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BOTTOM-UP FORCES MEDIATE NATURAL-ENEMY IMPACT IN A PHYTOPHAGOUS INSECT COMMUNITY

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Abstract. We employed a combination of factorial experiments in the field and laboratory to investigate the relative magnitude and degree of interaction of bottom-up factors (two levels each of host-plant nutrition and vegetation complexity) and top-down forces (two levels of wolf-spider predation) on the population growth of *Prokelisia* planthoppers (*P. dolus* and *P. marginata*), the dominant insect herbivores on *Spartina* cordgrass throughout the intertidal marshes of North America. Treatments were designed to mimic combinations of plant characteristics and predator densities that occur naturally across habitats in the field.

There were complex interactive effects between plant resources and spider predation on the population growth of planthoppers. The degree that spiders suppressed planthoppers depended on both plant nutrition and vegetation complexity, an interaction that was demonstrated both in the field and laboratory. Laboratory results showed that spiders checked planthopper populations most effectively on poor-quality *Spartina* with an associated matrix of thatch, all characteristics of high-marsh meadow habitats. It was also this combination of plant resources in concert with spiders that promoted the smallest populations of planthoppers in our field experiment. Planthopper populations were most likely to escape the suppressing effects of predation on nutritious plants without thatch, a combination of factors associated with observed planthopper outbreaks in low-marsh habitats in the field. Thus, there is important spatial variation in the relative strength of forces with bottom-up factors dominating under low-marsh conditions and top-down forces increasing in strength at higher elevations on the marsh.

Enhancing host-plant biomass and nutrition did not strengthen top-down effects on planthoppers, even though nitrogen-rich plants supported higher densities of wolf spiders and other invertebrate predators in the field. Rather, planthopper populations, particularly those of *Prokelisia marginata*, escaped predator restraint on high-quality plants, a result we attribute to its mobile life history, enhanced colonizing ability, and rapid growth rate. Thus, our results for *Prokelisia* planthoppers suggest that the life history strategy of a species is an important mediator of top-down and bottom-up impacts.

In laboratory mesocosms, enhancing plant biomass and nutrition resulted in increased spider reproduction, a cascading effect associated with planthopper increases on high-quality plants. Although the adverse effects of spider predation on planthoppers cascaded down and fostered increased plant biomass in laboratory mesocosms, this result did not occur in the field where top-down effects attenuated. We attributed this outcome in part to the intraguild predation of other planthopper predators by wolf spiders. Overall, the general paradigm in this system is for bottom-up forces to dominate, and when predators do exert a significant suppressing effect on planthoppers, their impact is generally legislated by vegetation characteristics.

Key words: bottom-up vs. top-down impact; habitat complexity; intertidal wetlands; intraguild predation; multitrophic interactions; phytophagous insect community; plant nutrition; planthopper; *Prokelisia* spp.; *Spartina alterniflora*; trophic cascades; vegetation structure.

INTRODUCTION

The historical controversy over the relative importance of “top-down” vs. “bottom-up” impact on phytophagous insect populations (e.g., Hairston et al. 1960, Ehrlich and Birch 1967) has been supplanted by a more

unified view (Price et al. 1980, Denno and McClure 1983, Hunter and Price 1992, Stiling and Rossi 1997, Letourneau and Dyer 1998, Denno and Peterson 2000, Forkner and Hunter 2000). The prevailing sentiment now is that top-down and bottom-up forces typically act in concert on herbivore populations and that host plants often set the stage on which natural enemies act (Denno and McClure 1983, Hunter and Price 1992, Hartvigsen et al. 1995, Forkner and Hunter 2000).

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Moreover, focus has shifted to elucidating how host plants and natural enemies interact to influence insect herbivore dynamics (Hunter and Price 1992, Denno and Peterson 2000, Forkner and Hunter 2000, Roda et al. 2000, Norton et al. 2001), which conditions promote or diminish the cascading effects of bottom-up and top-down forces (Polis and Strong 1996, Fagan 1997, Moran and Hurd 1998, Rosenheim 1998, Pace et al. 1999, Schmitz et al. 2000), and how other factors (e.g., herbivore and predator life-histories and physical disturbance) legislate the relative strength of each force (Moran et al. 1996, Beckerman et al. 1997, Schmitz et al. 1997, Denno and Peterson 2000).

From the growing number of studies assessing bottom-up and top-down effects, several predictions emerge relative to their impact on herbivores (Forkner and Hunter 2000). Among these are that (1) interactions between forces are commonplace, (2) the relative strength of both forces vary spatially and temporally, (3) the strength of top-down effects will increase with enhanced primary production, and (4) species identity (e.g., life history strategy) is as important a mediator of bottom-up and top-down forces as are productivity and the number of trophic levels in the food web (Oksanen et al. 1981, Oksanen 1990, Strong 1992, Polis et al. 1998, Denno and Peterson 2000, Forkner and Hunter 2000). Notably, however, rigorous experimental tests of these expectations under field conditions are rare for phytophagous insects (but see Stiling and Rossi 1997, Fraser 1998, Fraser and Grime 1998, and Forkner and Hunter 2000).

We employed a combination of factorial experiments in the laboratory and field to explore host-plant and natural enemy impacts on *Prokelisia* planthoppers (Hemiptera: Delphacidae), the predominant insect herbivores on cordgrass (*Spartina alterniflora*) throughout the Atlantic coastal marshes of North America (Denno et al. 2000). Specifically, we investigated the relative magnitude and degree of interaction of bottom-up factors (host-plant nutrition and vegetation structure) and top-down (invertebrate predators) forces on the population dynamics and growth of these herbivores. Invertebrate predation was selected as the focal top-down factor in this study because spider predators are the most abundant and devastating natural enemies of *Prokelisia* populations in this coastal region (Döbel and Denno 1994). Also, we chose plant nutrition (nitrogen content) as one bottom-up factor to manipulate because it has figured so prominently in elucidating the population dynamics of phytophagous insects, especially phloem feeders such as planthoppers (McNeill and Southwood 1978, White 1993). Moreover, vegetation structure (leaf litter/thatch) was selected as another plant-related variable because it is known to enhance the aggregative response of invertebrate predators and increase their ability to suppress prey populations (Riechert and Bishop 1990, Döbel and Denno 1994, Rypstra et al. 1999, Landis et al. 2000). Although these

bottom-up and top-down factors have been studied independently and have been shown to significantly impact populations of *Prokelisia* planthoppers (Denno 1983, Döbel and Denno 1994, Denno and Peterson 2000), no study has investigated their collective effects using factorial manipulations.

By manipulating plant nutrition (nitrogen fertilization), vegetation structure (thatch supplementation), and invertebrate predation (wolf spider augmentation), we addressed the following objectives with regard to their direct and interactive impacts on planthopper population growth. First, we examined the relative strength of bottom-up and top-down forces hypothesizing that plant-related effects would dominate (Hunter and Price 1992). Second, we predicted that enhanced *Spartina* productivity and nutrition would promote planthopper escape from natural enemy suppression in these highly mobile and fast-developing herbivores (Denno and Peterson 2000), an expectation contrary to conventional wisdom (Oksanen et al. 1981). Third, we anticipated that increasing vegetation complexity by adding thatch would enhance the impact of invertebrate predators (Döbel and Denno 1994), particularly on nitrogen-poor plants where planthopper growth is protracted and colonization is limited (Denno and Peterson 2000). Importantly, treatment combinations were designed to mimic conditions as they vary spatially across *Spartina* habitats in the field. Thus, a fourth objective was to compare the impact of our experimental treatment combinations on planthopper growth with similarly characterized *Spartina* habitats in the field where planthopper outbreaks are frequent (low marsh) and less common (high marsh; Denno and Peterson 2000).

Understanding the strength and interactive effects of bottom-up and top-down forces in phytophagous insect communities has important implications for both population ecology and agriculture. Despite the progress that has been made concerning the role of plant resources and natural enemies in the suppression of herbivorous insect populations (Hunter and Price 1992, Stiling and Rossi 1997, Forkner and Hunter 2000), our ability to predict their combined effects in most systems remains rather limited. Moreover, evaluating interactions between crop varieties and natural enemies is fundamental to establishing improved pest-management practices in agroecosystems (Hare 1994, Denno and Peterson 2000). The research presented here aims to advance our knowledge of the complex interactions that occur between host plant resources and natural enemies and their causal roles in the population ecology of a common and agriculturally important group of phytophagous insects, namely planthoppers.

METHODS

Study site and the cordgrass–planthopper–predator system

Field work was conducted on an expansive intertidal marsh in the Great Bay–Mullica River estuarine system

at the end of Great Bay Boulevard and just north of the Rutgers University Marine Station, Tuckerton, Ocean County, New Jersey, USA. The vegetation of this marsh and other mid-Atlantic marshes is dominated by the perennial cordgrass *Spartina alterniflora*, where it grows in extensive pure stands within the intertidal zone (Denno 1983, Gallagher et al. 1988). Within this zone, however, the structure of *Spartina* varies dramatically with elevation due to differences in tidal disturbance, nutrient subsidy, and litter decay (Denno 1983, Gallagher et al. 1988). Moving up an elevational gradient from low-marsh habitats (tidal creek banks) to high-marsh plateaus (meadows), *Spartina* plants generally decrease in nutrition (nitrogen content) and height, but increase in the amount of associated leaf litter (thatch; Denno 1983, Ornes and Kaplan 1989).

