Oecologia (2002) 132:549–558
DOI 10.1007/s00442-002-0989-2

PLANT ANIMAL INTERACTIONS

Tatyana A. Rand

Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution

Received: 14 December 2001 / Accepted: 17 May 2002 / Published online: 9 July 2002

Abstract Herbivore damage and impact on plants often varies spatially across environmental gradients. Although such variation has been hypothesized to influence plant distribution, few quantitative evaluations exist. In this study I evaluated patterns of insect herbivory on an annual forb, *Atriplex patula* var. *hastata*, across a salt marsh tidal gradient, and performed experiments to examine potential causes and consequences of variation in herbivory. Damage to plants was generally twice as great at mid-tidal elevations, which are more frequently inundated, than at higher, less stressful, elevations at five of six surveyed sites. Field herbivore assays and herbivore preference experiments eliminated the hypothesis that plant damage was mediated by herbivore response to differences in host plants across the gradient. Alternately, greater herbivore densities in the mid-marsh, where densities of an alternate host plant (*Salicornia europaea*) were high, were associated with greater levels of herbivory on *Atriplex*, suggesting spillover effects. The effect of insect herbivores on host plant performance varied between the two sites studied more intensively. Where overall herbivore damage to plants was low, herbivory had no detectable effect on plant survival or seed production, and plant performance did not significantly differ between zones. However, where herbivore damage was high, herbivores dramatically reduced both plant survival (>50%) and fruit production (40–70%), and their effects were stronger in the harsher mid-marsh than the high marsh. Thus herbivores likely play a role in maintaining lower *Atriplex* densities in mid-marsh. Overall, these results suggest that variation in herbivore pressure can be an important determinant of patterns of plant abundance across environmental gradients.

T.A. Rand (✉)
Department of Ecology and Evolutionary Biology,
Brown University, Providence, RI 02912, USA

Present address:
T.A. Rand, 348 Manter Hall, School of Biological Sciences,
University of Nebraska, Lincoln, NE 68588–0118, USA
e-mail: trand@unlserve.unl.edu
Tel.: +1-402-4720755, Fax: +1-402-4722083

Keywords Environmental gradients · Insect herbivory · Plant distribution · Salt marsh · Zonation

Introduction

Abiotic environmental factors have long been recognized to play an important role in mediating the relative importance and intensity of species interactions (Connell 1975; Menge and Sutherland 1987; Menge and Olson 1990; Dunson and Travis 1991). Thus, unraveling the nature of the complex interplay between biotic and abiotic processes is likely key to predicting patterns of organism distribution in ecological communities (Louda 1982; Smith 1987; Louda and Rodman 1996). In plant-insect systems, environmental modulation of interactions has been postulated to occur both indirectly, via effects on host plants, and through direct effects of abiotic factors on herbivore populations. It is well documented that underlying abiotic environmental factors can influence plant characteristics, which can subsequently impact insect herbivores. Some studies suggest that insect herbivores respond to improved plant quality, resulting from increases in nitrogen availability (White 1984) or decreases in plant defensive compounds (Rhoades 1979, 1983), when host plants are stressed. If so, the predicted result is increased herbivore impact on host plants under more stressful conditions. This prediction is supported by a number of studies that demonstrate a positive relationship between insect feeding damage to plants and various environmental stresses (Lewis 1984; Waring and Pitman 1985; Mattson and Haack 1987; Louda et al. 1987; Louda and Collinge 1992). However, more vigorous plants, presumably growing under more benign environmental conditions, can experience higher levels of herbivore pressure than stressed individuals under some circumstances (Price 1991). In either case, it is clear that abiotic factors can influence plant suitability and subsequent herbivory. Alternately, environmental factors may directly impact herbivore abundance thereby influencing levels of herbivory. Differences in insect abundance have been found to be important determinants of patterns of herbivory across sun-shade habitat boundaries (Collinge and Louda 1988; Louda and Rodman 1996) and along elevational gradients (Reynolds and Crossley 1997). Without careful study, it is often difficult to separate herbivore responses to environmentally induced differences in plant characteristics from direct responses of herbivores to the environmental conditions themselves (Larsson 1989; Jones and Coleman 1991).

Patterns of differential herbivore damage to plants across regional to local environmental gradients, as well as across smaller-scale habitat discontinuities, have been documented in several terrestrial environments (Louda 1989; Smith 1987; Louda et al. 1990; Osborne and Smith 1990). Thus, individual plants may experience very different levels of herbivore pressure across the range of abiotic conditions in which the species naturally occurs. Since herbivores can have important effects on critical demographic parameters such as survival and reproduction (Harper 1969; Louda et al. 1990; Louda and Potvin 1995; Crawley 1997), spatial variation in herbivory could influence patterns of plant distribution or abundance across adjacent habitat types (Harper 1969, 1977; Louda 1989; Louda and Rodman 1996). In fact, the available evidence suggests that herbivores can have important, spatially explicit, effects along gradients in elevation, soil moisture and light (Louda 1982, 1983; Louda and Rodman 1996). However, studies that examine how variation in insect herbivory across environmental gradients influences patterns of plant survival and reproduction remain relatively rare. Thus, we have few data with which to evaluate the general importance of differential insect herbivory as a potential mechanism determining plant distribution patterns.

In this study, I quantified patterns of insect herbivory on an annual forb, *Atriplex patula* var. *hastata* L., across a salt marsh tidal gradient and investigated the potential causes and consequences of the observed variation. In New England salt marshes, environmental conditions for plant growth are generally harshest at low and mid-marsh tidal elevations where frequent flooding results in high soil salinity and low soil oxygen availability (Bertness and Ellison 1987). A number of salt marsh plants, including *Atriplex*, are restricted to the mid and upper marsh zones due to their intolerance of the harsh physiological conditions in the low marsh zones (Bertness 1991; Hacker and Bertness 1999; Rand 2000). Within its physiological range, densities of *Atriplex* are highest towards the upper, terrestrial, border of the marsh where growing conditions are least harsh (Rand 2000). In other salt marsh systems, previous studies have demonstrated that salt marsh herbivores respond to changes in plant characteristics across tidal gradients (Hemminga and Soelen 1988; Hacker and Bertness 1995; Bowdish and Stiling 1998). Consequently, given the existence of a strong environmental gradient in New England salt marshes and evidence that *Atriplex* performance varies across this gradient, I predicted that herbivore pressure and impact on plants would vary across zones and thus play a role in generating patterns of plant distribution across the marsh. To evaluate this hypothesis, I addressed the following questions: (1) Does the extent of herbivore damage to *Atriplex* differ between two adjacent salt marsh zones that differ in abiotic environmental conditions? (2) Does the pattern of use reflect either herbivore response to differences in host-plant characteristics or differences in herbivore density? (3) Does insect damage to plants influence plant survival and reproduction and, if so, does this effect vary across zones?

