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Environmental gradients and herbivore feeding preferences in coastal salt marshes

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Abstract Current theories of plant-herbivore interactions suggest that plants may differ in palatability to herbivores as a function of abiotic stress; however, studies of these theories have produced mixed results. We compared the palatability of eight common salt marsh plants that occur across elevational and salinity stress gradients to six common leaf-chewing herbivores to determine patterns of plant palatability. The palatability of every plant species varied across gradients of abiotic stress in at least one comparison, and over half of the comparisons indicated significant differences in palatability. The direction of the preferences, however, was dependent on the plant and herbivore species studied, suggesting that different types of stress affect plants in different ways, that different plant species respond differently to stress, and that different herbivore species measure plant quality in different ways. Overall, 51% of the variation in the strength of the feeding preferences could be explained by a knowledge of the strength of the stress gradient and the type of gradient, plant and herbivore studied. This suggests that the prospects are good for a more complex, conditional theory of plant stress and herbivore feeding preferences that is based on a mechanistic understanding of plant physiology and the factors underlying herbivore feeding preferences.

Keywords Plant-herbivore interactions · Plant stress · Plant vigor · Salt marsh · Environmental stress

Introduction

Current theories of plant-herbivore interactions emphasize that these interactions may change across abiotic gradients. The plant stress hypothesis (White 1974, 1984) predicts that palatability of plants to herbivores will increase with abiotic stress, whereas the plant vigor hypothesis (Price et al. 1987; Price 1991) predicts instead that more vigorous plants—those that are least stressed—will be the most palatable. Both theories agree, however, that variation in abiotic conditions is likely to modify plant traits so as to produce variation in plant palatability.

Tests of the plant stress and plant vigor hypotheses have produced a variety of conflicting results (Waring and Cobb 1992; Koricheva et al. 1998) with some experiments supporting the first hypothesis (Paine et al. 1993; Cobb et al. 1997; Holopainen 2002) and others the second (Price 1988; Fernandes 1998; Forkner and Hunter 2000; Faria and Fernandes 2001; De Bruyn et al. 2002). One problem in trying to explain these diverse outcomes is that the typical study examines a single herbivore species feeding on a single plant species across a single gradient of stress in one type of natural system. Thus, we do not know whether the different outcomes observed in different studies are due to variation among herbivores, plants, different types of stress gradients, different types of natural system, or details of the experimental approach used in particular studies. Meta-analysis approaches (Koricheva et al. 1998) can only partially resolve these concerns. A more powerful approach would be to examine multiple herbivores and multiple plants within a single natural system, using a consistent methodology, and to compare palatability of the same plant species across more than one type of stress gradient. This is the approach we take here.

Salt marshes are an ideal system in which to study the effect of abiotic gradients on plant palatability, because two strong physical gradients occur across modest horizontal distances within single marshes (Pennings and Bertness 2001). Here, we examine plant palatability across flooding gradients, which occur across marsh elevation, and salinity gradients, which can be found in conjunction

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Table 1 Plant and edaphic characteristics along elevational and salinity gradients. Data are from Georgia except where indicated as from Texas. *ND* no data

Plant species	Elevational gradient					
	High elevation			Low elevation		
	Plant height (cm)	Soil salinity (PSU)	Soil water content (%)	Plant height (cm)	Soil salinity (PSU)	Soil water content (%)
<i>Batis maritima</i>	33	60	27	22	53	27
<i>Borrchia frutescens</i>	59	45	30	45	41	34
<i>Distichlis spicata</i>	40	45	40	43	46	55
<i>Iva frutescens</i>	119	51	20	71	63	14
<i>I. frutescens</i> (Tex.)	160	ND	ND	92	ND	ND
<i>Juncus roemerianus</i>	105	53	27	117	55	55
<i>Salicornia virginica</i>	24	67	26	27	55	38
<i>Spartina alterniflora</i>	48	66	61	125	44	57
<i>S. alterniflora</i> (Tex.)	98	ND	ND	72	ND	ND
Plant species	Salinity gradient					
	High salt			Low salt		
	Plant height (cm)	Soil salinity (PSU)	Soil water content (%)	Plant height (cm)	Soil salinity (PSU)	Soil water content (%)
<i>B. maritima</i>	10	173	18	25	73	26
<i>B. frutescens</i>	24	107	17	78	56	25
<i>B. frutescens</i> (Tex.)	31	ND	ND	51	ND	ND
<i>D. spicata</i>	20	102	22	33	57	39
<i>I. frutescens</i>	102	53	28	181	41	27
<i>J. roemerianus</i>	70	97	18	117	67	60
<i>Salicornia bigelovii</i> ^a	8	158	18	22	120	19
<i>S. virginica</i>	8	233	16	27	72	26
<i>S. alterniflora</i>	23	123	23	56	62	59

