

Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies

Andrea F. Huberty · Robert F. Denno

Received: 27 November 2005 / Accepted: 8 May 2006 / Published online: 23 June 2006
© Springer-Verlag 2006

Abstract Phytophagous insects have a much higher nitrogen and phosphorus content than their host plants, an elemental mismatch that places inherent constraints on meeting nutritional requirements. Although nitrogen limitation is well documented in insect herbivores, phosphorus limitation is poorly studied. Using factorial experiments in the laboratory and field, in which levels of soil nitrogen and phosphorus were manipulated, we studied the relative consequences of macronutrient limitation for two herbivores, namely the phloem-feeding planthoppers *Prokelisia dolus* and *P. marginata*. These planthoppers inhabit the salt marshes of North America where large stands of their *Spartina* host plant are found. Notably, these congeners differ in their dispersal abilities; *P. marginata* is dispersive whereas *P. dolus* is sedentary. Both nitrogen and phosphorus subsidies enhanced the nitrogen and phosphorus content of *Spartina*. When *P. dolus* and *P. marginata* were raised on plants with an enriched nitrogen signature, they exhibited greater survival, grew to a larger size, developed more rapidly, and achieved higher densities than on nitrogen-deficient plants. However, *P. marginata* experienced greater fitness penalties than *P. dolus* on

nitrogen-deficient plants. Phosphorus limitation and associated fitness penalties were not as severe as nitrogen limitation for *P. marginata*, and were not detected in *P. dolus*. The tempered response of *P. dolus* to N- and P-deficient *Spartina* is probably due to its greater investment in feeding musculature and hence ability to compensate for nutrient deficiencies with increased ingestion. To cope with deteriorating plant quality, *P. dolus* employs compensatory feeding, whereas *P. marginata* disperses to higher quality *Spartina*. When its option of dispersal is eliminated and *P. marginata* is confined on nutrient-deficient plants, its performance is drastically reduced compared with *P. dolus*. This research highlights the importance of interfacing herbivore life-history strategies with ecological stoichiometry in order to interpret the consequences of macronutrient limitation on herbivore performance and population dynamics.

Keywords Dispersal ability · Ecological stoichiometry · Nitrogen · Phosphorus · *Prokelisia* planthopper

Introduction

Insect herbivores have a decidedly higher nitrogen (~9% N) and phosphorus (~0.5% P) content than their host plants (~1.5%N, ~0.05%P) (Elser et al. 2000a; Fagan et al. 2002), a stoichiometric mismatch that places severe constraints on their ability to meet nutritional demands (Mattson 1980; Strong et al. 1984; Elser et al. 2000a). Thus, it is not surprising that nutrient limitation has been widely documented for a taxonomically diverse array of phytophagous insects (see

Communicated by Libby Marschall

A. F. Huberty · R. F. Denno
Department of Entomology, University of Maryland,
College Park, MD, USA

Present Address:
A. F. Huberty (✉)
USDA/APHIS/BRS, Unit 147, Riverdale, MD, USA
e-mail: ahuberty@terpalum.umd.edu

reviews by McNeill and Southwood 1978; Mattson 1980; Waring and Cobb 1992; White 1993; Awmack and Leather 2002; Huberty and Denno 2004).

The importance of nitrogen and phosphorus for insect herbivores has been demonstrated experimentally by manipulating the nutrient composition of their diet and measuring subsequent growth responses (Busch and Phelan 1999; Bentz and Townsend 2001; Chen and Welter 2002; Richardson et al. 2002). Physiologically, nitrogen is essential for growth (Kainulainen et al. 1996; Rossi et al. 1996; Kerslake et al. 1998), survival (Salim and Saxena 1991; Rossi et al. 1996; Ayres et al. 2000; De Bruyn et al. 2002), and reproduction (van Emden 1966; Rossi and Strong 1991; Bentz and Townsend 2001), due to its fundamental role in protein synthesis (Sternner and Elser 2002). Collectively, such studies demonstrate that nitrogen is consistently limiting for most invertebrates, both terrestrial (Slanksky and Feeny 1977; McNeill and Southwood 1978; Mattson 1980; White 1993; Elser et al. 2000a) and aquatic (Urabe and Watanabe 1992; Downing 1997; Hassett et al. 1997; Elser et al. 2000a). Moreover, nitrogen is thought to be the most limiting macronutrient for phytophagous insects (McNeill and Southwood 1978; Mattson 1980; Strong et al. 1984; White 1993; Polis 1999).

