et al. 1997). Because of the logistical difficulties inherent in working across geographic distances, most studies of latitudinal variation in plant palatability have not directly compared the palatability of high- and low-latitude plants (but see Steinberg et al. 1991, Swihart et al. 1994, Pennings et al. 2001). Instead, most studies have examined variation in plant traits such as tough-

ness, nutritional content, or the diversity, identity and concentration of secondary metabolites (e.g., Levin 1976, Rodriguez 1977, Coley and Aide 1991), or have worked with processed (lyophilized and pulverized) plant material (e.g., Bolser and Hay 1996). These approaches have created three caveats in our current understanding of latitudinal variation in plant palatability.

First, variation in a particular trait (say, phenolic content) does not necessarily imply variation in palatability, because herbivores may not be sensitive to variation in a particular plant trait (Steinberg and van Altena 1992, Steinberg et al. 1995). Moreover, since many traits combine to produce “palatability,” variation in one trait (say, phenolics) might be counteracted by opposite trends in another (say, toughness) with the result that no overall difference in palatability exists. Although this concern can be partially allayed by measuring as many plant traits as possible (e.g., Coley and Aide 1991, Coley and Barone 1996), it is logistically difficult to measure every single trait that might matter to herbivores, and hard to know how to integrate multiple trait measures into a single index of palatability.

Second, although the majority of studies to date have been consistent with the hypothesis that plant defenses increase at low latitudes (Hay and Fenical 1988, Coley and Aide 1991, Bolser and Hay 1996), a significant

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fraction of studies have found no, or the opposite, trend (Van Alstyne and Paul 1990, Steinberg 1992, Targett et al. 1992, Bryant et al. 1994, Swihart et al. 1994). Reconciling these divergent results is difficult because few studies have integrated direct measures of plant palatability with studies of plant traits that might affect palatability.

Third, many geographic studies have compared unrelated groups of plants, raising the possibility that phylogeny, rather than latitude, is the primary driver of palatability (or traits). This concern can be avoided by comparing congeners within multiple genera (Bolser and Hay 1996) or making intraspecific comparisons (Bolser and Hay 1996, Pennings et al. 2001).

Salt marshes offer an attractive system for examining latitudinal variation in plant palatability using approaches that avoid the above caveats. Salt marshes are a dominant intertidal habitat along the Atlantic coast of the United States (Pennings and Bertness 2001). The plant community of coastal salt marshes is comprised of relatively few species (Chapman 1974), making it logistically possible to study virtually the entire community. In addition, most of the 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.

We studied latitudinal variation in plant palatability in salt marshes on the Atlantic coast of the United States, working with the majority of the plant and herbivore species present in the community, comparing plants from New England with conspecifics from the South Atlantic Bight. We combined direct measures of plant palatability with measurements and experimental studies of plant traits in order to determine which traits might be responsible for observed variation in palatability. Results of palatability trials with fresh plants were published previously (Pennings et al. 2001), and demonstrated strong preferences for northern vs. southern individuals of all 10 plant species studied, regardless of season of plant collection or geographic origin of herbivore used. Here, we assess the relative importance of plant toughness, chemical defenses, and N content in producing this striking geographic pattern. Our experiments parallel those used by Bolser and Hay (1996) to study latitudinal variation in the palatability of seaweeds, and we draw comparisons between the results of the two studies in the discussion.

## METHODS

### Study sites

To ensure that working at any one site did not bias the results, we collected plants from four northern (Rhode Island, USA) and six southern (Georgia, USA) sites. The northern sites, located near 41°40' N latitude, were Hundred Acre, Rumstick, Haffenreffer, and Long Neck Cove, coded H, R, F, and N, respectively, in the figures. The southern sites, located near 31°25' N lat-

itude, were Airport, Shell, Island, Lighthouse, Marsh Landing, and Cabretta, coded A, S, I, L, M, and, C, respectively, in the figures. Long Neck is a protected cove of the Sakonnet River, near Common Fence Point, Rhode Island. All other sites are described in Pennings et al. (2001).

### Plants and herbivores

We worked with most plant species common at both northern and southern sites: *Aster tenuifolius*; *Iva frutescens* and *Solidago sempervirens* (Asteraceae); *Distichlis spicata*, *Spartina alterniflora*, and *Spartina patens* (Poaceae); *Salicornia europaea* and *Salicornia virginica* (Chenopodiaceae); and *Limonium carolinianum* (Plumbaginaceae). These nine species represented the majority of the species and >75% of the total plant biomass in both geographic locations (authors personal observation), and included 9 of the 10 species studied by Pennings et al. (2001). Feeding trials were conducted using three grasshopper and one crab species, selected because they were common at Sapelo Island, Georgia, and adapted well to laboratory conditions. The majority of the trials were conducted with the crab *Armases cinereum* (Grapsidae), coded Ac in the figures, because it was highly omnivorous and thus facilitated comparisons by allowing us to examine all the plants using a single consumer. A small number of additional trials were conducted with the grasshoppers *Orchelimum fidecinum* (Tettigoniidae), *Orphulella pelidna* (Acrididae), and *Paroxya clavuliger* (Acrididae), coded Of, Op and Pc respectively in the figures, to confirm that results from crab trials were typical of other consumers. In previous work, both northern and southern consumers preferred northern vs. southern plants, and results from crab trials were similar to results from 12 other consumers (Pennings et al. 2001). See Pennings et al. (2001) for additional information on the plants and consumers.

To ensure that our results did not vary over the growing season, we collected plants twice in each of two years (June and early September of 1997 and of 1998) for toughness, nutrient, and phenolic analyses. Feeding trials were conducted using plants collected in 1997. We will refer to June and September as "early" and "late" seasons, respectively.

### Toughness measurements

To compare the toughness of northern and southern plants, we measured toughness using two different techniques. These techniques, the penetrometer test and the ripping test, mimic different modes of herbivory, give similar rankings among plant species, and are described in Pennings et al. (1998). Briefly, the penetrometer test measures the force needed to penetrate a leaf with a thin rod, and the ripping test measures the force needed to rip a pin through a vertically oriented leaf. We did not use the ripping test with *D. spicata*

and *S. patens* because the force required to rip these plants was below the detection limit of the apparatus.

For each test, 10–20 individual leaves of each plant species were collected from each of two sites, returned on ice to the laboratory, and measured within 4 h. Values for individual leaves were averaged to yield a single value per species per site per season. Latitudinal differences in toughness were examined using a three-way ANOVA, with sites as replicates and latitude, season and year as main effects. Data for *Salicornia virginica* were analyzed with a two-way ANOVA because no plants of this species were collected early in 1997. Data were log transformed when appropriate to satisfy assumptions of ANOVA.