^a*S. bigelovii* was not included in elevational comparisons because it occurred across a narrow elevational range

with elevational gradients but also occur perpendicular to the flooding gradient as a function of local topography, hydrology and soil type. At the extreme high end of the salinity gradient, unvegetated bare patches (salt pans) occur in the high marsh (Chapman 1960; Pennings and Bertness 1999). Variation in flooding and salinity produce strong gradients of plant size within salt marshes (Valiela et al. 1978; Bertness et al. 1992; Howard and Mendelssohn 1999; Pennings and Bertness 2001; Richards et al., in press). Thus, these gradients in plant size provide an integrated measure of abiotic stress over time.

Variation in flooding in salt marshes affects a suite of biogeochemical properties of soils (Ponnamperuma 1972; Mausbach and Richardson 1994), including oxygen concentrations, levels of toxic sulfides, and the bioavailability of nitrogen (Drake 1989; Pezeshki 1997; Mendelssohn and Morris 2000). Flooding stress is least at the terrestrial border of the marsh, where soils are rarely inundated, and immediately adjacent to creekbanks, where rapid exchange of soil water with creek water is possible (Chapman 1960; Howes et al. 1981; Howes and Goehringer 1994). Salt stress limits plant growth both indirectly, by reducing soil water potential, and thereby making it difficult for plants to take up water, and directly, by damaging cellular processes (Poljakoff-Mayber 1975; Drake 1989; Mendelssohn and Morris 2000).

Some evidence exists that salt marsh plants vary in quality to herbivores across abiotic gradients. *Spartina alterniflora* leaves from low-stress, creekbank zones contain higher levels of nitrogen and lower concentrations of phenols than do leaves from high-stress, mid-marsh zones (Buchsbbaum et al. 1984; Bowdish and Stiling 1998), and are more vulnerable to snail grazing (Silliman and Bertness 2002). The shrub *Borrchia frutescens* supports fewer galls but higher densities of planthoppers under stressful, high-salinity conditions (Moon and Stiling 2000, 2002), and the shrub *Iva frutescens* is a better host for aphids under low-salinity conditions (Levine et al. 1998). Finally, growth of stem-boring larvae in European *Aster* is better at sites with lower salinities (Hemminga and van Soelen 1988). Despite these particular examples, however, we do not have a comprehensive understanding of how palatability of marsh plants varies across flooding and salinity gradients.

To obtain a more comprehensive understanding of variation in palatability of salt marsh plants, we worked with eight common salt-marsh plant species and six common leaf-chewing herbivores in a southeastern USA salt marsh. Using the same taxa, we examined variation in palatability across two stress gradients (flooding and salinity). Our results indicated that variation in plant palatability across physical stress gradients was ubiquitous, but that the direction of the variation was idiosyncratic. The magnitude of herbivore preferences, however, was predictable based on the magnitude of the variation in abiotic stress.

Materials and methods

Plants and herbivores

Most of the research (30 feeding trials) was done during June–August, 2000, on Sapelo Island, Georgia (31°27'N, 81°15'W). Field work was done in the salt marshes surrounding the island, and feeding trials at the University of Georgia's Marine Institute. We worked with eight plant species that were common and had distributions that spanned wide elevational and/or salinity gradients (Table 1). These eight species represented a majority of the species and >99% of the total plant biomass at the site (authors' personal observation). To document the environmental gradients experienced by each plant species, we periodically measured soil pore-water salinities and water content, and plant heights at the extremes of each environmental gradient for each plant species. To measure soil water content (percentage of initial soil mass consisting of water), we collected 5-cm-deep soil cores and measured water content gravimetrically. Soil salinity was estimated by rehydrating soils in excess deionized water, measuring the salinity of the supernatant with a refractometer after 24 h, and back-calculating to the original soil salinity. Since these data were collected opportunistically each time a particular plant was collected, rather than systematically, and thus varied in replication and were haphazard with respect to the monthly tidal cycle (i.e., spring versus neap tides), we simply present overall means as a rough guide to the nature of the stress gradients (Table 1). We used plant height as an integrated measure of all stresses experienced by the plants over time. All of the plants that we studied except *Salicornia bigelovii* are long-lived perennials, and their height is correlated with edaphic conditions (Richards et al., in press). All but *S. bigelovii* and *I. frutescens* are clonal, with extensive below-ground rhizomatous networks, consequently, measuring other aspects of size (such as the horizontal spread of particular genets) would have been highly problematic.

