Top-down, bottom-up, or side to side? Within-trophic-level interactions modify trophic dynamics of a salt marsh herbivore

Daniel C. Moon and Peter Stiling

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Many factors can influence the top-down and bottom-up dynamics of phytophagous insects. Although interactions between herbivore species have been frequently shown to be ecologically important, the effects of such horizontal trophic interactions on the relative roles of top-down and bottom-up forces have gone largely unstudied. In this paper we report on the results of a factorial field experiment in which we examined the effects of within-trophic-level interactions on the top-down and bottom-up dynamics of a salt marsh planthopper.
We manipulated the bottom-up effects of plant quality by increasing soil salinity, and manipulated top-down effects by decreasing the intensity of parasitoid attack with yellow sticky traps that removed hymenopteran parasitoids. We applied these treatments to plots in two patches of the host plant, one with low densities of lepidopteran stem borer larvae, and one with high densities of stem borers. We maintained the treatments and monitored planthopper density for ten months, from March through December 1999. Increased salinity significantly increased planthopper density within one month of the first application of salt. The rapid response of the planthopper to salt treatments suggested a chemical mechanism, perhaps mobilization of bound nitrogen. Yellow sticky traps, although significantly reducing parasitism of planthopper eggs, had little impact on hopper density. The density of lepidopteran stem borers, however, had an even greater impact on planthopper density than did salt treatments, with high stem borer plots supporting much lower densities of hoppers. Stem borer density also reduced the response of the planthopper to other treatments, especially salt supplementation. The results of this study show that the impact of within-trophic-level interactions can significantly change herbivore trophic dynamics and can be even more important than either top-down or bottom-up effects in determining herbivore density.

D. C. Moon and P. Stiling, Dept of Biology, Univ. of South Florida, Tampa, FL 33620, USA (dmoon@chuma.cas.usf.edu).

The examination of the relative roles of top-down and bottom-up effects on populations and communities continues to be a fertile field of ecological study. Although there have been many advances made in this area, many complex relationships remain to be disentangled. One facet of trophic dynamics that has recently received considerable attention from ecologists is how the roles and importance of top-down and bottom-up effects change under varying environmental conditions (Hunter and Price 1992, Hartvigsen et al. 1995, Floyd 1996, Preszler and Boecklen 1996, Hunter et al. 1997, Stiling and Rossi 1997, Forkner and Hunter 2000, Ritchie 2000, Moon and Stiling 2002). The overwhelming majority of these studies have focused on nutrients and productivity. In a recent example, Forkner and Hunter (2000) showed that the abundance of predaceous arthropods and the intensity of avian predation on phloem feeders was greater on fertilized oaks (*Quercus rubra*) than on unfertilized oaks. Given the fact that the nitrogen content of plant tissues is one of the most

consistently important determinants of herbivore density (Dixon 1970, Mattson 1980, Brodbeck et al. 1990, Rossi and Strong 1991, Waring and Cobb 1992, Moon et al. 2000), studies examining the bottom-up effects of increasing plant quality through fertilization are of vital importance.

There are a number of other factors that affect plant quality, however, that can be as important or even more so than fertilization. For salt marsh plants, one such factor is salinity and resulting salt stress. It has been well documented that salt stress can have profound impacts on salt marsh plants. For example, salinity can change chemistry (Cavalieri and Huang 1979, Jefferies et al. 1979, Cavalieri 1983), morphology (Longstreth and Nobel 1979, Kemp and Cunningham 1981, Hwang and Morris 1994, Hester et al. 1996), and reproduction (Haines and Dunn 1985, Shumway and Bertness 1992, Vernberg 1993, Srivastava and Jefferies 1995) of plants. Our previous research on *Borrichia frutescens* (Moon and Stiling 2000, 2002) has shown that salinity can significantly affect the quality and morphology of this species.

The effects of salt stress are not limited to salt marsh plants, but can impact the insects that feed on them as well. Variation in soil salinity levels has been shown to significantly affect insect herbivores in both natural (Brodbeck and Strong 1987, Hemminga and van Soelen 1988, Levine et al. 1997, Bowdish and Stiling 1998, Moon and Stiling 2000, 2002) and managed (Salim et al. 1990, Dunn et al. 1998) ecosystems. The most frequently invoked mechanistic explanation for stress effects on herbivores is White's (1978, 1993) stress hypothesis, which suggests that plants under stress will have more free, unbound nitrogen. For salt stress, this may indeed be the case, as many salt marsh plants respond to salt stress by mobilizing nitrogen in order to produce organic solutes that serve an osmoregulatory function (Jefferies 1977, 1980, Jefferies et al. 1979, Cavalieri 1983, Adam 1990). Stress can induce a number of other changes, such as altered defensive chemistry (Gould 1978, Rhoades 1979, Gershenzon 1984) in host plants that may significantly impact herbivores as well (Brodbeck and Strong 1987, Waring and Cobb 1992).