Materials and methods

Study system

The study was carried out at sites within six salt marshes in Narragansett Bay, Rhode Island, USA from 1997 to 1999. Narragansett Bay has semi-diurnal tides and a tidal amplitude of 0.8–2.0 m. All sites are typical southern New England salt marshes characterized by a dense cover of grasses and rushes that form distinct zones across the elevation gradient (Niering and Warren 1980). The lower marsh is dominated by *Spartina alterniflora* Loisel., which is replaced by *Spartina patens* (Aiton) Muhl., and then *Juncus gerardi* Loisel. towards the terrestrial border of the marsh. The upland border is dominated by *Iva frutescens* L. All species will subsequently be referred to by their generic names, with the exception of the *Spartina* species. Each marsh zone spans approximately 10–15 cm in tidal elevation, leading to differences in flooding frequencies from an average of 18 days per month in the *S. patens* zone to less than 1 day per month in the high marsh (Hacker and Bertness 1999).

Atriplex is largely restricted to the mid (*Juncus*) and high (*Iva*) zones, since it is intolerant of harsh physical conditions in the low marsh (Hacker and Bertness 1999; Rand 2000). *Atriplex* is fed upon by a chrysomelid beetle, *Erynephala maritima* (Lec.), which specializes on salt marsh plants in the Chenopodiaceae (Blake 1936). *Erynephala* is by far the most important herbivore on *Atriplex* in this system, and it makes characteristic oval grazing marks that are easily distinguished from those of other herbivores (personal observation). Both larval and adult stages feed on *Atriplex* as well as on *Salicornia europaea* L., another annual forb found predominantly at low marsh elevations (Ellison 1987). Adults overwinter and lay eggs in the early spring. Larvae hatch and begin feeding on seedlings in mid-May, and adults feed on plants through the end of September (personal observation).

Survey of herbivore damage across zones

To determine whether herbivore damage to *Atriplex* plants varied systematically across adjacent salt marsh zones, beetle damage was censused in the mid (*Juncus*) and high (*Iva*) zones at six study sites, at 2-week intervals from mid-June to the mid-August 1999. Study sites included three mainland salt marshes (Rumstick Cove, Hundred Acre Cove, and Sapowet) and three sites on Prudence Island (Coggeshall Cove, Providence Point, and Nag Creek). Thirty randomly selected *Atriplex* plants were tagged along 500 m of shoreline in each zone at each site, and the number of leaves that was damaged or undamaged by *Erynephala* was counted on each plant on each census date.

Plant palatability and herbivore abundance

Variation in herbivore pressure across zones could reflect either herbivore response to differences in plant characteristics or differences in herbivore density. Field assays of herbivore feeding pressure and laboratory tests of herbivore feeding preference were done to evaluate the influence of differences in plant palatability on insect feeding. In addition, I performed surveys of insect occurrence to determine whether herbivore densities varied across zones.

Field herbivory assays

To assess herbivore feeding pressure across zones, in the absence of potential differences in plant characteristics related to growth under different environmental conditions, I used greenhouse-grown plants transferred to the field for short-term assays. *Atriplex* individuals were grown from seed in the greenhouse in Metromix potting medium in pine-cells (plastic planting cones 5 cm diameter by 20 cm depth) until the 10–12 leaf stage. Plants were placed into the mid (*Juncus*) and upper (*Iva*) zones at Rumstick Cove and Nag Creek (*n*=10 plants / zone / site), by removing a plug of marsh peat and inserting the entire pine-cell into the soil until it was flush with the substrate surface. Assay plants were left in place for 1-week intervals in the beginning of June and in the last week of July 1997. They were then collected and the number of damaged and undamaged leaves per plant was determined. The lack of tidal flooding during the short duration of each assay, and the controlled soil conditions within the pine-cells, likely minimized environmental stress effects on host plant traits across zones in this test.

Herbivore preference experiments

Feeding trials were conducted twice during the growing season to test whether herbivores had a preference among plants from the different zones. Larvae were tested on 9 July and 18 August and adult beetles on 26 July and 28 August 1997. On the day of each feeding trial, *Atriplex* plants were collected from the mid (*Juncus*) and high (*Iva*) zones from two sites, Coggeshall Cove and Nag Creek. Plants were brought back to the laboratory and one, randomly selected, undamaged leaf was removed from each plant. Leaves from plants collected in the *Juncus* and *Iva* zones were paired by size (leaf length) and placed into plastic petri dishes (8 cm diameter). Larvae and adult beetles were collected from patches of the alternate host, *Salicornia*, at each site on the same day as plants were collected. A single beetle was placed equidistant from each leaf within each petri dish and allowed to feed for 8 h. This feeding interval was chosen to give the herbivores time to select plants and consume measurable amounts of tissue, without depleting resources (the area consumed was generally less than 50% of any leaf). The area consumed was measured on each leaf using a millimeter grid. Thirty replicates were run during each trial, except for adult trials in August, which were limited to 15 replicates because adult beetles were rare in the field on this date.

Sampling plant and herbivore densities across zones

To determine whether herbivore abundance varied across zones, and how this was related to host plant density, surveys of plant and insect densities were conducted during peak herbivore activity (mid-summer) at Providence Point and Nag Creek on 15 July 1999. At each site, the total number of host plants (*Atriplex* and *Salicornia*) as well as beetle larvae and egg clusters were counted in randomly placed 0.25 m^2 quadrats in the low (*S. patens*), mid (*Juncus*) and high (*Iva*) zones (*n*=80 quadrats / zone / site). Insects were counted by visually searching both host plant species, as well as surrounding vegetation and the substrate surface, for larvae and adults within each 0.25 m^2 quadrat. Similarly egg clusters, which are laid on the tips of the blades of dominant grasses and rushes, were counted within quadrats.

Herbivore exclusion experiment

An herbivore exclusion experiment was carried out in the field to examine the effect of herbivores on plant survival and seed production across zones. *Atriplex* seedlings, collected from natural populations in May, were brought to the greenhouse at Brown University and watered with tap water for 3 days to reduce subsequent transplant shock. These seedlings were transplanted into randomly located plots along 200 m of shoreline in both the mid (*Juncus*) and high (*Iva*) zones at Rumstick Cove and Nag Creek in the middle of May 1997. Plants that died during the first week were replaced. Each seedling was randomly assigned to one of three experimental treatments (*n*=40 plants / treatment / zone / site): (1) insecticide spray (Safer Insecticidal Soap), (2) water spray (procedural control), and (3) no spray (unmanipulated control). Treated plants were sprayed with 2–3 ml of water or insecticide solution weekly. The total number of leaves, number of leaves damaged by the beetles, and plant survival were monitored every 2 weeks throughout the growing season (May through early September). At the end of the growing season, surviving plants were harvested. Flowers and fruits were counted and pooled to estimate fruit number. Individuals of this annual plant that did not survive to reproductive maturity were scored as producing zero fruits. Each *Atriplex* flower produces a single fruit consisting of two fleshy bracts surrounding a single seed. Thus, my measure of reproductive output is an estimate of the mean seed production per seedling transplanted in each treatment-by-zone combination.