Six species of common consumers, including a crab, a beetle, a moth larva and three species of grasshopper were collected for

Table 2 Consumers used in palatability assays

Consumer species	Plant species tested
Decapoda	
<i>Armases cinereum</i> (Grapsidae)	<i>B. maritima</i> , <i>B. frutescens</i> , <i>D. spicata</i> , <i>I. frutescens</i> , <i>S. bigelovii</i> , <i>S. virginica</i>
Orthoptera	
<i>Orchelimum fidicinum</i> (Tettigoniidae)	<i>D. spicata</i> , <i>S. alterniflora</i>
<i>Orphulella pelidna</i> (Acrididae)	<i>D. spicata</i> , <i>S. alterniflora</i>
<i>Paroxya clavuliger</i> (Acrididae)	<i>B. frutescens</i> , <i>I. frutescens</i> , <i>J. roemerianus</i>
Coleoptera	
<i>Paria aterrima</i> (Chrysomelidae)	<i>I. frutescens</i>
Lepidoptera	
<i>Sparganothis</i> sp. (Tortricidae)	<i>S. bigelovii</i> , <i>S. virginica</i>

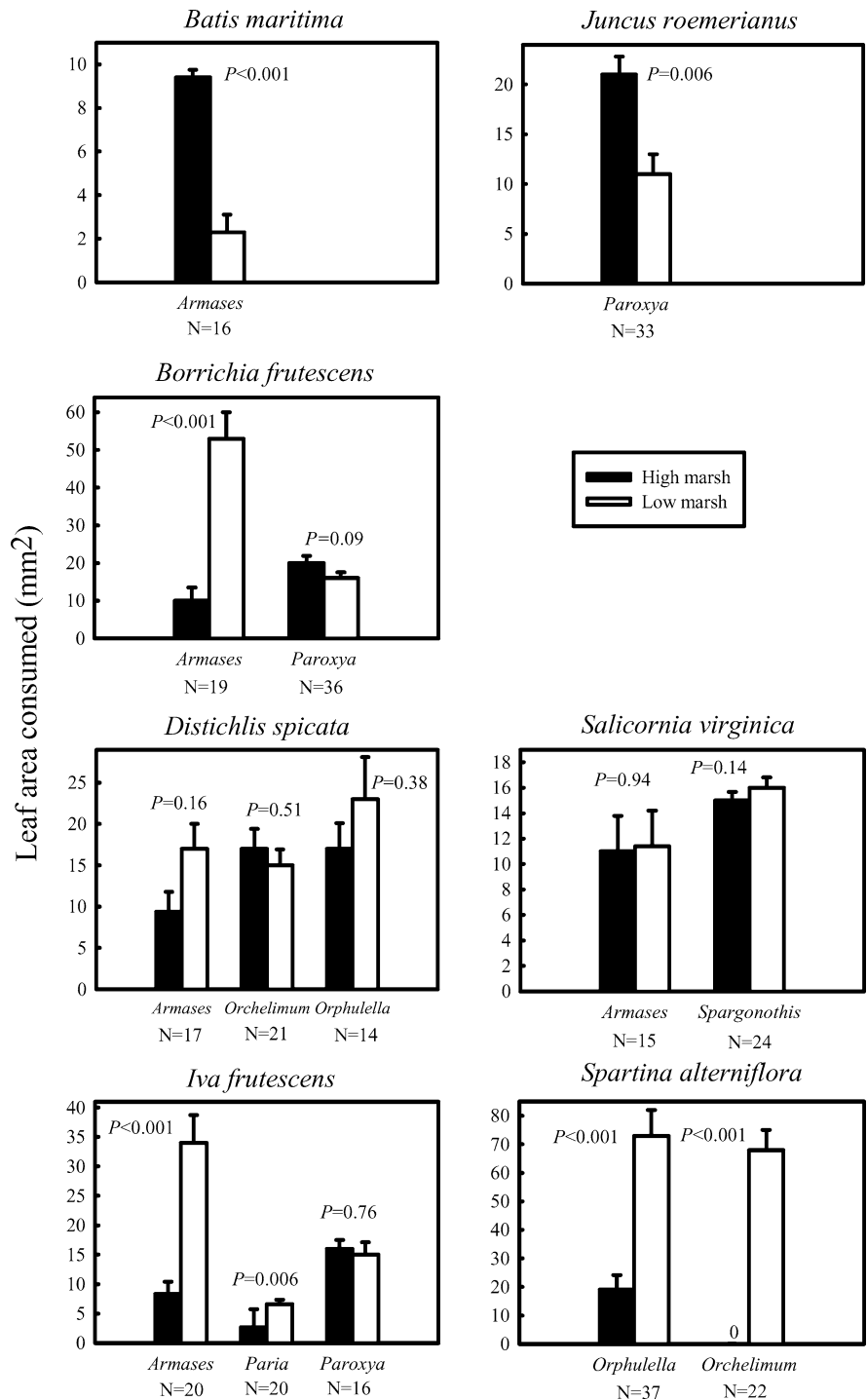
feeding trials (Table 2). Consumers ranged from specialists (e.g., *Sparganothis* sp., *Paria aterrima*) to moderate generalists (e.g., *Paroxya clavuliger*) to omnivores (*Armases cinereum*). The number of plant species that could be assayed with each herbivore species increased with diet breadth (Table 2).