While the effects of salt stress on plants and on their herbivores have been relatively well studied, the effect of salt stress on the balance between top-down and bottom-up effects is virtually unknown. In one of the few studies to look at the effects of stress on top-down and bottom-up effects, Hacker and Bertness (1995) found that stressed *Iva frutescens* plants supported greater densities of aphids because predation was lower on these smaller, stunted plants. No study to date, however, has manipulated both top-down pressure and bottom-up effects of host plant quality resulting from increased salt stress. This paucity of studies is surprising, considering the fact that one of the most well known theories of trophic dynamics, the Menge and Sutherland (1976, 1987) or MS hypothesis, predicts that the relative strengths of top-down and bottom-up effects can vary with stress levels. Perhaps this shortage of studies has arisen in part because of a general lack of agreement regarding what constitutes a stressful environment. There is little disagreement, however, that salt marshes are indeed stressful environments (Adam 1990, Bertness et al. 1992, Bertness and Hacker 1994, Levine et al. 1997). As such, the level of salt stress experienced by organisms living in such an environment may have strong impacts on top-down and bottom-up dynamics.

Another aspect of top-down and bottom-up dynamics that has gone virtually unstudied is the impact of within-trophic-level interactions among herbivores. For phytophagous insects, interspecific competition has been re-established as one of the pivotal factors in determining population dynamics (Damman 1993, Denno et al. 1995, 2000). In their review, Denno et al. (1995) showed that interspecific competition between herbivorous insects occurred in 76% of the cases examined. Interspecific competition has been shown to have strong impacts on the effects of host plants on herbivores (Haukioja and Niemela 1979, McClure 1980, Hanhimaki 1989, Moran and Whitham 1990, Hunter 1992, Masters and Brown 1992, Ritchie and Tilman 1992, Dankert et al. 1997, Denno et al. 2000), and has also been shown to impact the interaction between herbivores and their natural enemies (Fowler and MacGarvin 1986, Miller 1986, Settle and Wilson 1990, Bergvinson and Borden 1991). While the potential for horizontal trophic linkages to impact top-down or bottom-up forces in isolation has been well documented, the effects of within-trophic-level interactions have not been integrated into a simultaneous and factorial manipulation of both top-down and bottom-up effects. In this study we conducted a factorial field experiment in which we examined the effects of a lepidopteran stem borer on the trophic dynamics of the salt marsh planthopper *Pissonotus quadripustulatus* (Homoptera: Delphacidae). Here we show that competition from the stem borer can greatly affect the responses of the planthopper to bottom-up and top-down manipulations.

Methods

Study system

Our study centered around the phloem feeder *Pissonotus quadripustulatus* (Homoptera: Delphacidae) referred to hereafter by genus. *Pissonotus* is monophagous on *Borrichia frutescens* (Denno 1978), insert-

ing its mouthparts into the phloem tissue of the leaves of the plant and sucking the sap (Stiling 1994). Eggs are laid in the stems of *Borrichia*, just beneath the epidermis, with most eggs clustered around the nodes of the stem (Moon and Stiling 2000). *Pissonotus* is multivoltine with overlapping generations and is present on *Borrichia* year round (Moon and Stiling 2000). The host plant, *Borrichia frutescens* (Asteraceae) hereafter referred to by genus, is a rhizomatous perennial shrub, typically one meter or less in height. *Borrichia* is common in the intertidal zones, and just shoreward of the intertidal zones of the salt marshes around Tampa Bay, Florida (Antlfinger 1981, Stiling 1994).

The most common natural enemy of *Pissonotus* is the fairyfly *Anagrus* sp. nr *armatus* (Hymenoptera: Mymaridae), an egg parasitoid. *Pissonotus* eggs that have been parasitized by *Anagrus* are easily distinguishable from viable hopper eggs. Parasitized eggs are orange, eventually darkening to brown or black, while eggs that have not been parasitized are milky white in color (Moon and Stiling 2000). At our field site, *Pissonotus quadripustulatus* has few natural enemies other than *Anagrus*. *Pissonotus* is attacked by only 2 parasitoids other than *Anagrus*, a strepsipteran and a dryinid, and our preliminary observations indicated that the frequencies of parasitism by these two parasitoids at the study site used here were low. Our preliminary observations also indicated that predation on *Pissonotus* is mainly limited to spiders, which do not reach high densities at this field site.