Prior to the initiation of the field experiment, a greenhouse study was carried out to evaluate potential phytotoxic or enhancing effects of the insecticide on plant growth. Seeds were germinated in the greenhouse and seedlings (6–8 true leaves) were transplanted into plastic pine cells on 25 March 1997. Plants were watered daily and fertilized with a 20:40:20 NPK solution once every 2 weeks. Seedlings were randomly assigned to one of three treatments (*n*=20 seedlings / treatment) which were imposed on a weekly basis: (1) insecticide spray (Safer Insecticidal Soap), (2) water spray, and (3) no spray. Treated plants were sprayed with 2–3 ml of insecticide solution or water weekly. Plants were moved to randomly assigned new positions after spraying. Plants were harvested on 28 June, placed in a drying oven at 55°C for 1 week, and then weighed. Since this species sets seed erratically in a greenhouse environment, final biomass rather than seed production was used as a measure of plant performance.

Statistical analyses

Statistical analyses were carried out using JMP version 3.1 (SAS 1995). Data were transformed where necessary to meet assumptions of analysis of variance. All count data were ln (n+1) transformed and proportions were arcsine square root transformed.

Patterns of herbivore pressure between sites were analyzed using a type III two-way ANOVA, with site (random factor) and zone (fixed factor) as predictor variables. Post hoc contrast statements were used to compare least squares means between zones within each site. These tests were Bonferroni adjusted.

Larval and adult beetle preferences among leaves from plants collected from the high (*Iva*) or mid (*Juncus*) zones in feeding trials were examined using paired *t*-tests. Damage to plants placed across zones in each short-term field assay of herbivory was compared using a type III, two-way ANOVA, with site (random) and zone (fixed) as factors in the model. Analyses were conducted separately for each sampling date. Post hoc contrasts were used to compare least squares means between zones within each site. Numbers of herbivores and egg clusters within quadrats across the three marsh zones were converted to presence or absence per quadrat, due to the high frequency of zero values. Logistic regression analysis was used to test the null hypothesis that herbivore distribution (frequency of occurrence) was constant across zones. Where this analysis was significant, frequency of occurrence was compared between all zones (three comparisons using a chi-square analysis), and significance levels were Bonferroni adjusted to control for multiple tests.

Since herbivory was almost absent at Rumstick Cove in the year of the insecticide experiment, the two study sites were analyzed separately. Measurements of leaf damage and fruit number were analyzed using a two-way ANOVA for each site, with zone and insecticide treatment as factors in the model. The distribution of fruit number at Nag Creek was severely non-normal due to numerous zero values. Thus data were analyzed separately for each zone using a non-parametric median test, recommended for the sigmoidal distribution that was observed (SAS 1995). Cross-zonal comparisons were also made using a median test. Survivorship was analyzed using a logistic regression model on final data. Models were run for each site separately.

Results

Herbivore damage across zones

Percent leaf damage by beetles was consistently higher in the mid (*Juncus*) zone than the high (*Iva*) zone throughout the censusing interval when pooled across sites (Fig. 1 A). Differences in leaf damage across zones were analyzed for the second July census date (July 14 and 15), when herbivore damage was at its peak and before significant plant mortality in August. Damage to plants was significantly greater in the *Juncus* than *Iva* zones at all sites except one, where the trend was consistent with the pattern (main effect of Zone: $F_{1,5}=25.859$, $P=0.01$; Fig. 1B). However, the magnitude of the difference varied between sites as indicated by a significant site by zone interaction (Site×Zone: $F_{5,315}=3.981$, $P=0.001$). The level of herbivore pressure also varied between sites; at some sites percent leaf damage in the *Juncus* zone exceeded 70% compared to less than 5% at others (Site: $F_{5,315}=22.861$, $P=0.001$; Fig. 1B).

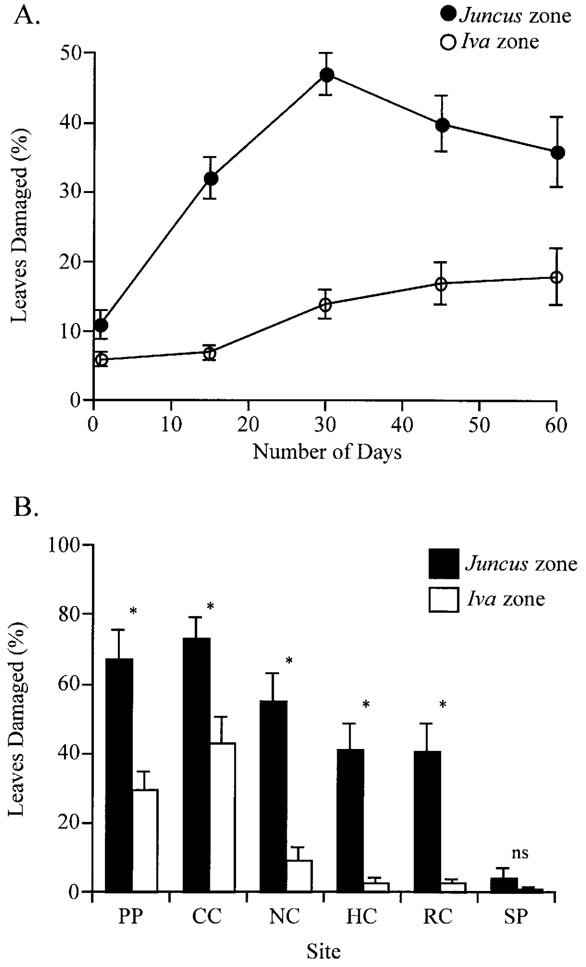

Fig. 1 **A** Herbivore damage to *Atriplex* across zones in mid-June through mid-August 1999. Each point represents a group mean ±1 SE, for each zone, across the six sites surveyed at each sampling date beginning on 15 June. **B** Herbivore damage to *Atriplex* across the mid (*Juncus*) and high (*Iva*) zones measured at the same six sites in mid-July. *Bars* represent means ±1 SE (n=30 plants / zone / site). *$P \leq 0.05$