For comparative purposes, four additional trials were conducted in October 2002 with a subset of the same plant and herbivore species, but collected from Surfside, Texas (28°58'N, 95°16'W) and returned to the laboratory at the University of Houston. We measured plant heights but did not collect edaphic data in Texas.

Feeding trials

Individual consumers were offered a choice between two undamaged leaves (or photosynthetic stems in the case of *Salicornia* spp.) from conspecific plants at opposite ends of the elevational and/or salinity gradient occupied by each plant species. Leaves or photosynthetic stems were standardized within each species for position in order to minimize any confounding effects of leaf age (typically, we collected the first fully expanded leaf, and avoided both leaves that were not fully expanded and leaves that appeared older and perhaps senescing). Leaves for individual assays were collected by hand from both ends of the environmental gradient in the field, placed in a cool and shaded ice chest, returned to the

Fig. 1 Georgia trials. Consumption of leaves from plants growing in high marsh vs. low marsh habitats in paired feeding trials. Data are means±1 SE; herbivore species and sample sizes are indicated below paired bars. The low marsh is the more stressful zone for all species except *S. alterniflora*, which experiences improved soil drainage at the lowest marsh elevations near to creekbanks (Mendelsohn and Morris 2000)

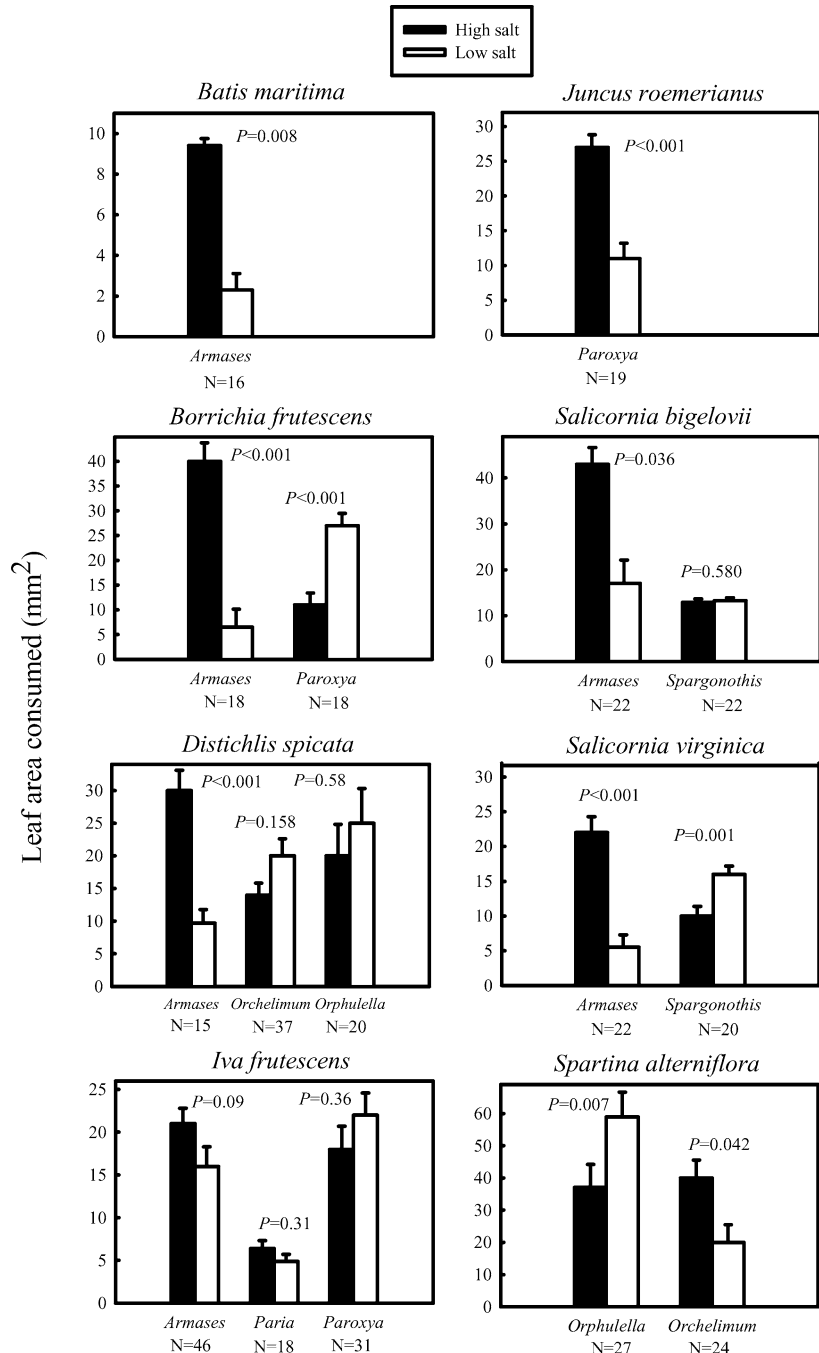


laboratory and immediately set up in feeding assays. Consumers were collected from the field by hand or with insect nets, returned to the laboratory, and immediately used in feeding assays. Consumers were housed individually within appropriate chambers (crabs, 500-ml glass jars with water; grasshoppers, screen cages; beetles and moth larvae, petri dishes). Individual replicates were checked twice a day and were terminated when substantial feeding (approximately 30%) on at least one leaf had occurred. Replicates in which neither diet was eaten after a period of 72 h provided no information on relative palatability of plants, and were omitted. Consumption was measured as mm² of leaf area consumed. Differences in consumption were compared between ends of the gradients using paired *t*-tests. Most preference assays (26) had 15–24 replicates, one had fewer (*n*=14) and seven had more (up to 46). Results did not appear to be a function of sample size, although there were a few assays that

were close to significance and probably would have attained significance had replication been sharply increased.

To determine whether the magnitude of herbivore preferences increased with increasing differences in plant stress, we used variation in plant height as an index of stress that was common to both gradients. We calculated the magnitude of herbivore preference as (consumption of preferred leaf–consumption of other leaf)/(consumption of preferred leaf) and the proportional difference in plant height as (height of taller plant–height of shorter plant)/(height of taller plant). Using multiple regression, we related this index of feeding preference to: (1) the proportional difference in plant height, (2) the type of gradient studied (elevation vs. salinity), (3) the type of herbivore studied (*Armases* vs. insects), and (4) the type of plant studied (species that accumulate salt in their tissues vs. species that exclude or excrete salt). The best regression model was chosen using Mallows's Cp statistic.