#### *Reconstituted-plant feeding trials*

To determine if variation in toughness influenced variation in palatability, we offered consumers a choice between reconstituted-plants from each geographic region. We reasoned that breaking down the physical structure of plants and reconstituting them into artificial diets would allow a comparison of plant chemical composition in the absence of differences in toughness. Thus, if consumers no longer discriminated between northern and southern plants in reconstituted form, it would suggest that toughness played a role in differences in palatability of fresh plants. This conclusion, however, would come with the caveat that chemical changes might have occurred during the processing of the plant material (see *Discussion*, below). Alternatively, if consumers still preferred reconstituted northern plants over southern conspecifics, it would suggest that differences in plant chemistry were responsible for differences in palatability.

Plants were frozen, lyophilized, and ground to a powder using a Wiley mill (mesh size = 40  $\mu\text{m}$ ). Plant powder from a northern site was reconstituted (0.2 g/mL) into a 4% agar diet and poured into one of two rectangular templates resting on mesh screen (mesh size = 1 mm<sup>2</sup>). Conspecific plant powder from a southern site was similarly reconstituted and poured into the second rectangular template. After the agar solidified, strips of mesh screen containing paired diets were presented to consumers in a two-choice feeding trial.

Consumers were housed within replicate glass jars containing water and the two conspecific diets. Replicates ( $n = 20$ ) were checked twice daily and terminated when substantial consumption of at least one diet occurred. Replicates in which neither diet was eaten after 72 h, or in which both diets were completely consumed between observations, provided no information on the relative palatability of northern vs. southern diets, and were omitted from the analysis. Consumption was measured as the area of each diet consumed (in square millimeters). Differences in consumption were compared between geographic locations using paired  $t$  tests, or, when assumptions of normality

or equal variance were not met, with Wilcoxon signed-rank tests.

#### *Chemical extract feeding trials*

To directly determine if differences in plant chemistry contributed to latitudinal variation in palatability, we compared the palatability of northern and southern plant extracts. Two solvent mixtures were used in the extractions in order to obtain compounds with a wide range of polarity. Plants were collected and frozen. Approximately 1 kg of plant material from each site in each season was macerated and extracted twice in 2:1 dichloromethane : methanol, followed by three extractions in 70:30 methanol : water. Each extraction used 300 mL of combined solvents. The solvent mixtures from the five extractions were combined and partitioned in a separatory funnel into one polar (methanol : water) and one nonpolar (dichloromethane) extract. The extracts were reduced to dryness using rotary evaporation and lyophilization.

Polar and nonpolar extracts were tested separately. Extracts from northern and southern plants were incorporated at natural concentrations (mass per volume) into a 4% agar diet, and presented to herbivores in two-choice feeding trials; trials were conducted and data analyzed as described above (see *Reconstituted-plant feeding trials*). Because we lacked detailed information on how various aspects of nutritional quality varied among plant species and geographic regions, we chose to incorporate the extracts into an agar diet that lacked additional nutritional constituents. The agar + extract diets were readily eaten by the consumers; however, results should be interpreted with caution because consumers may be more sensitive to secondary metabolites in diets with low nutritional quality (Duffy and Paul 1992, Hay et al. 1994).

#### *Nitrogen and phenolic concentrations*

Because geographic differences in plant N content might mediate palatability, we measured total N content of northern and southern plants. Plants were collected, lyophilized, and pulverized using an amalgamator. CHN analysis was performed at the University of Georgia Chemical Analysis laboratory using a Perkin-Elmer 240C elemental analyzer (Perkin-Elmer, Wellesley, Massachusetts, USA). Nitrogen content (proportion of dry mass) was arcsine (square-root) transformed and compared for each species with a three-way ANOVA (latitude  $\times$  season  $\times$  year). Individual plants ( $n = 4$ ) were nested within sites ( $n = 2$  plants per region per season per year), which were the unit of replication.

For most of the plant species that we studied, bioassay-guided fractionation experiments have not been performed to identify the secondary metabolite(s) that mediate palatability. In the case of *Spartina alterniflora*, however, there is evidence that the primary secondary metabolites are simple phenolics such as ferulic and coumeric acid (Valiela et al. 1979, Buchsbaum et

al. 1984, Rietsma et al. 1988, Newell and Porter 2000). We measured total phenolic content of *S. alterniflora* leaves using a standard Folin-Dennis reaction (Julkunen-Tiitto 1985, Zimmer 1997). Leaves were frozen after collection, lyophilized, and pulverized. Fifty milligrams (dry mass) of leaf material was extracted in 80% methyl alcohol 3 h, agitating extracts every 30 min. Fifty microliters of extract supernatant were reacted with 750  $\mu$ L deionized H<sub>2</sub>O, 200  $\mu$ L Folin-Ciocalteu reagent, and 1000  $\mu$ L 20% Na<sub>2</sub>CO<sub>3</sub>. The absorbance at 700 nm was measured on a spectrophotometer 20 minutes after addition of Na<sub>2</sub>CO<sub>3</sub>. Concentrations were calculated based on a standard curve using pure ferulic acid (Sigma Chemical Company, Saint Louis, Missouri, USA). Because Folin-Dennis measurements have a wide variety of limitations (Appel et al. 2001), results should be interpreted with caution.

## RESULTS

### Toughness measurements

Five plant species were tougher in the south than in the north, based on at least one of the two toughness measurements (Fig. 1). In no case did the data suggest that northern plants were consistently tougher than southern conspecifics.

**Penetrometer test.**—Most of the species tested, with the exception of *Aster tenuifolius* and *Solidago sempervirens*, varied in this measure of toughness as a function of latitude, season, or year; however, interactions between main effects often complicated unambiguous identification of latitudinal patterns (Table 1). Nevertheless, inspection of the data (Fig. 1) revealed that southern *Spartina alterniflora*, *S. patens*, *Limonium carolinianum*, and *Salicornia virginica* were tougher than northern conspecifics on more than half of the dates. Latitudinal variation in toughness of *Spartina patens* was particularly striking, varying as much as three-fold between southern and northern plants.

**Ripping test.**—Three of the plants tested, *A. tenuifolius*, *S. alterniflora* and *Salicornia virginica*, varied in this measure of toughness as a function of latitude. In the case of *A. tenuifolius* the magnitude of this difference varied between years (Table 1); however, southern plants had higher toughness measurements than northern plants on each date (Fig. 1). Latitudinal variation in toughness of *Spartina alterniflora* was particularly striking, with northern plants ripping at half the force of southern plants.

