FEEDING-INDUCED CHANGES IN PLANT QUALITY MEDIATE INTERSPECIFIC COMPETITION BETWEEN SAP-FEEDING HERBIVORES

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Abstract. Feeding-induced plant resistance is a well-documented phenomenon for leaf-chewing insects. Furthermore, feeding-induced resistance provides the mechanistic basis for many cases of delayed interspecific competition, whereby previous feeding by one species diminishes the performance of other herbivores which attack the same plant later in the season. This phenomenon, however, has been very poorly investigated for sap-feeding insects. The results we present here for salt marsh-inhabiting planthoppers (*Prokelisia dolus* and *P. marginata*) provide one of the few known examples of delayed, plant-mediated interspecific competition between two sap-feeding insects.

Three lines of experimental evidence from the laboratory, field cages, and open field plots provide support for the detrimental effects of previous feeding by one planthopper species on the subsequent survival and performance of the other. Laboratory experiments showed that prior feeding on cordgrass by one congener resulted in reduced performance of the other in the following generation. However, the effect was asymmetric. Prior feeding by *P. dolus* resulted in prolonged development and reduced body size (a correlate of fecundity) in *P. marginata,* whereas only development was protracted in *P. dolus* when plants were previously exposed to *P. marginata.* Consequently, *P. dolus* appears to be the superior competitor in the context of delayed, plant-mediated interactions. The negative effects of previous feeding by *P. dolus* on the development time, body size, and survival of *P. marginata* obtained in the laboratory were confirmed both in cages and on cage-free islets of cordgrass in the field. Feeding-induced reductions in host-plant quality by *P. dolus* may provide additional impetus for *P. marginata* to migrate from shared habitats on the high marsh to nutritionally superior plants in the low marsh rarely occupied by *P. dolus.*

The mechanism underlying the delayed competitive effects between *Prokelisia* planthoppers is most likely diminished plant nutrition, because feeding by *P. dolus* significantly reduces the concentration of essential amino acids in cordgrass. The asymmetry of plant-mediated competition between the *Prokelisia* species may be due to the ability of *P. dolus* to better tolerate feeding-depleted levels of plant nitrogen via compensatory feeding.

Even though these two planthoppers do not suffer significant fitness reductions during contemporaneous interactions, they compete severely in the context of feeding-induced plant resistance which is expressed later in the season. This result, coupled with the fact that most studies of interspecific interaction between herbivorous insects are contemporaneous, indicates that interspecific competition may be profoundly underestimated as a structuring force in phytophagous insect communities.

Key words: competition, plant-mediated; interspecific competition; intraspecific competition; planthopper; plant nutrition; plant resistance, induced; Prokelisia dolus; Prokelisia marginata; *salt marsh; sap-feeding insect;* Spartina.

Introduction

Historically, interspecific competition was thought to be too weak or infrequent to influence either the population dynamics or community structure of phytophagous insects (Hairston et al. 1960, Lawton and Strong 1981, Lawton and Hassell 1984, Strong et al. 1984). This conclusion was based largely on observational studies, since few experimental assessments

of competition were available for consideration (Denno et al. 1995). More recent reviews, based primarily on experimental studies, have found competition to be a far more important force in the population and community ecology of herbivorous insects than was once thought (Damman 1993, Denno et al. 1995).

For example, one current review, based on 193 pairwise species interactions involving herbivorous insects, found interspecific competition to occur in 76% of the cases (Denno et al. 1995). Moreover, interspecific competition occurred far more frequently between sap-feeding species such as aphids and scale insects than

between mandibulate folivores like lepidopterans and beetles, a finding which has been previously reported (Lawton and Strong 1981, Karban 1986, Denno and Roderick 1992). Most surprising was the finding that over half of the cases of interspecific competition among mandibulate herbivores involved delayed, plant-mediated competition, in which previous feeding by one species induced either nutritional or allelochemical changes in the plant that adversely affected the performance of another species feeding later in the season (Denno et al. 1995). In contrast, such delayed, plant-mediated competitive effects were rare for sap-feeding insects, comprising only 6% of the cases. On the one hand this guild difference may be real, but alternatively it may reflect an investigational bias in which most studies of feeding-induced changes by one species and their future consequences for other herbivores have been conducted using mandibulate folivores (Faeth 1986, Harrison and Karban 1986, Karban and Myers 1989, Tallamy and Raupp 1991, Dankert et al. 1997).

In fact, very few studies involving sap-feeders have explicitly investigated the consequences of previous feeding by one species on the subsequent performance of another sap-tapper in the following generation (Denno et al. 1995, but see McClure 1980). However, there is abundant evidence in the literature showing that heavy feeding by sap-feeding insects does induce long-term reductions in plant quality (McClure 1980, 1984, Olmstead et al. 1997), reductions that could potentially diminish the performance of other later-colonizing species (Denno et al. 1995).

The objectives of this report are two. First, we test for plant-mediated competitive interaction between two species of sap-feeding planthoppers, *Prokelisia dolus* and *Prokelisia marginata* (Hemiptera: Delphacidae), which co-occur on the intertidal salt marshes of North America (Denno et al. 1996). Second, we consider how such competitive effects bear on the migration dynamics of these planthoppers. Using a blend of laboratory and field experiments, we explicitly examine how previous feeding by one species affects the subsequent performance of the other in the following generation. This study takes on added significance, because neither species adversely affects the other's fitness (survival, development, and body size) when these two planthoppers interact concurrently at normal field densities (Denno and Roderick 1992). Contemporaneous interspecific interaction between the two species does, however, elicit the production of migratory forms (Denno and Roderick 1992). Moreover, the density-dependent effect of *P. dolus* on migrant production in *P. marginata,* whereby *P. marginata* emigrates annually from shared habitats, is much stronger than the reciprocal effect (Denno and Roderick 1992, Denno et al. 1996). One may ask why *P. marginata* migrates from shared habitats when there are few apparent direct fitness costs to be paid for remaining in a habitat with *P. dolus.* The

answer may lie in part with the adverse consequences of remaining on host plants previously occupied and nutritionally depleted by *P. dolus.* The demonstration of delayed competitive interactions in a system that lacks contemporaneous competition may help explain this apparent paradox. Furthermore, such a result would suggest that the historical focus on contemporaneous competitive interactions has led to a gross underestimate of the overall importance of interspecific competition in structuring phytophagous insect communities.

METHODS

Natural history and probability for interspecific interaction in Prokelisia *planthoppers*

Both *Prokelisia dolus* and *P. marginata* inhabit the intertidal marshes of North America and occur sympatrically throughout most of their geographic range (Wilson 1982, Denno et al. 1987, 1996). Along the Atlantic and Gulf coasts of North America, both species feed exclusively on the phloem sap of cordgrass, *Spartina alterniflora* (Denno et al. 1987, 1996). These two sap-feeders are by far the most abundant herbivorous insects on mid-Atlantic *Spartina* marshes with adult densities of both species frequently exceeding 1000 individuals/m^2, and nymphal densities of each occasionally surpassing 100 000 individuals/m^2 in their primary habitats (Denno and Grissell 1979, Denno et al. 1987; R. F. Denno, *unpublished data*). At our major study site in New Jersey, however, *P. dolus* is the more abundant of the two species comprising 66% of all planthopper individuals (Denno and Roderick 1992).

Heavy feeding by *P. dolus* significantly reduces the total concentration of amino acids and also diminishes the content of essential amino acids in *Spartina* (Bacheller and Romeo 1992, Olmstead et al. 1997). The consequence of low amino nitrogen in *Spartina* for planthoppers is reduced performance and reproductive potential, particularly for *P. marginata* (Denno et al. 1986, Cook and Denno 1994). Thus, the opportunity appears to exist for one species to influence the performance of the other through feeding-induced reductions in host-plant nitrogen.

Although these two multivoltine planthoppers differ in their population dynamics along the Atlantic coast, they do share the same habitats throughout much of the year when both consistently co-occur on the same individual plant (Denno et al. 1987, 1996, Denno and Roderick 1992). *P. marginata* is a very mobile species, undergoing annual interhabitat migrations between overwintering habitats on the high marsh (meadows of short-form *Spartina*) and summer sites for development in low-marsh habitats (stands of tall-form *Spartina*) (Denno et al. 1996). Low-marsh *Spartina* is nutritionally superior to high-marsh stands throughout much of the year (Denno 1983, Ornes and Kaplan 1989). However, *Spartina* in the low-marsh habitat is selectively

destroyed during winter by tides and shifting ice and is an unsuitable overwintering site for planthopper nymphs (Denno et al. 1996). Thus, low-marsh plants must be colonized each spring by migrants from high-marsh habitats. Dispersing adults of *P. marginata* colonize these nutritionally superior low-marsh plants, which results in larger and more fecund offspring compared to the offspring of nondispersing adults which develop on high-marsh *Spartina* at the same time (Denno and McCloud 1985, Denno et al. 1986, 1996). Fall migrations also occur in which dispersing adults fly to the high marsh and produce the overwintering generation of nymphs (Denno et al. 1996). On average, 80% of the *P. marginata* population occurs in low-marsh *Spartina* during the summer, whereas the remainder stays in high-marsh habitats (Denno et al. 1996). In contrast, *P. dolus* is far more sedentary and remains on the high marsh year-round (>90% of the population), dispersing locally within that habitat (Denno et al. 1996).