Plant palatability and herbivore abundance

Damage to transplanted plants in the short-term field assays of herbivory was higher in the mid (*Juncus)* than the high (*Iva*) zone, except early at one site where overall damage was very low (Fig. 2). Early in the season (June assays), herbivore damage to plants was significantly greater in the mid (*Juncus*) zone than the high (*Iva*) zone at Nag Creek while almost no herbivory occurred at Rumstick Cove, leading to a significant site by zone interaction term (Table 1). Percent leaf damage to plants at Rumstick Cove was very low, less than 5% across both zones, compared with Nag Creek where per-

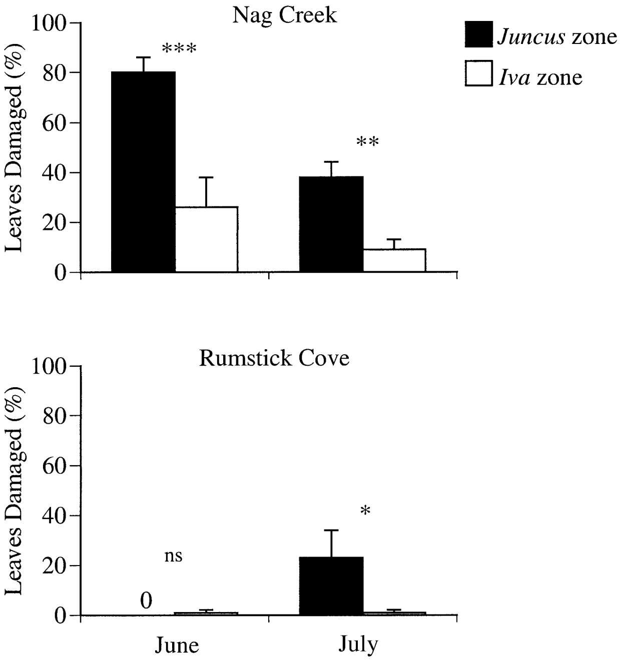

Fig. 2 Herbivore damage to greenhouse grown plants placed into the mid (*Juncus*) and high (*Iva*) zones for a singe week in June and July 1997. *Bars* represent means ±1 SE (n=10 plants / zone / site / month). Significance levels of post hoc contrasts for each between zone comparison are shown above bars. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

Table 1 Results of type III, two-way ANOVAs examining the effects of marsh zone [mid (*Juncus*) versus high (*Iva*)] on percent leaf damage to greenhouse grown plants placed into the marsh for one week at two sites in June and July 1997 (n=10 plants/zone/site/month)

	June			July		
Source	*df*	MS	*F*	*df*	MS	*F*
Site (*S*)	1	5.561	72.263***	1	0.323	3.524
Zone (*Z*)	1	1.352	0.834	1	1.585	204.593*
S×*Z*	1	1.622	21.07***	1	0.008	0.084
Error	34	0.077		31	0.092	

$^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$

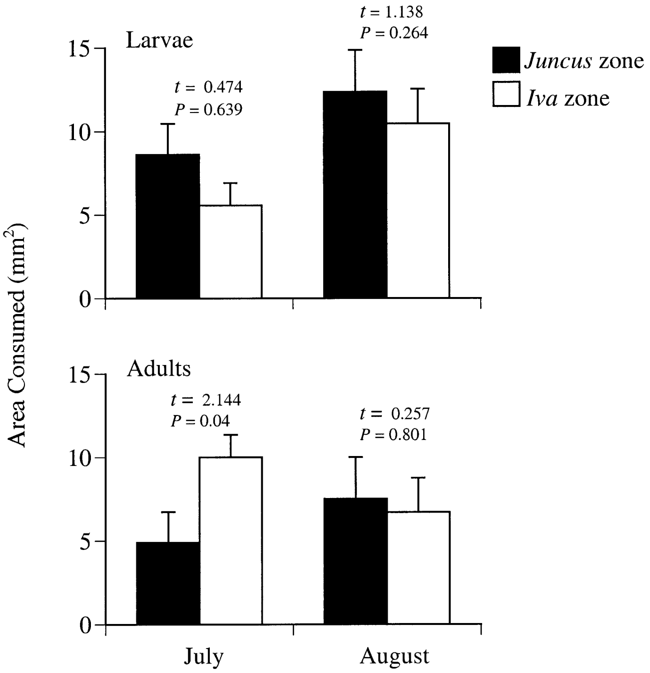

Fig. 3 Leaf area consumed by larval and adult beetles provided with a choice of *Atriplex* leaves collected from the mid (*Juncus*) or high (*Iva*) zones in early July and late August 1999. *Bars* represent means ± 1 SE. Results of paired t-tests for each trial are presented above bars

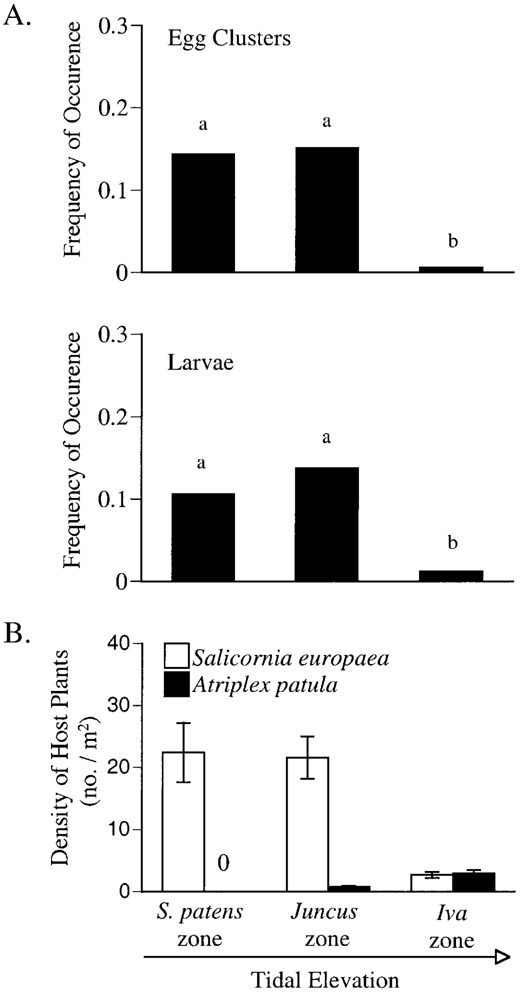

Fig. 4 **A** Distribution of beetle egg clusters and larvae across zones in July 1999. *Bars* represent frequency of occurrence measured on all vegetation in 0.25 m^2 quadrats across two sites (n=80 quadrats / zone / site). *Bars* with different letters differ significantly (χ^2, $P \leq 0.05$). **B** Distribution of host plants across marsh zones. *Bars* represent the mean ±1 SE number of plants per 0.25 m^2 quadrat across two sites (n=80 quadrats / zone / site)

cent leaf damage averaged 52% across zones and approached 80% in the *Juncus* zone. By late July damage to plants was significantly higher in the *Juncus* zone than the *Iva* zone at both sites, and damage levels did not vary significantly across sites (Fig. 2, Table 1).

