

## THE INFLUENCE OF A SALINITY AND NUTRIENT GRADIENT ON COASTAL VS. UPLAND TRITROPHIC COMPLEXES

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**Abstract.** We examined the relative strengths of top-down and bottom-up effects acting on insect herbivores feeding on five species of plants growing in coastal or upland regions of a Florida salt marsh. Three of the plant species, *Borrchia frutescens*, *Coccoloba uvifera*, and *Baccharis halimifolia*, grew close to the shore, while the two remaining species, *Myrica cerifera* and *Persea borbonia*, grew in upland areas with lower salinity and no tidal input. For each species, we added nitrogen fertilizer and reduced parasitism with sticky traps in a fully factorial design, and assessed the relative impacts of these bottom-up and top-down manipulations on the most common herbivores of each plant. We then used a within-study meta-analysis to integrate the results and quantitatively compare the strengths of top-down and bottom-up effects on the herbivores of these coastal and upland plants.

Both fertilization and reduction of parasitism resulted in significant increases in herbivore densities, and the effects of these treatments were only slightly more pronounced for herbivores of the upland plant species than the coastal plant species. The greatest difference, however, between coastal and upland systems was in the strength of the interaction between nutrients and parasitism. Fertilization strongly increased the effects of parasitism for herbivores of upland plants, but not coastal plants. Correlations between effect sizes and ambient salinity and foliar nitrogen levels showed that environmental stress levels may be principally responsible for the strength of interaction between bottom-up and top-down forces, but nutrient levels likely play a lesser role.

**Key words:** bottom-up; coastal gradient; fertilization; food chain; parasitoid; plant–insect interaction; top-down.

### INTRODUCTION

Ecologists have begun to appreciate the potential for abiotic heterogeneity to dramatically influence the relative importance of top-down and bottom-up forces (Chase 1996, Bowdish and Stiling 1998, Denno et al. 2002, Moon and Stiling 2002a). In spite of more than 700 studies addressing the roles of top-down and bottom-up effects published in the last decade, however, more questions have been generated than answered. While it is clear that more empirical data on the interplay between environment and trophic dynamics are still needed, the approaches we take will play a pivotal role in our ability to generalize across study systems (Halaj and Wise 2001, Hunter 2001). The majority of studies examining trophic relationships to date have focused on a single species or study system. As such, syntheses of trophic dynamics have consisted largely of qualitative comparisons among different studies, in which idiosyncrasies in both methodology and study system confound our ability to draw general conclusions (Hunter 2001). For this reason, we chose to take a multi-species approach to the study of top-down and bottom-up forces by employing identical experimental

design and methodology to examine five tritrophic systems along an environmental gradient.

Two of the environmental factors that have received the most attention with regard to their potential impact on trophic relationships are nutrient availability and environmental stress (Fretwell 1977, Menge and Sutherland 1976, 1987, Oksanen et al. 1981). One of the most frequently tested hypotheses in trophic ecology is that the strength of top-down forces increases with increasing nutrient and productivity levels (e.g., Stiling and Rossi 1997, Uriarte and Schmitz 1998, Forkner and Hunter 2000, Chase 2003). In spite of the attention this hypothesis has received, we have yet to reach a consensus, perhaps because other factors, both abiotic and biotic, modify the effects of nutrients and productivity (Ritchie 2000, Denno et al. 2002, Gratton and Denno 2003). Environmental stress is also believed to be an important determinant of trophic relationships, and it has been predicted that increasing levels of stress will result in greater importance of bottom-up processes (Menge and Sutherland 1976, Menge et al. 1995). The role of environmental stress, although important in trophic dynamic theory, has received considerably less attention than the role of nutrients. Nevertheless, stress, most frequently in the form of salinity or drought stress, has been shown in a number of studies to significantly impact the bottom-up and top-down influences on insect herbivores (Salim et al. 1990, War-

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ing and Cobb 1992, Bowdish and Stiling 1998, Moon and Stiling 2000, 2002a, c).