The spring exodus of *P. marginata* from the high marsh is triggered by a combination of deteriorating plant quality and crowding, both intraspecific crowding and interspecific crowding from *P. dolus* (Denno et al. 1985, 1986, 1996, Denno and Roderick 1992). *Prokelisia* planthoppers are wing dimorphic, with both volant macropters (migratory form) and flightless brachypters occurring in the same population, and the production of migratory forms is density dependent (Denno et al. 1985, 1996). Importantly, interspecific crowding is as strong a stimulus for the production of migrants as is intraspecific crowding, and the effect is reciprocal for both species (Denno and Roderick 1992). However, because migratory forms are triggered at a much lower density in *P. marginata* than *P. dolus,* interspecific interactions are asymmetric, with *P. dolus* having a far greater influence on the triggering of migrants in *P. marginata* than the reverse case (Denno and Roderick 1992).

Despite the predominant summer occupation of low-marsh habitats by *P. marginata,* the expansive meadows of *Spartina* on the high marsh are shared by both species during spring, fall, and winter, and to some degree, during the summer as well because not all *P. marginata* migrate to the low marsh (Denno et al. 1996). Thus, the opportunity for extensive interspecific interaction appears to exist. This report explicitly examines the possibility that spring feeding by *P. dolus* on the high-marsh habitat induces reductions in the quality of *Spartina* that hamper to some degree the summer occupation of this habitat by *P. marginata.*

Laboratory assessment of plant-mediated competition in Prokelisia planthoppers

To examine the effects of plant-mediated competition in *Prokelisia* planthoppers, *Spartina* plants were first exposed to one generation of feeding. Subsequently, the performance of a second cohort of planthoppers
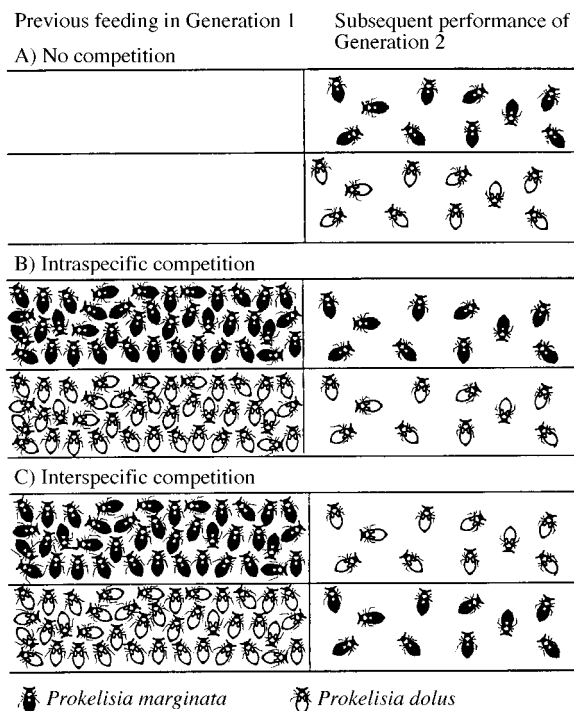

FIG. 1. Experimental design to test the effects of delayed, plant-mediated competition between the planthoppers *Prokelisia marginata* and *P. dolus. Spartina* plants were first exposed to one of two treatments: "previous feeding" by planthoppers (40 first-instar nymphs) or "no previous feeding." After 1 mo of feeding, all nymphs were removed from the "previous feeding" treatment. Subsequently, the performance (survival, development time to adult, and adult body size) of a second cohort of planthoppers (10 first-instar nymphs) was assessed 1 mo later on the same plants. Six different treatment combinations were established: two "no-competition" controls (A: no previous feeding followed by an assessment of each species performance on aged plants), two intraspecific treatments (B: previous feeding by either *P. dolus* or *P. marginata* followed by a subsequent assessment of that species' performance), and two interspecific treatments (C: previous feeding by either *P. dolus* or *P. marginata* followed by a subsequent assessment of the other species' performance).

was assessed one generation later on the same plants. Six different treatment combinations were established to explore the consequences of previous feeding, both by conspecifics and heterospecifics, on subsequent performance (Fig. 1).

Four competition (prior-feeding) treatments were established by caging 40 first instars of either *P. dolus* or *P. marginata* (one species per treatment) on plants and raising them to adults, after which time they were removed (Fig. 1). Subsequently, cohorts of 10 first instar conspecifics, either *P. dolus* or *P. marginata,* were caged on the previously fed-upon *Spartina* plants and their survival, development time to adult, and body size were measured. The densities of 40 and 10 nymphs per cage represent high and low field densities, respectively (Denno and Roderick 1992). There were two intraspe-

cific treatments (either *P. dolus* and *P. marginata*), in which previous feeding by one species was followed by a subsequent assessment of that species' second-generation performance. There were also two interspecific treatments, in which previous feeding by one species was succeeded by a subsequent assessment of the other species' performance. The duration of the previous-feeding treatment was designed to simulate one generation of plant exposure to planthoppers, and lasted ~1 mo.

Two ''no-competition'' (no previous feeding) controls were established in which plants initially remained planthopper-free for 1 mo. This period was the same length of time that plants in the competition treatments were exposed to previous feeding by planthoppers. After this planthopper-free period, 10 first-instar conspecifics were caged on the aged plants and their development time to adult and body size at eclosion were determined. A ''no-competition'' control was established for both *P. dolus* and *P. marginata.* Each of the six treatment combinations (the four competition treatments and the two controls) was replicated eight times.

Treatment cohorts were established by aspirating first-instar nymphs onto caged transplants of *Spartina* (both previously fed upon and not) and allowing them to develop to adults, at which time sex, survivorship (proportion surviving), development time to adult (in days), and body length (frons to end of abdomen in millimeters) were determined. The effect of competition treatment, planthopper species, sex, and their interaction on survivorship (sexes pooled), development time, and body length was analyzed using ANOVA and treatment means were compared with Sidak's adjustment for multiple comparisons (SAS 1990). The experimental design was a split-plot design with competition treatment and species assigned to whole plots (cages), and sex was associated with individuals. Thus, for development time and body size, competition treatments, species, and their interaction effects were tested with the cage variance (Error, cage), whereas sex and all remaining interactions were tested with the individual variance (Error, individual).

The *Spartina* plants used in the experiments were taken as transplants on 10 June 1990 from mud pannes at our study site near Tuckerton, Ocean County, New Jersey, USA. Plants (two per pot) were immediately transplanted into sand-filled pots (6.5 cm diameter). Potted transplants were maintained in four plastic-lined flats (1.0 × 0.7 m) filled halfway with water so that the sand was continuously wet, yet seedlings were never inundated. Flats received applications of a 3:1 mixture of ammonium nitrate (N:P:K, 34:0:0) and phosphoric acid (0:46:0). Seven grams of fertilizer were applied once every 2 wk to each flat. This fertilization rate results in plants with a soluble protein content (61.50 ± 6.04 mg/g, $\bar{X} \pm 1$ SD) representative of plants with moderate nutritional quality in the field (Denno

et al. 1985). All transplants were maintained in the greenhouse prior to their use in experiments.

Planthopper treatments were established in cages constructed of clear plastic cellulose butyrate tubing. Cages were 30.5 cm long and 3.8 cm in diameter with four holes (2.5 cm diameter) covered with organdy gauze for air circulation. Tube cages were capped at the top with screens for easy access. Tube cages were placed over the transplants in each pot by pressing them into the sand, and cohorts of first-instar nymphs were added as called for by the treatments.

All previous-feeding treatments (cohorts of 40 nymphs) were applied on 7 August 1990 by adding planthoppers to the caged transplants. No-competition control plants were also caged on this date. All planthoppers used in the previous-feeding treatments were removed on 1 September. The planthoppers (cohorts of 10) used to assess the consequences of previous feeding were added to the competition and no-competition treatments on 7 September. Treatment cages were randomly arranged in plastic trays and maintained at 25 ± 2°C on a 14:10 light : dark cycle in two incubators. The first-instar nymphs used in our experiments were taken from laboratory cultures after having been reared for one generation in the laboratory. The original planthopper stocks were established from gravid females collected in *Spartina* meadows at Tuckerton, Ocean County, New Jersey, USA.

Field assessment of plant-mediated competition in Prokelisia *planthoppers*

It was not logistically possible for us to examine all combinations of plant-mediated interspecific and intraspecific competition between *P. dolus* and *P. marginata* in the field. Thus, we explicitly focused our attention on the possibility that previous feeding by *P. dolus* on the high marsh results in deteriorated plant quality such that fitness reductions would occur in *P. marginata* were it to remain on the high marsh for a second generation. This emphasis extends from the knowledge that *P. marginata* undergoes a mass spring exodus annually from high-marsh habitats, which are shared with *P. dolus* (Denno et al. 1996).