Another herbivore feeding on *Borrichia* is a stem borer (Lepidoptera: Argyresthiidae), which, in the larval stages, feeds on the tissue layers beneath the epidermis. The presence of a stem borer is easily detected as its feeding leaves a roughened area of the stem, with the epidermis peeling and taking on a papery appearance. The as yet unknown lepidopteran species is multivoltine, with overlapping generations occurring year-round, although the greatest densities occur in the spring. Stem borer density is locally quite variable, with some patches of *Borrichia* having no borers at all, while other patches have as much as 80% of the stems occupied. Most (>90%) of *Borrichia* stems that are occupied contain only a single stem borer larva, although occasionally, as many as three have been found in one stem. This stem borer can compete directly and indirectly with the planthopper *Pissonotus*. The stem borer larvae consume the same tissue layers in which *Pissonotus* eggs are laid, and kill *Pissonotus* eggs as they bore through the stem. Stem borer activity may also make stems less attractive, either chemically or physically, to *Pissonotus*. Furthermore, large stem borer larvae excavate deep tunnels through the vascular tissue of the stem, girdling and frequently killing the stem. Thus, these stem borers may also reduce the number of stems available to *Pissonotus* in a patch.

Field methods and data analysis

On 1 March 1999, we staked out 16 2 m by 2 m plots in a large patch of *Borrichia frutescens* at Upper Tampa Bay park in Hillsborough County, Florida, USA. Eight of the plots were placed in a patch of *Borrichia* that had a high density of stem borers, typically between 50 and 80 borers per 100 stems. The other block of eight plots was placed in a patch of *Borrichia* that had a low density of stem borers, typically between 0 and 20 borers per 100 stems. Within each block of eight plots, both bottom-up and top-down forces were manipulated. Bottom-up manipulations consisted of increasing salt stress by adding salt to each of the appropriate experimental plots. We hand-broadcast 750 g of Morton's solar salt pellets over each plot biweekly. Top-down forces were manipulated by reducing parasitism pressure on *Pissonotus* by trapping hymenopteran parasitoids. This was accomplished with yellow Sticky Strips (Gempler's, Belleville, WI, USA), consisting of yellow plastic cards, 13 × 8 cm, coated with Tanglefoot adhesive. The fairyfly *Anagrus* sp nr *armatus* is attracted to the yellow cards, and gets stuck in the Tanglefoot. The efficacy of these cards in catching *Anagrus* wasps has been demonstrated many times previously (Cronin and Strong 1990, Stiling et al. 1991, Kruppa and Stiling, unpubl.). Five sticky traps were placed in each of four experimental plots, one near each of the corners, and one in the center of the plot. The traps were placed at the level of the tops of the *Borrichia* stems, close to where the wasps search for hosts, but still readily visible. Traps were collected every two weeks, and replaced by new cards. Collecting the traps every two weeks ensured that they were still sticky when collected, even in the wettest months of summer. Thus there was no lapse in the removal of parasitoids between trap applications.

We assigned the treatments, salinity (ambient and elevated) and traps (traps and no traps) randomly to plots within the high and low stem borer density blocks. The resulting design was fully factorial with three factors and two replicate plots per treatment combination, for a total of 16 plots. Pre-treatment data were collected on 1 March 1999, followed immediately by application of the first treatments. Post-treatment data were then collected through December 1999.

We assessed the degree to which salt supplementation increased salinity on the plots by measuring the interstitial soil water salinity. Twice each month we made a small depression, approximately 6 inches deep in the soil in a haphazardly chosen location in each plot. We then used a YSI model 33 salinity meter to measure the salinity of the water that pooled in the depression. The two measurements made each month were averaged to yield a monthly salinity measurement for each plot, which was then analyzed using repeated measures ANOVA to determine the effect of the treatments on salinity.

In order to assess the effects of the treatments on the host plant *Borrichia frutescens*, we measured percent foliar nitrogen, stem height, leaf area, and stem density. To measure the percentage of foliar nitrogen, every other month beginning in March, a leaf from each of ten randomly selected stems in each plot was collected from the same position on each stem (the lowest layer of leaves around the apical node). They were then returned to the lab, where they were freeze-dried in a Flexi-Dry lyophilizer (FTS Systems, Inc., Stone Ridge, New York, USA), ground in a Wiley mill, and analyzed for foliar nitrogen using a CE Instruments NC2100 CN Analyzer (CE Elantech, Inc., Lakewood, NJ, USA).