### Reconstituted-plant feeding trials

Twenty-six out of 47 (55%) trials with reconstituted plants resulted in greater consumption of the northern diet than of the southern diet (Fig. 2). In only one reconstituted trial was a southern plant preferred over a northern conspecific. The nature of the results varied between plant species, with five species displaying strong latitudinal trends, two displaying inconclusive

results, and two displaying no latitudinal trends. Grasshoppers preferred the northern diet in 8 of 11 trials and crabs in 18 of 36 trials ( $P = 0.30$ , Fisher exact test).

Over half of the trials with *Iva frutescens* (5 of 7), *Spartina alterniflora* (5 of 7), *S. patens* (5 of 6), *Salicornia europaea* (3 of 4) and *S. virginica* (3 of 4) resulted in significantly greater consumption of the northern plant than the southern conspecific. Two additional trials were marginally significant ( $P < 0.06$ ), and all the trials for these five species showed a trend towards greater consumption of the northern diet. Consequently, these assays provided strong evidence that, for these five species, there are latitudinal differences in plant quality other than, or in addition to, differences in toughness.

Half of the trials with *Aster tenuifolius* (2 of 4) and *Limonium carolinianum* (2 of 4) resulted in significantly greater consumption of the northern plant than the southern conspecific. In the case of *A. tenuifolius*, results depended upon which northern and southern sites were paired (e.g., one pair of sites displayed significant differences on both dates; the other pair did not). In the case of *L. carolinianum*, the results depended on season, with both early trials nonsignificant, and both late trials significant. For both species, at least one trial showed a nonsignificant trend towards greater consumption of southern plants. Because of the variability in these results, we consider them suggestive but not conclusive evidence for latitudinal differences in plant quality unrelated to toughness.

None of the trials with *Distichlis spicata* (0 of 6) and only one of the trials with *Solidago sempervirens* (1 of 5) resulted in significantly greater consumption of the northern plant than the southern conspecific. Moreover, one of the trials with *S. sempervirens* resulted in significantly greater consumption of the southern plant. For these species, the reconstituted-plant trials provided no evidence of latitudinal differences in plant quality unrelated to toughness.

### Chemical extract feeding trials

Overall, 6 out of 37 (16%) trials with nonpolar extracts and 23 of 37 (62%) trials with polar extracts resulted in significantly greater consumption of the northern than the southern diet (Fig. 3). Only one trial with a nonpolar extract and one trial with a polar extract resulted in significant preferences for the southern diets. Results varied among plant species, with four showing conclusive evidence for latitudinal differences in palatability of the polar extract, three showing suggestive but inconclusive results, and two displaying no latitudinal trends.

Over half the trials with polar extracts of *Iva frutescens* (5 of 5), *Spartina alterniflora* (4 of 4), *S. patens* (3 of 4, counting one trial with  $P = 0.054$ ), and *Salicornia europaea* (3 of 4) resulted in greater consumption of the northern than the southern diet. All nonsignificant trials with polar extracts of these species

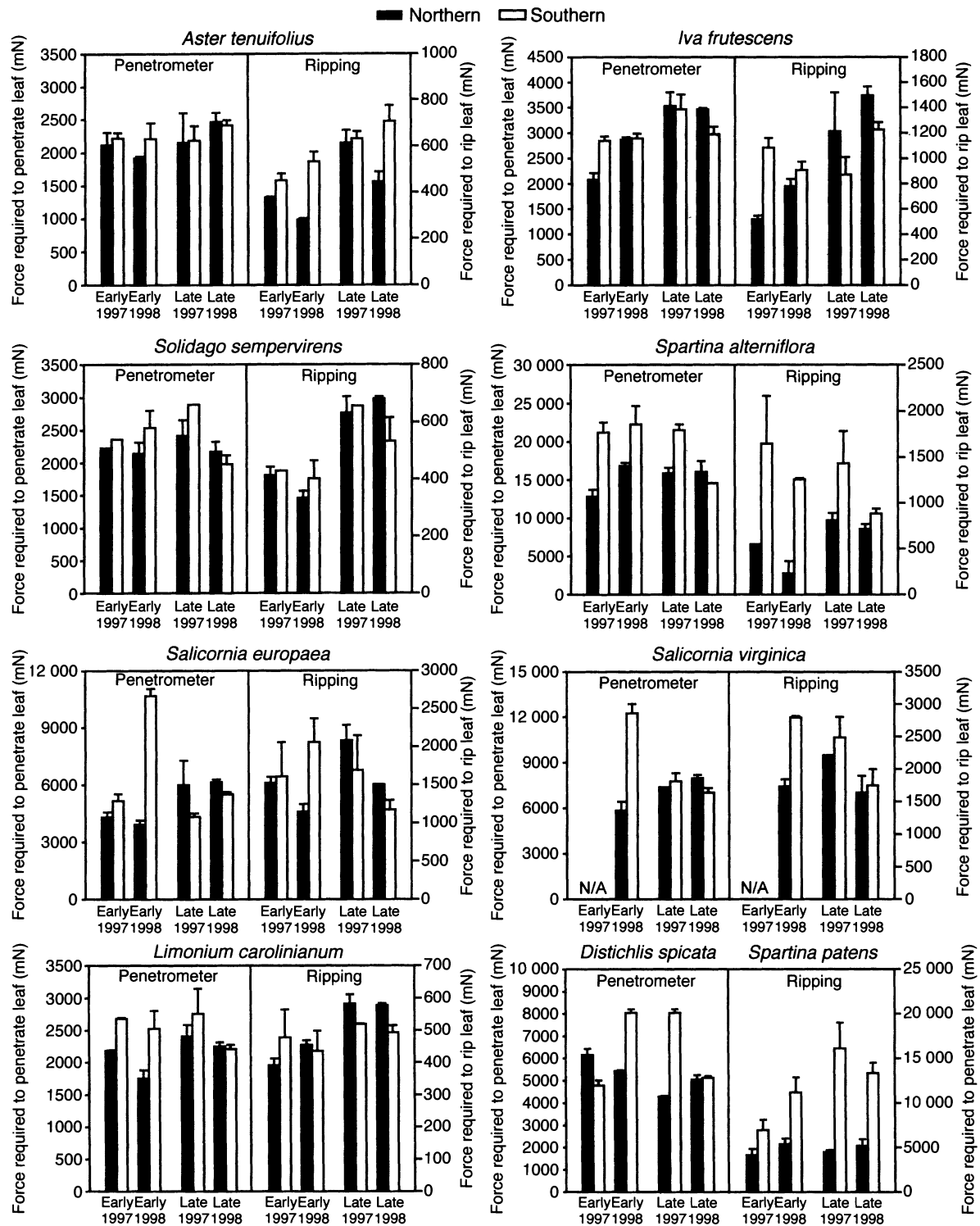


FIG. 1. Toughness of northern and southern plants, tested by penetrometer and ripping methods. Data are means and 1 SE. Season and year of collection are indicated below each bar.