We tested for competitive effects by conducting a manipulative experiment on an archipelago of small islets of *Spartina alterniflora* on the marsh (Fig. 2). Our study site is an expansive intertidal salt marsh in the Great Bay–Mullica River estuarine system at the end of Great Bay Boulevard just north of the Rutger's University Marine Station, Tuckerton, Ocean County, New Jersey, USA. This marsh is characterized by extensive meadows of short-form *Spartina* on the high marsh interrupted with flooded mud pannes and potholes (Denno et al. 1980, Döbel et al. 1990). Archipelagoes of *Spartina* islets (2–10 m² in area and separated from each other by 1–3 m) grow within the flooded habitats (Döbel and Denno 1994). A serpentine

Fig. 2. Experimental islets of *Spartina alterniflora* with field cages used to examine the effects of previous feeding (6 wk of exposure to *Prokelisia dolus*) on the survival and performance of a cohort of *P. marginata* established after the previous-feeding period. Altogether there were seven pairs of islets; one islet in each pair received the previous-feeding treatment, while the other went planthopper free for the 6-wk period. The archipelago of islets was located on an extensive intertidal marsh at Tuckerton, Ocean County, New Jersey, USA.

array of tidal creeks lined with tall-form *Spartina* occur throughout the marsh (Denno and Grissell 1979).

The effects of previous feeding by *P. dolus* on the subsequent survival and performance of *P. marginata* were examined on a set of *Spartina* islets in two ways: (1) in small field cages placed on islets and (2) on the cage-free portion of the same islets. We also attempted to examine plant-mediated competitive effects in the absence of field cages, a challenging task to say the least, because caging alone is known to induce changes in the amino acid composition and concentration of *Spartina* (Olmstead et al. 1997). Seven pairs of islets were selected in June 1997. One islet in each pair was assigned the previous-feeding treatment of *P. dolus*, whereas the other islet in the pair was kept almost free of planthoppers. Previous-feeding islets did not differ significantly in area (5.5 ± 2.3 m²) from no-competition islets (4.3 ± 1.3 m²; paired *t* test, $t = 1.614$, $P = 0.177$).

Field-cage assessment of competition.—The competitive effect of *P. dolus* on *P. marginata* was assessed in small field cages, placed two per islet into all 14 islets on 18 June 1997. Cylindrical cages (31 cm in height × 10 cm in diameter) were constructed of polyvinyl chloride drain pipe with two organdy-covered opposing rectangular ports (10 × 20 cm) cut into the wall. Each cage was twisted into the marsh surface such that 10–15 living culms of *Spartina* were enclosed. Cages on the seven previous-feeding islets were stocked individually with 160 early instars of *P. dolus* on 18 June, whereas cages on the seven no-competition islets remained unstocked and planthopper free. All cages were capped with organdy gauze to maintain the planthopper treatments. The density of 160 nymphs/cage (containing 10–15 *Spartina* culms) approximates both the high ''previous-feeding density'' used in our laboratory experiment (20 nymphs/culm) and the naturally occurring high densities in the field (Denno and Roderick 1992).

After approximately one month's time (one planthopper generation), all *P. dolus* were removed from the cages using a D-vac fitted with a small-diameter hose (3 cm). On 5 August each cage was stocked at a low density with 20 first-instar *P. marginata.* Just prior to adult eclosion on 28 August, all cages were removed from the islets, each cage still retaining the core of *Spartina* roots and living culms with planthoppers, and returned to the laboratory. The caged *Spartina* cores were maintained in water-filled plastic tubs, and each cage was checked every 2 d for the number of emerging adults until all individuals either eclosed or died. The survival and development time (both sexes pooled), and two measures of adult female body size (body length and tibia–tarsus length) were determined for planthoppers in each replicate. The effect of previous feeding by *P. dolus,* islet pair, and cage (nested within islet) on the survivorship (angular-transformed proportion of first instars molting to adults), development time (first instar to adult in days), body length (in millimeters) and tibia + tarsus length (in millimeters) were assessed using ANOVA (SAS 1990).

Cage-free assessment of competition.—The previous-feeding treatment was established on seven open islets (same islets which harbored the field cages) by stocking each islet repeatedly (on 18 and 24 June and 15 July 1997) with a high but natural density of *P. dolus* nymphs (Denno et al. 1987). Nymphs for the stocking treatment were obtained from *Spartina* meadows on the high marsh, habitats which are typically dominated by *P. dolus* at this time of the year (Denno et al. 1996). Companion voucher samples showed that on average, $35\,514 \pm 3319$ (mean ± SEM), $10\,270 \pm 960$, and 5152 ± 482 nymphs of *P. dolus* were added per square meter to the previous-feeding islets on 18 and 24 June and 15 July, respectively. The other islet in each pair was kept planthopper free by repeated vacuuming (on 18 and 24 June, 8, 15, and 22 July) with a D-vac suction sampler (see Döbel and Denno

1994). All 14 islets were sampled on 8 and 22 July to verify the success of the planthopper stocking and removal treatments.

To assess the effects of previous feeding by *P. dolus* on the survival and performance of *P. marginata,* all islets, both those exposed to *P. dolus* and those maintained hopper free, were defaunated on 29 July and again on 5 August using a D-vac suction sampler. Each islet was painstakingly vacuumed for 10 min to achieve nearly complete defaunation. On 5 August, following the second defaunation, first-instar nymphs of *P. marginata* were stocked onto each of the 14 islets. The islets subjected to previous feeding received 7420 ± 1003 nymphs/m² and the planthopper-free islets were stocked with 7614 ± 565 nymphs/m², treatment densities which did not differ significantly (paired *t* test, $t = -0.169$, $P = 0.869$). Nymphs for the stocking treatment were vacuumed from tall-form *Spartina,* a habitat which is selectively occupied by *P. marginata* (Denno et al. 1996). Companion, side-by-side samples were taken in this tall-form habitat. One sample was bagged for stocking each islet and the other was bottled in alcohol for later determination of the nymphal stocking density. To achieve similar stocking densities on all islets (number of nymphs per square meter), each stocking sample was adjusted for islet size by placing the D-vac sampling head (0.1 m²) once on the marsh surface in the tall-form habitat for each square meter of islet to be stocked. Thus, an islet with an area of 5 m² received nymphs vacuumed from 0.5 m² of tall-form *Spartina.* Because the average density of *P. marginata* in tall-form *Spartina* on 5 August was 73 414 ± 4722 nymphs/m², a density of approximately one order of magnitude less was used to stock the short-form *Spartina* growing on the experimental islets.

Subsequently, we sampled (using a D-vac) the paired islets on 22 and 28 August and 5 September to compare the density of *P. marginata* nymphs on islets previously fed upon by *P. dolus* with those not experiencing prior feeding. We also compared the body size of fifth-instar female nymphs and female brachypters between the two treatments. Female nymphs are easily identified, because just before molting their ovipositor is visible through the nymphal cuticle. Body size was assessed using two measures: (1) body length from the frons to the end of the abdomen (in millimeters), and (2) the combined lengths of the hind tibia and tarsus leg segments (in millimeters).

All islet sampling for planthoppers, both to verify the success of the *P. dolus* stocking and removal treatments (8 and 22 July) and to assess the effects of these treatments on the subsequent performance of *P. marginata* (22 and 28 August and 5 September), was done using a D-vac suction sampler (Denno and Roderick 1992). Specifically, one sample was taken on each islet on each of the five sampling dates. One sample consisted of two 30-s placements of the sampling head on the marsh surface such that a total of 0.2 m² of *Spartina*

was vacuumed. Planthoppers were killed in an ethyl-acetate jar, transferred to 95% ethanol sample bottles, and returned to the laboratory where they were counted.

Because the same islets were sampled repeatedly, the effect of the previous-feeding treatments on the density [$\log_{10}(N + 1)$] of *P. marginata* was analyzed using repeated-measures MANOVA employing profile analysis (von Ende 1993, Moran et al. 1996) with Treatment (2), Islet pair (7), and Time (4 dates) in the model. In profile analysis, a significant Time effect indicates that the response variable in question increases or decreases over time whereas the Treatment × Time interaction indicates whether the time trends differ between treatments (Moran et al. 1996). Data to verify the stocking and removal treatments of *P. dolus* were analyzed separately from those used to assess the treatment effects on the survival of *P. marginata.* ANOVA was used to examine the effect of the previous feeding treatments on the body length and tibia–tarsus length of *P. marginata* nymphs (28 August data only) and adult brachypters (5 September data only) (SAS 1990). Because macropterous adults of *P. marginata* can easily move among islets, they were excluded from all assessments of previous feeding on adult body size.

Results

Laboratory assessment of plant-mediated competition in Prokelisia planthoppers

Prior feeding on *Spartina* had significant adverse effects on the performance of *Prokelisia dolus* and particularly on *P. marginata.* For instance, development time was significantly extended in both species (males and females) when plants experienced previous feeding (Table 1, Fig. 3). Previous feeding imposed about a 4-d developmental delay on both sexes of *P. marginata,* whereas a 2-d developmental penalty occurred in *P. dolus.* Notably, the negative impact of previous feeding on the development of both species was as strong if the prior feeding resulted from heterospecifics as from conspecifics. In general, *P. dolus* developed quicker than *P. marginata* (22.1 ± 0.4 d and 26.0 ± 0.8 d, respectively; Table 1), and males, due to their smaller size, developed faster than females (23.3 ± 0.4 d and 24.7 ± 0.5 d; Table 1).