A powerful, although underused tool with which to examine the interactions between bottom-up, top-down, and abiotic forces is conducting experiments along natural environmental gradients (Preszler and Boecklen 1996, Chase 2003). Conducting factorial field experiments along the coastal-upland transition may be particularly valuable, because in these habitats there are often gradients of both nutrients and environmental stress (Adam 1990). Plants growing closer to the shore may experience soil pore water salinities that are 15–40‰ greater than salinity levels experienced by upland plants (D. C. Moon and P. Stiling, *unpublished data*). Coastal plants may also benefit from allochthonous nutrient input from marine systems (Polis and Hurd 1995, 1996), and coastal plants at our field site typically have higher foliar nitrogen concentrations than upland plants (D. C. Moon and P. Stiling, *unpublished data*). By imposing experimental manipulations on multiple tritrophic complexes along this gradient, we wished to examine how the relative importance of increasing plant quality by fertilization and decreasing parasitism by removing parasitoids is influenced by concurrent gradients in salinity and nutrient levels.

Simultaneous examination of multiple tritrophic systems will allow for a qualitative comparison among systems, but another tool must be used in order to quantitatively integrate the results of these separate studies. One of the most powerful tools available for quantitatively synthesizing the results of multiple experiments is meta-analysis (Hedges and Olkin 1985, Gurevitch and Hedges 1993). Meta-analysis has been used with increasing frequency by ecologists in recent years, and has been used to generate a new, integrated perspective on such issues as the importance of herbivory (Bigger and Marvier 1998), the interaction between competition and predation (Gurevitch et al. 2000), and the frequency and strength of aquatic (Brett and Goldman 1996) and terrestrial trophic cascades (Schmitz et al. 2000, Shurin et al. 2002). In this study, a factorial meta-analysis (Gurevitch et al. 2000) was used to quantitatively integrate the results obtained from the five tritrophic systems examined. This new technique, designed to synthesize the results of factorial experiments, generates effect sizes for main effects as well as the interactions between main effects (Gurevitch et al. 2000). Through the use of factorial meta-analysis, we explicitly tested how the importance of plant quality, parasitism, and the interaction between the two differ between coastal and upland systems.

#### METHODS

This study was performed on the coast of the Gulf of Mexico at Fort DeSoto Park in Pinellas County, Florida. We selected five of the most common plant species at our field site, *Borrchia frutescens*, *Coccoloba uvifera*, *Baccharis halimifolia*, *Myrica cerifera*,

and *Persea borbonia* for this study. Of the five host plant species, three (*Borrchia*, *Coccoloba*, and *Baccharis*) grew in more coastal areas, 30 m or less from shore, while two (*Myrica* and *Persea*) grew in upland hammocks at least 50 m from shore. All of these plant species support multiple species and guilds of herbivores, and in this study we examined the abundance of the three most common herbivores on each plant species (Table 1). All of the herbivores studied experience significant mortality from parasitoid attack, while predation from birds and spiders is a variable, but less frequent occurrence, accounting for no more than 5% of mortality. In Florida, all of these herbivore species have multiple generations between March and September when abundances are greatest. Details regarding the natural history of the species examined in this study can be found in digital Appendix A.

In January 2002, we established 16 1.5 × 1.5 m plots of *Borrchia*, and chose 16 *Coccoloba* plants and 16 *Baccharis* plants. All of these plants and plots were within ~30 m of shore. We then selected 16 plants each of *Myrica* and *Persea* that were ~80–100 m from shore. We chose plants from each species that were of approximately the same size; 1.5–2.0 m for *Coccoloba* and *Myrica*, and 2.0–2.5 m for *Baccharis* and *Persea*. All plants and plots were separated from one another by at least 2 m.

On 1 February 2002, we applied fertilization and parasitoid-removal treatments randomly to plants (or plots for *Borrchia*) of each species in a 2 × 2 factorial design, with four replicates per treatment combination. For *Borrchia*, fertilization treatments consisted of 200 g per plot of granular urea-based nitrogen fertilizer (46-0-0 NPK) applied to half of the plots. The same quantity of fertilizer was applied to half of each individual of the smaller species, *Coccoloba* and *Myrica*. For the larger species, *Baccharis* and *Persea*, we applied 350 g of the same fertilizer. Thus, the amount of fertilizer applied to each species was standardized, but adjusted for differences in biomass between species. Fertilizer was applied twice during the study, once on 1 February and once in May, approximately at the midpoint of the study. This fertilization regime successfully increased foliar nitrogen concentration of the plants of each species to approximately maximum naturally occurring levels (Moon and Stiling 2002a; D. C. Moon and P. Stiling, *unpublished manuscript*).

