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# INFLUENCE OF *Prokelisia* PLANTHOPPERS ON AMINO ACID COMPOSITION AND GROWTH OF *Spartina alterniflora*

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**Abstract**—The effects of feeding by the planthopper *Prokelisia dolus* on its host, *Spartina alterniflora*, were examined under conditions of both high and low plant-nitrogen subsidy. Phloem feeding by *P. dolus* reduced the concentrations of γ-aminobutyric acid, isoleucine, leucine, lysine, threonine, and valine in *S. alterniflora* leaves. In contrast, glutamic acid was the only amino acid that increased in plants fed upon by planthoppers, and this increase was only observed in plants in the high N-fertilizer treatment. Planthopper feeding reduced the total concentration of amino/imino acids tested, and the concentration of essential amino acids, although this difference was not quite statistically significant. Generally, concentrations of individual amino acids in *Spartina* were higher in the high N-fertilizer treatment. Planthopper feeding and nitrogen fertilization also significantly impacted *Spartina* growth and production. Culm elongation, new leaf production, and tiller elongation were reduced and leaf mortality was increased on plants fed upon by planthoppers. Furthermore, planthoppers showed enhanced survival on the high-N plants.

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Nitrogen fertilization also moderated the effects of sap feeding on plant growth because the reduction of culm elongation associated with planthopper feeding was more pronounced in the low N-fertilizer treatment. Thus, feeding by *P. dolus* adversely affected both the nutritional quality and growth of *Spartina*, effects that were tempered, in part, in plants receiving high nitrogen subsidy. Our results are discussed in the context of feeding-induced changes in plant quality and quantity as possible mechanisms mediating competitive interactions in *Prokelisia* planthoppers.

**Key Words**—Amino acids, Delphacidae, plant nitrogen, nutritional ecology, planthoppers, plant growth, sap-feeding insects.

## INTRODUCTION

Modification of host plant quality by feeding is a possible mechanism underlying intra- and interspecific competition among herbivorous insects (Schultz, 1988; Karban and Myers, 1989; Denno and Roderick, 1992; Damman, 1993; Denno et al., 1995; but see Faeth, 1992). Induced changes in attacked plants that reduce the suitability of hosts for later feeders include diminished nitrogen and carbohydrate availability (Cagampang et al., 1974; McClure, 1980; Inbar et al., 1995), increased levels of deterrents or toxic phytochemicals (Haukioja and Niemelä, 1979; Toumi et al., 1984; Tallamy and Raupp, 1991), diminished plant growth or altered plant structure (Berube, 1980; Fritz et al., 1986; Wellings and Dixon, 1987), and the release of volatiles that attract natural enemies (Price et al., 1980; Vet and Dicke, 1992). Although feeding-induced changes in host plant quality have been studied for mandibulate insects (e.g., Haukioja and Niemelä, 1979; Rhoades, 1983; Niemelä and Toumi, 1987; Tallamy, 1985), this phenomenon has been less well investigated for sap-feeding herbivores (Meyer, 1993; Dixon et al., 1993; Denno et al., 1995).

Poor plant nutrition can have very adverse effects on the performance and fitness of sap feeders such as planthoppers and aphids (McNeill and Southwood, 1978; Dixon, 1985; Denno et al., 1986; Cook and Denno, 1994). A probable mechanism by which sap feeders alter host plant quality for subsequent herbivores is by an induced change in plant nutrition, specifically amino nitrogen (McClure, 1980; Sōgawa, 1982; Denno and Roderick, 1992; Dixon et al., 1993). Sap-feeding insects are known to alter the levels of amino nitrogen in their host plants, and levels of free amino acids in attacked plants may increase, decrease, or remain unchanged depending upon the plant species (Weibull, 1988; Douglas, 1993; Sandström and Pettersson, 1994), plant phenology (Parry, 1977; Prestidge and McNeill, 1982; Dixon et al., 1993; Douglas, 1993), or the density of sap feeders (Cagampang et al., 1974; Sōgawa, 1982; Bacheller and Romeo, 1992). One potentially important consideration is that amino acid levels often increase immediately when plants are attacked, but then decrease with time

(Sōgawa, 1971; Bacheller and Romeo, 1992; Cook and Denno, 1994). Thus, the benefits of such pulses in available nitrogen for herbivores may be rather short-lived and may not be realized by subsequent-feeding herbivores that either attack plants later or have relatively extended developmental periods (Cook and Denno, 1994).

Nitrogen availability in host plant tissues is considered a limiting factor for many herbivores including sap feeders (McNeill and Southwood, 1978; Mattson, 1980; Raven, 1983). Nitrogen subsidy can dramatically increase the amount of total nitrogen and free amino acids available in phloem sap (Prestidge and McNeill, 1982; Pfeiffer and Burts, 1984; Cook and Denno, 1994), and densities of phloem feeders often increase following nitrogen fertilization of hosts (Cheng, 1971; Prestidge, 1982; Denno et al., 1985; Lightfoot and Whitford, 1987; Denno and Roderick, 1990), occasionally reaching outbreak proportions (Kenmore, 1980). What is not well understood is how the amount of nitrogen available to plants interacts with herbivore feeding to influence the concentration of free amino acids for subsequent herbivores.