The competition treatments also significantly affected body length compared to the ''no competition'' controls, but the effect was not the same (marginally) for both species (Table 1, Fig. 4). The body length of both sexes of *P. marginata* was dramatically reduced by previous feeding, both intraspecific feeding and interspecific feeding by *P. dolus.* Notably for females, prior feeding by *P. dolus* had a significantly stronger adverse effect on body length than did prior feeding by conspecifics. In contrast, none of the competition treatments affected the body length of either sex in *P. dolus* (Fig. 4). Independent of prior feeding, males were

TABLE 1. Analysis of variance results for the effects of competition treatment (no previous feeding, previous feeding by *Prokelisia dolus*, or previous feeding by *P. marginata*), planthopper species (*P. dolus* or *P. marginata*), sex, and their interaction on planthopper (A) development time, (B) body length (frons to end of abdomen), and (C) survivorship (sexes pooled).

Source of variation	df	MS	F	P
A) Development time (d)				
Competition treatment	2	443.30	8.00	0.001
Species	1	977.49	17.64	0.001
Treatment × Species	2	9.54	0.17	0.842
Error (cage)	40	55.42	...	...
Sex	1	157.07	29.30	0.001
Treatment × Sex	2	0.97	0.18	0.835
Species × Sex	1	24.56	4.58	0.033
Treatment × Species × Sex	2	1.84	0.34	0.709
Error (individual)	432	5.36	...	...
B) Body length (mm)				
Competition treatment	2	0.32	5.00	0.011
Species	1	0.01	0.16	0.694
Treatment × Species	2	0.17	2.59	0.087
Error (cage)	40	0.06	...	...
Sex	1	7.26	539.89	0.001
Treatment × Sex	2	0.18	1.35	0.260
Species × Sex	1	0.28	21.08	0.001
Treatment × Species × Sex	2	0.02	1.78	0.169
Error (individual)	431	5.80	...	...
C) Survivorship (%)				
Competition treatment	2	223.43	1.04	0.36
Species	1	4707.26	21.96	0.001
Treatment × Species	2	14.81	0.07	0.93
Error	45	14 229.64	...	...

significantly smaller than females, particularly for *P. dolus* (Table 1).

Prior feeding, either intraspecific or interspecific, imposed no detectable effect on survival (Table 1). On average, however, *P. dolus* survived significantly better (0.90 ± 0.26) than did *P. marginata* (0.67 ± 0.05) (Table 1).

Field assessment of plant-mediated competition in Prokelisia *planthoppers*

Field-cage assessment of competition.—Previous feeding by *P. dolus* significantly reduced the survival and performance of *P. marginata* (Fig. 5). Survival plummeted from $57 \pm 9\%$ in competition-free cages to $21 \pm 6\%$ on previously fed-upon plants ($F_{1,9} = 13.46$, $P = 0.005$), and development time was extended by previous feeding, from 28 ± 0.3 d in controls to 30 ± 0.6 d on plants previously infested with *P. dolus* ($F_{1,17} = 5.41$, $P = 0.032$). Significant competitive effects on female body size in *P. marginata* also occurred as evidenced by a shortened tibia + tarsus length ($F_{1,27} = 27.53$, $P = 0.0001$) and reduced overall body length ($F_{1,16} = 21.79$, $P = 0.0003$) when developing on plants previously exposed to *P. dolus* as compared to controls.

There was a significant effect of islet pair only on the survival of *P. marginata* ($F_{6,12} = 4.83$, $P = 0.01$), suggesting that harsher conditions may have prevailed at certain locations within the archipelago. Conditions may have also varied within the same islet as evidenced by a significant cage effect on both development time

($F_{9,165} = 2.17$, $P = 0.027$) and body length ($F_{9,65} = 2.30$, $P = 0.026$). For no response variable were there any significant treatment interactions with Islet pair or Cage ($P > 0.05$).

Cage-free assessment of competition.—We were effective in establishing and maintaining both the previous-feeding and no-previous-feeding treatments. Islets stocked with *P. dolus* nymphs carried significantly higher densities of *P. dolus* compared to those islets from which this species was repeatedly removed (Fig. 6; profile analysis, significant treatment effect, Wilks' lambda = 0.0953, $F_{1,6} = 56.93$, $P = 0.0003$). Populations of *P. dolus* declined with time on both islet treatments (significant Time effect, Wilks' lambda = 0.0932, $F_{1,6} = 58.39$, $P = 0.0003$), but they decreased much more in the "competition-relaxed" treatment as a result of repeated removal (significant Time × Treatment interaction, Wilks' lambda = 0.2266, $F_{1,6} = 20.48$, $P = 0.004$).

P. marginata developing on the open *Spartina* islets showed adverse consequences of previous feeding by *P. dolus*. Following the removal of *P. dolus* from all islets, the two islet treatments were stocked with virtually identical densities of *P. marginata* nymphs (~7500 nymphs/m^2) (Fig. 6). However, the survival of the two treatment groups differed dramatically thereafter. After stocking, populations of *P. marginata* nymphs declined on both islet treatments (significant Time effect, Wilks' lambda = 0.0096, $F_{1,6} = 136.78$, $P = 0.0002$), but they declined to much lower levels
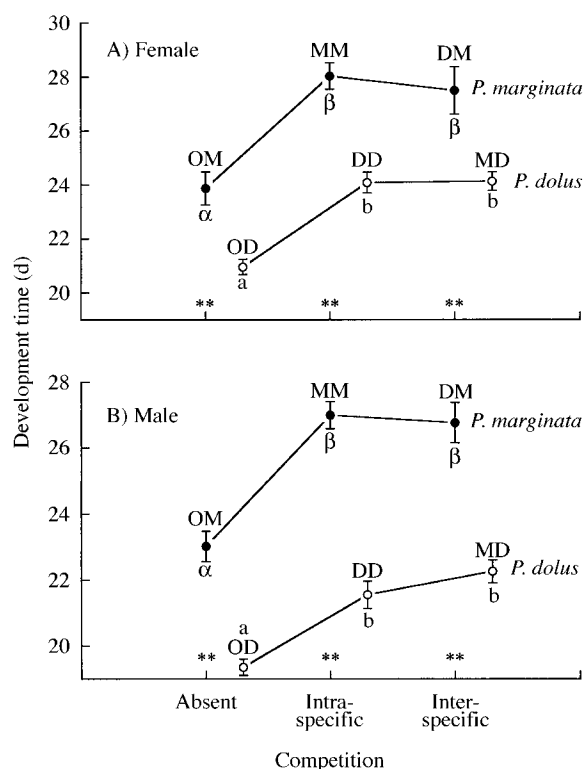
FIG. 3. The development time from nymph to adult (in days) of (A) female and (B) male *Prokelisia* planthoppers (*P. marginata* and *P. dolus*) raised on *Spartina* plants subjected to one of three competition treatments in the laboratory: no previous feeding (competition absent), previous feeding by conspecifics (intraspecific competition), or previous feeding by heterospecifics (interspecific competition). Capital letters above treatment means identify treatment combinations: OM = no previous feeding followed by an assessment of the development of *P. marginata,* MM = previous feeding by *P. marginata* followed by a subsequent assessment of that species' development time, DM = previous feeding by *P. dolus* followed by a subsequent assessment of *P. marginata*'s development time, OD = no previous feeding followed by an assessment of the development of *P. dolus,* DD = previous feeding by *P. dolus* followed by a subsequent assessment of that species' development time, and MD = previous feeding by *P. marginata* followed by a subsequent assessment of *P. dolus*'s development time. Means ($\pm$ 1 SE) with different letters (Greek for *P. marginata* and Roman for *P. dolus*) are significantly different ($P < 0.05$, ANOVA followed by Sidak's adjustment for multiple comparisons). Differences in development time between species but within the same competition treatment are indicated just above the abscissa (**$P < 0.01$; ANOVA). The effects of prior feeding by conspecifics (MM and DD) and heterospecifics (DM and MD) can be assessed by comparing these means with the appropriate "competition absent" treatment (OM or OD).
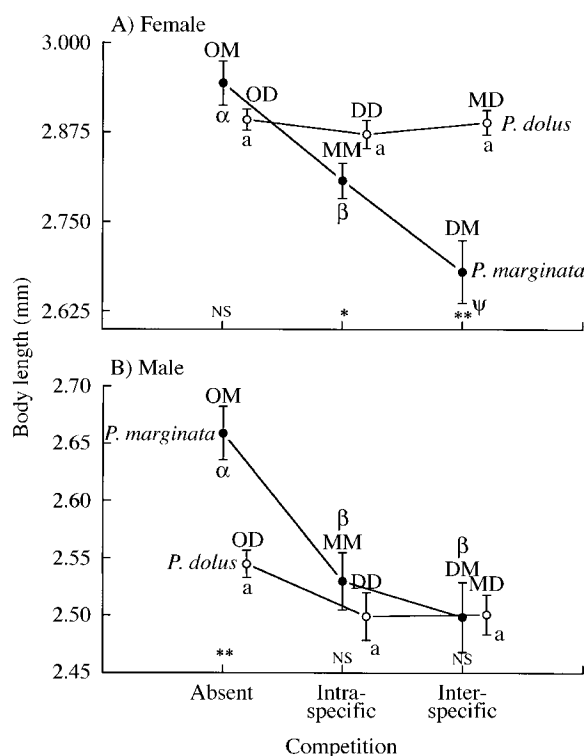
FIG. 4. The body length of adult (A) female and (B) male *Prokelisia* planthoppers (*P. marginata* and *P. dolus*) raised on *Spartina* plants subjected to one of three competition treatments in the laboratory: no previous feeding (competition absent), previous feeding by conspecifics (intraspecific competition), or previous feeding by heterospecifics (interspecific competition). Capital letters above treatment means identify treatment combinations: OM = no previous feeding followed by an assessment of the body length of *P. marginata,* MM = previous feeding by *P. marginata* followed by a subsequent assessment of that species body length, DM = previous feeding by *P. dolus* followed by a subsequent assessment of *P. marginata*'s body length, OD = no previous feeding followed by an assessment of the body length of *P. dolus,* DD = previous feeding by *P. dolus* followed by a subsequent assessment of that species body length, and MD = previous feeding by *P. marginata* followed by a subsequent assessment of *P. dolus*'s body length. Means 1 $\pm$ SE) with different letters (Greek for *P. marginata* and Roman for *P. dolus*) are significantly different ($P < 0.05$, ANOVA followed by Sidak's adjustment for multiple comparisons). Differences in body length between species but within the same competition treatment are indicated just above the abscissa (*$P < 0.05$, **$P < 0.01$, NS = not significant; ANOVA). The effects of prior feeding by conspecifics (MM and DD) and heterospecifics (DM and MD) can be assessed by comparing these means with the appropriate "competition absent" treatment (OM or OD).