In feeding preference experiments, the leaf area consumed by larvae did not significantly differ with zone of plant origin in either July or August (Fig. 3). Adult beetles consumed nearly twice as much leaf tissue on plants collected from the *Iva* zone in July, but there was no significant difference in August (Fig. 3).

Only two adult beetles were encountered during herbivore density surveys, thus analysis was not carried out for this life history stage. The frequency of occurrence of both larvae and egg clusters in 0.25 m^2 quadrats was significantly greater in the low (*S. patens*) and mid (*Juncus*) zones than at higher tidal elevations in the *Iva* zone (Logistic regression for larvae: Site χ^2=0.608 with P =0.435, Zone χ^2=15.105 with P=0.0005, an Site×Zone χ^2=0.193 with P=0.908; Logistic regression for egg clusters: Site χ^2=1.307 with P=0.242, Zone χ^2=23.918 with P=0.0001, and Site×Zone χ^2=0.854 with P=0.653; Fig. 4 A). The majority of the larvae (86%) were found on *Salicornia*. Despite overall low densities of larvae on *Atriplex*, larvae were found on a greater percentage of the plants growing in the *Juncus* zone (14.3%) than the *Iva* zone

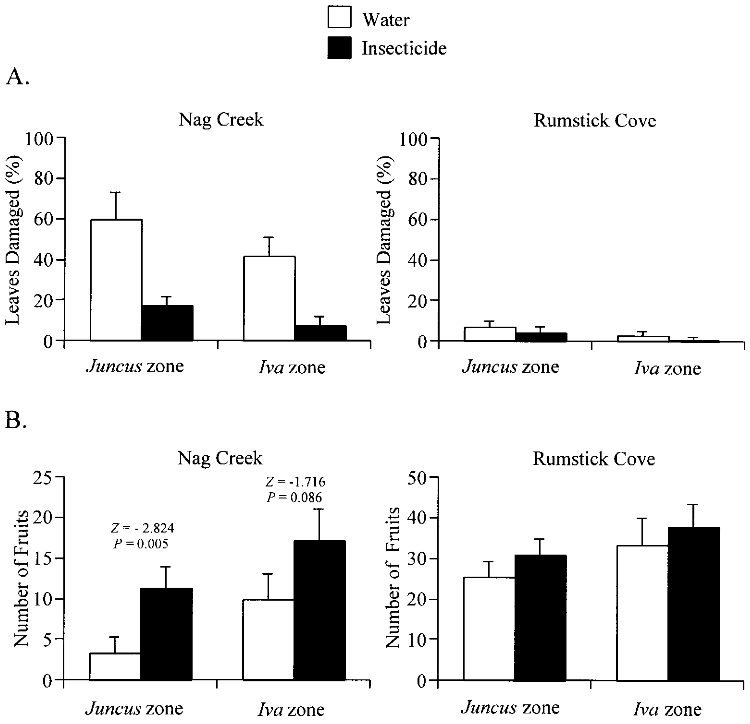

Fig. 5 **A** Herbivore damage to *Atriplex* plants across zones and insecticide treatments in the herbivore exclusion experiment at the time of peak damage in July 1997. *Bars* represent untransformed means ±1 SE (n=40 plants / zone / treatment / site). **B** Mean number (±1 SE) of fruits produced per seedling transplant across zones and insecticide treatments in the herbivore exclusion experiment. Results of a non-parametric median test are presented above bars for Nag Creek

Table 2 Summary of results of two-way ANOVAs examining effects of zone [mid (*Juncus*) versus high (*Iva*)] and insecticide treatment on percent leaf damage by herbivores and fruit production at Nag Creek and at Rumstick Cove. [~ analysis not performed due to non-normal distribution of data (see Materials and methods)]

	Herbivore damage			Fruit number		
Source	*df*	MS	*F*	*df*	MS	*F*
Nag Creek						
Zone	1	1.117	4.17*	~	~	~
Treatment	1	6.384	23.823***	~	~	~
Zone × Treatment	1	0.042	0.156	~	~	~
Error	93	0.268		~		
Rumstick Cove						
Zone	1	0.128	2.501	1	0.638	0.232
Treatment	1	0.0716	1.397	1	4.702	1.711
Zone × Treatment	1	0.004	0.072	1	1.301	0.473
Error	148	0.051		156	2.749	

$^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$

(2.5%). Patterns of host plant abundance varied dramatically across these same zones (Fig. 4B). *Salicornia*, an alternate host plant for the beetle, was over ten times as abundant as *Atriplex* overall, and its abundance peaked in the mid (*Juncus*) and low (*S. patens*) zones. *Atriplex* displayed the opposite pattern, with its highest densities in the upper *Iva* zone, and no individuals found in the low (*S. patens*) zone.

Herbivore exclusion

Results from the greenhouse study revealed that in the absence of herbivores, insecticide did not affect plant performance. There was no significant effect of treatment (sprayed with insecticide, sprayed with water, or controls) on final biomass (one-way ANOVA: $F_{2,\ 57}$=1.89, P=0.12) or the proportion of individuals flowering (χ^2=0.62, P=0.74).

In the field, no signifiant differences were found between unmanipulated control and procedural control (water) treatments in percent leaf damage (t=1.24, P=0.22), fruit number (t=0.88, P=0.38) or plant survival (χ^2=0.059, P=0.97). Hence, only water and insecticide treatments were compared in subsequent analyses. Neither treatment nor zone significantly affected herbivore damage to plants at Rumstick Cove, where herbivore pressure was always low, less than 10% (Fig. 5 A, Table 2). In contrast, percent leaf damage at Nag Creek was relatively high, exceeding 40%, in water treatments in both zones. Spraying plants with insecticide at this site significantly reduced levels of herbivore damage, by more than 75% (Fig. 5A, Table 2). Damage to *Atriplex* plants in the mid (*Juncus*) zone was signifi-