For phytophagous insects, phosphorus has not been considered as limiting as nitrogen, perhaps due to the paucity of research focus on this element. However, the few studies that have investigated phosphorus limitation indicate that it can affect survivorship (Clancy and King 1993; Ayres et al. 2000), fecundity (Popp et al. 1989), body size (Janssen 1994; Busch and Phelan 1999), oviposition preference (Skinner and Cohen 1994), growth rate (Perkins et al. 2004), and population density (Schade et al. 2003). Moreover, phosphorus limitation has been widely documented in many species of aquatic invertebrates, particularly in *Daphnia*, for which low levels of ambient phosphorus often result in reduced growth rate (Urabe et al. 1997, 2002; Urabe and Watanabe 1992; DeMott et al. 1998; Sternner and Schulz 1998; Elser et al. 2001; Makino et al. 2002; Xenopoulos et al. 2002) and reduced competitive superiority (Andersen 1997). Because phosphorus is required for nucleic acid synthesis (RNA) and thus protein production, its limitation can impose severe consequences for cellular function and ultimately the growth rate of consumers (Hessen and Lyche 1991; Elser et al. 1996, 2000a, b; Sternner and Elser 2002).

To date, no study has simultaneously investigated the consequences of nitrogen and phosphorus limitation for the survival and performance of terrestrial herbivorous insects. Using a combination of factorial

experiments in the laboratory and field, whereby levels of soil nitrogen and phosphorus were manipulated, this study examined the limiting roles of both macronutrients on the performance and population size of two phytophagous insects via their cascading effects on host plant quality. Two closely related planthoppers, *Prokelisia dolus* and *P. marginata* (Hemiptera: Delphacidae), were chosen for study explicitly because of dramatic differences in their sensitivity to host-plant nitrogen, competitive ability, and population dynamics (Cook and Denno 1994; Denno et al. 1996, 2000, 2002, 2003). Most notable is a striking difference in dispersal capability between these two congeners; *P. marginata* is highly dispersive whereas *P. dolus* is comparatively sedentary (Denno et al. 1996; Denno and Peterson 2000). Inversely associated with dispersal capability in these two phloem-feeding planthoppers is their ability to tolerate low plant nitrogen via feeding compensation (Denno et al. 2000; Huberty and Denno 2006). This relationship derives from a trade-off between flight musculature and the cibarial musculature associated with the ingestion of phloem sap, and thus their ability to enhance food intake on nutrient-deficient host plants (Huberty and Denno 2006). Thus, these two species apparently cope with deteriorating host-plant quality in two fundamentally different ways, *P. marginata* by emigrating to better quality host plants and *P. dolus* by increasing ingestion rate and thus tolerating periods of low plant quality (Denno et al. 2000; Huberty and Denno 2006).

Given the fundamentally discrepant mechanisms that underlie the ability of these species to cope with deteriorating plant quality, we anticipated that nitrogen and phosphorus limitation might affect them differently. Based on differences in feeding compensation, we predicted that, when confined to nitrogen-poor and phosphorus-deficient host plants, the sedentary species (*P. dolus*) would incur fewer performance penalties than the dispersive species (*P. marginata*), and that brachypters would be less adversely affected by nutrient limitation than macropters. Our specific objectives were to determine the effects of variable nitrogen and phosphorus subsidies on the performance and requisite elemental composition (N and P content) of *Prokelisia* planthoppers, and their cordgrass host plant *Spartina alterniflora*, which dominates the vegetation of intertidal salt marshes in eastern North America.