TABLE 1. Plant toughness: three-way ANOVA results of penetrometer (p) and ripping (r) tests.

Species	Test	Latitude	Season	Year	Latitude × Season	Latitude × Year	Season × Year	Latitude × Season × Year
<i>Aster tenuifolius</i>	p	0.549	0.253	0.605	0.508	0.861	0.251	0.660
	r	<0.001	<0.001	0.363	0.707	<b>0.006</b>	0.503	0.601
<i>Iva frutescens</i>	p	0.611	<0.001	0.560	<b>0.021</b>	<b>0.037</b>	<b>0.017</b>	0.512
	r	0.833	<b>0.003</b>	0.086	<b>0.008</b>	0.352	0.173	0.199
<i>Solidago sempervirens</i>	p	0.205	0.754	0.111	0.680	0.496	0.070	0.155
	r	0.818	<b>0.001</b>	0.302	0.245	0.479	0.860	0.213
<i>Distichlis spicata</i> †	p	<0.001	<0.001	<b>0.008</b>	<b>0.018</b>	<b>0.009</b>	<b>0.001</b>	<b>0.001</b>
<i>Spartina alterniflora</i>	p	<b>0.001</b>	0.165	0.624	<b>0.022</b>	<b>0.018</b>	<b>0.008</b>	0.253
	r	<b>0.004</b>	0.773	0.163	0.175	0.206	0.660	0.977
<i>S. patens</i> †	p	<0.001	<b>0.019</b>	0.412	<b>0.022</b>	0.894	0.091	0.137
<i>Salicornia europaea</i>	p	<b>0.007</b>	0.186	<b>0.002</b>	<0.001	<b>0.001</b>	<b>0.033</b>	<b>0.010</b>
	r	0.726	0.887	0.214	0.053	0.274	0.159	0.342
<i>S. virginica</i> ‡	p	<0.001	<b>0.010</b>	...	<0.001	...	...	...
	r	<b>0.039</b>	0.316	...	0.189	...	...	...
<i>Limonium carolinianum</i>	p	<b>0.018</b>	0.391	<b>0.041</b>	0.107	0.846	0.846	0.243
	r	0.517	<b>0.007</b>	0.950	0.100	0.306	0.658	0.474

Note: Significant results ( $P < 0.05$ ) are indicated in boldface.

† Measured only with penetrometer.

‡ Evaluated with two-way ANOVA because no measurements were made in early 1997.

showed a trend towards greater consumption of the northern diet. In addition, two of five trials with non-polar extracts of *I. frutescens* also resulted in greater consumption of the northern than the southern diet. All four of these plant species previously displayed strong latitudinal patterns in palatability of reconstituted plants, and we conclude that this earlier result was primarily driven by latitudinal variation in palatability of polar extracts.

The reconstituted-plant assays provided strong evidence for latitudinal differences in palatability of *Salicornia virginica*, and inconclusive evidence for *Aster tenuifolius* and *Limonium carolinianum*. In the chemical-extract trials with these species, half of the trials with polar extracts resulted in greater consumption of the northern than the southern diet (two out of four in each case). In the case of *A. tenuifolius*, the results again differed as a function of which sites were compared, but the pair of sites that consistently differed in palatability in the reconstituted-plant assays (Rumstick and Airport) did not differ in the polar-extract assays, and the pair of sites that consistently differed in palatability in the polar-extract assays (Hundred Acre and Marsh Landing) did not differ in the reconstituted assays. Similarly, results for *L. carolinianum* again differed by season, but whereas the reconstituted-plant assays displayed latitudinal differences only in the late season, the polar-extract assays displayed differences only in the early season. We consider these results suggestive but not conclusive evidence for latitudinal variation in plant palatability driven by extracts.

There was no evidence in the reconstituted-plant trials for latitudinal difference in palatability of *Solidago sempervirens* or *Distichlis spicata*, nor did these species display strong evidence for latitudinal variation in extract palatability. Two of five assays with polar ex-

tracts of *S. sempervirens* resulted in greater consumption of the northern than the southern diet. Results with *D. spicata* were mixed, with one assay indicating a preference for the northern diet, one a preference for the southern diet, and two no preference.

#### Nitrogen and phenolic concentrations

Northern populations of several plant species had higher N concentrations than did southern conspecifics (Fig. 4), but the magnitude of the differences often varied as a function of season or year, leading to significant interactions between the main effects (Table 2). Inspection of the data indicated that *Aster tenuifolius*, *Distichlis spicata*, *Spartina alterniflora*, *Salicornia europaea*, *S. virginica* and *Limonium carolinianum* had higher levels of N in the north than in the south on at least three of four dates. Differences were often larger early in the year than late in the year, leading to significant latitude × season interactions (Table 2).

At least three additional species, *Iva frutescens*, *Solidago sempervirens*, and *Spartina patens*, had higher levels of nitrogen in the north than in the south early in the year, but showed minimal differences or the reverse pattern late in the year. Given the shorter growing season in the north, these results are consistent with young, rapidly growing plants having high N content, and older, senescing plants having low foliar N content because of translocation to overwintering organs. In any case, because these species had a higher N content than southern conspecifics only in the spring, latitudinal variation in N content might explain differences in palatability that were observed in the spring, but could not explain differences in palatability that were observed in the fall (Pennings et al. 2001: Fig. 2).