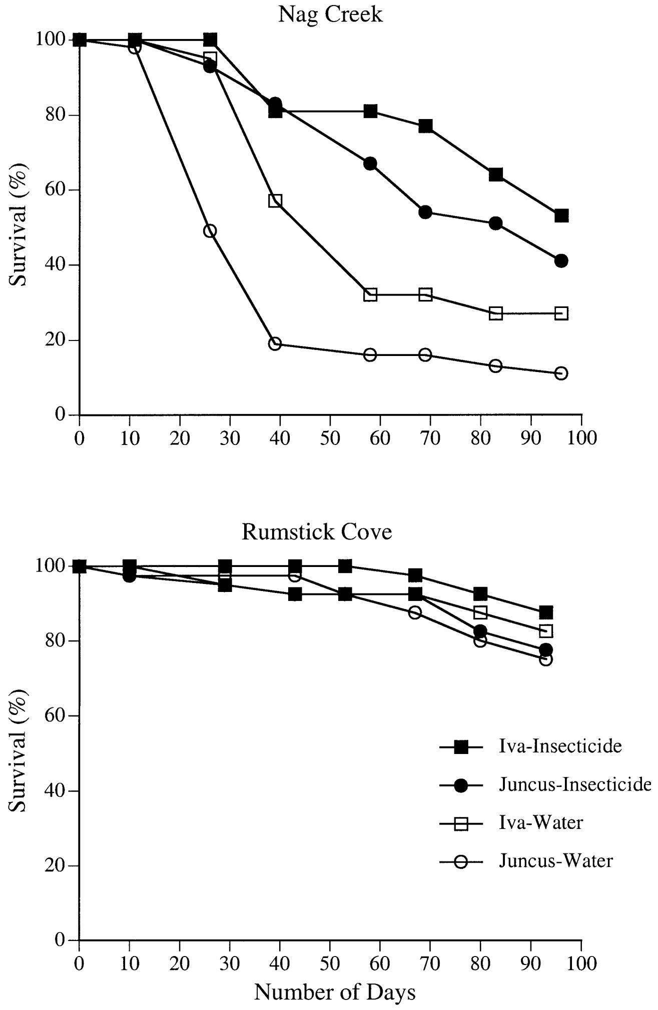

Fig. 6 *Atriplex* survival through time (beginning with the initiation of treatments on 17 June) across zones and insecticide treatments in the herbivore exclusion experiment

Table 3 Summary of results of logistic regression models examining effects of zone [mid (*Juncus*) versus high (*Iva*)] and insecticide treatment on the proportion of plants surviving to the end of the growing season at Nag Creek and at Rumstick Cove

Source	*df*	χ^2	*P*
Nag Creek			
Zone	1	1.509	0.2194
Treat	1	23.820	0.0001
Zone × Treatment	1	0.095	0.7580
Rumstick Cove			
Zone	1	0.269	0.6043
Treatment	1	0.736	0.3909
Zone × Treatment	1	1.502	0.2204

cantly greater than in the high (*Iva*) zone (Fig. 5A, Table 2).

Fruit production at Rumstick Cove, where herbivore pressure was low, did not significantly differ between treatments or zones, although there were trends toward lower production in the presence of herbivores and in the lower *Juncus* zone compared to the higher *Iva* zone (Fig. 5B, Table 2). Overall fruit production at Nag Creek tended to be lower in the *Juncus* zone (Z=1.791, P=0.073), and the impact of herbivores on seed production was zone-specific at this site. Herbivores significantly reduced the number of fruits in the *Juncus* zone by over 70% (Fig. 5B). The same trend was observed in the *Iva* zone but this was not significant (Fig. 5B).

Plant survival was markedly higher at Rumstick Cove, where herbivory was low, than at Nag Creek (Fig. 6). Plant survival at Rumstick Cove did not differ across herbivore treatments or zones (Table 3). In contrast at Nag Creek, where herbivory was higher, survival was significantly (more than 50%) greater when herbivores were excluded, and again, there was no significant effect of zone on survival (Fig. 6, Table 3). The overall effect of herbivores on survival did not significantly vary across zones, although there was a trend toward a greater effect in the mid (*Juncus*) than the high (*Iva*) zone (Fig. 6, Table 3).

Discussion

Patterns and potential causes of variation in herbivory

Herbivore damage to plants varied among sites and between salt marsh zones. Despite variation in the level of herbivore pressure, damage to plants was significantly greater in the mid-marsh (*Juncus*) zone than in the high-marsh (*Iva*) zone at five of the six surveyed sites, and the pattern was consistent at the sixth site. This strong zonal pattern in herbivore pressure was also consistent through time (Fig. 1). Interestingly, results from both the field herbivore assays and laboratory herbivore preference experiments strongly suggest that differences in host plant palatability were not responsible for generating the observed differences in herbivore damage across zones. Similar, greenhouse-grown, plants placed into the marsh for single week assays experienced the same patterns of damage as naturally occurring plants within each zone. Therefore even when plant quality was homogenized, herbivore damage was greater in the mid (*Juncus*) portion of the tidal gradient than in the upper (*Iva*) portion. Furthermore, neither larvae nor adult beetles showed a preference for leaves collected from the *Juncus* zone over the *Iva* zone either early or late in the growing season, and the opposite pattern was observed in one adult trial. Thus, spatial patterns of herbivore damage cannot be explained by environmentally driven differences in host plant palatability in this study. This contrasts with results of many earlier studies (Louda et al. 1987; Collinge and Louda 1988; Louda and Collinge 1992; Cobb et al. 1997).

Alternately, surveys of herbivore abundance demonstrated that the frequency of occurrence of larvae in 0.25 m^2 quadrats was more than five times higher in the low (*S. patens*) and mid (*Juncus*) zones than in the higher (*Iva*) zone (Fig. 4). A similar pattern was observed in the frequency of occurrence of egg clusters across this same gradient. While the majority of the larvae were found on *Salicornia*, larvae are quite mobile and frequently move between plants (personal observation). Furthermore, previous studies have demonstrated that *Atriplex* experiences much higher rates of herbivore damage when growing in association with *Salicornia* than in its absence (Rand 1999). Thus the increased abundance of herbivores at lower tidal levels most likely results in a spillover effect generating the observed patterns of increased larval occurrence on, and greater damage to, *Atriplex* in areas of high *Salicornia* density. Such associational susceptibility, or associational damage, has been found to be an important determinant of herbivore pressure in other plant-insect systems (Thomas 1986; Karban 1997; White and Whitham 2000), and is likely a major factor underlying the observed pattern of differential plant damage across zones in this study. However, a direct test of this hypothesis would require large-scale removal of *Salicornia* from the lower marsh. Finally, although differences in herbivore densities could themselves reflect the attraction of mobile herbivores to stressed plants in a given portion of the gradient, the lack of an herbivore preference for plant tissue from the more stressful marsh zone indicates that this is unlikely.