Stem height, leaf area, and stem density measurements were made monthly. Ten *Borrichia* stems from each plot were chosen at random and scored for stem height, measured in centimeters from ground to apical meristem. For leaf area, we randomly selected another set of ten stems per plot, and collected a leaf from the lowest layer of leaves at the apical node that did not show signs of senescence. The collected leaves were put on ice and returned to the lab, where the area was then measured using a CID model CI-202 leaf area meter (CID, Inc., Vancouver, WA, USA). Finally, we measured the density of stems by randomly placing a 0.5×0.5 m quadrat within each plot and counting the number of stem tips enclosed.

Additionally, to ensure that the difference in stem borer density between high and low borer blocks was maintained, as well as to examine the effects of our treatments on stem borer density, we made monthly censuses of stem borers. On each plot, we randomly selected 100 *Borrichia* stems and examined them for the presence of borers.
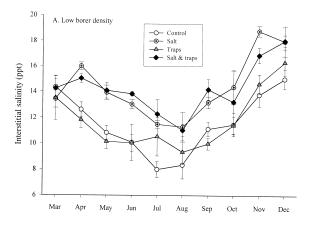
The effects of the treatments on *Pissonotus quadripustulatus* were assessed by monthly field counts of planthopper density. The abundance of *Pissonotus* feeding on *Borrichia* can be obtained easily by field counts because these planthoppers are 100% brachypterous (Stiling 1994) and do not fly away when approached or disturbed. For each plot, a randomly selected sample of 20 *Borrichia* stems per plot was observed for the abundance of planthoppers. We repeated this 3 times, and calculated a mean of the three counts that served as our data point for that plot in that month. Repeated measures ANOVAs were then used to determine treatment effects on *Pissonotus* density.

We also recorded the density of *Pissonotus* eggs, and the percentage of eggs that were parasitized by *Anagrus*. Each month, we collected ten randomly-selected stems from each of the sixteen plots and returned them to the lab. Each stem was then examined under a dissecting microscope. We used scalpels to strip away the epidermis of the entire stem and counted the total number of eggs per plot (10 stems), as well as the percentage of those eggs that had been parasitized. Although the

number of eggs varied among plots and among months, percent parasitism values were never based on fewer than 24 eggs, usually many more. Egg density and parasitism data were then analyzed with repeated measures ANOVA. All statistical procedures used throughout the study were performed using the SYSTAT 9 statistical program (Wilkinson 1999).

Results

Addition of salt pellets significantly increased interstitial soil water salinity (F = 35.436, df = 1,12, P < 0.001). Salinity increased by an average of 3 ppt (a 27% increase) on salt-supplemented plots compared to plots that were not salted (Fig. 1). This increase was maintained over the course of the study, even during the wettest months of the summer when salinities are lowest. Salinities were very similar on low and high stem borer density plots (Fig. 1).
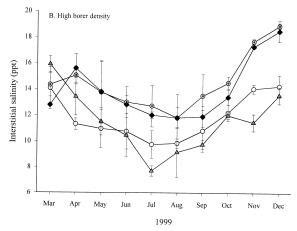

Fig. 1. Mean ($\pm$ 1 SE) salinity (ppt) of soil water measured at a depth of 15 cm in each treatment and control plot from A) low stem borer density plots and B) high stem borer density plots.

Table 1. Summary of results (P values) of repeated measures ANOVA on 4 response variables measured for *Borrichia frutescens*.

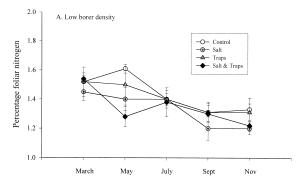| Source	Foliar nitrogen	Stem height	Leaf area	Stem density
Between subjects				
Borer	0.172	0.470	0.432	0.147
Salt	0.001	0.064	<0.001	0.085
Traps	0.896	0.897	0.904	0.934
Borer × Salt	0.120	0.678	0.582	0.538
Borer × Traps	0.432	0.794	0.336	0.950
Salt × Traps	0.833	0.895	0.730	0.617
Borer × Salt × Traps	0.574	0.854	0.423	0.874
Within subjects				
Time	<0.001	<0.001	<0.001	<0.001
Time × Borer	0.452	0.678	0.611	0.056
Time × Salt	0.244	0.451	0.028	0.294
Time × Traps	0.914	0.812	0.916	0.756
Time × Borer × Salt	0.290	0.909	0.222	0.920
Time × Borer × Traps	0.221	0.969	0.477	0.794
Time × Salt × Traps	0.800	0.618	0.935	0.241
Time × Borer × Salt × Traps	0.618	0.761	0.195	0.307