The monophagous planthopper *Prokelisia dolus* Wilson (Hemiptera: Delphacidae) feeds on the perennial cordgrass *Spartina alterniflora* Loisel. throughout the intertidal salt marshes of North America (Denno and Roderick, 1992; Denno et al., 1995). The soluble protein content of *Spartina* declines as *Prokelisia* densities increase over the summer in the field (Denno et al., 1985). Nitrogen availability to plants is most limited in the high marsh (Cavalieri and Huang, 1981) where *Prokelisia* species occur sympatrically for much of the growing season (Denno and Roderick, 1992). This study explores one possible mechanism underlying the direct and delayed effects of competition between *Prokelisia* planthoppers, namely feeding-induced changes in the amino acid chemistry and growth of their host plant.

To test the hypothesis that sap feeding alters plant physiology, we used a factorial experiment to examine the effect of *P. dolus* on the growth and amino acid composition of *S. alterniflora*. Our specific objectives were to determine: (1) if the amino acid composition and growth of *Spartina* plants differ when they are grown with and without planthoppers, and (2) if nitrogen fertilization modifies any planthopper-induced differences in plant growth or amino acid chemistry.

## METHODS AND MATERIALS

*Experimental Design.* To evaluate the potentially interactive effects of feeding by *Prokelisia dolus*, feeding duration, and nitrogen subsidy on the growth and nutrition of *Spartina*, we compared the growth and amino acid composition of plants grown with or without planthoppers under high or low N-fertilizer regimes. Specifically, we used a 3 × 2 × 2 factorial design with planthoppers

(present, absent, and a cage control), N-fertilizer subsidy (low or high), and feeding duration (nine and 15 days after planthoppers were established on plants) as main factors. Uncaged plants served as cage controls and were used to evaluate any effect of caging on plant growth and chemistry independent of planthopper effects.

*Spartina alterniflora* plants were grown from seed in sand-filled pots (6.3 cm) placed in plastic-lined flats (1.0 × 0.7 $m^2$) filled to 3 cm with water. The two nitrogen subsidy treatments (low and high) were established by fertilizing plants biweekly at two rates (1 g/flat or 7 g/flat) with a 3 : 1 mixture of ammonium nitrate (N/P/K, 34 : 0 : 0) and phosphoric acid (0 : 46 : 0) for three months prior to their use in the experiment. Two flats of plants were fertilized for each nitrogen treatment and were maintained in the greenhouse (see Denno et al., 1985, for details). The two fertilizer regimes result in plants with soluble nitrogen contents that span those that occur naturally in the field (Denno et al., 1985, 1986).

Because plants were fertilized prior to the application of planthopper treatments, we measured the dry weight of five randomly selected plants from each N-fertilizer treatment on the same day that the planthopper/cage treatments were applied (day 0). The average biomass value for each N-fertilizer treatment was determined and subtracted from the final values to adjust for initial differences in plant mass between the two N-fertilizer treatments. Prior to the random application of planthopper/cage treatments, all *Spartina* seedlings were thinned to three stems per pot.

Planthoppers were established on plants by placing 200 field-collected adults of *P. dolus* within a cage constructed of clear plastic cellulose butyrate tubing (see Denno and Roderick, 1992, for details). Planthoppers were collected in *Spartina* meadows near Tuckerton, Ocean County, New Jersey, three days prior to their use in the experiment. Each of the six planthopper/cage × fertilizer treatment combinations was replicated at least 10 times. The effect of feeding duration on plant growth and chemistry was evaluated by assessing half of the replicates after nine days of exposure to planthoppers and measuring the other half after 15 days of exposure.

*Amino Acid Extraction and Analysis.* Plants for amino acid analysis were harvested nine or 15 days after planthoppers were established on treatment plants. Whole-plant samples (leaves from all three stems) were collected in the greenhouse, placed immediately on Dry Ice, and taken to the laboratory where they were lyophilized and then ground in a Wiley mill. Whole-leaf samples, rather than phloem exudate, were used as indicators of the chemical composition of phloem sap.

Powdered leaf material (50 mg) was extracted 3× with 2.0 ml MCW (MeOH–$CHCl_3$–$H_2O$, 12 : 5 : 1). Combined supernatant was separated into an upper aqueous and a lower $CHCl_3$ phase by the addition of 1.5 ml $H_2O$ and 1.0

ml $CHCl_3$. The aqueous layer was removed, dried under a stream of air, and redissolved in 0.5 ml of 25% EtOH. Samples for the amino acid analyses were prepared by drying 0.1 ml of the above solution under air and redissolving in 0.5 ml of pH 2.0 analyzer buffer (Singh et al., 1973), which is described below.

Amino acids were separated using a Dionex model MBF/SS amino acid/peptide analyzer. The organic nitrogen compounds analyzed included all essential amino acids, nonessential amino acids, and the imino acids proline (Pro) and pipecolic acid (PIP). Extracts were loaded onto a 0.4 × 12.0-cm column packed with DC-5A cation exchange resin (Dionex Corp.). OPA (*o*-phthaldialdehyde) was used as the postcolumn fluorescence detection reagent. Fluorescence was measured with a Gilson Fluorometer with wavelength of excitation 360 nm and emission 455 nm. Integration of peak areas was performed using a Shimadzu C-R3A Chromatopac data processor. Peaks were identified by absolute retention time and quantified by relation to standards of known concentration.