Although determining the factors underlying differences in insect abundance across the marsh was beyond the scope of the study, such differences could reflect direct responses of herbivores to the abiotic environment, variation in rates of predation across the gradient, or differences in overall resource availability. The most plausible explanation in this case is resource availability, that herbivore densities reflect the total abundance of host plants. Total host plant density is highest in the low (*S. patens*) and mid (*Juncus*) zones because of the presence of *Salicornia*, which is more than 10 times as abundant as *Atriplex* (Fig. 4B). Herbivorous insects are commonly found to be more abundant in areas of high host plant density (Root 1972; Kareiva 1983; Bach 1994). Thus, it is likely that high absolute densities of plant resources, driven by the presence of *Salicornia*, maintain herbivores at greater densities in the low marsh, leading to increased use of *Atriplex* there. The influence of changes in vegetation composition along gradients, particularly densities of alternative host plants, as a potential mechanism generating variation in herbivore abundance/pressure has rarely been examined (but see Parker and Root 1981). These results suggest that it warrants more attention.

Variation in herbivore abundance or damage across tidal or salinity gradients has been observed in insect-plant assemblages in other salt marsh studies (Foster 1984; Hemminga and Soelen 1988, 1992; Hacker and Bertness 1995; Bowdish and Stiling 1998) and insects and crabs in mangrove studies (Smith 1987; Ellison and Farnsworth 1993; Sousa and Mitchell 1999; Osborne and Smith 1990). In some of these studies herbivore abundance or plant damage was found to be highest in the more stressful portion of the gradient for plant growth (Ellison and Farnsworth 1993; Hacker and Bertness 1995), as in the present study. However, in other cases the opposite pattern was observed (Hemminga and Soelen 1988). The lack of a consistent pattern likely reflects both the complexity of most ecological gradients, with multiple factors varying in tandem, and the fact that “stress” affects species to different degrees depending on their unique biological tolerances. Furthermore, the relationship between stress and herbivory can result from several different underlying direct or indirect mechanisms. First, two of the above studies invoked plant quality as a potentially important factor driving insect distribution patterns across stress gradients. In one case insects were found to respond negatively to salinity-induced changes in their hosts (Hemminga and Soelen 1988), while in another case nitrogen availability was found to be more important than salt stress in determining insect densities on host plants (Bowdish and Stiling 1998). Second, herbivores may directly respond to the underlying environmental conditions, such as in some mangrove systems where crab seed predators prefer lower to higher tidal elevations (Sousa and Mitchell 1999). Third, herbivore densities may also reflect changes in predation pressure on them across gradients (Hacker and Bertness 1995). Finally, this study suggests that changes in host plant composition may influence patterns of herbivore density and impact across environmental gradients. Thus, ecological complexity may preclude the development of a comprehensive predictive framework relating environmental stress and herbivory.

Effects of herbivores on host-plant performance

Differences in herbivore pressure between adjacent habitats or across gradients, such as those observed in this study, have the potential to influence patterns of host plant distribution and abundance if herbivores significantly impact key plant demographic parameters (Harper 1969; Louda 1982, 1983; Louda and Rodman 1996). Herbivore damage to plants in the insect exclusion experiment varied between the two experimental sites. These two sites represent extremes along the continuum of herbivore damage observed in the multi-site survey of naturally occurring plants (Figs. 1, 5A). Transplants at Rumstick Cove experienced damage similar to the lowest levels observed in the multi-site survey (<10% of leaves damaged), whereas plants at Nag Creek experienced damage levels similar to the more highly impacted sites (>60% of leaves damaged in the mid (*Juncus*) zone and >40% in the high (*Iva*) zone). At Rumstick Cove, where insect damage was low, herbivores did not affect plant survival or reproductive output, and there were no differences in herbivore pressure across zones. In contrast at Nag Creek, where damage to plants was high, herbivory was significantly higher in the mid (*Juncus*) than the high (*Iva)* zone. Yet the magnitude of the difference in herbivore pressure between zones at Nag Creek was lower than at most of the survey sites, where damage tended to be at least 50% lower in the *Juncus* zone than the *Iva* zone (Fig. 1B). Thus the differential effect of herbivores on plant performance across zones is likely often stronger than that observed in the herbivore exclusion experiment.

Clearly herbivorous leaf feeding beetles can have a large influence on host plant densities when herbivore abundance is high. Overall, herbivores dramatically reduced *Atriplex* survival at Nag Creek, by over 70% in the mid (*Juncus*) zone and just less than 50% in the high (*Iva*) zone. Patterns of plant survival were influenced much more by the effects of herbivores than differences in environmental conditions between marsh zones (Fig. 6). However, overall, abiotic stress likely contributed to *Atriplex* mortality as survival was relatively low even in the absence of herbivores.

Herbivores also reduced seed production by *Atriplex* in the mid (*Juncus*) zone at Nag Creek. Fruit number there was 66% lower than it would have been in the absence of herbivores (Fig. 5). When herbivores were excluded, fruit production in the *Juncus* zone increased to levels similar to those found higher in the marsh in the *Iva* zone, where it did not significantly differ between treatments. *Atriplex* is an annual plant without a substantial seed bank, and its seedling recruitment has been shown to be seed limited (Rand 2000). Therefore, reductions in seed production in a given year, resulting from the influence of insect herbivores on either plant survival or reproductive output, will reduce seedling recruitment the following year. Thus, herbivores likely limit *Atriplex* population densities at the lower portion of its range.

The effect of herbivores varied between the two intensively studied sites, as is commonly observed in studies of insect herbivory (Huntly 1991; Bach 1994; Bevill et al. 1999). However, populations of beetles at Rumstick Cove have been observed to reach high densities every 2–3 years (personal observation). Furthermore, the levels of herbivore damage documented in the experiment at Nag Creek, where herbivores dramatically impacted plant survival and reproductive output, were similar to those found at the majority of sites in the survey of herbivore damage in 1999 (Figs. 1, 5A). Thus, cumulatively the data suggest that levels of herbivore damage are commonly high enough to have a major impact on plant survival and seed production. The large impact of beetle herbivores on *Atriplex* survival, coupled with the consistent pattern of differential damage to plants across zones, suggest that herbivores may be an important factor contributing to the differential abundance of *Atriplex* across zones in salt marsh habitats. These results reinforce those of other studies that suggest that consumers can be important determinants of plant distribution and abundance across environmental gradients (Louda 1982, 1983, 1989; Smith 1987; Louda and Rodman 1996). This study further lends support to the accumulating evidence that herbivores can play an important, yet under appreciated, role in salt marsh systems (Pennings and Bertness 2000).

Acknowledgements Mark Bertness, John Bruno, Svata Louda, Todd Minchinton, Doug Morse, Matt Paulson, Steve Pennings, Annie Schmitt and three anonymous reviewers provided valuable comments and suggestions on the manuscript. Paul Schmidt and Sammy Hotimsky provided essential field assistance at critical moments. I also thank Al Beck for facilitating the use of field sites on the Narragansett Bay National Estuarine Research Reserve, and Fred Jackson for maintaining plants in the greenhouse. This research was funded in part by a NSF Doctoral Dissertation Improvement Grant (DEB-9801521). Further support was provided by National Science Foundation and A.W. Mellon Foundation grants to M.D. Bertness.