Addition of salt pellets produced a number of stress-related changes in *Borrichia*. For example, salt supplementation significantly reduced the foliar nitrogen concentration of *Borrichia* leaves (Table 1). Plants from salt supplemented plots contained, on average, 1.40% foliar nitrogen, while plants from plots that were not salted contained an average of 1.51% (Fig. 2). There was a significant effect of time on foliar nitrogen concentration (Table 1), as was there on stem height, leaf area, and stem density reflecting the seasonality common among the plant response variables measured.

Increased salinity also reduced the growth of *Borrichia* (Table 1), as stems from salted plots averaged 7 cm less (a 23% reduction) in height than did stems from non-salted plots. The difference in stem height was evident within one month of the first treatment application. Increased salt stress also significantly reduced (by 18%) average area of *Borrichia* leaves (Table 1). Mean leaf area was most markedly different among treatments in late spring when the growing season started, but decreased as leaf area declined on all plots through the fall, as evidenced by a significant interaction between salt supplementation and time (Table 1).

Interestingly, increased salinity resulted in a slight (8%) decrease in the density of *Borrichia* stems per plot, although this decrease was not significant at the $P = 0.05$ level (Table 1). The decrease in stem density on salt supplemented plots was again most visible during the spring and summer growing season of *Borrichia*, although time did not interact significantly with salt treatments.

Stem borer density did not affect any of the other plant response variables measured, and did not interact with any other treatment, or with time, except for stem density, as mentioned above (Table 1). Parasitoid removal treatments had no effect on the plant variables measured (Table 1). Means from trapped plots were close to control means in all months of the study.

The difference in stem borer density between high and low borer plots was highly significant ($F = 1765.489$, df = 1,8, $P < 0.001$) and was maintained throughout the study (Fig. 3). High borer plots averaged 50.24 stem borers per 100 stems over the ten months of the study, while low borer plots averaged only 9.81 stem borers per 100 stems. Increased salinity
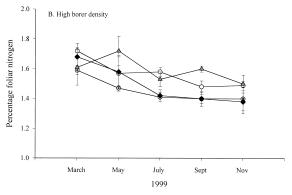

Fig. 2. Mean (± 1 SE) percent foliar nitrogen of *Borrichia frutescens* leaves from A) low stem borer density plots and B) high stem borer density plots.
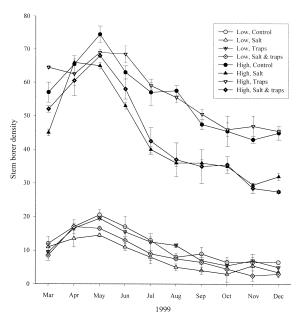
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Fig. 3. Mean (± 1 SE) number of stems with stem borer larvae out of 100 *Borrichia frutescens* stems sampled per plot.
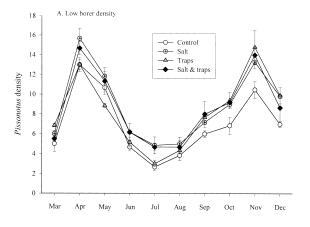
resulted in a significant decrease in stem borer density ($F = 62.401$, df $= 1,8$, $P < 0.001$), but this decrease was most evident on high borer plots (Fig. 3), and there was a significant interaction between salt treatments and stem borer density ($F = 23.612$, df $= 1,8$, $P = 0.001$). Stem borer density changed with time ($F = 105.233$, df $= 9,72$, $P < 0.001$), peaking in the spring, and declining through the remainder of 1999 (Fig. 3). This seasonal pattern was more pronounced on high borer plots (Fig. 3), reflected in a significant interaction between time and borer density ($F = 17.893$, df $= 9,72$, $P < 0.001$).

Stem borer density had strong effects on the density of *Pissonotus* (Table 2). Planthopper densities were markedly greater on plots with low stem borer density throughout the study (Fig. 4). In addition to achieving higher peak densities, planthoppers also sustained greater densities on low stem borer plots during periods of decline, such as the summer and late fall (Fig. 4), although time did not interact significantly with stem borer density (Table 2).