Parasitoid removal treatments consisted of adding 13 × 8 cm yellow Sticky Strips traps (Gempler's, Belleville, Wisconsin, USA) to half of the plants or plots of each species (Moon and Stiling 2002a, b, c). Traps were changed every other week to ensure that they remained sticky. For *Borrchia*, we used the same density of traps, 5 per plot, we had used in previous experiments (Moon and Stiling 2002a, b, c). We applied the same number of traps (6–7) per plant to half of the individuals of *Coccoloba* and *Myrica*. For the larger species, *Baccharis* and *Persea*, we increased the num-

TABLE 1. The three most common insect herbivores, along with their classification by guild and primary hymenopteran parasitoid, for five host plant species along a coastal–upland gradient.

Herbivore species, by host plant	Feeding guild	Primary hymenopteran parasitoid
<i>Borrchia frutescens</i> (Asteraceae)		
<i>Pissonotus quadripustulatus</i> (Homoptera: Delphacidae)	phloem feeder	<i>Anagrus</i> sp. nr <i>armatus</i> (Mymaridae)
<i>Asphondylia borrichiae</i> (Diptera: Cecidomyiidae)	gall maker	<i>Torymus umbilicatus</i> (Torymidae)
<i>Argyresthia</i> sp. (Lepidoptera: Argyresthiidae)	stem borer	unidentified species (Eulophidae)
<i>Coccoloba uvifera</i> (Polygonaceae)		
Leaf miner species one (Lepidoptera: Nepticulidae)	leaf miner	<i>Closterocerus cinctipennis</i> (Eulophidae)
Leaf miner species two (Lepidoptera: Nepticulidae)	leaf miner	<i>Aprostocetus</i> sp. (Eulophidae)
<i>Hexeris enhydri</i> (Lepidoptera: Thyrididae)	stem borer	unidentified species (Braconidae)
<i>Baccharis halimifolia</i> (Asteraceae)		
<i>Neolasioptera lathamii</i> (Diptera: Cecidomyiidae)	gall maker	<i>Torymoides sulcius</i> (Torymidae)
<i>Liriomyza trifolii</i> (Diptera: Agromyzidae)	leaf miner	<i>Closterocerus</i> sp. (Eulophidae)
<i>Amauromyza maculosa</i> (Diptera: Agromyzidae)	leaf miner	<i>Neochrysocharis</i> sp. (Eulophidae)
<i>Persea borbonia</i> (Lauraceae)		
<i>Phyllocnistis magnoliella</i> (Lepidoptera: Gracilariidae)	leaf miner	unidentified species (Eulophidae)
<i>Trioza magnoliae</i> (Homoptera: Psyllidae)	gall maker	<i>Psyllaephagus</i> sp. (Encyrtidae)
<i>Urodus parvula</i> (Lepidoptera: Yponomeutidae)	leaf chewer	unidentified species (Encyrtidae)
<i>Myrica cerifera</i> (Myricaceae)		
<i>Nepticula myricifoliella</i> (Lepidoptera: Nepticulidae)	leaf miner	<i>Zagrammosoma americanum</i> (Eulophidae)
Leaf miner species two (Lepidoptera: Nepticulidae)	leaf miner	unidentified species (Eulophidae)
Hesperiid leaf tier (Lepidoptera: Hesperidae)	leaf tier	unidentified species (Braconidae)

ber of traps to 7 or 8 depending upon the size of the individual. Pre-treatment data were collected on 1 February 2002, and this was followed immediately by application of fertilizer and positioning of sticky traps. The experiments were then maintained through September 2002, when insect densities declined.

We measured the interstitial soil salinity at a depth of 15 cm in each plot of *Borrchia* and at the base of each individual of the other species using an Aquaterr Instruments model 200-48 soil meter (Aquaterr Instruments Incorporated, Costa Mesa, California, USA). We also measured the nitrogen content of leaves from each species in July. A mature undamaged leaf was collected from each of ten randomly selected branches from each individual plant of *Coccoloba*, *Baccharis*, *Myrica*, and *Persea*, and ten randomly selected *Borrchia* stems in each plot. Leaves were then dried, ground in a Wiley mill, and analyzed for foliar nitrogen (expressed as percentage of dry mass) using a CE Instruments NC2100 CN Analyzer (CE Elantech, Incorporated, Lakewood, New Jersey, USA).