on *Spartina* islets previously exposed to *P. dolus* (significant Time $\times$ Treatment interaction, Wilks' lambda = 0.1315, $F_{1,6} = 8.81$, $P = 0.031$). On the "competition" islets, populations of *P. marginata* fell from 7420 $\pm$ 1003 nymphs/m² on 5 August to 1607 $\pm$ 562 nymphs/m² on 22 August, and by early September populations had declined to 204 $\pm$ 80 nymphs/m². Contrast

this pattern of survival with that for *P. marginata* on the "no-competition" islets, on which populations fell from the initial stocking density of 7614 $\pm$ 565 nymphs/m² to only 3083 $\pm$ 467 nymphs/m² on 22 August, and to 675 $\pm$ 300 nymphs/m² on 5 September. Thus, nymphal survival was generally much higher on islets from which *P. dolus* had been removed (signif-
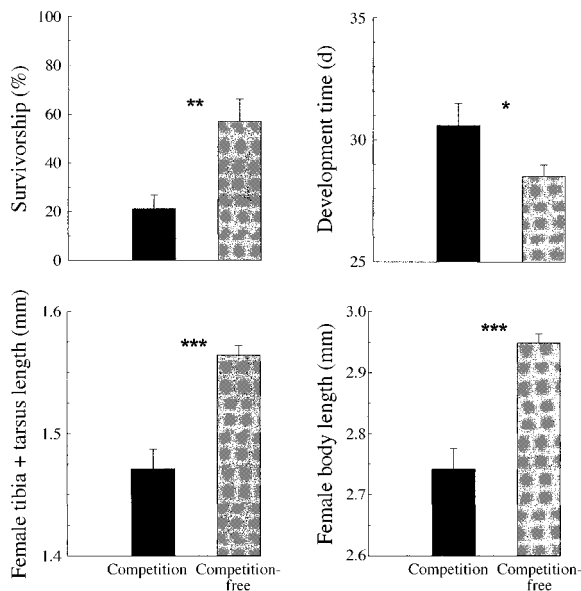
FIG. 5. Survivorship (both sexes pooled), development time (both sexes pooled), tibia + tarsus length (females only) and body length (females only) of *Prokelisia marginata* subjected to one of two competition treatments. Cohorts of *P. marginata* (20 first-instar nymphs) were either raised on plants that were exposed to *P. dolus* (160 nymphs/cage) for 1 mo (competition treatment) or they were raised on plants that experienced no prior feeding by *P. dolus* (competition-free treatment). Treatments were established in field cages placed on *Spartina* islets in the field at Tuckerton, New Jersey. Islets were paired such that one islet in the pair received the competition treatment, while the other was assigned the competition-free control. Differences between treatment means are indicated (ANOVA): *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

icant Treatment effect, Wilks' lambda = 0.197, $F_{1,6}$ = 24.46, $P = 0.0026$). The abrupt decline of nymphal densities following 22 August on all islets resulted in part from nymphs molting to adults. There were no significant effects of islet pair on nymphal density ($P > 0.05$).

Female nymphs and brachypterous adults of *P. marginata* were also significantly smaller (indexed by tibia + tarsus length) on islets previously exposed to *P. dolus* than they were on islets experiencing the no-previous-feeding treatment (Fig. 7; $F_{1,116}$ = 5.71, $P = 0.019$ for nymphs, $F_{1,79}$ = 5.79, $P = 0.018$ for brachypters). Using body length as a less accurate surrogate for body size (due to shrinkage in alcohol), there was a nonsignificant trend toward reduced body size on islets previously stocked with *P. dolus* (Fig. 7). Thus, results from both field-cage and open-islet experiments provide consistent and strong evidence for a delayed interspecific effect of *P. dolus* on the survival and performance of *P. marginata*.

DISCUSSION

Interspecific interactions between phytophagous insects are frequently mediated through feeding-induced changes in either plant nutrition or allelochemistry (Hunter 1992, Damman 1993, Denno et al. 1995). Induced plant responses often involve reductions in plant nitrogen (McClure 1980, Masters and Brown 1992, Olmstead et al. 1997) or changes in a variety of secondary chemicals (Haukioja and Niemelä 1979, Schultz 1988, Hanhimäki 1989, Haukioja et al. 1990, Karban and Myers 1990), both of which can adversely influence other herbivorous insects (Damman 1993, Denno et al. 1995). Such feeding-induced changes in plant physiology can occur immediately and diminish
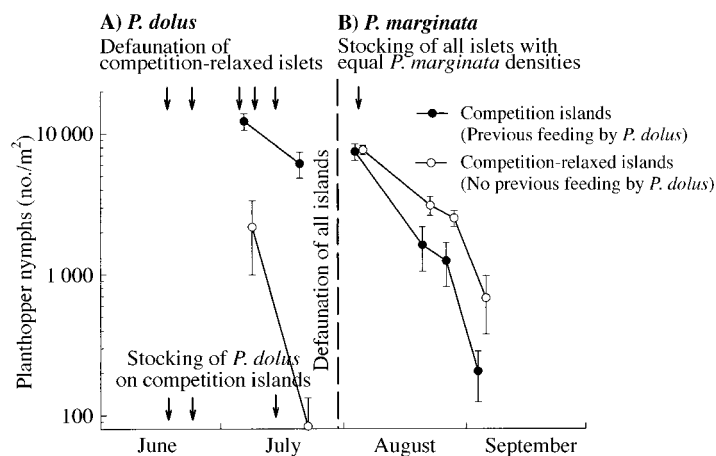

FIG. 6. Effect of plant-mediated competition (previous feeding by *Prokelisia dolus*) on the fate of cohorts of *P. marginata* stocked onto paired islets of *Spartina* in the field at Tuckerton, New Jersey. One islet in each pair was assigned the "competition" treatment (achieved by repeated stocking with *P. dolus* during June and July; stocking dates are indicated by arrows along the abscissa), whereas the other islet in the pair received the "competition-relaxed" treatment [achieved by repeated vacuuming during June and July; defaunation dates are indicated by arrows in (A)]. The density of *P. dolus* achieved on the "competition" and "competition-relaxed" islets is shown in (A). In late July (vertical dashed line), all islets were defaunated of planthoppers by repeated vacuuming. In early August, each islet was stocked with first-instar nymphs of *P. marginata* at a density of ~7500/m². The change in cohort density on the "competition" and "competition-relaxed" islets is shown in (B). Cohorts of *P. marginata* decreased in size much more on islets exposed to *P. dolus* than on "competition-relaxed" islets ($P = 0.031$, repeated-measures ANOVA). Bars represent ±1 SE.
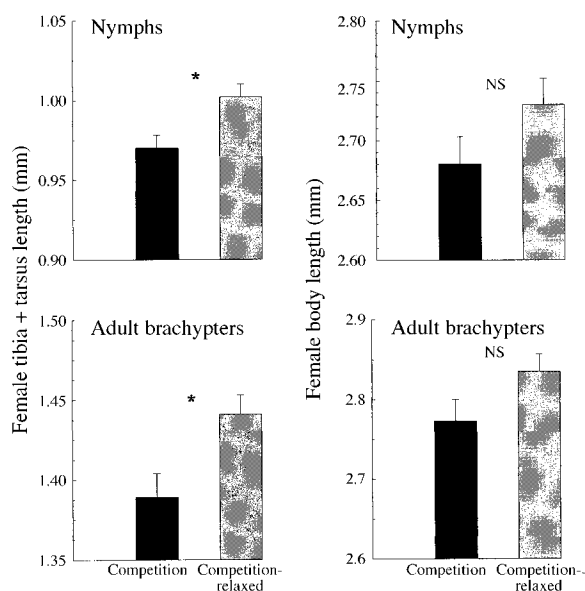
FIG. 7. Body size (tibia + tarsus length) of female nymphs and brachypterous adults of *Prokelisia marginata* subjected to one of two competition treatments on islets of *Spartina* in the field at Tuckerton, New Jersey. Cohorts of *P. marginata* (~7500 first-instar nymphs/m²) either developed on islets that were exposed to *P. dolus* for 6 wk (competition treatment) or they developed on plants that experienced little prior feeding by *P. dolus* (competition-relaxed treatment). Differences between treatment means are indicated (ANOVA): *$P < 0.05$, NS = not significant. Bars represent +1 SE.