The most abundant phytophagous insects on *Spartina* are two monophagous, phloem-feeding planthoppers, *Prokelisia dolus* and *P. marginata* (Denno et al. 2000). Both planthoppers insert their eggs in leaf blades, are trivoltine, overwinter as nymphs, are similar in size (3 mm), and have comparable generation times (~40 d) and growth rates (Denno et al. 1989, 2000). The two planthoppers are wing dimorphic with both migratory adults (macropters with fully developed wings) and flightless adults (brachypters with reduced wings) occurring in the same population (Denno and Peterson 2000). *P. dolus*, however, is a relatively sedentary species (most adults are flightless) that occurs primarily in high-marsh habitats (Denno et al. 1996). By contrast, *P. marginata* is a highly mobile species (most adults are macropterous) along the Atlantic coast and undergoes annual interhabitat migrations between high-marsh and low-marsh habitats. Outbreaks of both planthopper species are associated with nitrogen-rich host plants, but most striking are the outbreaks of *P. marginata* that occur frequently on low-marsh *Spartina* (Denno and Peterson 2000).

Wolf spiders are the major predators of the active stages of planthoppers on mid-Atlantic salt marshes (Döbel et al. 1990, Döbel and Denno 1994). Of the hunting spider species on the marsh, *Pardosa littoralis* (5–6 mm) is the most abundant, with densities frequently exceeding 200 individuals/m². *Pardosa* is a voracious predator with a per capita consumption rate of 70 planthoppers/d (Döbel and Denno 1994). *Prokelisia* planthoppers typically comprise 61% of the diet of *Pardosa*, and both planthopper species are similarly vulnerable to attack. *Pardosa* and other invertebrate predators decrease in abundance down the elevational gradient, a pattern associated with the paucity of thatch in low-marsh habitats (Döbel et al. 1990). Other common predators in the field are the mirid bug *Tytthus vagus* (Hemiptera: Miridae) that feeds exclusively on planthopper eggs (Finke and Denno 2002), and a diversity of web-building spiders, particularly *Grammonota trivittata* (Araneae: Linyphiidae; Döbel et al. 1990).

Laboratory assessment of bottom-up and top-down forces on planthopper population growth

To examine the direct and interactive effects of host plant nutrition, vegetation structure, and spider predation on the growth of planthopper populations, we conducted a full factorial experiment in laboratory mesocosms containing *Spartina* transplants. Two levels each of plant nutrition (high or low nitrogen fertilization), vegetation structure (thatch present or absent), and spider density (zero or five per mesocosm) were all crossed. Each mesocosm was stocked with adult planthoppers (*Prokelisia dolus*), and planthopper populations were allowed to grow over a 2-mo period, after which time they were censused to determine the effect of the eight treatment combinations on population growth. This time period spans approximately two planthopper generations (see Denno et al. 1989).

Spartina plants used in the experiment were transplanted from the Tuckerton field site on 15 May 1997 into sand-filled, plastic flower pots (30 cm diameter). Nine *Spartina* culms were haphazardly placed in each of 200 pots. Pots were then maintained outside in eight water-filled wading pools (2 m diameter) in the nursery-greenhouse area at the University of Maryland. All pools were fertilized with a 3:1 mixture of ammonium nitrate (N-P-K: 34-0-0) and phosphoric acid (0-46-0). High-quality plants were achieved by fertilizing each of four pools biweekly (early June to early August) with 24 g of the mixture, whereas low-quality plants were established by fertilizing the other four pools with 3.5 g of the mix (Denno et al. 1985, Denno and Roderick 1992).

On 1 August 1997, 40 pots with transplants were randomly selected from the high-quality treatment pools, as were 40 others from the low-quality treatment pools, and all were moved inside to the laboratory and placed in 10 smaller wading pools (1.1 m diameter). The pools, each containing eight pots (one of each treatment combination) were arranged in two rows of five with two 1000-w sodium-vapor lamps suspended 2 m above each row of pools. All transplants were caged on 4 August by placing a cylindrical, clear plastic (cellulose butyrate) mesocosm (22 cm in diameter by 30 cm in height) over each pot. Each mesocosm contained six organdy-covered ports (6 cm in diameter) and was fitted with an organdy-covered lid.

The vegetation structure treatment was applied by placing either 25 g or 0 g of dry, field-collected *Spartina* thatch onto the bottom of each mesocosm. On 6 August, each mesocosm was stocked with 13 adult, field-collected planthoppers (10 females and three males of *P. dolus*), and the spider treatment (either zero or five *Pardosa* per mesocosm) was applied the next day. Spiders were field-collected in early August and represented a mix of medium to large immatures of both sexes (4–6 mm in body length).

Planthopper and spider populations were censused

on 6 October after aspirating all animals from each mesocosm. Any reproduction by *Pardosa* wolf spiders (females carrying egg sacs) was also assessed. To determine treatment effects on the above-ground biomass of *Spartina* (g dry mass per mesocosm), all plants in each mesocosm were harvested on 7 October, oven-dried at 80°C for 48 h, and then weighed. The biomass of dead plant material (g dry mass of thatch and senescent leaves) remaining in each mesocosm was similarly determined.

Initial planthopper and spider densities (13 and five individuals per mesocosm, respectively, convert to 342 and 130 individuals/m², respectively) were selected to represent mean densities that occur naturally on the marsh (Döbel and Denno 1994, Denno et al. 1996). Likewise, levels of thatch and nutrient subsidy (fertilization) were selected to produce plants and vegetation structures that span the naturally occurring range of these variables (Döbel and Denno 1994, Denno et al. 1985).

The effects of plant nutrition, thatch, spiders, and their interactions on the final population size of the planthopper population (log-transformed density per mesocosm) were analyzed using ANOVA (SAS Institute 1995). ANOVA was also used to examine treatment effects on the live biomass of *Spartina* and the amount of remaining thatch. Because predator effects on prey density can cascade down to influence plant biomass (Gómez and Zamora 1994, Hartvigsen et al. 1995, Moran et al. 1996), we determined the relationship between live *Spartina* biomass and final planthopper density for the two plant-nutrition treatments using analysis of covariance with planthopper density as the covariate (SAS Institute 1995). Plant nutrition and thatch effects on the number of spiders remaining in mesocosms at the end of the experiment were also evaluated using ANOVA, and a *t* test was used to compare spider reproduction (number of egg sacs per female) on plants in the two fertilization categories. For all analyses, normality assumptions were checked and log transformations were used when necessary to normalize variances across treatments. Means (± 1 SE) are reported untransformed.

Field assessment of bottom-up and top-down forces on planthopper population growth

To test for the interactive effects of plant nutrition, vegetation structure, and spider predation on planthopper population growth in the field, we conducted a manipulative experiment on an archipelago of small, uncaged *Spartina* islets located in a flooded mud-flat area on the high marsh at the Tuckerton field site (see Denno et al. 2000). Islets averaged 1.85 ± 0.13 m² in area, and were separated from each other by 1–3 m. However, the number of islets was limited at our study site, so we selected a subset of the eight possible treatment combinations to explore. From the full factorial design we used in the lab experiment, we chose those treat-

ments for which planthoppers were most and least likely to escape natural enemy impact. In all, three bottom-up treatments (fertilized islets without thatch, nonfertilized islets with thatch, and nonfertilized without thatch) were each crossed with two spider-predation treatments (spiders added vs. not).

We expected planthoppers to escape spider suppression on fertilized islets without thatch, a treatment designed to mimic low marsh conditions (Denno et al. 1996, Denno and Peterson 2000). In contrast, we hypothesized that spiders would be most effective in suppressing planthopper populations on nonfertilized islets, particularly on those with thatch, a treatment designed to simulate the structure and nutrition of *Spartina* growing on high-marsh meadows (Döbel and Denno 1994). Each of the six treatment combinations was replicated nine times, except for the two nonfertilized thatch-free combinations with and without spider augmentation that were each replicated four times (44 total islets).

All islets were selected on 21 May 1999 and each was raked repeatedly to remove ambient thatch. To achieve high and low levels of plant nutrition, *Spartina* islets were either fertilized or not with a 3:1 mixture of granular ammonium nitrate (N-P-K: 34-0-0) and phosphoric acid (0-46-0). Each "high-quality islet" received eight applications of the fertilizer mixture at a rate of 60 g·m⁻²·date⁻¹, applied biweekly from 21 May to 15 July. Because high-marsh *Spartina* in general has a low nitrogen content (Denno 1983, Ornes and Kaplan 1989), "low-quality islets" were achieved by withholding fertilizer. The two vegetation-structure treatments were achieved by adding field-collected dry thatch (700 g dry mass/m²) or not to the appropriate islets on 4 June.