In order to assess the effects of top-down and bottom-up manipulations on the 15 herbivore species, we conducted monthly field counts of insect densities. For the herbivores feeding on *Borrchia*, we counted the number of *Pissonotus* planthoppers per 20 stems, *Asphondylia* galls per 200 stems, and *Argyresthia* stem borers per 50 stems on each plot. For *Coccoloba*, the number of leaf miners per 10 leaves, and *Hexeris* borers per 50 leaf nodes were counted. We examined 100 *Baccharis* branch terminals for *Neolasioptera lathamii* galls, and 100 leaves for *Liriomyza* and *Amauromyza* leaf miners each month. Densities of all herbivores on

*Myrica* and *Persea* were assessed by examining 100 leaves per plant of all individuals of each species. All insect densities were summed over the eight months of the study for data analysis.

Parasitism rates, expressed as percentages, were assessed for 11 of the 15 herbivore species. Parasitism of leaf miners and gall makers was assessed by examining mines and galls for emergence holes throughout the study and noting whether the holes were made by herbivores or parasitoids as described in Appendix A. Parasitism of *Pissonotus* eggs was conducted once in June. Ten randomly selected *Borrchia* stems were collected from each plot and returned to the lab where they were dissected under a microscope, and the percentage of dark-colored parasitized eggs was recorded (Moon and Stiling 2000). Parasitism rates of the four remaining herbivore species, *Argyresthia* sp. on *Borrchia*, *Hexeris enhydri* borers on *Coccoloba*, hesperid leaf tiers on *Myrica*, and *Urodus parvula* caterpillars on *Persea*, could not be determined because destructive methods would have been necessary, and densities of these insects were not high enough to allow for such collections.

#### Data analysis

Treatment effects were tested using two-way ANOVAs. Parasitism data for most species were log-transformed prior to analysis to meet normality and homoscedasticity assumptions of the model. All statistical procedures were carried out using the SYSTAT 9 statistical package (SPSS 1999).

A factorial meta-analysis was performed on the data to quantitatively synthesize results across species. For

each herbivore species we calculated the effect size (Hedges'  $d$ ) and sampling variance of fertilization or parasitoid removal manipulations at control and experimental levels. We also calculated an effect size and sampling variance for the interaction between factors. These calculations are similar to the procedures for calculating main effects and interactions in ANOVAs, and were carried out following the methods detailed in Gurevitch et al. (2000). Effect sizes for main effects and interactions were considered significant if 95% confidence intervals did not overlap zero. A significant interaction indicates that fertilization altered the strength of top-down forces. A positive sign of the interaction term indicates that top-down effects on herbivores were significantly greater at increased resource levels than at control resource levels. Significant differences between interactions between groups of studies were tested using the  $Q_b$  statistic generated from the mixed model, with  $P$  values estimated from randomization. Fail-safe values were also calculated using Rosenthal's method with  $\alpha = 0.05$ .

### RESULTS

Mean interstitial soil salinities for each plant species varied approximately with their degree of tidal influence (Fig. 1). *Borrchia frutescens*, which received regular tidal inundation, experienced the greatest salinities, with the two other coastal plants, *B. halimifolia* and *C. uvifera*, experiencing somewhat lower salinities. The two upland species, *P. borbonica* and *M. cerifera*, which experience no tidal influence, averaged only 2 and 1 ppt salinity respectively in the surrounding soil (Fig. 1).

The mean unmanipulated percentage of foliar nitrogen for each host plant species showed a similar pattern (Fig. 1). The three coastal species had higher ambient foliar nitrogen concentrations than the two upland species. Addition of nitrogen fertilizer significantly increased the nitrogen content of all five plant species ( $P < 0.001$  in all cases).

Addition of yellow sticky traps reduced parasitism levels significantly for all of the 11 herbivore species for which data were collected ( $P < 0.02$  in all cases). Parasitism levels were decreased from an average of 49.9% to 32.6%. A full data and ANOVA table can be found in Appendix B.