The analyzer was equipped with a modified Dionex secondary amine kit (model SAA 26401) for detecting imino acids. Chl-T was used as the oxidant for opening the imino rings of Pro and PIP prior to reaction with OPA (Bleecker and Romeo, 1982). The oxidation reaction temperature was maintained in a delay coil for 60 sec at a constant 111.5°C by a Haake circulating hot oil bath (model E2).

Two amino acid analyzer runs were performed on each sample, one for the primary amino acids and a second for imino acids. Amino acids were sequentially eluted from the column using six buffers (A–F) of increasing pH in a constant 0.2 M solution of $Na^+$ cations. Seventeen of 20 protein amino acids and γ-aminobutyric acid were resolved in the system. The amides asparagine and glutamine coeluted with serine (Asx). An abbreviated second run, utilizing buffers A, B, and F and a Chl-T delay coil prior to mixing with OPA detected Pro and PIP (Bleecker and Romeo, 1982).

Amino acid analyzer buffers contained 2.0 g NaOH, 8.76 g NaCl, 0.25 g $Na_2EDTA$, and 1.0 ml phenol per liter solution. The sample buffer and buffers A, B, and C were brought to the desired pH of 2.0, 3.1, 3.5, and 4.2, respectively, by titrating with formic acid (99%). Eluent D was titrated to pH 7.1 with $H_3PO_4$ (85%), and eluent E was brought to pH 10.0 with 3.5 g $H_3BO_3$ and two pellets of NaOH. An additional regenerant buffer, eluent F, contained 4.0 g NaOH, 5.84 g NaCl, 0.25 g $Na_2EDTA$, and 1.0 ml phenol per liter.

A three-way factorial of analysis of variance was used to evaluate the effects of planthoppers, N-fertilizer levels, time, and their interactions on *Spartina* amino/imino acid composition. Sidak's *t* tests were used to compare interaction means. Prior to final analyses, residuals were examined for normality (Shapiro-Wilk test) and homoscedasticity (Levene's test, Milliken and Johnson, 1984). Throughout the text and tables, means are expressed with one standard error

and amino acid concentrations are expressed as nanomoles per gram *Spartina* dry mass.

Although the experimental treatments were randomized in 3 × 2 × 2 factorial design, data from caged plants and uncaged plants were analyzed separately for ease of presentation of results. The results from the partial analyses did not differ from those of the more complex factorial ANOVA.

*Plant Growth.* Just prior to their harvest for amino acid analysis, all plants were measured to determine the effects of planthoppers, feeding duration, and fertilization on growth. The following plant parameters were measured on days 9 and 15: culm elongation per stem (average elongation in centimeters for the three stems per pot); leaf gain per stem; number of dead leaves per stem; number of tillers produced per pot; tiller growth (total elongation in centimeters for tillers in the pot); and dry biomass (pooled biomass of all tillers and stems in the pot). Dry biomass measurements (grams) were made on plants harvested for the amino acid analysis (total of the three-stem harvest). After nine and 15 days, we determined planthopper densities and calculated planthopper loads (load = number of planthoppers per gram dry mass *Spartina*) for each replicate. Three-way analyses of variance, as described in the previous section, were used to evaluate differences in plant growth parameters among treatments and treatment combinations.

## RESULTS

*Planthopper and N-Fertilization Effects on Amino Acid Composition of* Spartina. Planthoppers significantly reduced the concentrations of Ile, Leu, Lys, Thr, and Val in plants on which they fed compared to planthopper-free controls (Figure 1; Table 1). Concentrations of Trp were initially increased by planthopper-feeding in the high N-fertilizer treatment but this increase was not observed in the low N-treatment or in either fertilizer treatment after 15 days (significant three-way interaction in Table 1). Planthoppers also reduced, but not quite statistically, the total concentration of essential amino acids ($\bar{X}$ = 5581 ± 376 nmol/g) compared to control plants ($\bar{X}$ = 6320 ± 458 nmol/g; $F_{1,42}$ = 3.69, $P < 0.07$).

Planthoppers significantly reduced the concentrations of GABA and Ala, but they did not significantly reduce the concentration of any other nonessential amino acid (Table 1, Figure 1). In fact, Ala concentrations were only reduced by planthopper feeding after nine days in the low-N treatment, and no significant differences existed between the planthopper and control plants after 15 days (three-way interaction in Table 1). Glutamic acid was the only amino acid that increased significantly in plants fed upon by planthoppers. Concentrations of Glu increased in response to planthopper feeding in plants in the high N-fertilizer treatment; no significant planthopper effect was detected in the low N-fertiliza-