Fig. 2 Georgia trials. Consumption of leaves from plants growing in high-salt vs. low-salt habitats in paired feeding trials. Data are means±1 SE; herbivore species and sample sizes are indicated below *paired bars*. The high-salt habitat is more stressful to all plant species than the low-salt habitat



Results

Seventeen of 30 feeding trials (57%) in Georgia yielded a significant preference for one or the other end of an elevational or salinity gradient. However, details of results varied among plant and herbivore species within each environmental gradient.

Elevational gradient

Variation in plant height indicated that we sampled across an elevational gradient that was wide enough to affect plant performance for four of the seven plant species studied (Table 1). In contrast, the remaining three species (*Distichlis spicata*, *Juncus roemerianus*, *S. virginica*) varied little in height across their elevational range. In all seven cases, salinity varied little across the elevational ranges of the plants, indicating that we were successful in sampling an elevational gradient that was relatively unconfounded by salinity variation.

Seven of the 14 feeding trials indicated a significant preference for plants from one end or the other of the elevational gradient (Fig. 1). Four trials indicated a preference for plants from the low-stress end of the gradient, and three for the high-stress end. Trials with *D. spicata* and *S. virginica*, two of the species which varied the least in height across their elevational range, comprised five of the seven non-significant trials. In the case of *S. alterniflora* only, note that the preference by both *Orchelimum fidicinum* and *Orphulella pelidna* for plants growing at the lower end of the elevational gradient indicates a preference for the low-stress end of the gradient. For *S. alterniflora*, which was the only plant that we studied to occupy the low marsh, low-elevation plants are taller and less stressed than high-elevation plants because of increased water drainage near to creek banks (Mendelssohn and Morris 2000).

Salinity gradient

Variation in plant height and soil salinity indicated that we sampled across a salinity gradient that was wide enough to produce variation in plant performance for all eight of the species studied. In many cases, salinity varied inversely with soil water content, suggesting that the salinity gradient was partially confounded either with soil type (which affects water-holding capacity) or flooding, despite our efforts to standardize elevation. For simplicity, however, we refer to this gradient as a salinity gradient while recognizing that other factors likely co-varied with salinity.