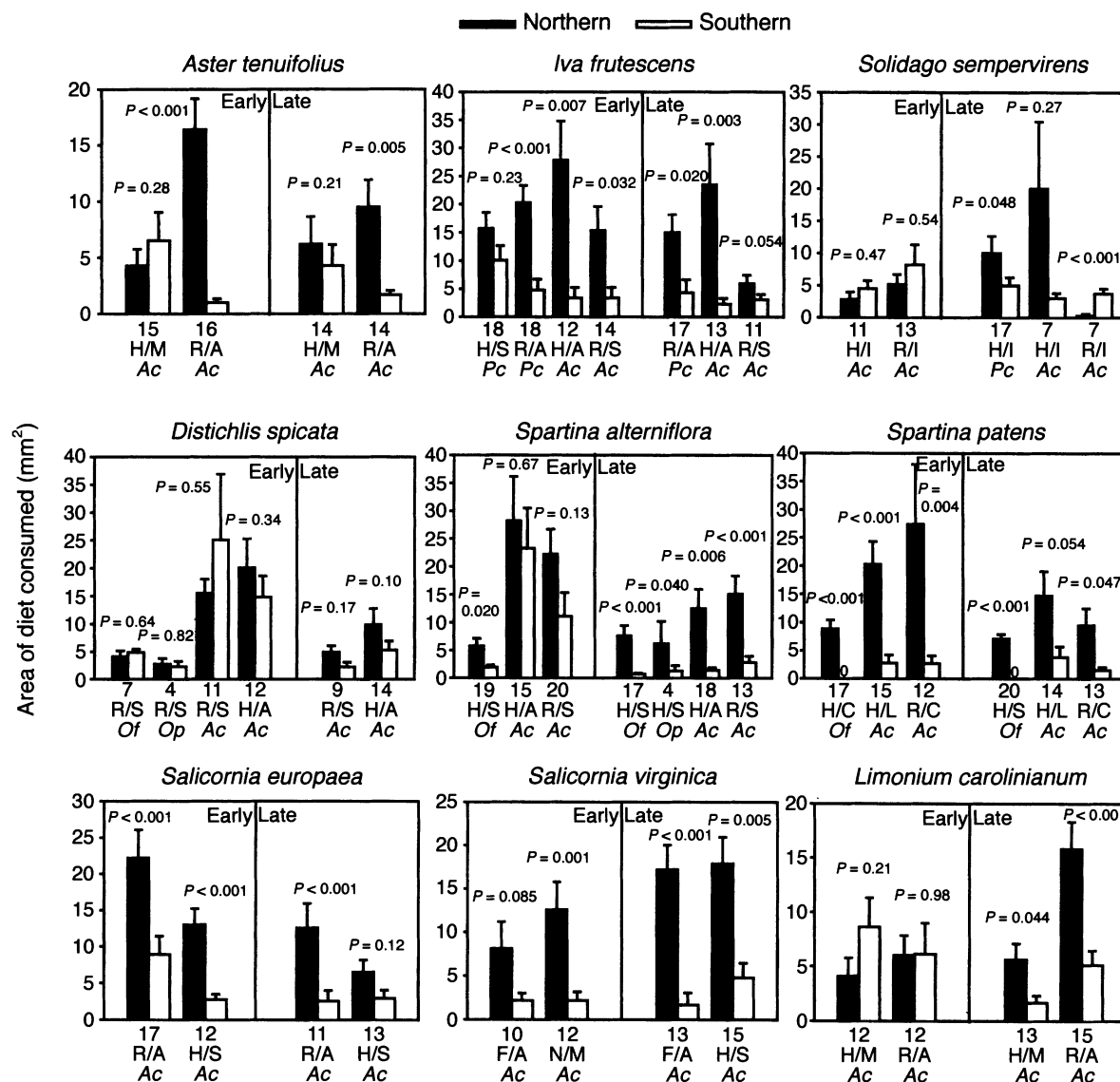


FIG. 2. Consumption of reconstituted northern vs. southern plants in two-choice feeding trials. Data are means and 1 SE. Sample sizes, sites, and herbivore used are indicated below paired bars. For site abbreviations see *Methods: Study sites*. Herbivore key: Ac = *Armases cinereum*, Of = *Orchelimum fidicinum*, Op = *Orphulella pelidna*, Pc = *Paroxya clavuliger*.

Phenolic concentrations of *Spartina alterniflora* were almost 30% greater in the south ( $3.16 \pm 0.10\%$  of dry mass [mean + 1 SE]) than in the north ( $2.45 \pm 0.13\%$ ,  $P < 0.0001$ , ANOVA, results did not vary by year or season). This result is consistent with the latitudinal differences in palatability of polar extracts observed in most comparisons with this species (Fig. 3).

Overall, we found strong evidence that all species of salt marsh plants demonstrate latitudinal variation in palatability when presented to herbivores in an intact form (Pennings et al. 2001). When we examined individual plant traits, we found that all but one species exhibited latitudinal variation in at least one trait (Table 3). Five species were tougher in the south than the north. Five species were less palatable in the south than

the north when tested in reconstituted form. The polar extracts of four of these five species were less palatable in the south than the north. Finally, nitrogen content was lower for six species, and phenolic concentration higher for one species, in the south than the north.

#### DISCUSSION

Along the Atlantic coast of the United States, southern salt-marsh plants are less palatable than northern conspecifics (Pennings et al. 2001). Here, we have begun to identify the plant traits that are responsible for this variation. Plant toughness, secondary chemistry, and nitrogen content all varied with latitude in some plant species, but experimental evidence linking trait variation to variation in palatability was strongest for