Prior to the application of the spider treatment, all islets were defaunated three times (June 10, 16, and 25) to remove ambient planthoppers and spiders and to equalize initial arthropod densities among treatments. Using a D-vac suction sampler (D-Vac, Ventura, California, USA), each islet was vacuumed for 10 min to achieve nearly complete defaunation (Denno et al. 2000). The spider augmentation treatment was initiated on 30 June, and was applied on five subsequent dates as well (8, 15, 21, and 28 July, and 3 August) to insure intended density levels despite emigration. On each date, *Pardosa* wolf spiders were applied at a rate of 100 individuals/m² to those islets calling for spiders. Spiders (large immatures) for this treatment were obtained by vacuuming neighboring *Spartina* meadows with a D-vac suction sampler (Denno et al. 2000).

Planthoppers could freely colonize all islets following the final defaunation on 25 June, and all treatments were in place by 30 June. Subsequently, the effect of the treatments on planthopper population size (individuals/m²) was assessed on four dates during the next 6-wk period (30 June, 8 and 28 July, and 17 August). Populations of planthoppers and spiders were censused

using a D-vac vacuum sampler (Denno and Roderick 1992, Denno et al. 2000). One sample was taken on each islet on each of the four sampling dates and consisted of two 10-s placements of the sampling head on the marsh surface such that 0.2 m² of *Spartina* was vacuumed. Arthropods (*Prokelisia* nymphs, adults of *P. dolus* and *P. marginata*, the pooled adults and immatures of *Pardosa* wolf spiders, and other predators) were killed in an ethyl-acetate jar, transferred to 95% ethanol sample bottles, and returned to the laboratory where they were counted. Nymphs of the two *Prokelisia* species were pooled because sorting them accurately to species is extremely difficult.

To verify the effectiveness of the fertilizer and thatching treatments, the aboveground biomass (g dry mass/m²) and nitrogen content (%) of *Spartina* were assessed once (25 August) on each islet, as was the biomass of dead plant material (g dry mass/m² of the thatch supplement and accumulated senescent leaves). One vegetation sample was taken on each islet by clipping all aboveground biomass within a 0.047 m² wire frame (Wiegert 1962). Living vegetation was separated from dead plant material, the dead fraction was further sorted into thatch (remainder of original supplement) and recently senesced leaves, and the three fractions were oven dried at 80°C for 24 h before weighing. The nutritional content of the live fraction was determined by grinding each dried sample to a powder in a Wiley mill, passing it through a 1-mm mesh screen, and analyzing it for percent nitrogen using a CHN automated analyzer (Soils Testing Laboratory, University of Maryland, College Park, Maryland, USA).

Treatment effects on the final population density of planthoppers and predators were assessed on 17 August (wolf spiders excepted) using ANOVA (SAS Institute 1995). Treatment effects on the density of stocked wolf spiders were assessed on samples taken one date earlier on 28 July to coincide with their peak seasonal abundance and when planthopper nymphs were large and most vulnerable to spider predation (see Döbel et al. 1990, Döbel and Denno 1994). Moreover, assessing the abundance of stocked spiders on this earlier date reflected a more robust assessment of the predation pressure that potentially influenced the final density of planthoppers on 17 August. Mirid egg predators were assessed on 17 August because ovipositing planthopper adults and thus eggs were abundant during this time. Treatment effects on the density of adult planthoppers were also examined on 8 July to coincide with the time when planthoppers migrate and colonize new habitats (Denno et al. 1996). The model design was a factorial (3 × 2) with three bottom-up treatments (fertilized islets without thatch, and nonfertilized islets with and without thatch) each crossed with two top-down treatments (wolf spiders added vs. not). Following ANOVA, treatment means were compared using Tukey-Kramer hsd tests (SAS Institute 1995).

Our three-by-two field design did not allow us to

estimate the interactive effects of fertilizer and thatch with spiders because both bottom-up treatments were subsumed in the "plant-treatment" category. In cases where the bottom-up plant treatments of both fertilizer and thatch appeared to influence arthropod densities (as indicated by Tukey-Kramer hsd tests), additional two-way ANOVAs (fertilizer by spider and thatch by spider with Bonferroni adjusted α levels) were performed to specifically elucidate the nature of the bottom-up effect and possible interactions with spiders.

Dependent variables were the density of planthoppers (pooled *Prokelisia* nymphs, and adults of *P. marginata* and *P. dolus*) and predators (pooled immatures and adults of the lycosid wolf spider *Pardosa*, pooled nymphs and adults of the mirid egg predator *Tytthus*, and the pooled total of all other spiders which consisted mostly of *Grammonota trivitatta*). Preliminary analysis revealed that even log-transformation of density data failed to homogenize variances among treatments for planthoppers and wolf spiders (SAS Institute 1995). Thus, treatment effects on all planthoppers (pooled *Prokelisia* nymphs, adults of *P. marginata* and *P. dolus*) and the wolf spider *Pardosa* were assessed using ANOVA on rank-transformed density data across the 44 islets (Potvin and Roff 1993). Treatment effects on the mirid bug *Tytthus*, and on the pooled total of all other spider species were assessed using ANOVA on log-transformed densities ($N + 1$ individuals/m²). Treatment effects on plant parameters were examined using ANOVA for each dependent variable: nitrogen (angular-transformed percentage), live biomass (log-transformed g/m²), and dead biomass (log-transformed g/m²), and means were compared using Tukey-Kramer HSD tests (SAS Institute 1995). All means (± 1 SE) are reported untransformed.

Top-down and bottom-up impacts on planthopper population size: correspondence between laboratory and field assessments

Our field assessment was conducted on noncaged islets of *Spartina* where both planthoppers and wolf spiders could freely emigrate and immigrate. Other planthopper predators such as the mirid bug *Tytthus* and the web-building spider *Grammonota* could colonize the islets and possibly confound the impact of the imposed treatments. These nonmanipulated predators could directly diminish planthopper populations or they could serve as intraguild prey and indirectly reduce the impact of *Pardosa* wolf spiders on planthoppers (see Finke and Denno 2002). Thus, to assess if our lab findings scaled up under field conditions, we compared the relative impacts of the bottom-up and top-down treatments on final planthopper density between the controlled laboratory experiment and our field assessment where other confounding factors might come into play.

In all, six treatment combinations were common to both experiments: fertilized islets without thatch, and

TABLE 1. Analysis of variance results (F values and significance levels) for the effects of nutrient subsidy (high or low fertilization rate), vegetation structure (thatch added or not), spider predation (present or absent), and their interactions on the density of *Prokelisia dolus* (log-transformed density per mesocosm), aboveground live biomass (g dry mass per mesocosm) and the dead plant biomass (g dry mass thatch plus senescent leaves per mesocosm) of *Spartina alterniflora* after 2 mo of growth in the laboratory.

| Source of variation | df | <i>P. dolus</i> nymphs | <i>Spartina</i> biomass | |
|--|----|---------------------------|-------------------------|-----------|
| | | | Live | Dead |
| Fertilization | 1 | 14.96*** | 97.01**** | 95.02*** |
| Thatch | 1 | 10.82** | 2.35 | 721.29*** |
| Fertilization \times Thatch | 1 | 1.61 | 3.19 | 31.73*** |
| Spider predation | 1 | 54.26*** | 10.73** | 0.18 |
| Fertilization \times Predation | 1 | 1.45 | 0.25 | 7.46** |
| Thatch \times Predation | 1 | 10.31** | 5.99* | 0.25 |
| Fertilization \times Thatch \times Predation | 1 | 4.7* | 0.03 | 0.66 |
| Error | 72 | | | |

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; **** $P \leq 0.0001$.

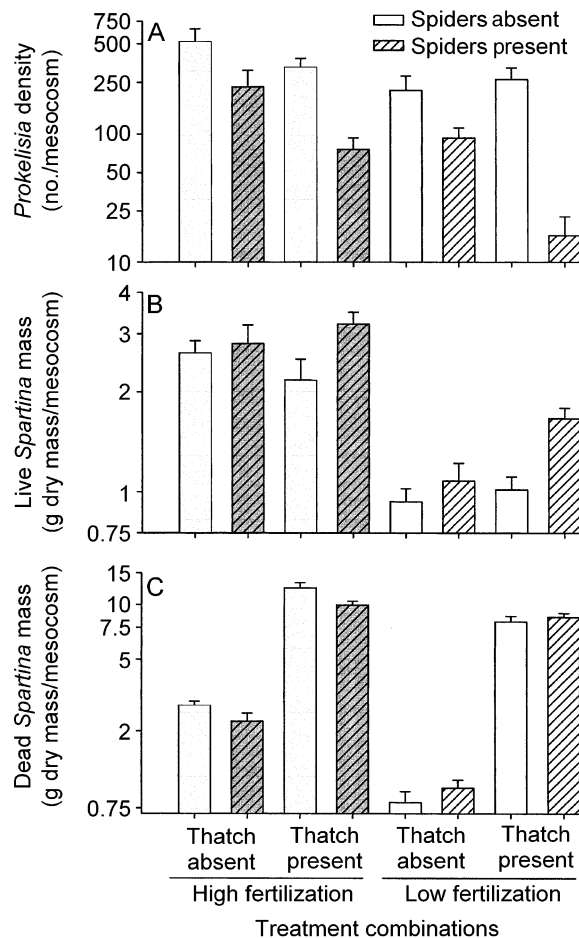


FIG. 1. Effects of nitrogen subsidy (high or low fertilization rate), vegetation structure (thatch present or absent), and wolf-spider predation (zero or five per mesocosm) crossed in a full-factorial design on the (A) population density of the planthopper *Prokelisia dolus*, (B) live aboveground biomass of *Spartina* (g dry mass), and (C) dead biomass of *Spartina* (g dry mass) after two months in laboratory mesocosms. Means \pm 1 SE are presented.

nonfertilized islets with and without thatch, each crossed with two levels of wolf spider predation. The relationship between the final density of planthoppers in laboratory mesocosms and the final density that accrued on islets was determined for the six treatment combinations using correlation.