Ten of 16 feeding trials indicated a significant preference for plants from one end or the other of the salinity gradient (Fig. 2). Seven trials indicated a preference for plants growing in high salinity soil, and three for plants growing in low salinity soil. Trials with *I. frutescens*, which displayed the weakest salinity gradient,

comprised three of the six non-significant trials. In three cases (*B. frutescens*, *S. virginica*, *Spartina alterniflora*), different herbivores displayed opposite salinity preferences for the same species of plant. In general, the crab *A. cinereum* preferred plants from the high end of the salinity gradient (five of five significant comparisons), whereas results with insects were inconsistent (three trials preferred low-salinity plants; two preferred high-salinity plants).

Texas feeding assays

Two of four Texas feeding trials indicated a significant preference for plants from one end or the other of the elevation or salinity gradients (Fig. 3). As in Georgia (Fig. 2), *P. clavuliger* preferred *B. frutescens* from low vs. high salt areas. In contrast to results from Ga. (Fig. 2); however, *A. cinereum* displayed no preference for *B. frutescens* from low vs. high salt areas. Our Texas study site had a small tidal range and no distinct “creebank” habitat for *S. alterniflora*, and this species displayed little variation in height at this site (Table 1). Perhaps as a result, *O. pelidna* displayed no preference for *S. alterniflora* plants across the elevational gradient (Fig. 3a); however, the trend towards preferring lower elevation plants was in the direction of the significant result obtained in GA (Fig. 1). The largest difference in results was for *Iva*. In GA (Fig. 1), *A. cinereum* preferred *I. frutescens* from low marsh elevations (Fig. 1), but in Texas the same consumer preferred *Iva* from high marsh elevations (Fig. 3).

General patterns in feeding preferences

Across all assays conducted in Georgia, the magnitude of herbivore feeding preferences was fairly predictable ($r^2=0.51$, $P=0.0009$, Table 3). In particular, the magnitude of feeding preferences increased with the proportional

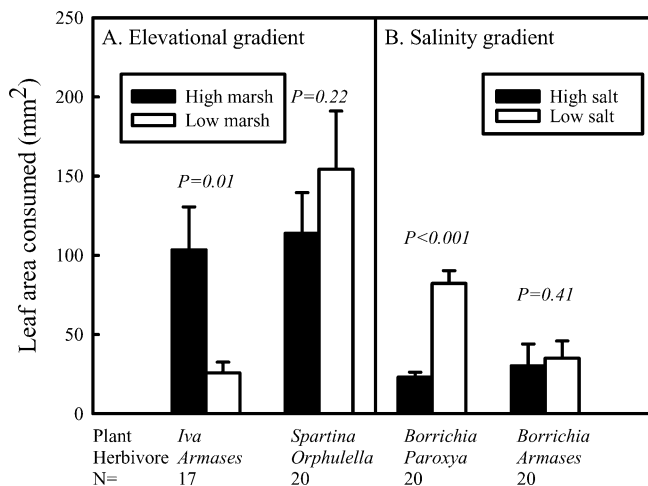


Fig. 3a, b Texas trials. Consumption of leaves from plants growing in **a** high marsh vs. low marsh habitats in paired feeding trials or **b** high salt vs. low salt habitats. Data are means±1 SE; plant species, herbivore species and sample sizes are indicated below paired bars

difference in heights of the plants compared (Fig. 4). Feeding preferences were also affected by gradient type (for a given difference in plant height, the elevational gradient produced stronger feeding preferences than did the salinity gradient, Fig. 4a), and by herbivore type (for a given difference in plant height, *Armasenes* had stronger feeding preferences than did insects, Fig. 4b). Plant type (salt accumulators vs. excluders and excreters) did not significantly affect feeding preferences ($P=0.12$), but was included in the best regression model selected by Mallows' C_p statistic (Table 3). Including the four Texas assays in the regression did not alter any of these conclusions (results not shown).

Discussion

Previous authors have argued that strong physical gradients in salt marshes mediate the palatability of selected marsh plants to particular herbivores (Denno et al. 1986; Hemminga and van Soelen 1988; Bowdish and Stiling 1998; Levine et al. 1998; Moon and Stiling 2000). Our results document that similar differences in plant palatability are ubiquitous across the entire salt marsh plant community. For each of the eight plants studied, at least one herbivore discriminated between plants from opposite ends of an elevational or a salinity gradient. In several cases, however, results differed among herbivores, or among gradients, indicating that different herbivore species perceive plant quality in different ways, and that different types of stress gradients may have different effects on plant quality.