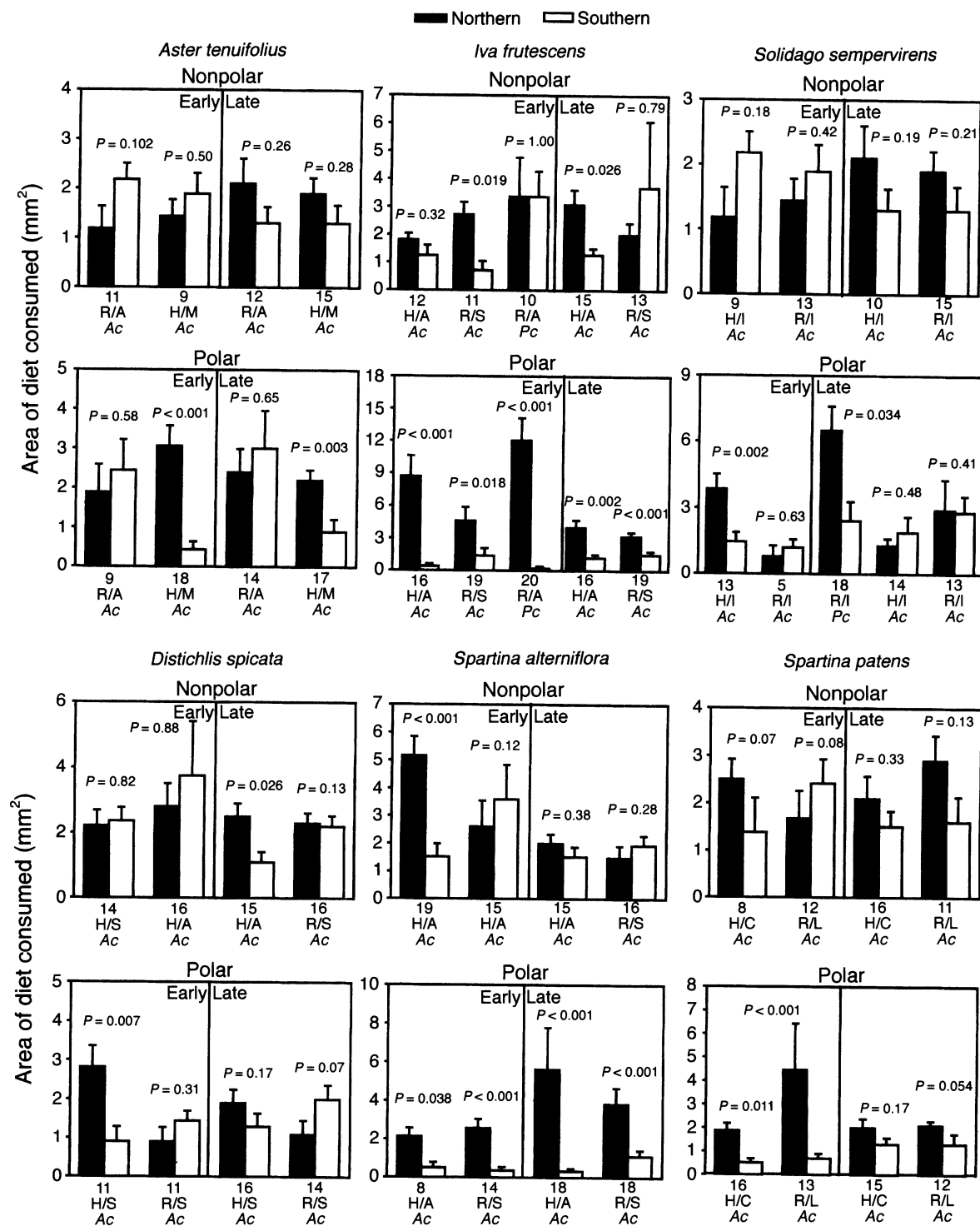


FIG. 3. Results of feeding trials with polar and nonpolar plant extracts. Data (consumption of northern vs. southern diets in two-choice feeding trials) are means and 1 SE. Sample sizes, sites, and herbivore used are indicated below paired bars. For site abbreviations see *Methods: Study sites*. Herbivore key: Ac = *Armases cinereum*, Pc = *Paroxya clavuliger*.

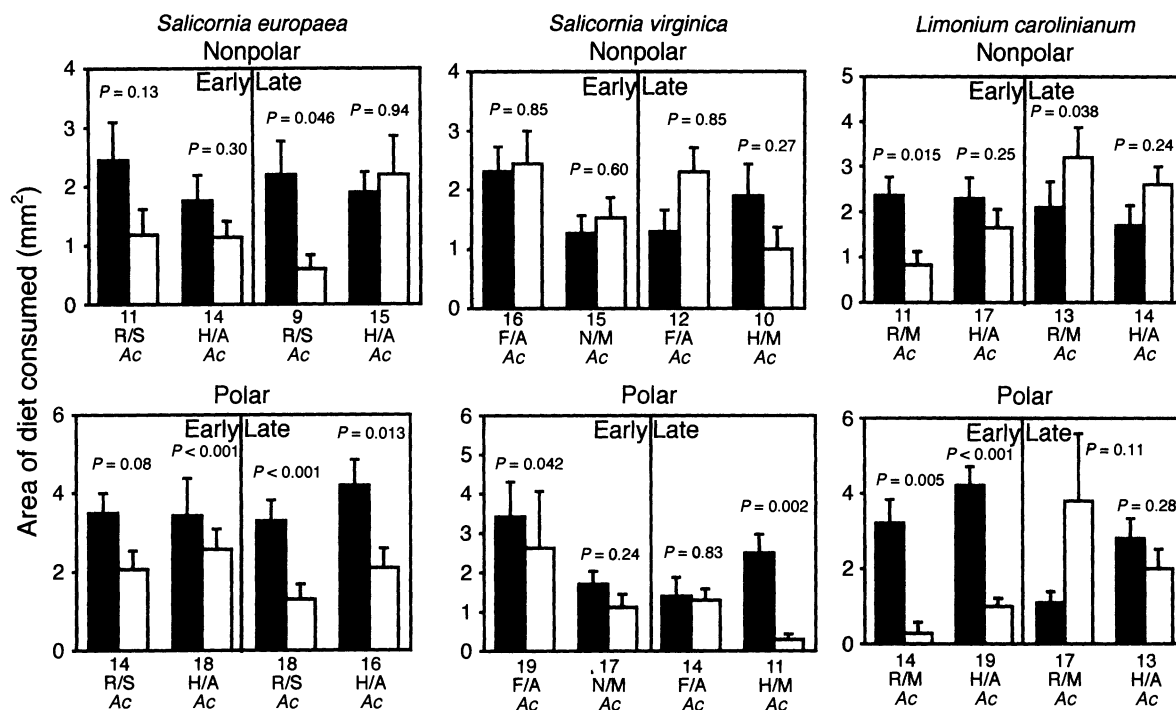


FIG. 3. Continued.

polar extracts. Results with reconstituted plants and plant traits were less striking than previous results with fresh plant material, suggesting that studies that work with reconstituted plants, or that focus only on plant traits, are likely to underestimate variation in plant palatability. Many of our results are similar to results from a latitudinal comparison of seaweed palatability by Bolser and Hay (1996), suggesting that similar processes may occur in both systems.

In at least five salt-marsh plant species, southern individuals were tougher than northern conspecifics in at least one measure of toughness. For none of these species did latitudinal differences in palatability totally disappear when plants were compared in reconstituted form; however, in two cases (*Aster tenuifolius* and *Limonium carolinianum*) the reconstituted assays were ambiguous, suggesting that removing differences in toughness removed some of the differences in palatability. Nevertheless, the three plants with the strongest differences in toughness (*Salicornia virginica*, *Spartina alterniflora*, and *S. patens*) also showed clear differences in palatability in reconstituted assays when differences in toughness were removed. Thus, latitudinal variation in toughness was not the only trait leading to latitudinal variation in palatability; however, latitudinal variation in toughness could have reinforced palatability differences caused by other plant trait(s). Pennings et al. (1998) found that variation in toughness was the primary factor affecting feeding preferences of *Armases cinereum*, the crab used here in most of our assays; however, their study focused on comparing dif-

ferent plant species which varied in toughness by >2 orders of magnitude. In comparison, the intraspecific differences in toughness across latitude that we report here were modest (up to 3-fold). We conclude that although intraspecific variation in toughness could have contributed to latitudinal differences in palatability, it was not of overriding importance.