References

Bach CE (1994) Effects of a specialist herbivore (*Altica subplicata*) on *Salix cordata* and sand dune succession. Ecol Monogr 64:423–445

Bertness MD (1991) Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:125–137

Bertness MD, Ellison AM (1987) Determinants of pattern in a New England salt marsh plant community. Ecol Monogr 57:129–147

Bevill RL, Louda SM, Stanforth LM (1999) Protection from natural enemies in managing rare plant species. Conserv Biol 13:1323–1331

Blake DH (1936) A redisposition of *Monoxia puncticollis* and allied species. J Wash Acad Sci 26:423–430

Bowdish TI, Stiling P (1998) The influence of salt and nitrogen on herbivore abundance: direct and indirect effects. Oecologia 113:400–405

Cobb NS, Mopper S, Gehring CA, Caouette M, Christensen KM, Whitham TG (1997) Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. Oecologia 109:389–397

Collinge SK, Louda SM (1988) Herbivory by leaf miners in response to experimental shading of a native crucifer. Oecologia 75:559–566

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence form field experiments. In: Cody ML, Diamond J (eds) Ecology and evolution of communities. Belknap Press of Harvard University Press, Harvard, Mass. pp 460–490

Crawley MJ (1997) Plant-herbivore dynamics. In: Crawley MJ (ed) Plant ecology. Blackwell, London, pp 401–474

Dunson WA, Travis J (1991) The role of abiotic factors in community organization. Am Nat 138:1067–1091

Ellison AM (1987) Effects of competition, disturbance, and herbivory on *Salicornia europaea*. Ecology 68:576–586

Ellison AM, Farnsworth EJ (1993) Seedling survivorship, growth, and response to disturbance in Belizean mangal. Am J Bot 80:1137–1145

Foster WA (1984) The distribution of the sea-lavender aphid *Staticobium staticis* on a marine salt mash and its effect on host plant fitness. Oikos 42:97–104

Hacker SD, Bertness MD (1995) A herbivore paradox: why salt marsh aphids live on poor quality plants. Am Nat 145: 192–210

Hacker SD, Bertness MD (1999) Experimental evidence for factors maintaining salt marsh plant species diversity in a New England salt marsh. Ecology 80:2064–2073

Harper JL (1969) The role of predation in vegetation diversity. Brookhaven Symp Biol 22:48–62

Harper JL (1977) Population biology of plants. Academic Press, New York

Hemminga MA, van Soelen J (1988) Estuarine gradients and the growth and development of *Agapanthia villosoviridescen*s (Coleoptera), a stem borer of the salt marsh halophyte *Aster tripolium*. Oecologia 77:307–312

Hemminga MA, van Soelen J (1992) The performance of the leaf mining microlepidopteran *Bucculatrix maritime* (Stt.) on the salt marsh halophyte, *Aster tripolium* (L.), exposed to different salinity conditions. Oecologia 89:422–427

Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. Annu Rev Ecol Syst 22:477–503

Jones CG, Coleman JS (1991) Plant stress and insect herbivory: toward an integrated perspective. In: Mooney HA, Winner WE, Pell EJ, Chu E (eds) Response of plants to multiple stresses. Academic Press, New York, pp 249–247

Karban R (1997) Neighborhood affects a plant's risk of herbivory and subsequent success. Ecol Entomol 22:433–439

Kareiva P (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 259–289

Larrson S (1989) Stressful times for the plant stress-insect performance hypothesis. Oikos 65:277–283

Lewis AC (1984) Plant quality and grasshopper feeding: effects of sunflower condition on preference and performance in *Melanopus defferentialis*. Ecology 63:836–843

Louda SM (1982) Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. Ecol Monogr 52:25–41

Louda SM (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Halplopappus venetus* (Asteraceae), along a climatic gradient. Ecology 64:511–521

Louda SM (1989) Differential predation pressure: a general mechanism for structuring plant communities along complex environmental gradients. Trends Ecol Evol 4:158–159

Louda SM, Collinge SK (1992) Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. Ecology 73:153–169

Louda SM, Potvin MA (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. Ecology 76:229–245

Louda SM, Rodman JE (1996) Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, Bittercress). J Ecol 84:229–237

Louda SM, Dixon PM, Huntly NJ (1987) Herbivory in sun versus shade at a natural meadow-woodland ecotone in the Rocky Mountains. Vegetatio 72:141–149

Louda SM, Keeler KH, Holt RD (1990) Herbivore influences on plant performance and competitive interactions. In: Grace JB, Tilman D (eds) Perspectives in plant competition. Academic Press, New York, pp 413–444

Mattson WJ, Hack RA (1987) The role of drought in the outbreak of plant-eating insects. BioScience 37:110–118

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57

Menge BA, Sutherland JP (1987) Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress. Am Nat 130:730–757

Niering WA, Warren RS (1980) Vegetation patterns and processes in New England salt marshes. BioScience 30:301–307

Osborne K, Smith TJ (1990) Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegetatio 89:1–6

Parker MA, Root RB (1981) Insect herbivores limit the habitat distribution of a native composite, *Machaeranthera canescens*. Ecology 62:1390–1392

Pennings SC, Bertness MD (2000) Salt mash communities. In: Bertness MD, Hay ME, Gaines SD (eds) Marine community ecology. Sinauer, Sunderland, Mass. pp 1–27

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

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

Rand TA (2000) Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. J Ecol 88:608–621

Reynolds BC, Crossley DA (1997) Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. Environ Entomol 26:1232–1239

Rhoades DF (1979) Evolution of plant chemical defenses against herbivores. In: Rosenthal GA, Janzen DH (eds) Herbivores: their interaction with secondary plant metabolites. Academic Press, New York, pp 3–54

Rhoades DF (1983) Herbivore population dynamics and plant chemistry. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 155–220

Root RB (1972) Organization of plant arthropod associations in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 43:95–124

SAS (1995) JMP statistics and graphics guide, version 3.1. SAS Institute, Cary, N.C.

Smith TJ (1987) Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. Estuar Coast Shelf Sci 25:43–52

Sousa WP, Mitchell BJ (1999) The effect of seed predators on plant distributions: is there a general pattern in mangroves? Oikos 86:55–66

Thomas CD (1986) Butterfly larvae reduce host plant survival in vicinity of alternative host species. Oecologia 70:113–117

Waring RH, Pitman GB (1985) Modifying lodgepole pine (*Pinus contorta*) stands to change susceptibility to mountain pine beetle (*Dendroctonus ponderosae*) attack. Ecology 66:889–897

White JA, Whitham TG (2000) Associational susceptibility of cottonwood to a box elder herbivore. Ecology 81:1795–1803

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105