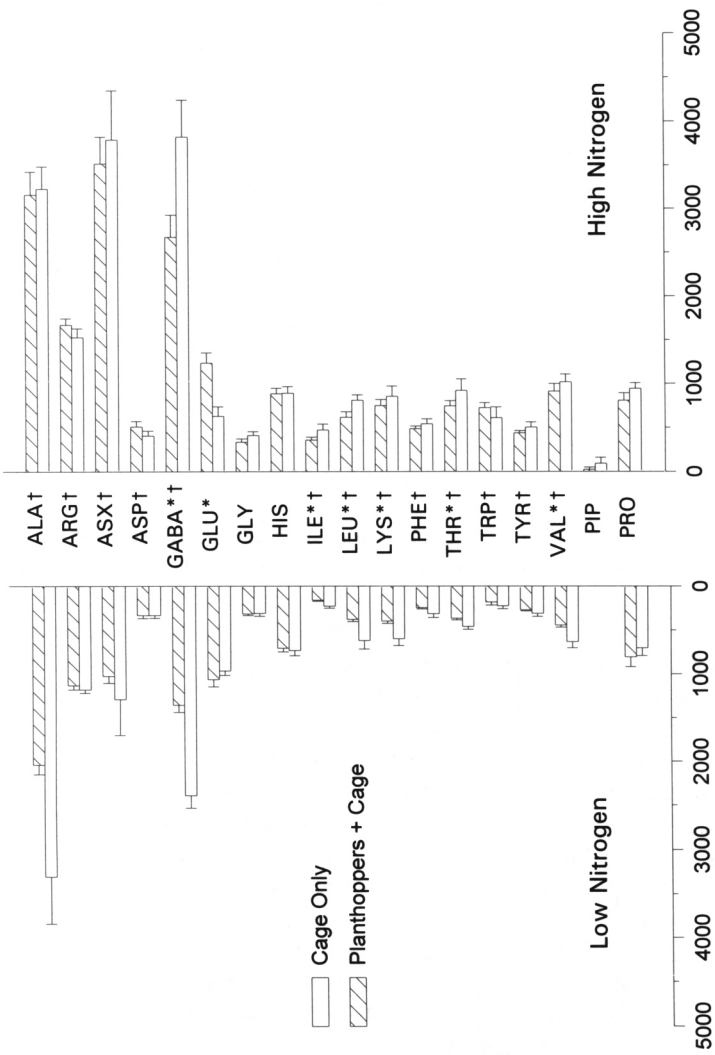


FIG. 1. Amino/imino acid concentrations of *Spartina alterniflora* caged with or without *Prokelisia dolus* planthoppers. Plants were randomly assigned to low or high N-fertilizer treatments. Asterisks (*) indicate significant differences between the planthopper treatment and controls (Table 1). Daggers (†) indicate significant differences between low and high N-fertilizer treatments (Table 1).

TABLE 1. ANALYSES OF VARIANCE RESULTS FOR EFFECTS OF PLANTHOPPERS, N-FERTILIZER TREATMENTS, AND TIME ON CONCENTRATIONS OF ESSENTIAL AND NONESSENTIAL AMINO ACIDS IN *Spartina alterniflora*[a]

| | | Essential amino acids | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Source of variation | *df* | Arg | His | Ile | Leu | Lys | Phe | Thr |
| Planthoppers | 1 | 26,993 | 4,440 | 98,618*** | 536,513** | 305,047* | 44,525 | 208,736* |
| Fertilizer | 1 | 2,144,528*** | 288,800** | 554,846*** | 551,859** | 1,030,724*** | 623,001*** | 2,079,481*** |
| Planthopper × fertilizer | 1 | 71,443 | 0.92 | 7,261 | 9,845 | 209,776 | 128 | 17,071 |
| Time | 1 | 142,599 | 7,113 | 57,273* | 128,017 | 89,582 | 8,987 | 57,577 |
| Planthopper × time | 1 | 125,363 | 815 | 40,453 | 26,498 | 12,216 | 7,311 | 88,307 |
| Fertilizer × time | 1 | 335,504* | 270,693* | 72,758* | 6,807 | 227,487 | 82,308* | 78,733 |
| Planthopper × fertilizer × time | 1 | 28.2 | 33,245 | 39,182 | 50,823 | 60,457 | 26,413 | 126,561 |
| Error | 42 | 49,202 | 40,193 | 13,017 | 47,967 | 62,874 | 13,528 | 52,076 |

[a] $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

tion treatment (Figure 1; significant planthopper × fertilizer interaction in Table 1).

As expected, N fertilization increased the concentrations of most amino acids assayed (Figure 1). Specifically concentrations of Asp, Leu, Lys, Thr, and Val were significantly greater in plants receiving more nitrogen (Figure 1; Table 1). Concentrations of Arg, Asx, GABA, Ile, Phe, and Tyr were greater in plants in the high N-fertilizer treatment on both sampling days, but the difference was much greater on day 15 (significant fertilizer × time interaction term in Table 1).

There were no statistically significant effects of planthoppers, time, N fertilizer, or interactions on Gly, the two imino acids, or the two sulfur-containing compounds (Met and Cys). Concentrations of total amino/imino compounds in plants on which planthoppers fed were significantly lower ($\bar{X}$ = 15,700 ± 1120 nmol/g) than controls ($\bar{X}$ = 18,100 ± 1390 nmol/g; Table 1). As expected, the total concentration of amino/imino acids was significantly influenced by N-fertilization (significant fertilizer × time interaction term in Table 1). Total amino/imino acids were higher in plants in the high-N treatment on day 9 (high-N $\bar{X}$ = 17,840 ± 1291 nmol/g; low-N $\bar{X}$ = 13,544 ± 1227 nmol/g; $P < 0.05$; Sidak's *t* test), but the effect of fertilization was much greater by day 15 (high-N $\bar{X}$ = 23,077 ± 1551 nmol/g; low-N $\bar{X}$ = 11,838 ± 656 nmol/g; $P < 0.05$; Sidak's *t* test).