In at least four and as many as seven of the plants (depending on the rigor of the evidence demanded), latitudinal variation in the palatability of polar extracts contributed to latitudinal variation in palatability of fresh plants. For all but two of these seven species, which were ambiguous for both tests, latitudinal differences in palatability were also found in the reconstituted-plant assays. In the one case in which we quantified variation in a class of secondary metabolites, the phenolic concentration of *Spartina alterniflora* was higher in southern plants than in northern conspecifics. Thus, for these species we can link variation in palatability of fresh plants to variation in palatability of reconstituted plants (indicating that factors in addition to toughness are important) to variation in palatability of polar extracts—and in one case, potentially to variation in the concentration of phenolics. Documenting latitudinal variability in concentrations of individual secondary metabolites must await bioassay-guided identification of which secondary metabolites in each plant are distasteful to consumers. Moreover, because phenolic assays measure a broad group of compounds that may differ in activity and include compounds that are not true phenolics (Appel et al. 2001, Kubanek et

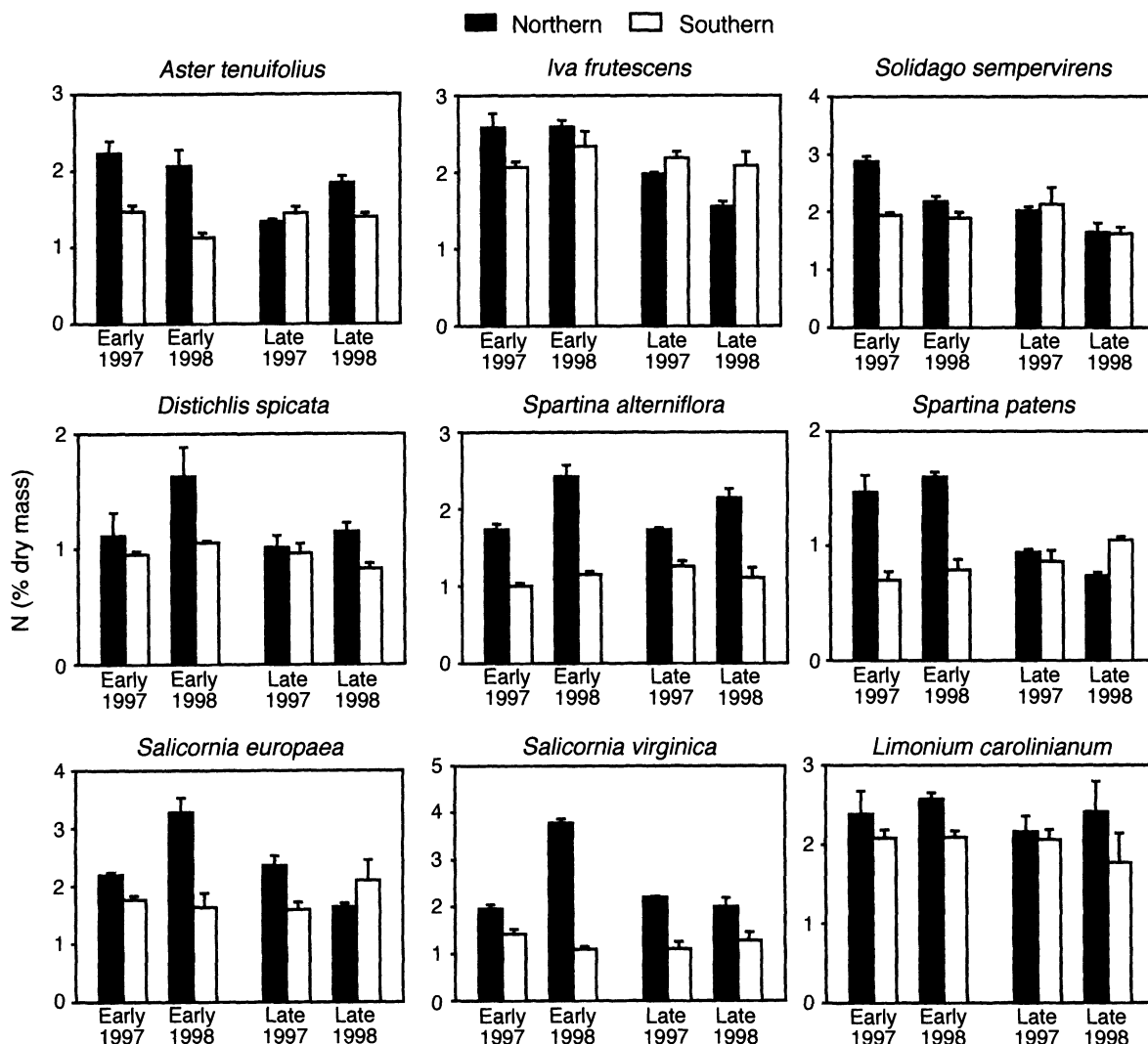


FIG. 4. Nitrogen content of northern and southern plants. Year and season of collection are presented below each bar.

al. 2001), the phenolic measurements should be considered preliminary until confirmed by quantification of individual compounds followed by feeding assays with compounds at natural concentrations. Bolser and Hay (1996) similarly found that the palatability of ex-

tracts correlated with palatability of reconstituted seaweeds better than did other seaweed traits.

Nitrogen content in several plant species was higher in the north than the south. This variation could arise from several sources. Northeastern estuaries are typi-

TABLE 2. Plant nitrogen content: results of three-way ANOVAs.

Species	Latitude	Season	Year	Latitude × Season	Latitude × Year	Season × Year	Latitude × Season × Year
<i>Aster tenuifolius</i>	<0.001	<b>0.017</b>	0.967	<0.001	<b>0.024</b>	<b>0.003</b>	0.273
<i>Iva frutescens</i>	0.896	<0.001	0.392	<0.001	0.096	<b>0.025</b>	0.757
<i>Solidago sempervirens</i>	<b>0.009</b>	<0.001	<b>0.001</b>	<b>0.005</b>	<b>0.050</b>	0.206	<b>0.018</b>
<i>Distichlis spicata</i>	<b>0.007</b>	0.052	0.101	0.458	0.081	0.117	0.816
<i>Spartina alterniflora</i>	<0.001	0.974	<0.001	0.069	<0.001	<b>0.027</b>	0.605
<i>Spartina patens</i>	<0.001	<b>0.001</b>	0.279	<0.001	0.125	0.382	0.134
<i>Salicornia europaea</i>	<0.001	0.059	0.287	<b>0.005</b>	0.883	0.078	<0.001
<i>Salicornia virginica</i>	<0.001	<0.001	<b>0.009</b>	<b>0.013</b>	<0.001	<b>0.010</b>	<0.001
<i>Limonium carolinianum</i>	<b>0.015</b>	0.195	0.906	0.999	0.223	0.546	0.489

Note: Significant results ( $P < 0.05$ ) are indicated in boldface.

TABLE 3. Summary of results of tests for plant traits responsible for latitudinal variation in palatability of nine salt-marsh plant species: "yes" indicates that we unambiguously identified latitudinal variation in a trait, "maybe" indicates results were equivocal, and "no" indicates that we found little evidence for latitudinal variation.