the performance of a co-occurring species (short-term effect), or they may persist to adversely impact the fitness of potential competitors in subsequent generations or seasons (delayed effect) (McClure 1980, Neuvonen et al. 1988, Damman 1993, Denno et al. 1995).

Short-term, interspecific effects are known for sap-feeding insects (McClure 1980, 1984), leaf-chewing insects (Masters and Brown 1992, Ritchie and Tilman 1992), and phytophagous mites (Karban and English-Loeb 1988, English-Loeb et al. 1993), but delayed induced effects have been studied almost exclusively with mandibulate insects (West 1985, Faeth 1988, Hanhimäki 1989, Hunter 1992, Denno et al. 1995, Dankert et al. 1997). Long-lasting induced plant resistance has also been shown to mediate interspecific interactions between phytophagous mite species (Karban and English-Loeb 1988, English-Loeb et al. 1993). Spring feeding by leaf-chewing insects can have profound negative effects on a variety of insect guilds which occur during the summer and fall on oak trees (West 1985, Hunter 1987, Hunter and West 1990). Spring-feeding caterpillars so affect the suite of late-season herbivores and other community members in this system that they have been termed ''keystone herbivores'' (Hunter 1992). Despite their apparent primal importance in leaf-chewer dominated systems, such delayed interspecific effects have gone virtually unexplored for sap-feeding insects (but see McClure 1980).

Our results for *Prokelisia* planthoppers provide one of the few known examples of delayed, plant-mediated interspecific competition between two sap-feeding insects. Three lines of experimental evidence from the laboratory, field cages, and open field plots provide consistent support for the detrimental effects of previous feeding by one planthopper species on the subsequent survival and performance of another. Data from laboratory experiments showed that prior feeding on *Spartina* by one congener resulted in the diminished performance of the other in the following generation, but the adverse effect was not symmetric. Prior feeding by *P. dolus* resulted in prolonged development and reduced body size in *P. marginata,* whereas only development was protracted in *P. dolus* when plants were previously exposed to *P. marginata* (Figs. 3 and 4). Furthermore, the interspecific effect of prior feeding on the body size of *P. marginata* was much stronger than the intraspecific effect (Fig. 4). The consequence of reduced body size in female *P. marginata* is severe and translates into profoundly reduced fecundity (Denno and McCloud 1985). For example, reducing body length from 2.94 mm (absence of competition) to 2.68 mm (interspecific competition with *P. dolus*) results in a 32% reduction in average daily fecundity when these body-length values (Fig. 4) are used to predict fecundity (average daily fecundity = $-22.621 + 10.598 \times$ body length; Denno and McCloud 1985). The body size of *P. dolus* was unaffected by previous feeding, either from conspecifics or from *P. marginata*. These data collectively suggest that the delayed consequences of prior feeding are much stronger for *P. marginata* than they are for *P. dolus*. Thus, *P. dolus* appears to be the superior competitor in the context of delayed, plant-mediated interactions.

Prior feeding by *P. dolus* negatively affected the development, body size, and survival of *P. marginata* in the field as well (Figs. 5, 6, and 7). Delayed interspecific competition resulted in smaller females (2.72 mm) with a predicted fecundity 28% less than females not experiencing the effects of prior feeding (2.95 mm) (Fig. 5, Denno and McCloud 1985). The benefits gained by reduced interspecific competition must be particularly strong for *P. marginata* because they are undoubtedly offset in part by the penalties imposed by contemporaneous intraspecific competition. For instance, intraspecific crowding has very adverse effects on the body size and survival of *P. marginata* (Denno and Roderick 1992). For our field cage and laboratory experiments we were able to minimize the effects of contemporaneous intraspecific competition by assessing delayed interspecific effects on low densities of *P. marginata*. This strategy was not prudent for the open-islet experiment because we wanted to ensure a reasonable stocking density that ultimately would result in a potentially detectable difference between the two treatments. Thus, we stocked the islets with a moderate density of *P. marginata* (7500 nymphs/m²). Knowing

that our islets on average carried an aboveground *Spartina* dry-weight biomass of 250 g/m^2 (R. F. Denno, *unpublished data*), we were able to calculate an average stocking load of 30 nymphs/g *Spartina.* This load value represents a moderate level of intraspecific crowding for *P. marginata,* one that results in minor fitness penalties (see Denno and Roderick 1992). Thus, because nymphal densities were much higher on the ''no-competition'' islets compared to those exposed to *P. dolus* (Fig. 6), individuals on the ''no-competition'' islets probably incurred greater reductions in survival and body size due to intraspecific competition. Despite this probable intraspecific penalty, nymphs on the ''no-interspecific-competition'' islets survived better and molted at a larger body size than individuals experiencing islets previously infested with *P. dolus* (Figs. 6 and 7).

The mechanism underlying the delayed competitive effects in *Prokelisia* planthoppers is very likely diminished *Spartina* nutrition. For example, feeding by *P. dolus* significantly reduces the total concentration of free amino acids and of essential amino acids in *Spartina* (Olmstead et al. 1997). Although feeding-induced reductions of several amino acids occur after only 9 d of feeding, decreases in others are much more delayed (Olmstead et al. 1997). Because the fitness (body size) of *P. marginata* is negatively affected when feeding on amino nitrogen-deficient *Spartina* (Denno et al. 1985, 1986, Cook and Denno 1994), previous feeding by *P. dolus,* and the associated long-term reductions in amino nitrogen this species induces, strongly suggest the mechanistic basis for the delayed competitive effect of *P. dolus* on *P. marginata.* Furthermore, the rapid nymphal development of *Prokelisia* planthoppers (Denno et al. 1989), coupled with the slow reduction of plant nitrogen due to planthopper feeding, may explain why previous feeding rather than contemporaneous feeding has more impact on planthopper performance (see Denno and Roderick 1992). Feeding-induced allelochemistry is probably a much less likely explanation for plant-mediated competitive effects because complex secondary chemicals such as glucosinolates, terpenoids, alkaloids, flavonoids, and phenolics are either absent or occur in low concentrations in grasses (Culvenor 1970, Butler and Bailey 1973, Harborne and Williams 1976, McNeill and Southwood 1978, van Etten and Tookey 1979, Prestidge and McNeill 1983).

Although competitive effects are generally asymmetric between phytophagous insects (Lawton and Hassell 1981, Strong et al. 1984, Denno et al. 1995), one can ask why this might be the case for *Prokelisia* planthoppers, whereby the penalties imposed by previous feeding are much more severe for *P. marginata* (Figs. 3 and 4). Why should *P. marginata* be more susceptible to diminished plant nitrogen than *P. dolus*? The answer may lie with a fundamental difference in the ability of these two planthoppers to compensate for low nitrogen by increasing their intake of phloem sap. Planthoppers and leafhoppers feed by inserting their stylets into phloem and xylem tissues, respectively (Backus 1985, Cook and Denno 1994). Then using a cibarial pump, cell sap is ingested. The cibarial pump is driven by a series of dilator muscles which insert on the interior of the face (Backus 1985). Species which pull against negative cell pressure typically have very enlarged cibarial-dilator muscles and very large faces for their attachment (Backus 1985). In contrast, phloem-feeding taxa, which often experience a positive cell pressure, have smaller cibarial dilators and less expanded faces. Consequently, ingestion capability appears to be positively related to face size and commitment to cibarial musculature (Backus 1985). *P. dolus* has a much broader face and commitment to subtending cibarial musculature than *P. marginata* (Denno et al. 1987; R. F. Denno, *unpublished data*). Thus, *P. dolus* may be more capable of increasing food uptake in response to any reductions in plant nitrogen, either natural or those induced by previous feeding, than *P. marginata.* Furthermore, feeding by *P. dolus* may deplete plant nitrogen more than feeding by *P. marginata.* This supposition may explain why previous feeding by *P. dolus* has more dire consequences on the body length of female *P. marginata* than previous feeding by conspecifics (Fig. 4).