Plant traits likely to matter to herbivores, such as nutrient and phenol content, are known to vary in *Spartina* across elevational gradients (Buchsbaum et al. 1984; Bowdish and Stiling 1998), and likely vary in similar ways in other salt marsh plants. We found that plants from different ends of the elevation gradient often differed in palatability to herbivores. The direction of the preferences, however, depended on the species examined. In some cases (e.g., *Iva* in GA) herbivores preferred plants of from the high-stress end of the elevational gradient, in other cases (e.g., *Batis* in GA) they preferred plants from the low-stress end. This variation in results suggests that flooding stress affects different species of plants in different ways, that different herbivores respond to different plant traits, or both.

Table 3 Multiple regression analysis of feeding preferences^a

Predictor	Coefficient	<i>P</i>
Constant	-1.099	0.005
Plant height	1.017	0.0003
Gradient type	0.296	0.007
Herbivore type	0.250	0.005
Plant type	0.133	0.12

^aAdjusted $r^2=0.51$, $F_{4,25}=6.60$, $P=0.0009$

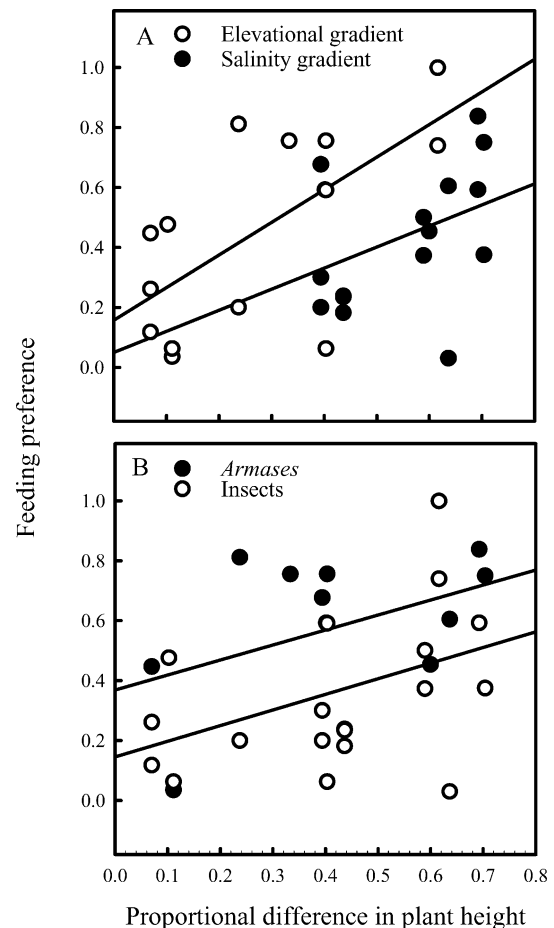


Fig. 4 Georgia trials, the magnitude of herbivore feeding preferences vs. proportional difference in plant height. **a** Comparing gradients, **b** comparing herbivore groups. For illustrative purposes, linear regression lines for individual data categories are shown; however, data were analyzed using multiple regression (Table 3)

Comparisons of palatability across elevation were more likely to be significant when there was a strong difference in physical stress between the ends of a gradient. For example, the difference in height between *S. virginica* at the low versus the high ends of the elevational gradient was only 3 cm (proportional difference=0.11), and no differences in palatability were observed. Similarly, *Distichlis* was also found over a narrow elevational gradient with only a 3 cm difference (proportional difference=0.07) in plant height between the lower to the upper end of the gradient, and no differences in palatability were observed. The results with *Distichlis* may also have been affected by the timing of our experiment. Pennings et al. (2001) found that herbivores ate more *D. spicata* in early summer (June) than in late summer (September), suggesting a decline in palatability over the summer. We conducted our trials in August, and might have observed stronger differences in palatability had we conducted trials earlier in the summer.

As with the elevational gradient, plants from different ends of the salinity gradient often differed in palatability to herbivores. The direction of the preferences, however,

again depended on the herbivore species examined. Five of five significant trials with *A. cinereum* indicated a preference for plants growing at the high end of the salinity gradient. In contrast, four of six significant trials using insects indicated a preference for plants growing at the low end of the salinity gradient. In several cases (*Borrchia*, *Salicornia*, *Spartina*), different consumer species had opposite feeding preferences across the salinity gradient for the same species of plant, again emphasizing that different herbivores may perceive plant quality in different ways. Plants experiencing salt stress commonly increase tissue concentrations of salts and/or nitrogen-based osmotica (Flowers et al. 1977, 1986; Rozema et al. 1985). Salt in food stimulates feeding by *Armases* (Pennings et al. 1998), likely explaining the preference of this crab for plants from the high end of the salinity gradient. Most herbivores would be expected to prefer foods with higher nitrogen content (White 1984), but this may have been partially counterbalanced in the case of insects by higher salt levels and/or by other changes in plants growing in high-salinity soils. For example, high salinity often induces increased succulence in leaves (Hacker and Bertness 1995), which probably also increases toughness.