The densities of all 15 herbivores studied were influenced significantly by both fertilization ( $P < 0.05$  in all cases; Appendix C) and reduction of parasitism ( $P < 0.05$  in all cases). For *Borrchia frutescens*, all three herbivores responded positively to fertilization, although the greatest responses were observed for *P. quadripustulatus* and *Argyresthia* sp., which almost doubled in density on fertilized plots (Fig. 2). Fertilization resulted in a more moderate increase in gall density. For all three herbivores, the effect of reduced parasitism was less than the effect of fertilization. Moreover, the combination of fertilizer and sticky traps

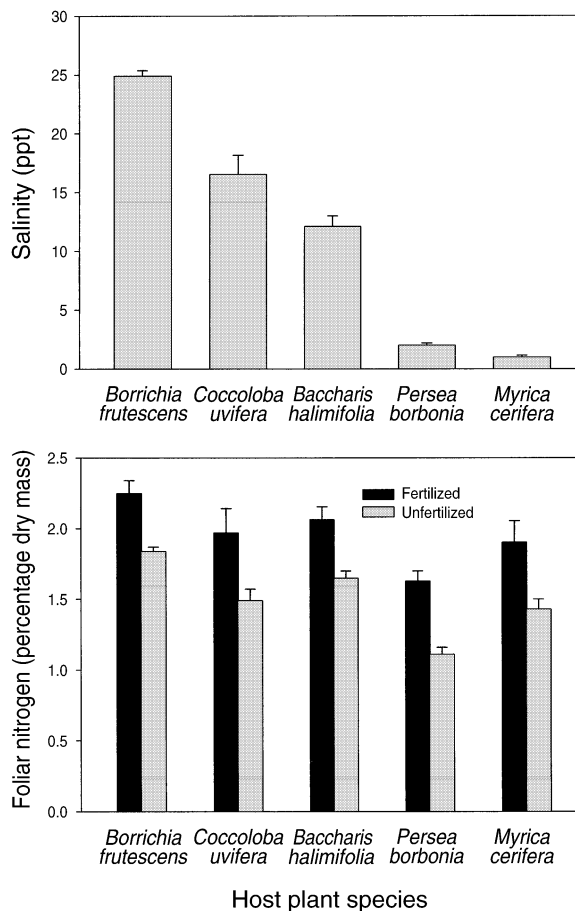


FIG. 1. Mean  $\pm$  1 SEM ambient interstitial soil salinity (in ppt) and foliar nitrogen concentrations measured as percentage of dry mass for fertilized and control plants of five host plant species used in the study.

yielded only modest increases in density above those observed on fertilized plots (Fig. 2).

A similar pattern was found for the herbivores of *Coccoloba uvifera* (Fig. 2). The leaf miners and stem borers that feed on this plant species exhibited a mean increase in density of 81% on fertilized plots, and a mean increase of 38% on plots that received sticky traps. There was not a significant interaction between treatments for any of the herbivore species ( $P > 0.10$  in all cases), as the effects of fertilization and reduction of parasitism were approximately additive (Fig. 2).

The effects of bottom-up and top-down manipulations on the herbivores of *Baccharis halimifolia* were more equitable than those observed for *Borrchia* or *Coccoloba* (Fig. 2). Fertilization and reduction of parasitism both more than tripled the density of the gall maker *Neolasioptera lathami*, and doubled the densities of the leaf miners *Amauromyza maculosa* and *Liriomyza trifolii*. Again, these treatments acted additively on herbivore density, and there were no significant interactions between treatments for any of the three species ( $P > 0.20$  in all cases).