The reduced ability of *P. marginata* to cope with low plant nitrogen goes far to explain its mobile life history and the partial role that *P. dolus* apparently plays in its population dynamics. Prestidge and McNeill (1982) argue that responses to host-plant nitrogen have selected for two discrepant life history styles in sap-feeding insects. First, there are species with highly specific nitrogen requirements which are very mobile (macropterous) and actively track specific nutritional requirements. Second, there are species which are more tolerant of fluctuating levels of host-plant nitrogen and these tend to be much less mobile (brachypterous). *P. marginata* and *P. dolus* appear to fit these categories. *P. marginata* undergoes annual interhabitat migrations between persistent overwintering habitats on the high marsh and temporary but more nitrogen-rich *Spartina* habitats located on the low marsh (Denno et al. 1996). In laboratory choice tests, *P. marginata* selects nitrogen-rich over nitrogen-poor plants on which to feed and oviposit (Denno 1985), and it suffers significant reductions in body size/fecundity when raised on nitrogen-poor plants (Cook and Denno 1994). In the field, macropterous adults of *P. marginata* accumulate rapidly on and emigrate less from nitrogen-rich host plants (Denno et al. 1980, Cook and Denno 1994). Moreover, this planthopper can show dramatic population increases on fertilized plots of *Spartina* (Denno 1983, 1985, Cook and Denno 1994). In contrast, *P. dolus* is far more sedentary (brachypterous), colonizes nitrogen-rich plants less, and remains on the high marsh year round, where it incurs depressed levels of plant nitrogen par-

ticularly during the summer months (Cook and Denno 1994, Denno et al. 1996).

We argue that the spring exodus of *P. marginata* from shared habitats on the high marsh is enhanced by *P. dolus* which induces long-term depletions in the quality of *Spartina* that further limit the summer occupation of this habitat by *P. marginata.* In late May prior to the migration of *P. marginata,* >85% of both species' populations co-occur on the high marsh (Denno et al. 1996). Our data strongly suggest that if *P. marginata* were to remain in habitats dominated by *P. dolus,* its fitness would be diminished considerably the following generation (Figs. 6 and 7). We further contend that feeding by *P. dolus* exacerbates the inherent summer contrast between nitrogen-poor *Spartina* on the high marsh and nitrogen-rich cordgrass in the low marsh (Denno 1983, Denno et al. 1986, 1996), and provides additional impetus for *P. marginata* to migrate to low-marsh *Spartina.* Thus, although the fitness consequences of contemporaneous interactions between these two planthoppers appear mild (Denno and Roderick 1992), *P. dolus* imposes severe delayed competitive effects on *P. marginata.* It would be unreasonable to suggest that all feeding-induced reductions in plant nitrogen on the high marsh result from *P. dolus,* because previous feeding by conspecifics also results in the diminished performance of *P. marginata* in the next generation (Figs. 3 and 4). However, we emphasize that *P. dolus* can be far more abundant than *P. marginata* during spring and summer on the high marsh (Denno et al. 1996; R. F. Denno, *unpublished data*), and that previous feeding by *P. dolus* has far greater consequences on certain fitness components of *P. marginata* than does previous feeding by conspecifics (Fig. 4).

It could be argued on the basis of the inherent disparity in plant nitrogen between high-marsh and low-marsh *Spartina* during summer (Denno 1983, Ornes and Kaplan 1989) that a nitrogen-sensitive species like *P. marginata* (Denno et al. 1980, Denno 1985) would migrate to the temporary, low-marsh habitat independent of any competitive effects imposed by *P. dolus.* After all, temporal and spatial change in plant nitrogen has been implicated as a major factor underlying host-plant alternation and habitat shifts in a variety of migratory phytophagous insects, particularly aphids (McNeill and Southwood 1978, Prestidge and McNeill 1983, Moran 1988, 1990, Dixon 1998). Nonetheless, evidence suggests that competition from *P. dolus* also contributes importantly to the migration dynamics of *P. marginata.* For instance, the proportion of migratory forms in New Jersey populations of *P. marginata* is variable and positively density dependent (Denno and Roderick 1992, Denno et al. 1996). Moreover, the observed fraction of macropterous forms in high-marsh populations of *P. marginata* cannot be explained on the basis of conspecific density alone, which on average predicts a fraction of macropters 34% less than that actually observed (Denno and Roderick 1992). Only

by factoring in the density of *P. dolus* as well can the proportion of migratory morphs in high-marsh populations of *P. marginata* be accurately predicted (Denno and Roderick 1992). Thus, when *P. dolus* is common in a shared high-marsh habitat, proportionally more migrants are produced by *P. marginata* and a smaller fraction of the population (20% on average) remains in the local habitat (Denno and Roderick 1992, Denno et al. 1996). Consequently, we suggest that *P. dolus* induces reductions in host-plant quality that further intensify the contrast between high-marsh and low-marsh plant nutrition and provides added incentive for interhabitat migration in *P. marginata.*

Sharing a common tissue resource may increase the opportunity for plant-mediated competition to occur between sap-feeders, especially if the mechanism involves feeding-induced reductions in amino nitrogen. In general, interspecific competition is thought to be intensified between sap-feeders which share a common plant-tissue resource, even if the sap-feeders are spatially separated on the plant (Moran and Whitham 1990, Denno et al. 1995). Both known cases of delayed competition in sap-feeders involve species pairs which feed in the same tissue type, *Prokelisia* planthoppers in the phloem (this report) and diaspidid scale insects in mesophyll tissue (McClure 1980). The one study which failed to find any effects of feeding-induced plant resistance involved previous feeding by caterpillars on birch leaves and its possible influence on the subsequent performance of a phloem-feeding aphid (Martin et al. 1994). Although damage-induced increases in allelochemicals (phenolics) are common in this system (Haukioja and Niemelä 1979), sap-feeders may avoid their effects by feeding in the phloem where such compounds occur in low concentrations (Buckley 1987, Martin et al. 1994). However, other studies have detected community-level effects of leaf damage by chewing insects on sap-feeders as a pooled grouping (Danell and Huss-Danell 1985, Haukioja et al. 1985, Fowler and MacGarvin 1986). Nevertheless, the data at hand suggest that sharing a common tissue resource promotes both contemporaneous and delayed competitive interactions between sap-feeders (Denno et al. 1995). Furthermore, the feeding-induced depletion in amino nitrogen appears to be the most likely mechanism underlying interspecific competition between sap-feeders.

Historically, feeding-induced plant resistance is a well-documented phenomenon for leaf-chewing insects and phytophagous mites (Faeth 1986, Karban and Myers 1989, Tallamy and Raupp 1991, Dankert et al. 1997). In contrast, this phenomenon has been poorly investigated for sap-feeding insects (Denno et al. 1995). Our data show that the primary mechanism underlying interspecific competition in *Prokelisia* planthoppers is previous feeding by one species and its long-term consequences for congeners which feed on the same plant one generation later. Importantly, the fitness

of neither *Prokelisia* species is adversely affected when these species feed contemporaneously at natural densities on the same plant (Denno and Roderick 1992). Thus, failure to detect interspecific competition in contemporaneous interactions does not necessarily constitute evidence for dismissing competition as an important factor in community dynamics. Because most investigations of interspecific competition between sap-feeding insects have been cases of contemporaneous interaction (Damman 1993, Denno et al. 1995), and because sap-feeders are often prominent community members (Cook and Denno 1994), interspecific competition as a structuring force in phytophagous insect communities may be substantially underestimated.

LITERATURE CITED

Bacheller, J. D., and J. T. Romeo. 1992. Biotic and abiotic stress effects on nitrogen chemistry in the salt marsh cordgrass *Spartina alterniflora* (Poaceae). Chemoecology **3**:74–80.

Backus, E. A. 1985. Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior. Pages 163–194 *in* L. R. Nault and J. G. Rodriguez, editors. The leafhoppers and planthoppers. Wiley, New York, New York, USA.

Buckley, R. 1987. Ant-plant-Homoptera interactions. Advances in Ecological Research **16**:53–85.

Butler, G. W., and R. W. Bailey. 1973. Chemistry and biochemistry of herbage. Academic Press, London, UK.

Cook, A., and R. F. Denno. 1994. Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense and host plant specialization. Pages 114–139 *in* R. F. Denno and T. J. Perfect, editors. Planthoppers: their ecology and management. Chapman and Hall, New York, New York, USA.

Culvenor, C. C. J. 1970. Toxic plants—a re-evaluation. Search **1**:103–110.

Damman, H. 1993. Patterns of interaction among herbivore species. Pages 132–169 *in* N. E. Stamp and T. M. Casey, editors. Caterpillars: ecological and evolutionary constraints on foraging. Chapman and Hall, New York, New York, USA.

Danell, K., and K. Huss-Danell. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. Oikos **44**:75–81.

Dankert, B. A., D. A. Herms, D. Parry, J. M. Scriber, and L. A. Haas. 1997. Mediation of interspecific competition between folivores through defoliation-induced changes in host quality. Pages 71–88 *in* A. Raman, editor. Ecology and evolution of plant-feeding insects in natural and man-made environments. International Scientific Publications, New Delhi, India.