*Caging Effects on Amino Acid Composition of* Spartina. After 15 days, concentrations of Ala, GABA, Glu, and Trp were higher in caged plants than uncaged controls (Table 2). Caged plants in the high N-fertilizer treatment also

| Mean square values | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Nonessential amino acids | | | | | | |
| Trp | Val | Ala | Asx | Asp | Gaba | Glu | Tyr | Total amino/imino acids |
| 9,442 | 271,240* | 6,077,317* | 1,180,235 | 17,717 | 14,577,603*** | 1,178,319*** | 32,695 | 80,188,369* |
| 2,519,911*** | 2,109,323*** | 2,982,128 | 70,662,106*** | 162,061* | 21,906,005*** | 122,319 | 372,334*** | 725,519,220*** |
| 69,517 | 16,835 | 3,914,761* | 30,543 | 25,827 | 52,019 | 670,323** | 2,773 | 8,012,140 |
| 161,406 | 85,509 | 27,029 | 2,658,514 | 232,405** | 3,476,736* | 1,225,860*** | 10,162 | 48,283,362 |
| 19,506 | 19,446 | 3,945,842* | 406 | 419 | 1,466,768 | 36,999 | 8,927 | 3,161 |
| 284,353* | 181,082 | 7,054,914** | 13,629,960*** | 54,965 | 2,883,158* | 299,115 | 60,003* | 173,195,751** |
| 206,442* | 109,831 | 3,657,559* | 4,125,985 | 262 | 1,807,394 | 3,266 | 31,633 | 64,405,778 |
| 42,282 | 61,255 | 856,080 | 1,088,675 | 27,755 | 576,900 | 91,760 | 11,820 | 17,030,000 |

had higher levels of Arg, His, and total amino/imino acids than did caged plants in the low-N treatment, but no difference in the concentrations of these amino acids existed between control (uncaged) plants in the two N-fertilizer treatments (Table 2). Concentrations of Asx were greater in the high N-fertilizer treatment in both control and caged plants, but within the high-N treatment, caged plants had more than twice the Asx than controls (Table 2). The other amino/imino acids assayed did not show a response to plant caging.

To summarize the cage effects, amino acids levels in caged plants were generally high relative to controls, and this difference was often marked when nitrogen availability to the plant was high (cage × fertilizer interaction in Table 2). This may represent a stress response of plants to the cages because increased concentrations of free amino acids have been associated with plant stress (Cagampang et al., 1974; Stewart and Larher, 1980). In contrast, in the low N-fertilizer treatment, amino acid levels in caged and control plants generally did not differ significantly (Table 2). Thus, in the absence of sufficient nitrogen, *Spartina* plants may not exhibit the same stress response.

*Planthopper and N-Fertilizer Effects on* Spartina *Growth.* Planthopper feeding negatively impacted *Spartina* growth and development. New leaf production and tiller elongation were reduced and the number of dead leaves were increased on *Spartina* fed on by planthoppers (Table 3, Figure 2). Culm elongation was also significantly reduced by planthopper feeding, but the difference in culm elongation was greater in plants in the low N-fertilizer treatment (control plant $\bar{X} = 8.1 \pm 1.16$ cm; planthopper treatment $\bar{X} = 3.48 \pm 0.332$ cm; $P < 0.01$; Sidak's $t$ test) than in the high-N treatment (control plant $\bar{X} = 4.1 \pm 0.89$ cm; planthopper treatment $\bar{X} = 1.50 \pm 0.262$ nmol/g; $P < 0.001$, Sidak's $t$ test;

TABLE 2. AVERAGE ($\bar{X} \pm 1$ SE) AMINO ACID CONCENTRATIONS (nmol/g) IN CONTROL AND CAGED *Spartina alterniflora* PLANTS AFTER 15 DAYS[a]

| | | Caged plants | Control plants | $F_{1,16}$ |
|---|---|---|---|---|
| Means comparisons for significant caging effects | | | | |
| Ala | | 2950 ± 253 | 2285 ± 234 | 5.52* |
| GABA | | 3560 ± 436 | 2800 ± 304 | 4.89* |
| Glu | | 930 ± 94 | 603 ± 83 | 8.57** |
| Trp | | 496 ± 148 | 224 ± 62 | 5.41* |
| Means comparisons for significant Cage* Fertilizer interactions | | | | |
| N-Fertilizer | | | | |
| Arg | High | 1720 ± 128* | 1370 ± 146† | 5.38* |
| | Low | 1205 ± 61 | 1334 ± 35 | |
| His | High | 100 ± 98* | 776 ± 56† | 7.57* |
| | Low | 640 ± 59 | 799 ± 57 | |
| ASX | High | 4860 ± 490* | 2065 ± 523*† | 13.82** |
| | Low | 696 ± 121 | 628 ± 92 | |
| Total | High | 25740 ± 1810* | 17130 ± 2150† | 8.65** |
| | Low | 12550 ± 970 | 13120 ± 933 | |

[a] Plants were randomly assigned to low or high N-fertilizer treatments ($n = 10$) and were grown in a greenhouse. Interaction means were compared using Sidak's $t$ tests ($P < 0.05$). For comparisons of interaction means, daggers (†) indicate significant differences between caged and control plants within fertilizer treatments and asterisks (*) indicate significant differences between high and low N-fertilizer treatments within columns.