The bottom-up effects of altered plant quality through increased salt stress significantly increased the density of *Pissonotus* planthoppers (Table 2). Within one month of the first application of salt, the density of planthoppers was higher on salt supplemented plots, and remained higher for most months of the study (Fig. 4). This increase in herbivore density occurred before many of the plant response variables exhibited a response to treatments, perhaps suggesting some rapid change in plant chemistry with increased

salt stress. Interestingly, salt treatments interacted significantly with stem borer density (Table 2), as there was a reduced effect of salt treatments on *Pissonotus* density on plots with high stem borer density (Fig. 4).

Although parasitoid removal treatments significantly reduced parasitism of *Pissonotus* eggs ($F = 13.411$, df $= 1,8$, $P = 0.006$), this did not translate into a significant main effect of traps on *Pissonotus* density (Table 2). The yellow sticky traps reduced parasitism of *Pissonotus* eggs from an average of 59% to 38%, but there was no noticeable change in planthopper density until the fall of 1999. In the fall, however, planthopper density on trapped plots did increase relative to control plots (Fig. 4), and this was reflected in a marginally significant interaction between traps and time (Table 2). There was also an interaction between salt and parasitoid removal treatments (Table 2). *Pissonotus* density on plots receiving both treatments remained close to the densities observed on
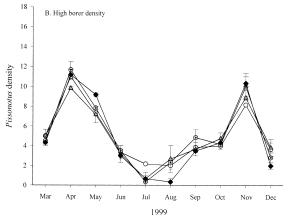

Fig. 4. Mean (± 1 SE) number of *Pissonotus quadripustulatus* per 20 *Borrichia frutescens* stems from A) low stem borer density plots and B) high stem borer density plots.

Table 2. Results of repeated measures ANOVA on the effect of stem borer density, salt, and parasitoid removal treatments on *Pissonotus* density.

Source	Sum of squares	df	Mean square	F ratio	P value
Between subjects					
Borer	263.503	1	263.503	618.740	<0.001
Salt	15.845	1	15.845	37.205	<0.001
Traps	0.311	1	0.311	0.729	0.418
Borer × Salt	7.212	1	7.212	16.935	0.003
Borer × Traps	1.230	1	1.230	2.889	0.128
Salt × Traps	6.316	1	6.316	14.831	0.005
Borer × Salt × Traps	1.903	1	1.903	4.469	0.067
Error	3.407	8	0.426		
Within subjects					
Time	1585.431	9	176.159	173.564	<0.001
Time × Borer	15.216	9	1.691	1.666	0.113
Time × Salt	22.096	9	2.455	2.419	0.018
Time × Traps	16.849	9	1.872	1.845	0.075
Time × Borer × Salt	15.282	9	1.698	1.673	0.111
Time × Borer × Traps	5.770	9	0.641	0.632	0.766
Time × Salt × Traps	14.156	9	1.573	1.550	0.147
Time × Borer × Salt × Traps	4.938	9	0.549	0.541	0.840
Error	73.077	72	1.015		

plots receiving salt only, and did not increase further in the fall when *Pissonotus* densities on trapped plots increased (Fig. 4).

Stem borer density and increased salinity also significantly affected the mean number of *Pissonotus* eggs found in each stem (F = 16.588, df = 1,8, P = 0.004 and F = 8.056, df = 1,8, P = 0.022, respectively). We found an average of 17.2% more *Pissonotus* eggs in each *Borrichia* stem on plots with low stem borer density than on plots with high stem borer density (Fig. 5). At the level of individual stems, eggs were found in stems with and without stem borer larvae, although the mean number of eggs per stem was significantly lower for stems with stem borers (mean of 1.16, N = 687 stems sampled) than for stems without stem borers (mean of 3.27, 913 stems sampled, P < 0.001 one-way ANOVA on log transformed data).

Similarly, the mean number of *Pissonotus* eggs in each *Borrichia* stem was 14.3% greater on salt supplemented plots than on plots that did not receive salt (Fig. 5). The interaction between stem borer density and salt treatments on *Pissonotus* egg density was marginally significant (F = 4.646, df = 1,8, P = 0.063), as the effect of increased salinity on *Pissonotus* egg density was much greater on plots with low stem borer density than on plots with high stem borer density (Fig. 5). There was also a significant effect of time on egg density (F = 41.816, df = 9,72, P < 0.001), reflecting the seasonal variation in oviposition (Fig. 5). Time interacted significantly with both stem borer density and salt treatments (F = 2.281, df = 9,72, P = 0.026 and F = 2.275, df = 9,72, P = 0.025, respectively). Both treatments had greater effects during pulses in egg density, especially during the fall pulse (Fig. 5). Parasitoid removal treatments had no noticeable effect on egg densities (F = 0.410, df = 1,8, P = 0.540).
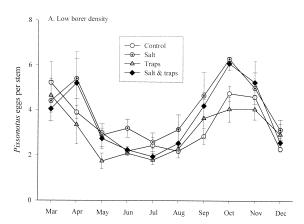
Discussion