RESULTS

Laboratory assessment of bottom-up and top-down forces on planthopper population growth

Host-plant factors, specifically host-plant nutrition and vegetation structure, legislated the ability of *Pardosa* wolf spiders to suppress populations of *Prokelisia dolus* (see Plate 1). The following discussion elucidates the details of this complex interactive effect. Planthoppers generally achieved larger populations when raised on high-quality *Spartina* (significant fertilization effect) when thatch was absent (significant thatch effect) and when spiders were absent (significant predation effect; Table 1, Fig. 1A). There was also a significant two-way interactive effect of spider predation and thatch on planthopper population size, whereby spiders suppressed planthopper populations relatively more when thatch was present than when it was absent (Table 1, Fig. 1A). A three-way interactive effect of plant quality, vegetation structure, and spider predation on planthopper population size resulted because the suppressing effect of spiders in the presence of thatch was relatively greater on low-quality plants than on high-quality plants (Table 1, Fig. 1A). Thus, spiders were most able to deter planthopper population growth on poor-quality plants with thatch. Under these treatment conditions, populations grew to only 16 ± 6 (mean \pm 1 SE) planthoppers per mesocosm. By contrast, planthopper populations escaped much of the suppressing effects of spiders on highly nutritious and thatch-free vegetation, where a final density of 189 ± 79 planthoppers per mesocosm was achieved. In the absence of predation on high-quality, thatch-free *Spartina*,



PLATE 1. Planthoppers (*Prokelisia marginata* and *P. dolus*) feeding on the phloem sap of *Spartina alterniflora*, a cordgrass that dominates the vegetation of intertidal marshes along the Atlantic coast of North America. Plant resources and spider predation interact in complex ways to impact the population growth of these planthoppers. The degree that spiders suppress planthopper populations depends on both plant nutrition and vegetation complexity. Spiders are most likely to check planthoppers on poor-quality *Spartina* with an associated matrix of leaf litter. In this system, bottom-up forces legislate the strength of top-down impacts. Photo by Hartmut Döbel.

planthopper populations erupted to 516 ± 140 individuals per mesocosm (Fig. 1A).

Differences in planthopper population growth among treatments containing wolf spiders were not attributable to the differential survival of spiders. Although the mean number of spiders decreased from 5 to 2.8 ± 0.2 individuals per mesocosm, there was no effect of either plant nutrition ($F_{1,36} = 0.59, P = 0.45$), thatch ($F_{1,36} = 0.59, P = 0.45$), or their interaction ($F_{1,36} = 1.05, P = 0.31$) on final spider density. There was, however, a significant effect of plant nutrition on wolf spider reproduction. Female wolf spiders produced more egg sacs when they were in mesocosms containing high-quality *Spartina* (0.55 ± 0.12 per female) than they did in arenas with nutrient-poor plants (0.10 ± 0.14 per female; $t = 2.28, df = 38, P = 0.03$). The enhanced reproduction of spiders on high-quality plants was associated with the higher density of planthopper prey on these plants compared to less nutritious ones (Fig. 1A). It is important to note that the egg sacs

carried by females at the termination of the experiment had not yet hatched and did not elevate the density of spiders in mesocosms.

Fertilization and spider predation both influenced the aboveground live biomass of *Spartina* in mesocosms. Strongest were the direct effects of fertilizer level on plant biomass (significant fertilization effect, Table 1), where plants in the high-fertilizer treatment attained greater biomass than plants receiving a low-nutrient subsidy (Fig. 1B). Spider density also influenced plant biomass, but to a much lesser degree. In general, the presence of spiders enhanced the live biomass of *Spartina* (significant spider effect), an effect that was intensified when thatch was present (significant thatch by spider interaction; Table 1, Fig. 1B). These predation effects on plant biomass were most likely indirect and cascaded down via their influence on planthopper density. Within a nutrient subsidy level, the greatest biomass of *Spartina* was attained when both spiders and thatch were present (Fig. 1B), and it was under these conditions that planthopper populations were most suppressed by spiders (Fig. 1A).

Additional analysis further supports that spider effects on plant biomass were leveled indirectly through reductions in planthopper density. For instance, there was a significant negative relationship between the biomass of *Spartina* in mesocosms and the final size of the planthopper population, a relationship that resulted on plants receiving both high ($y = 0.708 - 0.141x; R^2 = 0.17, P = 0.008$) and low ($y = 0.237 - 0.111x; R^2 = 0.23, P = 0.002$) fertilizer subsidies (Fig. 2). Analysis of covariance showed that although there was a

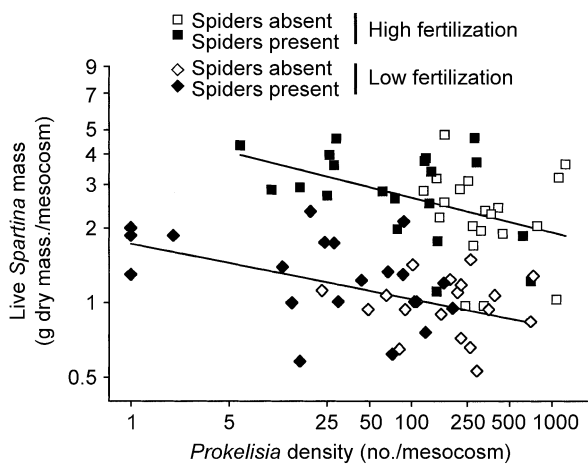


FIG. 2. Relationship between the live biomass of *Spartina* and planthopper (*Prokelisia dolus*) population size after 2 mo of growth on plants receiving high (squares) and low (diamonds) fertilizer subsidies in laboratory mesocosms. There was a significant effect of nutrient subsidy ($P < 0.001$) and planthopper density on plant biomass ($P < 0.0001$, ANCOVA). The smallest planthopper populations and the highest values for plant biomass occurred in mesocosms containing wolf spiders (filled symbols), a pattern that resulted on plants receiving either fertilizer treatment.

TABLE 2. Analysis of variance results (F values and significance levels) for the effects of three bottom-up plant treatments (fertilized vegetation without thatch augmentation, non-fertilized vegetation without thatch augmentation, and nonfertilized vegetation with thatch augmentation), two spider predation treatments (*Pardosa* wolf spiders added vs. not), and their interaction on the nitrogen content (angular-transformed percentage), aboveground live biomass (g dry mass per m²) and dead biomass (g dry mass thatch plus senescent leaves per m²) of *Spartina alterniflora* on islets at Tuckerton, New Jersey, USA.

| Source | df | Nitrogen content (%) | <i>Spartina</i> biomass | |
|-----------------------------------|----|----------------------|-------------------------|-------|
| | | | Live | Dead |
| Plant treatment | 2 | 96.27**** | 78.96*** | 4.54* |
| Spider addition | 1 | <0.01 | 0.31 | <0.01 |
| Plant treatment × Spider addition | 2 | 0.01 | 0.17 | 0.29 |
| Error | 38 | | | |

* $P \leq 0.05$; *** $P < 0.001$; **** $P \leq 0.0001$.

clear direct effect of fertilizer level on plant biomass ($F_{1,76} = 13.57$, $P < 0.001$), there was also a highly significant effect of planthopper density ($F_{1,76} = 18.21$, $P < 0.0001$). Planthopper density and fertilizer level did not interact to affect the biomass of *Spartina* ($F_{1,76} = 0.26$, $P = 0.61$). Notably, the lowest planthopper populations and the highest associated values for plant biomass occurred in mesocosms containing spiders (filled symbols), a pattern that emerged for both fertilizer treatments (Fig. 2).

ANOVA verified the effectiveness of our thatching treatment as evidenced by a highly significant effect of thatch addition on the amount of dead plant biomass remaining in mesocosms at the end of the experiment (Table 1, Fig. 1C). The small amount of dead plant material present in those treatments without thatch augmentation resulted from *Spartina* leaves that senesced during the course of the experiment. For these treatments, more dead plant material accumulated in mesocosms receiving a high fertilizer subsidy (significant fertilizer effect, Table 1), an effect that was linked to outbreeding planthopper populations (Fig. 1A) and enhanced plant senescence. Spiders diminished slightly the amount of dead plant material on heavily fertilized plants without thatch, an effect that did not occur on lightly fertilized plants (significant fertilizer by spider predation interaction; Table 1, Fig. 1C). This interactive effect was indirect and was associated with the adverse effects of spider predation on planthopper population size (Fig. 1A), which in turn reduced leaf senescence.