Denno, R. F. 1983. Tracking variable host plants in space and time. Pages 291–341 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Denno, R. F. 1985. Fitness, population dynamics and migration in planthoppers: the role of host plants. Pages 623–640 *in* M. A. Rankin, editor. Migration: mechanisms and adaptive significance. Contributions in Marine Science Volume 27. Marine Science Institute, University of Texas at Austin Press, Port Aransas, Texas, USA.

Denno, R. F., L. W. Douglass, and D. Jacobs. 1985. Crowding and host plant nutrition: environmental determinants of wing-form in *Prokelisia marginata*. Ecology **66**:1588–1596.

Denno, R. F., L. W. Douglass, and D. Jacobs. 1986. Effects of crowding and host plant nutrition on a wing-dimorphic planthopper. Ecology **67**:116–123.

Denno, R. F., and E. E. Grissell. 1979. The adaptiveness of wing-dimorphism in the salt marsh-inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Ecology **60**:221–236.

Denno, R. F., and E. S. McCloud. 1985. Predicting fecundity from body size in the planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Environmental Entomology **14**:846–849.

Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition revisited and resurrected. Annual Review of Entomology **40**:297–331.

Denno, R. F., K. L. Olmstead, and E. S. McCloud. 1989. Reproductive cost of flight capability: a comparison of life history traits in wing dimorphic planthoppers. Ecological Entomology **14**:31–44.

Denno, R. F., M. J. Raupp, D. W. Tallamy, and C. F. Reichelderfer. 1980. Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Ecology **61**:859–867.

Denno, R. F., and G. K. Roderick. 1992. Density-related dispersal in planthoppers: effects of interspecific crowding. Ecology **73**:1323–1334.

Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Döbel, M. D. Eubanks, J. E. Losey, and G. A. Langellotto. 1996. Habitat persistence underlies the intraspecific dispersal strategies of planthoppers. Ecological Monographs **66**:389–408.

Denno, R. F., M. E. Schauff, S. W. Wilson, and K. L. Olmstead. 1987. Practical diagnosis and natural history of two sibling salt marsh-inhabiting planthoppers in the genus *Prokelisia* (Homoptera: Delphacidae). Proceedings of the Entomological Society of Washington. **89**:687–700.

Dixon, A. F. G. 1998. Aphid ecology. Chapman and Hall, London, UK.

Döbel, H. G., and R. F. Denno. 1994. Predator planthopper interactions. Pages 325–399 *in* R. F. Denno and T. J. Perfect, editors. Planthoppers: their ecology and management. Chapman and Hall, New York, New York, USA.

Döbel, H. G., R. F. Denno, and J. A. Coddington. 1990. Spider community structure in an intertidal salt marsh: differences along an elevational gradient. Environmental Entomology **19**:1356–1370.

English-Loeb, G. M., R. Karban, and D. Hougen-Eitzman. 1993. Direct and indirect competition between spider mites feeding on grapes. Ecological Applications **3**:699–707.

Faeth, S. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. Ecology **67**:479–494.

Faeth, S. 1988. Plant-mediated interactions between seasonal herbivores: enough for evolution or coevolution? Pages 391–414 *in* K. C. Spencer, editor. Chemical mediation of coevolution. Academic Press, New York, New York, USA.

Fowler, S. V., and M. MacGarvin. 1986. The effects of leaf damage on the performance of insect herbivores on birch, *Betula pubescens*. Journal of Animal Ecology **55**:565–573.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960.

Community structure, population control and competition. American Naturalist **44**:421–425.

Hanhimäki, S. 1989. Induced resistance in mountain birch: defence against leaf-chewing insect guild and herbivore competition. Oecologia **81**:242–248.

Harborne, J. B., and C. A. Williams. 1976. Flavonoid patterns in leaves of the Graminae. Biochemical Systematics and Ecology **4**:267–280.

Harrison, S., and R. Karban. 1986. Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. Oecologia **69**:354–359.

Haukioja, E., and P. Niemelä. 1979. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. Oecologia **39**:151–159.

Haukioja, E., P. Niemelä, and S. Sirén. 1985. Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation, in the mountain birch *Betula pubescens* ssp. *tortuosa.* Oecologia **65**:214–222.

Haukioja, E., K. Ruohomaki, J. Senn, J. Suomela, and M. Walls. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. Oecologia **82**:238–247.

Hunter, M. D. 1987. Opposing effects of spring defoliation on late-season oak caterpillars. Ecological Entomology **12**:373–382.

Hunter, M. D. 1992. Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. Pages 287–325 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resources distribution on animal-plant interactions. Academic Press, New York, New York, USA.

Hunter, M. D., and C. West. 1990. Variation in the effects of spring defoliation on the late season phytophagous insects of *Quercus robur*. Pages 123–135 *in* A. D. Watt, S. R. Leather, M. D. Hunter, and N. A. C. Kidd, editors. Population dynamics of forest insects. Proceedings of the Natural Environment Research Council Institute of Terrestrial Ecology Conference, Intercept, Edinburgh, UK.

Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. Ecology **67**:1063–1072.

Karban, R., and G. M. English-Loeb. 1988. Effects of herbivory and plant conditioning on the population dynamics of spider mites. Experimental and Applied Acarology **4**:225–246.

Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics **20**:331–348.

Lawton, J. H., and M. P. Hassell. 1981. Asymmetrical competition in insects. Nature **289**:793–795.

Lawton, J. H., and M. P. Hassell. 1984. Interspecific competition in insects. Pages 451–495 *in* C. B. Huffaker and R. L. Rabb, editors. Ecological entomology. Wiley, New York, New York, USA.

Lawton, J. H., and D. R. Strong. 1981. Community patterns and competition in folivorous insects. American Naturalist **118**:317–338.

Martin, M.-A., N. Cappuccino, and D. Ducharme. 1994. Performance of *Symydobius americanus* (Homoptera: Aphididae) on paper birch grazed by caterpillars. Ecological Entomology **19**:6–10.

Masters, G. J., and V. K. Brown. 1992. Plant-mediated interactions between two spatially separated insects. Functional Ecology **6**:175–179.

McClure, M. S. 1980. Competition between exotic species: scale insects on hemlock. Ecology **61**:1391–1401.

McClure, M. S. 1984. Influence of cohabitation and resinosis on site selection and survival of *Pineus boerneri* Annand and *P. coloradensis* (Gillette) (Homoptera: Adelgidae) on red pine. Environmental Entomology **13**:657–663.

McNeill, S., and T. R. E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. Pages 77–98 *in* J. S. Harborne, editor. Aspects of plant and animal coevolution. Academic Press, London, UK.

Moran, M. D., T. P. Rooney, and L. E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. Ecology **77**:2219–2227.

Moran, N. A. 1988. The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. American Naturalist **132**:681–706.

Moran, N. A. 1990. Aphid life cycles: two evolutionary steps. American Naturalist **136**:135–138.

Moran, N. A., and T. G. Whitham. 1990. Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. Ecology **71**:1050–1058.

Neuvonen, S., S. Hanhimäki, J. Suomela, and E. Haukioja. 1988. Early season damage to birch foliage affects the performance of a late season herbivore. Journal of Applied Entomology **105**:182–189.

Olmstead, K. L., R. F. Denno, T. C. Morton, and J. T. Romeo. 1997. Influence of *Prokelisia* planthoppers on the amino acid composition and growth of *Spartina alterniflora.* Journal of Chemical Ecology **23**:303–321.

Ornes, W. H., and D. I. Kaplan. 1989. Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. Marine Ecology Progress Series **55**:63–72.

Prestidge, R. A., and S. McNeill. 1982. The role of nitrogen in the ecology of grassland Auchenorrhyncha (Homoptera). Symposium of the British Ecological Society **22**:257–281.

Prestidge, R. A., and S. McNeill. 1983. Auchenorrhyncha—host plant interactions: leafhoppers on grasses. Ecological Entomology **8**:331–339.

Ritchie, M. E., and D. Tilman. 1992. Interspecific competition among grasshoppers and their effect on plant abundance in experimental field environments. Oecologia **89**:524–532.

SAS. 1990. SAS user's guide. SAS Institute, Cary, North Carolina, USA.

Schultz, J. C. 1988. Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology **69**:896–897.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants. Harvard University Press, Cambridge, Massachusetts, USA.

Tallamy, D. W., and M. J. Raupp. 1991. Phytochemical induction by herbivores. Wiley, New York, New York, USA.

van Etten, C. H., and H. L. Tookey. 1979. Chemistry and biological effects of glucosinolates. Pages 471–500 *in* G. A. Rosenthal and D. H. Janzen, editors. Herbivores: their interaction with secondary plant metabolites. Academic Press, New York, New York, USA.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

West, C. 1985. Factors underlying the late seasonal appearance of the lepidopterous leaf-mining guild on oak. Ecological Entomology **10**:111–120.

Wilson, S. W. 1982. The planthopper genus *Prokelisia* in the United States (Homoptera: Fulgoroidea: Delphacidae). Journal of the Kansas Entomological Society **55**:532–546.