TABLE 3. ANALYSES OF VARIANCE RESULTS FOR EFFECTS OF PLANTHOPPERS, N-FERTILIZER, AND TIME ON GROWTH (CULM ELONGATION, LEAF GAIN, AND TILLER ELONGATION) AND LEAF LOSS OF *Spartina alterniflora*

| | | Mean square values[a] | | | |
|---|---|---|---|---|---|
| Source of variation | *df* | Culm elongation | Leaf gain | Tiller elongation | Dead leaves (*N*) |
| Planthoppers | 1 | 153.5*** | 3.40*** | 83.6* | 14.50*** |
| Fertilizer | 1 | 106.4*** | 0.07 | 36.04 | 0.02 |
| Planthopper × fertilizer | 1 | 12.3* | 0.006 | 58.3 | 3.46 |
| Time | 1 | 81.5*** | 2.07*** | 66.7* | 0.43 |
| Planthopper × time | 1 | 67.3*** | 0.55 | 9.28 | 0.14 |
| Fertilizer × time | 1 | 6.18 | 0.05 | 108.9* | 5.92* |
| Planthopper × fertilizer × time | 1 | 6.23 | 0.12 | 0.97 | 0.51 |
| Error | 42 | 2.26 | 0.16 | 15.78 | 0.99 |

[a] *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

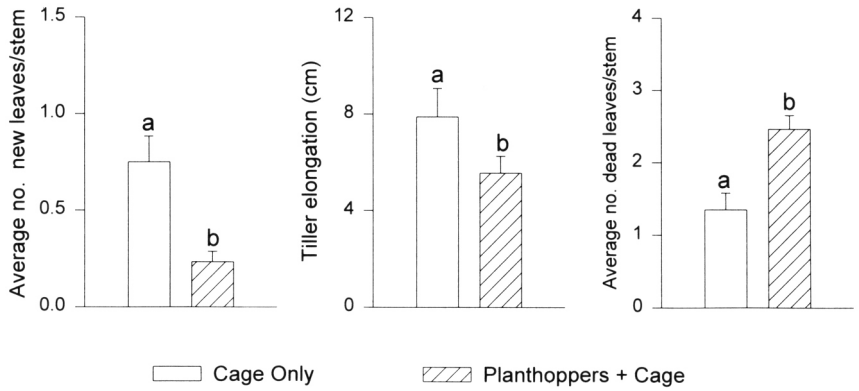


FIG. 2. Number of new leaves per stem, tiller elongation, and dead leaves ($\bar{X} \pm 1$ SE) on *Spartina alterniflora* plants grown with or without *Prokelisia dolus* planthoppers. Significant differences between control and planthopper treatments are indicated by different letters (Table 3).

significant planthopper × fertilization interaction in Table 3). A significant planthopper × time interaction also existed for culm elongation (Table 3) because this parameter did not differ between controls ($\bar{X} = 3.6 \pm 0.62$ cm) and the planthopper treatment on day 9 ($\bar{X} = 2.34 \pm 0.373$ cm; $P > 0.05$; Sidak's $t$ test), but was reduced in the planthopper treatment by almost 75% by day 15 (planthopper treatment $\bar{X} = 2.58 \pm 0.397$ cm; control plant $\bar{X} = 8.6 \pm 1.13$ cm; $P < 0.01$; Sidak's $t$ test).

Because N fertilizer had been applied to *Spartina* plants three months prior to the application of the planthopper/cage treatments, it was not surprising that the initial dry biomass readings (on day 0) from plants in the high-N treatment were almost three times ($\bar{X} = 0.276 \pm 0.069$ mg/plant) that observed in the plants in the low treatment ($\bar{X} = 0.094 \pm 0.0216$ mg/plant; $F_{1,8} = 6.33$, $P < 0.036$). After subtracting this initial difference, the final dry biomass values did not differ between plants in the two fertilizer treatments ($F_{1,42} = 0.43$, $P > 0.50$). Planthoppers slightly reduced the dry biomass of plants on which they fed ($\bar{X} = 0.72 \pm 0.053$ mg) compared to controls ($\bar{X} = 0.77 \pm 0.057$ mg) but this difference was not statistically significant ($F_{1,42} = 0.64$, $P > 0.40$).

Nitrogen fertilization of *Spartina* plants appeared to enhance the survival of *P. dolus*. Planthopper densities were greater on plants in the high-N treatment ($\bar{X} = 45.8 \pm 3.83$ individuals/stem) than in the low-N treatment ($\bar{X} = 35.5 \pm 2.72$ individuals/stem; $F_{1,25} = 12.65$, $P < 0.01$), and planthopper densities in both fertilizer treatments were higher on day 9 ($\bar{X} = 69.1 \pm 1.25$ individuals/

stem) than on day 15 ($\bar{X}$ = 38.8 ± 0.84 individuals/stem; $F_{1,25}$ = 14.93, $P < 0.001$).