Field assessment of bottom-up and top-down forces on planthopper population growth

Our resource manipulations were successful in enhancing both the nutritional quality and biomass of *Spartina* and its physical structure (thatch). Fertilization significantly increased the nitrogen content of *Spartina* from 1.5% to 2.3% and aboveground live biomass from ~400 g/m² to 950 g/m² (significant plant treatment effect; Table 2, Fig. 3A and B). Moreover, neither spider addition nor thatch supplementation affected the nitrogen content or live biomass of *Spartina*

(Table 2, Fig. 3A and B). Thus, natural enemy effects did not cascade down to influence either the nutritional quality or biomass of *Spartina* in the field.

There was a significant effect of plant treatment on the biomass of dead plant material (thatch and senescent leaves) present on the *Spartina* islets, an effect that resulted entirely from thatch addition (Table 2, Fig. 3C). Of the 800 g/m² of thatch added to nonfertilized islets in early June, 362 ± 73 g/m² and 429 ± 35 g/m² remained in late August on treatment islets that were and were not stocked with spiders, respectively. By contrast, no thatch of the sort we added was present on the dethatched islets, although some senescent leaf material occurred by the end of the experiment (Fig. 3C).

The spider augmentation treatment was effective in elevating the density of *Pardosa* wolf spiders on experimental islets. Within the fertilizer and thatch treatments, wolf spider density was significantly higher on islets stocked with spiders than on islets not augmented with these predators (significant spider addition effect; Table 3, Fig. 4A). Notably, some *Pardosa* wolf spiders did colonize nonstocked islets. There was also a significant plant-treatment effect on wolf spider density, an effect that resulted in part from more spiders, both released individuals and ambient immigrants, remaining on and/or colonizing fertilized islets compared to nonfertilized ones (Table 3, Fig. 4A). A two-way ANOVA on only the thatch-free treatments further supported the fertilizer effect on wolf spider density ($F_{1,22} = 51.8$, $P < 0.0001$). Moreover, on unfertilized islets, wolf spider density was generally higher on islets supplemented with thatch (157 ± 21 individuals/m²) than on islets not receiving a thatch subsidy (109 ± 5 individuals/m², Fig. 4A), a pattern corroborated by two-way ANOVA (significant thatch effect, $F_{1,22} = 9.8$, $P = 0.005$).

Bottom-up treatments influenced the 8 July colonization density of the two *Prokelisia* species differently. Adults of *P. marginata* (mostly macropters) selectively colonized fertilized islets in enormous numbers (significant plant treatment effect; Table 3, Fig. 5A), whereas the adults of *P. dolus* (mostly flightless brachypters)

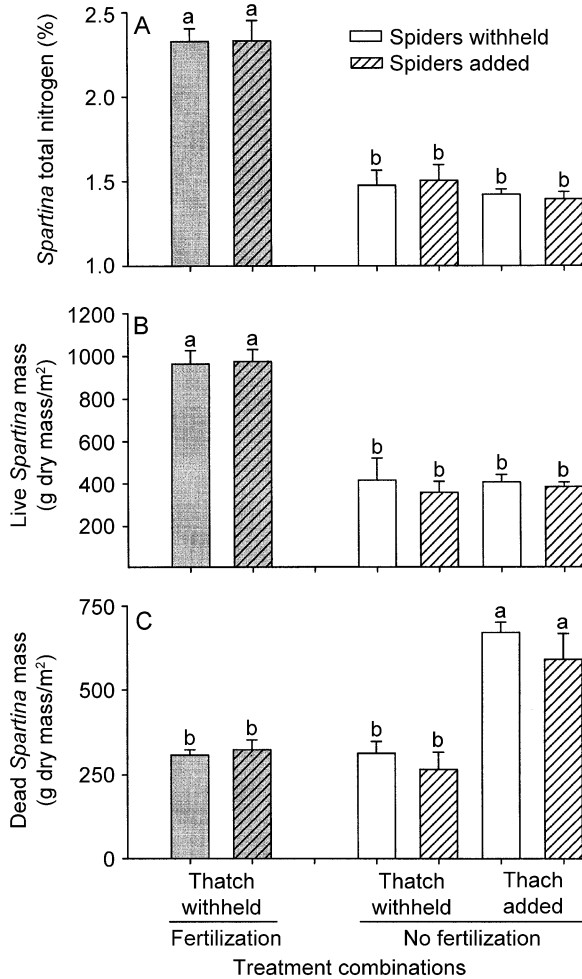


FIG. 3. Effects of nutrient subsidy (fertilization), vegetation structure (thatch), and spider augmentation on the (A) nitrogen content (% dry mass), (B) live aboveground biomass (g dry mass/m²), and (C) dead biomass (g dry mass of thatch and senescent leaves/m²) of *Spartina* cordgrass measured (25 August 1999) on experimental islets at Tuckerton, New Jersey, USA. Six treatment combinations were applied to islets: three host-plant treatments (fertilized islets without thatch and nonfertilized islets with and without thatch) each crossed with two spider-predation treatments (wolf spiders added vs. not). Means + 1 SE that do not share letters are significantly different ($P < 0.05$, ANOVA followed by Tukey-Kramer hsd test).

colonized at much lower densities and were similarly abundant on all islets regardless of treatment (Table 3; Fig. 5B). The difference in colonization ability between the two planthopper species undoubtedly explains why *P. marginata* ultimately attained higher densities than *P. dolus* on all experimental islets, particularly those islets that were fertilized (compare axes of Fig. 5C with 5D). During this early stage of islet colonization, neither the spider-addition treatment nor the thatch treatment had any effect on adult density for either planthopper species (Table 3, Fig. 5A and B).

Despite the initial difference in the impact of the

fertilization treatment on the colonization density of *P. marginata* and *P. dolus*, the plant and predation treatments had a similar effect on the final population size of both planthopper species by mid-August (significant plant and spider-addition effects on adults and nymphs, Table 3). In general, adults of both *P. marginata* and *P. dolus* and their nymphs were more abundant on fertilized islets than on nonfertilized ones (Fig. 5C–E). Two-way ANOVA further corroborated a significant positive fertilizer effect on the adult density of *P. marginata* and *P. dolus* as well as nymphs ($F_{1,22} = 21.2$, $P = 0.0002$, $F_{1,22} = 6.2$, $P = 0.02$, $F_{1,22} = 8.5$, $P = 0.008$, respectively). In particular, adults of *P. marginata* and nymphs erupted to very high densities (2000–5000 individuals/m²) on fertilized islets. Also, adults of *P. marginata* and nymphs generally achieved higher densities on nonfertilized islets without thatch than on nonfertilized islets supplemented with thatch (Fig. 5C and E; significant thatch effect, $F_{1,22} = 10.3$, $P = 0.004$ and $F_{1,22} = 6.1$, $P = 0.02$, respectively).

Bottom-up factors mediated the impact of the spider-augmentation treatment on planthopper density. Although the addition of wolf spiders to islets resulted in significant overall reductions in the final density of

TABLE 3. Analysis of variance results (F values and significance levels) for the effects of three bottom-up plant treatments (fertilized vegetation without thatch augmentation, nonfertilized vegetation without thatch augmentation, and nonfertilized vegetation with thatch augmentation), two spider predation treatments (*Pardosa* wolf spiders added vs. not), and their interaction on the population size (no. per m²) of wolf spiders, *Tythus vagus* egg predators, other spider species (pooled total), and the planthoppers *Prokelisia marginata* (adults only), *Prokelisia dolus* (adults only) and *Prokelisia* nymphs (both species pooled) on islets of *Spartina alterniflora* at Tuckerton, New Jersey, USA.

| Arthropods | Source of variation | | |
|----------------------------|---------------------|------------------|----------------|
| | Plant treatment | Spider treatment | Plant × Spider |
| Predators | | | |
| Wolf spiders | 42.43*** | 86.74*** | 0.14 |
| <i>Tythus vagus</i> | 93.69*** | 44.33*** | 4.96* |
| Other spider species | 11.90*** | 1.22 | 1.72 |
| Planthoppers | | | |
| <i>P. marginata</i> adults | | | |
| 8 July | 34.91*** | 0.01 | 1.25 |
| 17 August | 41.88*** | 7.99** | 2.91* |
| <i>P. dolus</i> adults | | | |
| 8 July | 0.89 | 2.53 | 0.22 |
| 17 August | 19.73** | 7.38** | 1.31 |
| <i>Prokelisia</i> nymphs | | | |
| 17 August | 30.79*** | 8.20** | 4.66* |
| df | 2, 38 | 1, 38 | 2, 38 |

Notes: Treatment effects were assessed twice for *Prokelisia* adults, once on 8 July when ambient nymphs were molting to adults that could colonize islets, and again on 17 August after six weeks of population growth. Wolf spiders were assessed on 28 July, and other predators were censused on 17 August.