The two gradients sometimes produced parallel patterns in feeding preference by particular consumers. For example, *Armases* always preferred *Borrchia* from the high-stress end of the gradient (low elevation or high salt). In other cases, the same consumer exhibited opposite preferences for the same species of plant growing across the two gradients. For example, *Armases* preferred *Batis* from the low-stress end of the elevational gradient (high elevation) but the high-stress end of the salt gradient (high salt). *Paroxya* similarly preferred *Juncus* from the low stress end of the elevational gradient and the high-stress end of the salt gradient.

Our results argue that no simple relationship exists between plant stress and herbivore preferences. Different types of stress gradient may produce different effects on plant palatability. Different plant species may respond to a particular gradient by increasing or decreasing in palatability (Renaud et al. 1990). Finally, different herbivores may respond differently to stress effects on the same plant species, perhaps because the different herbivores respond to different plant traits (Cronin and Hay 1996). In sum, we argue that understanding how herbivores respond to plant stress will require a more detailed understanding of how plant traits respond to different types of stress, and of which plant traits matter to particular herbivores.

Although we could not predict the direction of herbivore feeding preferences for plants from different ends of stress gradients, we were able to explain a large amount (51%) of the variation in preference strength based on a knowledge of the strength of the stress gradient and the type of gradient, plant and herbivore studied (Table 3). The most general result was that as the magnitude of the stress gradient (measured by plant height) increased, the magnitude of the feeding preference also increased. There were also differences between the two stress gradients (for

a given difference in plant height, the elevational gradient produced stronger feeding preferences than did the salinity gradient, Fig. 4a) and among herbivores (*Armases* had stronger feeding preferences than did insects, Fig. 4b). The fact that we were able to predict half of the variation in preference strength based on these fairly crude indicator variables suggests that the prospects are high for a general understanding of the relationship between abiotic stress and herbivore feeding preferences. Our results suggest, however, that this general relationship will be conditional upon a number of factors, rather than being a simple relationship that applies to all taxa. We thus echo the conclusions of reviews of the plant stress and plant vigor hypotheses, which have previously noted that the results often differ between types of stress and herbivore feeding guild, and have called for a better understanding of how plant physiology responds to different types of stress (Waring and Cobb 1992; Koricheva et al. 1998). Koricheva et al. (1998) also point out that few studies of these hypotheses have used multiple levels of stress. Our ability to predict the magnitude of herbivore preferences was based in large part on our ability to infer the strength of the stress gradients based on variation in plant height. We suggest that using multiple levels of stress, and/or measuring the degree of plant stress, will prove to be useful approaches in generating a better understanding of how herbivores respond to plants growing across abiotic gradients.

We chose to work with plants growing across natural abiotic gradients in the field, thereby avoiding any potential artifacts involved in mimicking stress gradients in the laboratory (Koricheva et al. 1998). This approach, however, carries the caveat that a variety of factors in addition to stress may have varied across the gradients we examined. For example, damage from the snail *Littoraria* to the grass *S. alterniflora* varies sharply across the elevational gradient because of variation in predation on *Littoraria* from marine consumers (Silliman and Bertness 2002), and variation in feeding by *Littoraria* could produce variation in plant quality to other herbivores. The presence of uncontrolled or unmeasured factors such as this is likely why we were able to explain only 51% of the variation in feeding preferences. On the other hand, the fact that we documented patterns in feeding preference across natural gradients in the field suggests that our results are robust despite the presence of interfering factors, and that they are likely to matter in real natural systems. In particular, the variation in plant quality that we documented for every plant species that we studied is likely to have important implications for herbivore distributions across the salt marsh landscape.

Pennings et al. (2001) previously demonstrated latitudinal variation in palatability of many of the same plant species that we studied here: ten species of salt marsh plants from high latitudes were consistently more palatable to 13 species of herbivores than were conspecific plants from low latitudes. Our results indicate that plant palatability may also vary across environmental gradients within a geographic region, but for two reasons our results

do not cast doubt on the latitudinal pattern previously reported. First, this study focused on comparing plants across the extremes of environmental gradients; however, for the previous latitudinal comparisons, plants were collected from the center of their local ranges in a manner that was standardized among geographic regions. Second, the latitudinal differences in palatability previously observed were typically much stronger than the local differences reported here, and were consistent among all plants and herbivores, whereas the preferences reported here varied as a function of plant and herbivore species. Thus, we conclude that the palatability of salt marsh plants varies on both geographic and local scales, but that the geographic variation is stronger and more predictable than the local variation.

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