Planthopper loads were also influenced by N fertilization. On day 9, planthopper loads were higher on plants in the high N-fertilizer treatment ($\bar{X}$ = 265 ± 37.1 individuals/g *Spartina* dry mass) than in the low-N treatment ($\bar{X}$ = 175 ± 17.4 individuals/g *Spartina* dry mass; $P < 0.05$, Sidak's $t$ test; $F_{1,25}$ = 10.36, $P < 0.01$), but by day 15, loads were similar between the two fertilizer treatments (high-N $\bar{X}$ = 116 ± 11.2; low-N $\bar{X}$ = 161 ± 18.5 individuals/g *Spartina* dry mass; $P > 0.05$; Sidak's $t$ test). The lack of difference in planthopper loads between the two fertilizer treatments on day 15 was due to the reduced biomass of plants in the low nitrogen treatment rather than to any increase in planthopper survival.

*Caging Effects on* Spartina *Growth.* A significant interaction between caging and fertilization effects existed for both culm elongation ($F_{1,32}$ = 4.26, $P < 0.05$) and new leaf production ($F_{1,32}$ = 3.99, $P < 0.05$). Culm elongation in the high-N treatment did not differ between caged plants ($\bar{X}$ = 4.1 ± 0.89 cm) and the uncaged controls ($\bar{X}$ = 3.6 ± 0.78 cm; $P > 0.05$, Sidak's $t$ test). In contrast, in the low N-fertilizer treatment, culm elongation was greater for the caged plants ($\bar{X}$ = 8.1 ± 1.16 cm) than for uncaged plants ($\bar{X}$ = 5.4 ± 0.96 cm; $P < 0.05$, Sidak's $t$ test). This difference may have been the result of etiolation by plants stressed in the low N-fertilizer treatment.

The number of new leaves produced by caged plants in the high N-fertilizer treatment ($\bar{X}$ = 0.80 ± 0.223) was significantly less than that produced by control plants ($\bar{X}$ = 1.30 ± 0.144; $P < 0.05$, Sidak's $t$ test), but caging did not affect new leaf production in the low fertilizer treatment ($\bar{X}$ = 0.70 ± 0.161) compared to controls ($\bar{X}$ = 0.63 ± 0.135; $P > 0.05$, Sidak's $t$ test). Dry plant biomass ($F_{1,32}$ = 2.40, $P > 0.05$) and the number of dead leaves ($F_{1,32}$ = 0.26, $P > 0.05$) did not differ between caged and control plants.

Although tiller production did not differ between caged and control plants ($F_{1,32}$ = 3.23, $P > 0.05$), tiller elongation was negatively affected by caging. Tiller elongation of caged plants ($\bar{X}$ = 7.9 ± 1.18 cm) was dramatically less than that of controls ($\bar{X}$ = 15.3 ± 2.72 cm; $P < 0.05$; $F_{1,32}$ = 6.88, $P < 0.05$). Thus, caging appears to negatively affect *Spartina* growth and elongation of new shoots.

## DISCUSSION

Modification of host plant quality has been implicated as an important factor promoting intra- and interspecific competition among sap-feeding insects (McClure, 1980; Moran and Whitham, 1990; Inbar et al., 1995), but the mechanisms of host plant alteration and how such modifications impact subsequent

herbivores are not clear (Wellings and Dixon, 1987; Meyer, 1993; Denno et al., 1995). In this study, we provide evidence that *Prokelisia dolus* significantly reduces host plant quality by limiting plant growth and decreasing the levels of certain amino acids.

Specifically, we determined that the available surface area of *Spartina* plants was reduced as a consequence of a decrease in culm and tiller elongation, production of new leaves, and an increase in leaf mortality associated with planthopper feeding (Figure 2, Table 3). Three potential consequences of decreased plant surface area include reduced photosynthesis (Fitter and Hay, 1981; Crawley, 1983), a reduction in available nutrients (Schaffer and Mason, 1990), and increased herbivore crowding (Dixon and Logan, 1972, 1973). For many wing-dimorphic herbivores including *P. dolus*, intra- and interspecific crowding can trigger the production of migratory forms, and as a consequence there is an increase in emigration from crowded habitats (Dixon, 1985; Lamb and MacKay, 1987; Denno et al., 1985; Denno and Roderick, 1992; Denno and Peterson, 1995).

Feeding by *P. dolus* also significantly reduced the concentrations of GABA, Ile, Leu, Lys, Thr, and Val (Figure 1). Although some of these amino acids are considered essential for aphid growth and reproduction (Dadd and Krieger, 1968; Leckstein and Llewellyn, 1973; Emden, 1973), it is not clear if reductions in these compounds adversely impact the performance of planthoppers. Koyama (1992) found that no single amino acid is essential for growth of the white-backed planthopper, *Sogatella furcifera* (Horvath) (Hemiptera: Delphacidae), with the possible exception of sulfur-containing compounds (Cys or Met). Furthermore, yeastlike endosymbiotes may provide essential nutrients if specific amino acids are absent from the diets of planthoppers (Houk and Griffiths, 1980; Campbell, 1989). Perhaps more importantly in our study, planthopper feeding reduced the total concentration of amino acids in *Spartina* leaves, thereby reducing the amino nitrogen quality of these host plants for subsequent herbivores.