* $P \leq 0.05$; ** $P \leq 0.001$; *** $P \leq 0.001$.

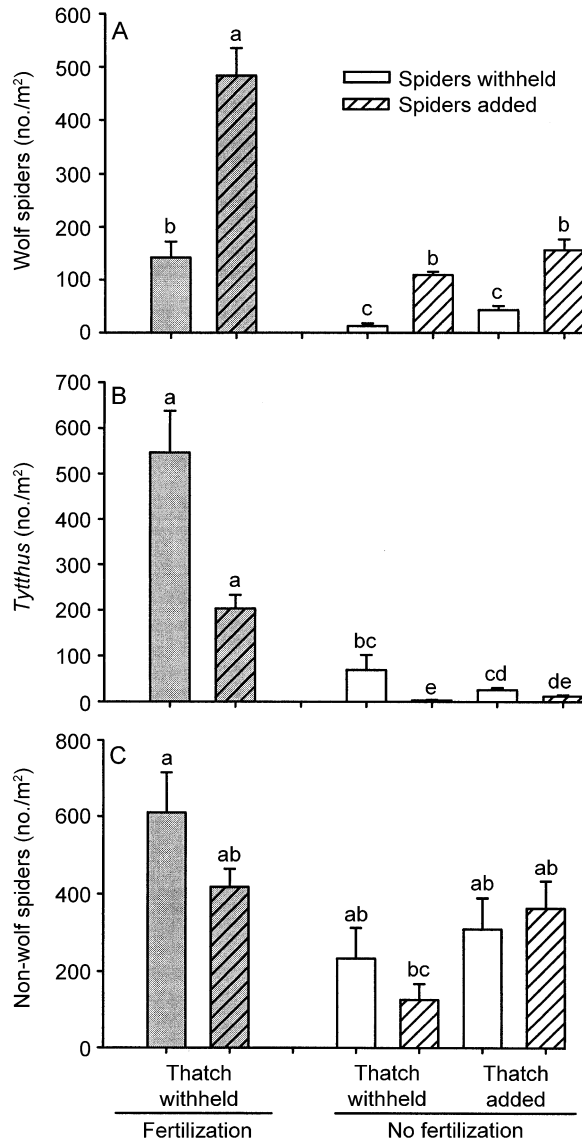


FIG. 4. Effects of nutrient subsidy (fertilization), vegetation structure (thatch), and spider augmentation on the density of (A) lycosid wolf spiders, (B) mirid egg predators (adults and nymphs of *Tyttthus vagus* pooled), and (C) non-lycosid spider species (pooled) on experimental *Spartina* islets at Tuckerton, New Jersey, USA. Lycosids were censused on 28 July, whereas other predators were assessed on 17 August 1999. Treatments and means separation tests are as in Fig. 3.

planthopper adults and nymphs (significant spider-addition effect, Table 3), the suppressing effect of spiders was relatively greater on nonfertilized islets than on fertilized ones, particularly for adult *P. marginata* and nymphs which were mostly this species (significant plant treatment by spider addition interactions for *Prokelisia* nymphs and *P. marginata* adults; Table 3, Fig. 5C and E). The greater suppressing effect of spiders on nonfertilized islets than fertilized ones was further documented using two-way ANOVA which found a

significant interactive effect of fertilization and spider addition on both *Prokelisia* nymphs ($F_{1,22} = 9.5$, $P = 0.006$) and *P. marginata* adults ($F_{1,22} = 5.2$, $P = 0.03$). For example, spiders reduced populations of *P. marginata* adults and *Prokelisia* nymphs by 50% and 16% on fertilized plants and by 81% and 64% on nonfertilized host plants, respectively (compare thatch-free treatments in Fig. 5C and E). A similar but nonsignificant trend also occurred for *P. dolus*, whereby the density of adults was reduced more on nonfertilized islets (50%) than on fertilized islets (26%; compare thatch-free treatments in Fig. 5D). These results occurred even though the density of wolf spiders was significantly higher on fertilized islets (~500 individuals/m²) than on nonfertilized ones (100–200 individuals/m²; Fig. 4A).

Thatch also affected planthopper populations negatively, whereby smaller populations of *P. marginata* and *P. dolus* adults and *Prokelisia* nymphs occurred on nonfertilized islets with thatch than on thatch-free islets (Fig. 5C–E; significant thatch effect with two-way ANOVA, $F_{1,22} = 15.1$, $P = 0.0008$, $F_{1,22} = 4.3$, $P = 0.05$, $F_{1,22} = 10.9$, $P = 0.003$, respectively). Moreover, a significant interactive effect of spiders and thatch resulted for adults of *P. marginata* ($F_{1,22} = 6.8$, $P = 0.016$) and *Prokelisia* nymphs ($F_{1,22} = 8.8$, $P = 0.007$) because of the contrasting spider effect on thatched and nonthatched islets (Fig. 5C and E). Unlike results from the laboratory experiment (Fig. 1A), spiders showed a greater negative impact on planthoppers on nonthatched islets than in thatched ones. This result occurred not because spiders were ineffective at suppressing planthoppers in thatch. Indeed, of all the treatment combinations, planthopper populations were the smallest on thatched islets augmented with spiders, but they remained low as well on thatched islets where spiders were withheld (Fig. 5C–E). This pattern likely resulted from a significant level of predation from ambient wolf spiders and other predators that immigrated to these thatchy control islets (Fig. 4A–C).

Other nonmanipulated predators colonized the experimental islets and were affected by the bottom-up and wolf spider-addition treatments. For the mirid egg predator *Tyttthus*, the bottom-up and spider-addition treatments significantly impacted its density (Table 3). Populations of this predator were generally higher on fertilized islets than nonfertilized ones, and lower on islets augmented with wolf spiders (Fig. 4B). This latter effect is consistent with the intraguild predation of mirids by wolf spiders. The suppressing effect of spiders on mirids was relatively greater on nonfertilized islets than on fertilized islets (Fig. 4B) as evidenced by a significant fertilizer by spider interaction ($F_{1,22} = 5.5$, $P = 0.02$). Moreover, on nonfertilized islets, thatch moderated the impact of wolf-spider predation on mirids (significant thatch by spider interaction; $F_{1,22} = 5.3$, $P = 0.03$). The reduced effect of spiders on mirids on

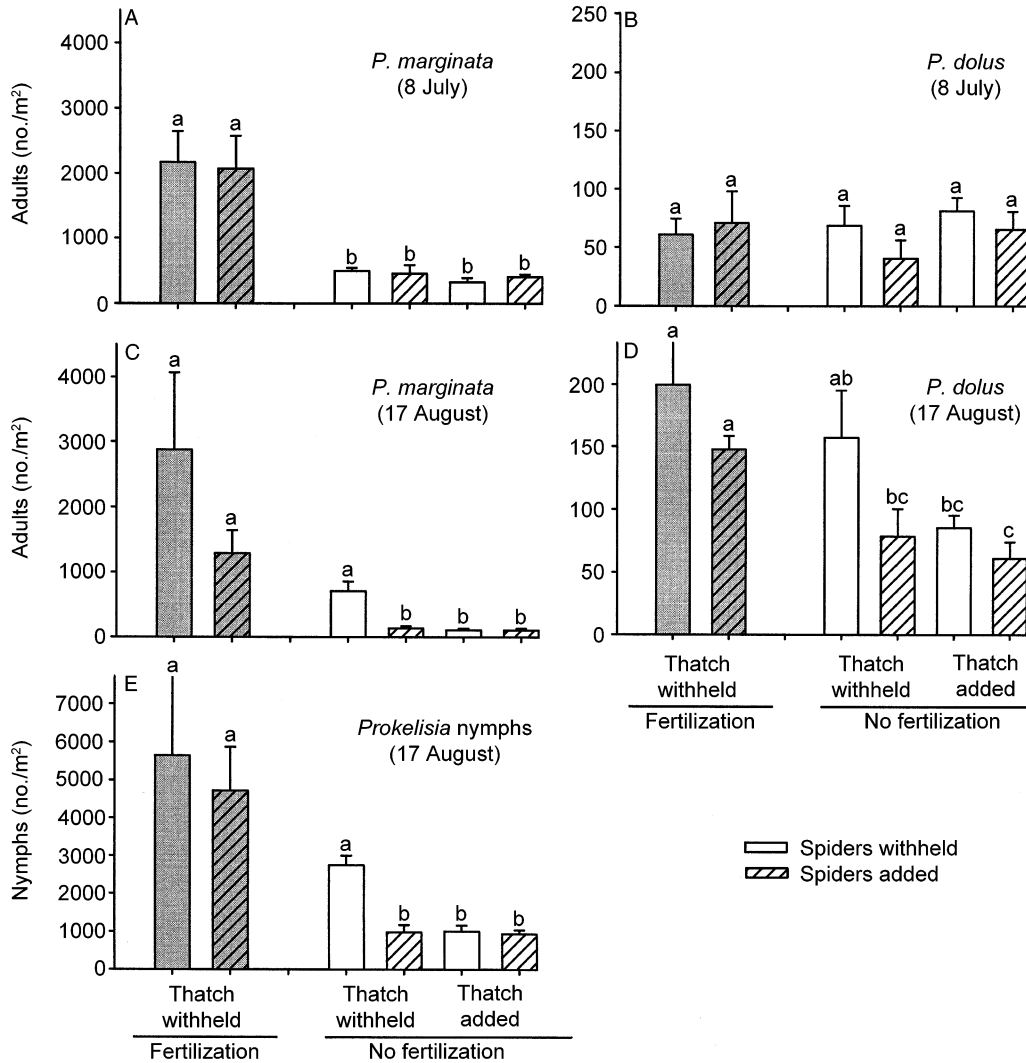


FIG. 5. Effects of nutrient subsidy (fertilization), vegetation structure (thatch), and spider augmentation on the colonizing density (8 July) of (A) *Prokelisia marginata* adults and (B) *P. dolus* adults, and on the late-season density (17 August) of (C) *P. marginata* adults, (D) *P. dolus* adults, and *Prokelisia* nymphs (both species pooled) on experimental *Spartina* islets at Tuckerton, New Jersey, USA. Spider augmentation occurred once before 8 July and five times before 17 August. Treatments and means separation tests are as in Fig. 3.