	<i>Aster tenuifolius</i>	<i>Iva frutescens</i>	<i>Solidago sempervi- rens</i>	<i>Distichlis spicata</i>	<i>Spartina</i>		<i>Salicornia</i>		<i>Limonium carolini- anum</i>
					<i>alter- niflora</i>	<i>patens</i>	<i>europaea</i>	<i>virginica</i>	
Palatability of fresh plants	yes	yes	yes	yes	yes	yes	yes	yes	yes
Toughness									
Penetrometer	no	no	no	maybe	yes	yes	maybe	yes	yes
Ripping	yes	no	no	n/a	yes	n/a	no	yes	no
Palatability of reconstituted plants	maybe	yes	no	no	yes	yes	yes	yes	maybe
Palatability of extracts									
Nonpolar	no	maybe	no	no	no	no	no	no	no
Polar	maybe	yes	no	no	yes	yes	yes	maybe	maybe
Nitrogen content	yes	no	maybe	yes	yes	maybe	yes	yes	yes

Notes: An "n/a" entry indicates that the trait was not measured for this species. Results for fresh plants are from Pennings et al. (2001).

cally more eutrophic than southeastern ones (Bricker et al. 1999). The shorter growing season in northern marshes might require a higher N content to allow for rapid growth. Finally, low N content of southern plants might be an adaptive response to reduce palatability to herbivores (McNeill and Southwood 1978, Denno and McClure 1983, White 1984, 1993, Augner 1995, but see Valentine and Heck 2001). Whether latitudinal variation in N contributes to variation in plant palatability is unclear, for three reasons. First, *Armases cinereum*, the consumer used in most of our studies, does not appear to respond strongly to variation in plant N content (Pennings et al. 1998). Second, differences in N content were most pronounced early in the growing season, but differences in palatability were observed both early and late (Pennings et al. 2001). Third, we did not perform experiments in which we manipulated N content in order to assess consumer responses. Thus, our data are consistent with the hypothesis that differences in N content contribute to latitudinal variation in palatability of fresh plants, but do not directly test this hypothesis. In comparison, Bolser and Hay (1996) ruled out protein content as an explanation for latitudinal differences in palatability of seaweeds.

A potential caveat to our results is that most of our assays were conducted with a single consumer species that is found only in southern marshes. It is possible that another species of consumer might have reacted differently in our assays. For example, a northern consumer might have been more sensitive to variation in secondary chemistry (Cronin et al. 1997). In our previous study of fresh plants (Pennings et al. 2001), however, a suite of 13 consumers, including *Armases*, exhibited similar patterns of preference for northern vs. southern plants, regardless of consumer species or geographic origin. Moreover, results in our present paper of 14 assays with three species of southern grasshopper were qualitatively similar to results of parallel *Armases* assays. Thus, although the use of different consumers

might have altered some of the details of our results, the overall patterns and conclusions likely would not have changed.

Overall, as we moved from fresh plants to reconstituted plants to extracts, latitudinal differences in palatability decreased. Thus, all nine species of plants differed in palatability in assays with fresh plant material, but only five unambiguously differed in palatability in reconstituted assays, and only four in assays with extracts. For one species, *Solidago sempervirens*, no traits differed across latitude. Similarly, Bolser and Hay (1996) were only able to trace latitudinal differences in palatability of reconstituted seaweeds to extracts in about two thirds of the cases. Three explanations might account for these "dampening differences." First, if more than one plant trait contributes to differences in palatability, tests that eliminate some plant traits will find less striking differences. For example, if differences in palatability are partially driven by factors other than secondary metabolites, this part of the variation will not be present in tests with extracts. Second, each time plant material is processed, various chemical components may volatilize, decompose, or react with each other. Thus, each step in handling the plant material may destroy or dilute the traits of interest. Finally, variation in palatability could be partially caused by traits that were not investigated here. Many traits combine to determine plant palatability, and variation in traits such as the content of water, salt, silica, or nutrients other than nitrogen could have contributed to latitudinal gradients in palatability. Regardless of the explanation, this pattern suggests that studies that work with reconstituted plants, or look only at plant traits, may underestimate latitudinal differences in palatability of fresh plants. As discussed earlier (see *Introduction*) it is also possible that studies that focus on plant traits may overestimate latitudinal differences in palatability if the studied traits do not affect palatability.

One plant trait that we did not study that might vary with latitude is salt content. Southern marshes are typically saltier than northern marshes because of increased evapotranspiration at lower latitudes (Pennings and Bertness 1999, 2001). To the extent that the salt concentration of plant tissues reflects that of the soil, southern plants might be saltier than northern ones (however, in pilot studies, latitudinal differences in ash content were neither large nor consistent). High salt concentration might deter feeding by some herbivores, but not by *Armases*, which prefers a high-salt diet (Pennings et al. 1998). Moreover, feeding preferences by *Armases* for fresh plant material did not differ from those of other consumers (Pennings et al. 2001). Thus, although we lack experimental data evaluating the role that salt concentration might play in feeding preferences of most marsh herbivores, we doubt that it is a general explanation for the latitudinal patterns in palatability observed by Pennings et al. (2001).

No single plant trait varied in a way that was consistent with latitudinal variation in plant palatability for every species. Rather, all the traits varied with latitude in several, but not all, plants. This diversity of trait differences across latitude is not surprising. Because "palatability" is determined by many traits, plants can be "unpalatable" in different ways. Because a wide variety of consumers including sap-sucking insects, leaf-chewing insects, crabs, snails, and mammals eat salt marsh plants (Pennings and Bertness 2001), different types of defenses may be selected for by different consumers. Moreover, abiotic factors such as edaphic or climate conditions also vary with latitude and may act concurrently with consumers to exert selective pressure on plants. Plant responses to edaphic conditions or climate may indirectly affect traits important to consumers, further increasing the diversity of mechanisms responsible for latitudinal gradients in plant palatability.

In this paper we have evaluated the potential for plant toughness, secondary chemistry, and N content to determine latitudinal patterns of plant palatability. Although a great deal more work remains to be done (we lack experimental studies addressing the role of N content, and we lack knowledge about the secondary metabolites present in each plant species), our results are a first step towards explaining the proximate plant traits that contribute to latitudinal variation in plant palatability in Atlantic coast salt marshes. The ultimate evolutionary mechanisms behind this latitudinal variation in plant palatability and plant traits, however, remain to be investigated. Our work has been presented in the context of standard biogeographic theories arguing that consumer-prey interactions are more intense at lower latitudes, and hence that prey defenses should be better developed at lower latitudes (Mithen et al. 1995). Some circumstantial evidence supports the hypothesis that herbivore pressure is greater in low- than high-latitude salt marshes (Pennings et al. 2001), but a variety of

other factors, including climate, length of growing season, salinity, and anthropogenic eutrophication also may differ between low- and high-latitude salt marshes, and could play a role in latitudinal differences in plant traits and palatability. Future work by our group will evaluate these possibilities in more detail.

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