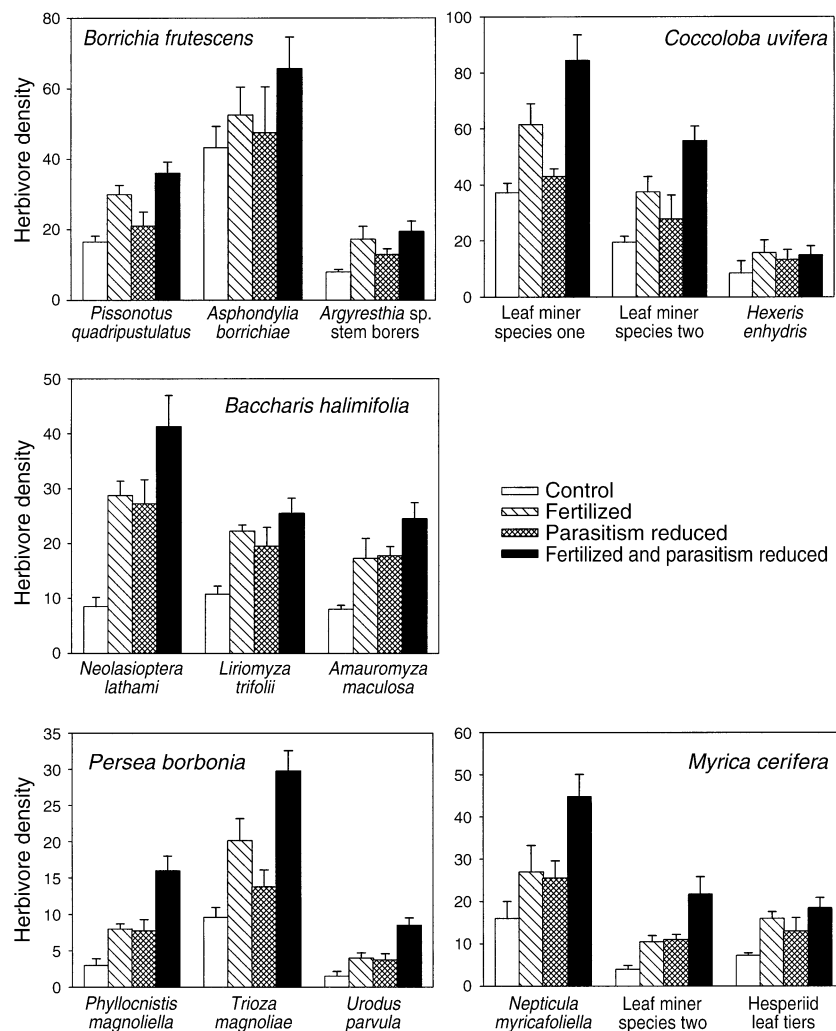


FIG. 2. Mean  $\pm$  1 SEM densities of the three most common herbivore species on each of five host plant species: *Borrichia frutescens*, *Coccoloba uvifera*, *Baccharis halimifolia*, *Persea borbonia*, and *Myrica cerifera*. Data are totals for the eight months of the study;  $N = 4$  (four replicate plants or plots per treatment). Densities were measured as no. individuals, but number of stems or leaves counted varied by plant host species (see *Methods* for units).

Two herbivores of *Persea borbonia*, the leafminer *Phyllocnistis magnoliella* and the geometrid moth *Urodus parvula*, responded almost equally to fertilization and reduction of parasitism (Fig. 2). On plants that received either fertilizer or sticky traps, densities of leaf miners and *U. parvula* caterpillars were >150% greater than those found on control plants. Fertilization more than doubled the density of galls made by the psyllid *Trioza magnoliae*, and reducing parasitism resulted in an increase in gall density of 47%. The greatest impact on the densities of these three herbivore species, however, was found on plots that received both fertilizer and sticky traps (Fig. 2), and there was a trend toward a significant interaction between treatments on the density of the leaf miner *P. magnoliella* ( $P = 0.078$ ).

The effects of bottom-up and top-down manipulations on the herbivores of *Myrica cerifera* were similar

to those described for the herbivores of *P. borbonia* (Fig. 2). For two of the herbivores, fertilization and parasitism reduction treatments influenced density nearly equally (Fig. 2). Each treatment resulted in approximately a 65% increase in the density of *Nepticula myricafoliella* and a 170% increase in the density of the agromyzid. The greatest increases in the densities of leaf miners were found on plots receiving both treatments (Fig. 2). This resulted in a trend toward an interaction between treatments for *N. myricafoliella* ( $P = 0.084$ ), and a significant interaction for the agromyzid leaf miner ( $P = 0.034$ ). Hesperid leaf tiers responded more strongly to fertilization than to parasitism reduction treatments, and did not exhibit a trend for an interaction between treatments ( $P = 0.155$ ).

Quantitative synthesis of our results revealed a number of patterns, some of which were not apparent through qualitative examination of the data. Overall,

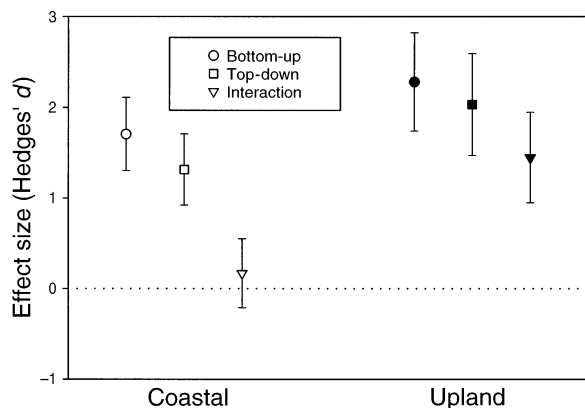


FIG. 3. Effect sizes (Hedges'  $d$ ) and 95% confidence intervals for the bottom-up effects of fertilization, top-down effects of parasitism reduction, and interaction between treatments for herbivores of coastal ( $N = 9$ ) and upland ( $N = 6$ ) plant species. Effects are significant if confidence intervals do not overlap zero.