thatched islets may have contributed to the overall low planthopper populations there (Fig. 5C–E).

Other spider species (pooled total of mostly web-builders) were affected solely by the bottom-up treatments (significant plant-treatment effect, Table 3), whereby these predators achieved higher densities on fertilized than on nonfertilized islets (Fig. 4C; significant fertilizer effect, $F_{1,22} = 27.6$, $P < 0.0001$). Wolf spider augmentation did not significantly influence the density of these other spider species (Table 3), although there was a trend toward reduced populations on thatch-free islets where *Pardosa* was released (Fig. 4C; marginally significant spider effect, $F_{1,22} = 3.7$, $P = 0.07$). Thus, any intraguild predation of smaller web-building spider species by *Pardosa* appeared to be less pronounced than that incurred by mirids. On nonfertilized

islets, these spiders were generally more abundant on thatched islets than on islets lacking thatch (Fig. 4C; significant thatch effect, $F_{1,22} = 5.7$, $P = 0.03$).

Top-down and bottom-up impacts on planthopper population size: correspondence between laboratory and field assessments

Overall, the relative impact of the six bottom-up and spider predation treatments on the density of *Prokelisia* planthoppers was very similar on open islets in the field and in confined mesocosms in the lab. Treatment means in the field and laboratory were significantly correlated when the density of *P. dolus* ($r = 0.85$, $P = 0.03$) was used to assess treatment effects (Fig. 6). When the pooled density of *Prokelisia* nymphs was used to assess treatment effects, the relationship was marginally sig-

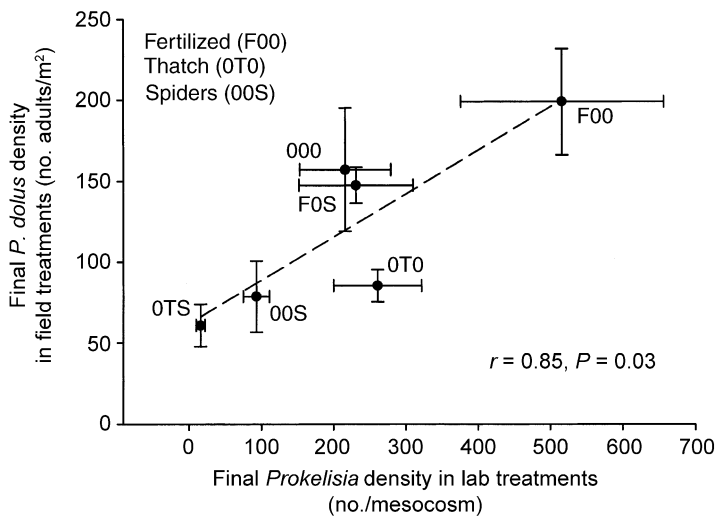


FIG. 6. Relationship between the impact of six experimental treatments (three host-plant treatments [fertilized plants without thatch and nonfertilized plants with and without thatch] each crossed with two spider-predation treatments [wolf spiders added vs. not]) on the density of *Prokelisia* planthoppers on open *Spartina* islets in the field at Tuckerton, New Jersey, USA, and the impact of the same six treatments on the density of planthoppers in confined mesocosms in the laboratory. Correlation was based on the final density of *Prokelisia dolus* (adults) after three months growth on experimental islets of *Spartina* in the field and the final density of *P. dolus* (adults and nymphs) after two months growth in experimental mesocosms in the laboratory ($r = 0.85$, $P = 0.03$). F = fertilized *Spartina*, T = thatch added, S = *Pardosa* wolf spiders added, 0 = no treatment applied. Thus, F00 = fertilized *Spartina* without thatch and without spiders added. Means \pm 1 SE are shown.

nificant ($r = 0.78$, $P = 0.06$). In both field and mesocosm assessments, planthoppers attained their highest density on fertilized *Spartina* plants that lacked thatch and were not augmented with wolf spiders. The lowest density of planthoppers occurred on poor-quality *Spartina* with thatch and supplemented with wolf spiders.

DISCUSSION

There is now widespread evidence that top-down and bottom-up forces interact to affect populations of phytophagous insects (Forkner and Hunter 2000). Results of our experiments also confirm complex interactive effects between plant-related factors and predators on the population growth of salt marsh planthoppers (Figs. 1A and 5C–E). In general, the extent to which spiders suppressed planthoppers depended on both plant nutrition and vegetation structure, an interaction that was demonstrated experimentally both in the field and laboratory. For the most part, spiders restrained planthoppers most effectively on poor-quality *Spartina* with an associated matrix of thatch, and planthopper populations generally escaped the suppressing effects of predation on nutritious plants without thatch (Fig. 5C–E). Thus, the general paradigm in this system is for bottom-up primacy whereby predation does not offset the colonization-enhancing and growth-promoting effects of host-plant nutrition on planthopper populations under most circumstances. Moreover, when predators do exert a significant suppressing effect on planthopper populations, their impact is mediated to a great extent by host-plant characteristics, namely plant nutrition and vegetation structure. Thus, our hypothesis that host plant-related effects would dominate in this system was confirmed, as espoused by Hunter and Price (1992) for phytophagous insects in general. The dominance of bottom-up impacts on phytophagous arthropods has been demonstrated by others, both empirically (Auer-

bach et al. 1995, Forkner and Hunter 2000) and using modeling approaches (Gutierrez et al. 1994). Thus, plants often set the dynamic stage on which herbivorous insects and their natural enemies interact (Denno and McClure 1983, Hunter and Price 1992).

Nonetheless, the paradigm of plant primacy is a general one, and for salt-marsh planthoppers, there is important spatial variation across habitats in the relative strength of bottom-up and top-down forces. We designed our top-down and bottom-up treatment combinations to mimic naturally occurring spatial variation in these factors in the field. Nitrogen-rich *Spartina* free of thatch and with few associated spider predators are characteristics of low-marsh habitats (Denno 1983, Döbel et al. 1990). It was this combination of factors that promoted the largest planthopper populations in our experiments (Fig. 6), and also fosters outbreaks in the field (Denno and Peterson 2000). The high nitrogen content of low-marsh *Spartina* promotes mass colonization, enhances survival and fecundity, and encourages rapid population growth of *Prokelisia* planthoppers (Olmstead et al. 1997, Denno and Peterson 2000). The paucity of thatch and greater tidal disturbance combine to reduce populations of many predators including *Pardosa* wolf spiders in low-marsh habitats (Döbel et al. 1990). The rarity of natural enemies, coupled with superior *Spartina* nutrition and the ability of planthoppers to induce reductions in plant nitrogen when they feed (Denno et al. 2000), all contribute to the boom-and-bust dynamics of planthopper populations in low-marsh habitats (Denno and Peterson 2000). Thus, bottom-up forces generally prevail at lower elevations on the marsh.

In contrast, invertebrate predators appear to play a greater role in planthopper suppression in certain high-marsh habitats. Our experiments show that wolf spiders are often most effective in suppressing planthoppers on nitrogen-poor plants with associated thatch (Fig. 6),

characteristics typical of *Spartina* growing on high-marsh meadows. Other manipulative experiments conducted on the high marsh also demonstrate that thatch promotes an aggregative response of spiders that in turn enhances planthopper suppression on nutrient-poor *Spartina* (Döbel and Denno 1994). Thatch was also shown to foster greater planthopper suppression in laboratory mesocosms, where spiders could not immigrate from nearby habitats (Fig. 1A). This result suggests that spiders may capture planthoppers with greater efficiency in thatchy habitats, perhaps as a result of the scaffold-like structure of thatch that may provide greater access to leaf-feeding planthoppers for a ground-foraging predator. Thus, increasing vegetation complexity by adding thatch did not apparently provide hiding sites and thus a refuge from predation, a finding contrary to the view that heterogeneity enhances enemy-free space (Murdoch et al. 1989, Messina et al. 1997). Nonetheless, these experiments confirm our hypothesis that complex vegetation with thatch often intensifies the impact of spider predation both by encouraging predator aggregation and by increasing capture efficiency, a result shown for other systems as well (Landis et al. 2000).