Addition of salt pellets significantly increased the interstitial salinity of treated plots, and this increase was maintained for the duration of the study by repeated applications. Salinity on salt supplemented plots averaged 18 ppt, a value within the range of naturally occurring salinities experienced by the organisms studied (Moon and Stiling 2000, and unpubl. data). Similarly, parasitism of *Pissonotus* eggs from plots receiving sticky traps was reduced from an average of 59% to 38%, values that were also within the range of natural variability for this system (Moon and Stiling 2000, 2002). As such, our treatments mimic naturally occurring conditions and our results provide insight into how trophic dynamics among the same species of organisms can vary over distances of meters or less.

Increasing salt stress through the addition of salt pellets reduced all of the response variables measured for *Borrichia*. The effect of salt stress on these variables was most pronounced during the growing season when these variables increased naturally on plots that were not salted. This suggests that salt stress has an overall inhibitory effect on growth and reproduction in *Borrichia* as it does in a number of other plants (Longstreth and Nobel 1979, Kemp and Cunningham 1981, Haines and Dunn 1985, Shumway and Bertness 1992, Vernberg 1993, Hwang and Morris 1994, Srivastava and Jefferies 1995, Hester et al. 1996).

Percent foliar nitrogen was significantly lower on salt supplemented plots than on plots with ambient salinity. These results agree with those of Bowdish and Stiling (1998) who found that increased soil salinity resulted in a decrease in the percentage of foliar nitrogen in *Spartina alterniflora*. The decrease in percent foliar nitrogen on salt supplemented plots represents another

component of the stress complex that accompanies high salinity, and, along with ion toxicity and unfavorable water balance, could account for the changes seen in *Borrichia*.

Although there was less total nitrogen in the leaves on plants on salt supplemented plots, *Pissonotus* showed an almost immediate positive response to salt treatments. All responses of the host plant to salt supplementation, other than chemical ones, became evident after the increase in *Pissonotus* density was detected. Moreover, salt supplementation actually decreased stem growth, leaf area, and a number of other plant response variables, indicating that these aspects of host plant quality probably did not contribute to the increase in *Pissonotus* density. Part of the stress hypothesis proposed by White (1978) suggested that one component of the stress response of plants is the mobilization of bound nitrogen, and this unbound nitrogen is more accessible to herbivores. This mechanism may have contributed to the observed increases in planthopper density on salt supplemented plants, but
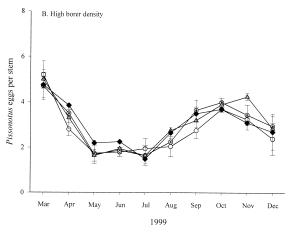
our measurements of the percentage of total nitrogen in plant tissues would not be able to account for such mobilization, as differentiation between bound and unbound nitrogen would be required.

Removal of parasitoids with yellow sticky traps reduced the percentage of *Pissonotus* eggs that were parasitized by *Anagrus*. Parasitism was markedly reduced within one month of treatment application, and remained lower for the duration of the study. This reduction in parasitism produced a small time-dependent increase in *Pissonotus* density. Such a time delay may occur because treatments must first affect the parasitoid, and would then only be expressed as planthoppers emerged from eggs over time. Increased salinity reduced the effect of traps on *Pissonotus* density, as traps did not produce an increase in planthopper density over and above the increase resulting from increased salinity on plot receiving both treatments. This result lends some support the prediction of the Menge and Sutherland (1976, 1987) model that top-down effects would be less important under more stressful conditions.

The densities of lepidopteran stem borers also play a prominent role in this ecosystem, and are perhaps even more important than salinity levels. There was a significant interaction between time and stem borer density on the density of *Borrichia* stems, as stem density declined over the course of the study on high stem borer plots. This reduction in stem density occurred as stem borer larvae girdled and killed a number of *Borrichia* stems (Moon and Stiling, pers. obs.).