Feeding by *P. dolus* also increased concentrations of Glu (Figure 1). Glutamic acid is a sucking stimulant for the brown planthopper, *Nilaparvata lugens* (Hemiptera: Delphacidae) (Sōgawa, 1982), and increased ingestion may be a compensatory mechanism for accelerating nutrient intake on nitrogen-deficient plants (McNeill and Southwood, 1978; Cook and Denno, 1994). Moreover, increased levels of Glu inhibit feeding altogether in some aphids and may indicate an overall deterioration in nutritional quality of the host plant (Srivastava et al., 1983; Weibull, 1988; Douglas, 1993).

Phloem-feeding insects leave stylet sheaths in plant tissues that disrupt phloem transport above the feeding site. As a consequence, local amino acid concentrations may temporarily increase (Cagampang et al., 1974; Sōgawa, 1982; Bacheller and Romeo, 1992). With the exception of Glu, such dramatic increases in amino acid concentrations did not occur in our study. This may be

due to one or more of the following reasons. First, marked increases in free amino acid concentrations are typically associated with high densities of planthoppers. Although the densities used in our experiment (initially 70 planthoppers/stem) represented the highest densities that occur in natural populations (Denno et al., 1986; Denno and Roderick, 1992), they were lower than those reported to cause the most dramatic increases in amino acid concentrations by Cagampang et al. (1974) and Bacheller and Romeo (1992). In these studies, increases in amino acid concentrations were much less or not observed at lower planthopper densities.

Although planthoppers can increase local amino acid concentrations under high-density conditions, plants may rapidly deteriorate and become unsuitable for planthopper feeding (Cagampang et al., 1974; Cook and Denno, 1994). Thus, mobile planthopper females may take advantage of temporary pulses of induced amino nitrogen, but they may not select such plants for oviposition on the basis of such cues as increased Glu that may signal the onset of plant deterioration (see Cook and Denno, 1994).

Second, some of the differences between our study and those reported for planthoppers feeding on rice (Sōgawa, 1971, 1982; Cagampang et al., 1974) may be due to differences between the physiology of *Spartina* and rice or differences in how these plants respond to phloem feeding. Numerous studies indicate that amino acid concentrations within the phloem vary among plant species and cultivars (Weibull, 1988; Douglas, 1993; Sandstöm and Pettersson, 1994).

Finally, the environment in which plants grow likely impacts the responses of plants to phloem feeders. In a study similar to ours, Bacheller and Romeo (1992) grew *S. alterniflora* under saline conditions and found dramatic increases in plant stress-associated compounds. In our experiment, salt was not added to the plant culturing medium. Thus, we did not observe significant increases in asparagine, an amide associated with plant stress (Brodbeck and Strong, 1987), or proline, which is specifically associated with osmotic stress in *Spartina* (Cavalieri and Huang, 1981).

In this study, the performance of both plant and herbivore was enhanced by increased nitrogen availability. Fertilization dramatically increased concentrations of most of the nitrogen compounds assayed (Figure 1); plant growth and production was enhanced by N fertilization; and planthopper survival was higher on plants in the high-N treatment. These results were anticipated because increased nitrogen availability from fertilization often results in enhanced insect performance or population increase (Waring and Cobb, 1989; Cook and Denno, 1994). Increased nitrogen availability may ameliorate the effects of planthopper feeding because a significant planthopper × fertilizer interaction did exist for culm elongation (Table 3) and two of the nitrogen compounds assayed (Ala and Trp) (Table 1). Thus, both nitrogen availability and planthopper feeding influ-

ence *Spartina* growth and amino acid composition, and these bottom up and lateral forces have potentially interactive effects.

Our results provide a possible explanation for the plant-mediated competitive effects observed in both contemporaneous and delayed interactions of *Prokelisia* planthoppers. In a previous study, neither survivorship, development time, nor body size of *P. dolus* was adversely affected by intra- or interspecific crowding by its congener, *P. marginata* Van Duzee (Denno and Roderick, 1992). However, in another study, the development time of *P. dolus* was significantly extended on plants on which planthoppers had previously fed (Denno et al., 1995; R. Denno and J. Cheng, unpublished data). Thus, *P. dolus* is sensitive to delayed competition resulting from intra- and interspecific interactions, but does not suffer negative effects from contemporaneous interactions with *P. marginata*.

Our results indicate that the concentrations of several amino acids in *Spartina* are reduced by planthopper feeding. Some amino acids (e.g., Ala, Arg, Asx, GABA, Leu) decreased after only nine days of exposure to planthoppers, while decreases in others were more delayed. Furthermore, our study indicated that subsequent generations of planthoppers encounter plants with fewer leaves and smaller culms and tillers. As a result, feeding by planthoppers may induce both qualitative and quantitative changes in *Spartina* plants that could adversely affect the performance of future generations of planthoppers. These impacts may be even more dramatic in nature than we observed in our experiment because our comparisons were made on caged plants in which the concentrations of several amino acids and culm elongation were artificially increased by caging.

In the *Prokelisia/Spartina* system, competitive interactions could be mediated by both reductions in plant growth and surface area as well as diminished plant nutrition. Although reductions in host plant growth associated with sap feeding have been documented for a number of insect species (e.g., Dixon, 1971; Cockfield et al., 1987; Meyer and Root, 1993), our study adds to the comparatively sparse literature detailing how phloem feeders adversely affect both the growth and amino nitrogen profiles of their host plants (see Cagampang et al., 1974; Sōgawa, 1982; Wellings and Dixon, 1987).

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