Spiders and other invertebrate predators are far more abundant at higher elevations on the marsh (Döbel et al. 1990, Denno and Peterson 2000). Thus, there is substantial spatial variation in the strength of top-down and bottom-up forces on planthopper populations across habitats on the marsh. In general, plant quality diminishes up the elevational gradient (Gallagher et al. 1988, Ornes and Kaplan 1989), and both the abundance of thatch and invertebrate predators increase (Denno 1983, Döbel et al. 1990). The result is an increase in the relative strength of predation at higher elevations.

By fertilizing *Spartina* islets we were able to increase both its nitrogen content and biomass (Fig. 3). These host-plant effects promoted planthopper increases (Fig. 5) that then cascaded to the third trophic level where invertebrate predators became more abundant. Not only did more of the *Pardosa* spiders remain on fertilized islets (Fig. 4A), but densities of nonmanipulated enemies such as the egg predator *Tytthus* and other spider species (*Grammonota*) were higher on fertilized islets (Fig. 4B and C). Predator increases on fertilized *Spartina* islets probably resulted from a combination of increased aggregation, enhanced reproduction, and reduced emigration in areas of elevated planthopper density. Such numerical responses have been shown independently for *Pardosa* and *Tytthus* in other studies (Döbel and Denno 1994, Finke and Denno 2002). Similarly, in our laboratory experiment, *Pardosa* wolf spiders produced significantly more egg sacs on heavily fertilized *Spartina* plants that supported higher densities of planthoppers. Thus, for *Pardosa*, both an immediate aggregative response and a time-lagged reproductive response are the cascading results of enhanced plant quality.

Others have also shown that increases in host plant productivity and nutrition elevate the densities of herbivorous arthropods which in turn foster increases in natural enemy populations at the third trophic level (Hartvigsen et al. 1995, Fraser and Grime 1998, Polis et al. 1998, Forkner and Hunter 2000). In several cases involving herbivorous arthropods, bottom-up effects travel up through the food web where the effect of enhanced enemy density cascades back down to impact adversely herbivores at trophic levels beneath (Hartvigsen et al. 1995, Stiling and Rossi 1997, Fraser and Grime 1998, Polis et al. 1998, Forkner and Hunter 2000). These studies support the contention that the strength of top-down forces increases with enhanced primary productivity (Oksanen et al. 1981), and for herbivorous arthropods are consistent with the trophic view that "what goes up must come back down" (Forkner and Hunter 2000).

Notably, however, this cascading effect did not occur in this study, despite the elevated numbers of *Pardosa* and other natural enemies on fertilized islets (Fig. 4). *Prokelisia* planthoppers, especially *P. marginata*, escaped spider predation more on fertilized *Spartina* islets than on nonfertilized islets (Fig. 5). We argue that highly mobile herbivores such as planthoppers colonize nutritious host plants in very high numbers (Denno 1983, Denno et al. 1996) and in so doing partially escape natural enemy impact (Denno and Peterson 2000).

The effect of a mobile life style on colonization can be seen by comparing the early July densities of the flight-capable *P. marginata* with those of the more sedentary *P. dolus* on fertilized and nonfertilized islets (Fig. 5A and B). Soon after islets were available for colonization, very high densities of *P. marginata* macropters (>2000 individuals/m²) selectively settled on fertilized islets, whereas <500 adults/m² colonized nonfertilized islets. This pattern contrasted with that for *P. dolus*, where the flightless adults were less common and similarly abundant on all islets regardless of fertilizer subsidy. The high initial density of colonizing macropters coupled with the enormous number of eggs they deposit (Denno and Peterson 2000), undoubtedly contributed to the escape of *P. marginata* from spider suppression on fertilized islets by mid-August (Fig. 5C).

For the less mobile *P. dolus*, spiders were more effective in suppressing populations across all plant treatments in the field, although there was a trend toward greater restraint on nonfertilized compared to fertilized islets (Fig. 5D). The reduced dispersal ability of this species (Denno et al. 2000) coupled with its delayed population increase on nitrogen-rich plants (Denno and Peterson 2000), diminished escape from spider predation on fertilized plants in the field.

In general, mobile species of herbivores appear to be less influenced by top-down forces than are sedentary species (Denno and Peterson 2000). When prey

are more mobile and fecund than their primary predators, as is the case for *P. marginata* and *Pardosa*, predators often exhibit a weak numerical response to increasing prey density, predator-prey dynamics uncouple, and prey populations erupt (Döbel and Denno 1994). We argue that when very mobile and short-lived herbivores are involved, enhanced plant quality may promote their escape from top-down forces rather than cascade back down to adversely affect their local density via elevated predator abundance (Denno and Peterson 2000). More likely is rapid population growth followed by density-dependent dispersal, a phenomenon that occurs frequently in *P. marginata* (Denno and Roderick 1992). Because dispersing planthoppers colonize high-quality *Spartina* patches en masse in other habitats (Denno and Peterson 2000), what goes up in one habitat may come down elsewhere to adversely impact plant resources. Thus, local bottom-up effects on consumers (the mass build-up of migrants in this case) can influence spatial subsidies across habitats (colonists) and affect food-web dynamics at a regional spatial scale (Polis and Hurd 1996). Nonetheless, our results for *Prokelisia* planthoppers suggest that the life history strategy of a species is an important mediator of top-down and bottom-up impacts.

There has been considerable dispute in the ecological literature as to whether the top-down effects of natural enemies cascade down through the food web to benefit primary producers (Polis and Strong 1996, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001). It is thought that factors such as food-web diversity, omnivory, and intraguild predation, buffer communities against trophic cascades (Strong 1992, Polis and Strong 1996, Fagan 1997, McCann et al. 1998, Schmitz et al. 2000), although exceptions exist (Moran and Hurd 1998, Pace et al. 1999). For terrestrial food webs dominated by phytophagous arthropods, there is support both for (Moran et al. 1996, Beckerman et al. 1997, Schmitz et al. 1997, Letourneau and Dyer 1998, Moran and Hurd 1998, Halaj and Wise 2001) and against (Forkner and Hunter 2000, Schmitz et al. 2000, Halaj and Wise 2001) enemy effects that cascade down to either reduce herbivory or enhance plant biomass.

Results from our experiments are consistent with the notion that emergent interactions (e.g., intraguild predation and omnivory) dampen predator-mediated cascades. In laboratory mesocosms, where only spiders and planthoppers interacted, predator effects traveled down resulting in increased cordgrass biomass (Fig. 1B). By contrast, we found no experimental evidence for this cascade in the field where predators other than wolf spiders were present. Here, the addition of wolf spiders had no effect on *Spartina* biomass or nutrition and neither fertilization nor thatch augmentation altered this pattern (Fig. 3A and B). Other prey, in particular intraguild prey, were present in the field that were excluded from the laboratory experiment. Both mirid egg predators and web-building spiders were

common on the experimental islets and there was convincing evidence that wolf spiders fed extensively on mirids as well as planthopper prey. For instance, the addition of *Pardosa* wolf spiders significantly reduced mirid populations, particularly on nonfertilized islets without thatch (Fig. 4B), a trend that also occurred with nonwolf spider species (Fig. 4C). We argue that these smaller predators served as intraguild prey for *Pardosa*, partially relaxed *Pardosa* predation on planthoppers, and diminished the opportunity for top-predator effects to cascade down and affect *Spartina* biomass. Notably, the intraguild predation of mirids by *Pardosa* wolf spiders, particularly in thatch-free habitats, has been documented independently (Finke and Denno 2002). Thus, our findings are consistent with the view that reticulate interactions such as intraguild predation buffer food webs from enemy-driven trophic cascades (Strong 1992, Fagan 1997, McCann et al. 1998, Schmitz et al. 2000).

Alternatively, the use of *Spartina* transplants may have promoted the cascading effects of spider predation on cordgrass biomass in laboratory mesocosms. Field plants with long-established root systems may have been more tolerant of elevated planthopper densities on islets where spiders were withheld. Although we do not rule out that differences in plant tolerance contributed to the discovery of a trophic cascade in the laboratory, we argue that the apparent intraguild predation of mirids by wolf spiders (Fig. 4B) is an equally plausible explanation for the attenuation of top-down effects in the field.

Key to understanding bottom-up vs. top-down forces in this system is the life history strategy of the dominant herbivores, whereby mobility and rapid population growth tend to uncouple predator-prey dynamics both spatially and temporally. In an environment of variable plant nutrition and vegetation structure, planthoppers can both colonize and exploit high-quality host plants and partially elude their less responsive predators (Denno and Peterson 2000). The default is strong bottom-up impact and predator effects that often do not cascade down to dramatically affect herbivore populations. Only in certain habitats where predators aggregate and herbivores develop slowly, both dictated by plant-related factors, do predators exert a significant adverse effect.

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