Stem borer density also had a substantial impact on the density of *Pissonotus* planthoppers, and produced differences in planthopper density of even greater magnitude than those resulting from increased salinity. Planthopper density was always much lower on plots with high stem borer densities. The difference in *Pissonotus* density between high and low stem borer treatments was most pronounced during periods of decline in planthopper density, with the areas that have low stem borer density serving as a form of refuge for *Pissonotus* during those times. We found similar results in another experiment in which fertilization treatments increased the densities of the same stem borers studied here (Moon and Stiling, unpubl.). In that experiment, *Pissonotus* densities did not differ among plots prior to treatment application, but in plots where stem borer density increased following treatment application, stem borer densities did not change or were even reduced in spite of well-documented (Moon and Stiling 2000, and unpubl.) beneficial effects of fertilization.

There are a number of ways in which stem borer larvae could negatively impact *Pissonotus*. As mentioned previously, stem borer larvae kill *Pissonotus* eggs that have been laid in the same tissue layers that they bore through. Stiling and Strong (1983) described a similar mechanism occurring in the stems of *Spartina*

Fig. 5. Mean (± 1 SE) number of *Pissonotus quadripustulatus* eggs per stem from A) low stem borer density plots and B) high stem borer density plots.

alterniflora. In their study, however, stem-boring larvae would actively seek out and kill or "murder" their competitors. In this study, *Pissonotus* eggs may or may not be actively sought, but such a mechanism is plausible, as we did find planthopper eggs in stems harboring stem borers, but the mean number of eggs per stem was lower for these stems than for stems without borers. Stem borer larvae may also make stems less attractive to *Pissonotus* by changing plant chemistry (Haukioja and Niemela 1979, McClure 1980, 1989, West 1985, Hanhimaki 1989, Ritchie and Tilman 1992, Denno et al. 2000). Although stem borer density did not significantly affect the total foliar nitrogen content of *Borrichia*, relatively little is known about the chemistry of this plant and whether or not (or how well) it is defended.

The results we have reported here show that high densities of stem borers may also indirectly reduce planthopper densities by reducing the density of the host plant. Such a reduction in host plant density probably does not explain all of the impact of the stem borer on *Pissonotus*, as the effect of borer density on the planthopper was evident at the beginning of the study, when stem densities were not significantly different. Most likely, a number of mechanisms contribute to the negative impact of the stem borer on *Pissonotus*.

It is important to realize that stem borer densities were not experimentally manipulated, and thus, the evidence for competition between herbivores in this study is indirect. It is unlikely, however, that these two herbivores are simply responding in an opposite manner to a common environmental or host plant attribute. As stated above, we have also found that, in another study (Moon and Stiling, unpubl.), an increase in stem borer density on fertilized plots suppressed the response of *Pissonotus* to increased host plant quality. Furthermore, we have found that these two herbivores respond similarly to bottom-up manipulations when their densities remain relatively low, but become negatively correlated with one another when they become crowded on less abundant host plants (Moon and Stiling, unpubl.). We have only recently begun to appreciate the potential for strong interactions between these two herbivores, and direct manipulations of herbivore densities are needed to fully understand the nature of these interactions.

Stem borer density also affected the response of *Pissonotus* to elevated salinity. There was much less of an increase in planthopper density on salt supplemented plots that had high densities of stem borers than on salt supplemented plots with low borer densities. This is in spite of the fact that elevated salinity decreased stem borer density on the high stem borer plots. The reduced response of *Pissonotus* to increased salinity on high stem borer plots may reflect a reduced capacity of resident planthoppers to reap the rewards of increased salinity, and/or reduced immigration of planthoppers

into these plots. We do know that the effects of the treatments on *Pissonotus* are attributable, at least in part, to differential reproduction. Treatment effects on the number of eggs found per stem mirror those on planthopper density, and these treatment effects are most noticeable during the pulses in egg density, which precede the pulses in planthopper density. It is also likely that planthoppers immigrate into favorable plots, and emigrate out of less favorable ones, because although completely brachypterous at our field site, *Pissonotus* can still hop freely among plants. For other delphacid planthoppers, *Prokelisia dolus* and *Prokelisia marginata*, environmental conditions (Denno et al. 1980, 1996), host plant nutrition (Denno 1983, 1985, Denno et al. 1985) and competition (Denno et al. 1985, 1986, Denno and Roderick 1992) have all been shown to significantly affect immigration and emigration rates. Since we did not measure planthopper movement, however, we can not comment on the degree to which this occurred in our study.

The results reported here are important because they show that interactions between herbivores can be even more important than either top-down or bottom-up effects, supporting the conclusions of Denno et al. (1995) that competition among insect herbivores is frequent, important, and often underestimated. Our results also show that within-trophic-level interactions can substantially impact relationships between trophic levels, and as such should be considered in examinations of top-down and bottom-up dynamics.

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