the bottom-up effects of fertilization were greater than the top-down effects of reducing parasitism (Fig. 3), although not significantly so ( $Q_b = 3.11$ ,  $P = 0.149$ ), and the effects of both treatments were very large. Also, the main effects of fertilization and parasitism reduction were greater for herbivores of upland plants than coastal plants (Fig. 3). For fertilization, the difference between coastal and upland species was not statistically significant ( $Q_b = 4.14$ ,  $P = 0.148$ ), but for parasitism reduction it was ( $Q_b = 6.71$ ,  $P = 0.002$ ). There was also a significant difference between the strength of the interaction between treatments for herbivores of coastal vs. upland plants ( $Q_b = 40.39$ ,  $P < 0.001$ , Rosenthal's fail-safe value = 279.8), and this was evident in the fact that the interaction between fertilization and parasitism reduction was only significant for upland herbivores (Fig. 3).

When the effect sizes of the interaction terms for each species of herbivore were plotted against the ambient salinity and foliar nitrogen levels of their respective host plants and analyzed using Pearson's product-moment correlations, the relationship was significant for salinity, but not nitrogen (Fig. 4). The strength of the interaction term increased with decreasing salinity ( $r = 0.542$ ,  $P = 0.037$ ). Thus, the strongest interaction between fertilization and parasitoid reduction was observed for the herbivores of *Myrica cerifera*, while the weakest interaction between treatments occurred on *Borrichia* (Fig. 4). For foliar nitrogen levels, a similar trend was suggested by the data, but the relationship was not significant ( $r = 0.378$ ,  $P = 0.105$ ).

#### DISCUSSION

Fertilization and yellow sticky traps resulted in perturbations of approximately equal strength. Fertilization resulted in an average 32% increase in foliar nitrogen, and traps resulted in an average 34% reduction

in parasitism. Both fertilization and parasitism reduction treatments had strong effects in all tritrophic complexes. This shows that both top-down and bottom-up forces are important in these systems, supporting the suggestion that the interplay of these two factors will strongly influence the densities of phytophagous insects (Price et al. 1980, Stiling and Rossi 1997, Uriarte and Schmitz 1998, Forkner and Hunter 2000).

The strong effects of fertilization on herbivore densities on all plant species suggests that even for coastal plants, which may receive allochthonous nutrient inputs (Polis and Hurd 1995, 1996), nitrogen levels limit herbivore densities. There were considerable differences in the effect of fertilization among herbivore species, with increases in density ranging from 21% to 238%. Overall, the greatest effects of fertilization were observed for herbivores on upland plants. It has been suggested that bottom-up forces should be stronger in more stressful habitats (Menge and Sutherland 1976, 1987). The results we have reported here would seem to contradict this prediction, as bottom-up effects of fertilization were greater for herbivores of upland plants. It has also been suggested, however, that the bottom-up forces of plant quality, particularly nitrogen

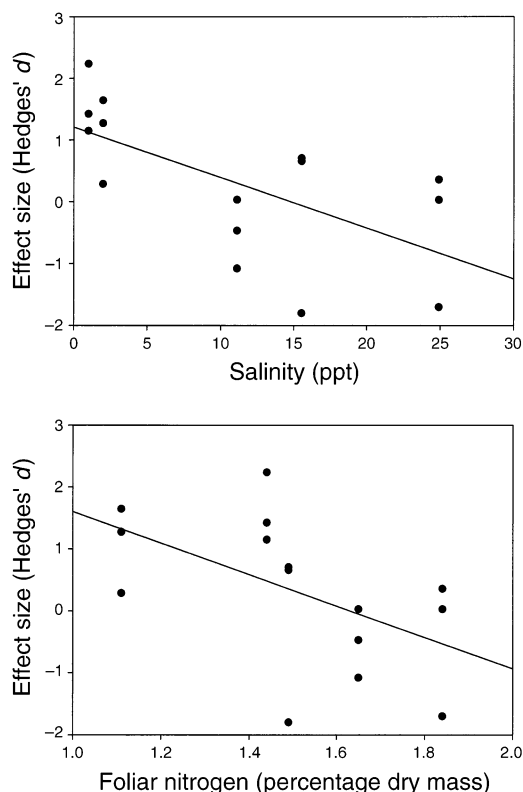


FIG. 4. Correlations of effect sizes of interaction terms with ambient soil pore water salinity and foliar nitrogen concentrations of each host plant species. Each data point represents the effect size for one herbivore species, with three data points or species at the mean salinity or nitrogen level of the respective host plant.

levels, should be stronger in areas that are nutrient-poor (Fretwell 1977, Oksanen et al. 1981). This may have indeed been the case in our study, as coastal plant species had higher ambient levels of foliar nitrogen. Thus, nutrient availability and stress levels may interact to determine the importance of the bottom-up effects of plant quality for insect herbivores.

Reduction of parasitism had strong effects on herbivore density in this study, increasing significantly the densities of all 15 herbivore species studied. Overall, the effects of top-down manipulations were stronger on herbivores of upland plants than coastal ones. This seems to support the suggestion that top-down forces should be more important in less stressful areas (Menge and Sutherland 1976, 1987), but seems to contradict the predictions of Fretwell (1977) and Oksanen et al. (1981). Again, it appears as though an interaction between the concurrent gradients in nutrients and salinity determine the strength of top-down and bottom-up forces. These findings lend strong support to the idea that environmental heterogeneity will set the stage upon which trophic dynamics act (Hunter and Price 1992).

The greatest difference between coastal and upland systems in this study was the strength of the interaction between fertilization and reduction of parasitism. For herbivores on coastal plants, the strength of the interaction between treatments was near zero, while for herbivores on upland plants, the interaction was very large, indicating that the strength of top-down effects was greatly increased by nutrient additions. Correlations between the effect sizes of the interaction between treatments and the ambient salinity and foliar nitrogen levels for each of the five host plant species suggests that the strength of the interaction between bottom-up and top-down forces is influenced more strongly by salinity. Thus, environmental stress in the form of increased salinity may limit the synergism between treatments and suggests that nutrient additions may increase the strength of top-down forces, but only in more favorable environments. Increased soil salinity has been shown to interfere with absorption of nitrogen by plants, inhibit growth, and alter plant chemistry (Jeffries and Perkins 1977, Osgood and Zieman 1993, Bowditch and Stiling 1998). It is possible that increased salinity makes insect hosts or the plants they feed on less attractive to parasitoids by altering their chemical signature. It is also possible that host plant-related mortality is greater for herbivores feeding on plants in more saline areas. It is important to note, however, that there was also a trend for an effect of ambient host plant foliar nitrogen concentrations on the strength of the interaction between top-down and bottom-up forces. Therefore, it is likely that there is meaningful interplay between these two abiotic factors.

It has been suggested that drawing general conclusions about the relative roles of top-down and bottom-up effects in influencing and regulating herbivore den-

sities will require new approaches as well as more complete use of the empirical data we generate (Hunter 2001, Walker and Jones 2001). Factorial field studies provide a powerful tool with which to examine the interactions among top-down and bottom-up factors and environmental variation (Forkner and Hunter 2000, Hunter 2001), while application of meta-analysis techniques minimizes the confounding effects of variability among species, facilitating the generation of general conclusions about the roles of top-down and bottom-up forces. The results of our study show that the strengths of top-down and bottom-up forces, and especially the interaction between the two, vary along a coastal gradient. Our results suggest that a complex interaction between salinity and nutrient availability result in data that sometimes support, and sometimes contradict, predictions of the current trophic dynamic theories such as the Exploitation Ecosystems Hypothesis (Oksanen et al. 1981) and the Menge and Sutherland (1976) hypothesis. Integration of these theories, as well as quantitative synthesis of multiple study systems, may bring us closer to a consensus regarding the roles of top-down and bottom-up forces.

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#### APPENDIX A

A summary of the natural history of the plants and insects examined in this study is available in ESA's Electronic Data Archive: *Ecological Archives* EO85-085-A1.

#### APPENDIX B

Treatments means and ANOVA results for parasitism rates of 11 herbivore species in 2002 are available in ESA's Electronic Data Archive: *Ecological Archives* EO85-085-A2.

#### APPENDIX C

A summary of ANOVA results for the densities of the 15 herbivore species studies in 2002 is available in ESA's Electronic Data Archive: *Ecological Archives* EO85-085-A3.