This research aims to elucidate the singular and interactive effects of nitrogen and phosphorus limitation on the performance of two abundant phytophagous insects and to examine the interface between life-history strategy and the consequences of macronutrient limitation. Moreover, this work contributes to a

broader need to understand the relative roles of nitrogen and phosphorus in the nutritional ecology of phytophagous insects, two macronutrients that can have important consequences for species interactions, food-web dynamics, and ecosystem function (Coll and Guershon 2002; Sterner and Elser 2002; Vanni et al. 2002; Denno and Fagan 2003).

Materials and methods

Study site and system

Macronutrient limitation on planthopper density and *Spartina* growth was studied on an expansive salt marsh in the Great Bay–Mullica River estuarine system just north of the Rutgers University Marine Station, Tuckerton, Ocean County, New Jersey, USA (39°30.8'N, 74°19.0'W). The vegetation of this marsh is dominated by the perennial cordgrass *S. alterniflora*, where it grows in extensive pure stands in the intertidal zone (Gallagher et al. 1988; Denno et al. 1996; Mendelsohn and Morris 2000).

Within the intertidal zone, the structure and nutritional content of *S. alterniflora* varies dramatically with elevation due to differences in nutrient subsidy by tides and salinity (Webb 1983; Gallagher et al. 1988; House et al. 1998). Moving up an elevational gradient from low-marsh habitats (tidal creek banks) to high-marsh plateaus (meadows), *Spartina* plants generally decrease in nutrient content (N and P) and size (Ornes and Kaplan 1989; Denno et al. 2005). Although N uptake in *Spartina* is limited under conditions of elevated salinity on the high marsh (Mendelsohn 1979; Webb 1983), salt stress also promotes increases in N-containing osmoprotectants, such as proline, that may benefit phytophagous insects (Cavaliere and Huang 1981; Bacheller and Romeo 1992; Naidoo et al. 1992). However, increased salinity can result in lowered cell turgor pressure (Drake and Gallagher 1984), which subsequently may reduce a phloem feeder's access to stress-elevated nitrogen (Huberty and Denno 2004). Thus, natural variation in the N and P content of *Spartina* occurs in the field presenting potential local problems to herbivores that must meet their nutrient demands.

Prokelisia marginata and *P. dolus* are the most abundant herbivores on Atlantic coastal marshes where they feed exclusively on *S. alterniflora* (Denno et al. 2002). Overall, *P. marginata* is more sensitive to fluctuating plant nitrogen than its congener (Cook and Denno 1994; Denno et al. 2002, 2003). For example, although adults of both wing-dimorphic species select the most N-rich individual plants on which to feed and

oviposit at a small spatial scale, adults of *P. marginata* (mostly flight-capable macropters) are able to rapidly colonize N-enriched stands of *Spartina* in the field at much higher densities than adults of *P. dolus* (mostly flight-less brachypters), a response that ultimately results in much higher densities of *P. marginata* (Denno et al. 2002). Moreover, *P. dolus* appears to withstand N-deficient plants better than *P. marginata*. For instance, previous feeding by *Prokelisia* planthoppers significantly reduces the amino nitrogen content of *Spartina* (Olmstead et al. 1997), an effect that has far greater fitness consequences for *P. marginata* than *P. dolus* (Denno et al. 2000). The ability of *P. dolus* to better compensate for nutrient-deficient phloem sap by increasing its ingestion rate probably underlies its reduced sensitivity to depleted plant nitrogen (Huberty and Denno 2006). Notably, nothing is known about phosphorus limitation in these planthoppers and how it might interact with plant nitrogen to affect their performance.

Laboratory experiment

A 4×4 full factorial experiment was initiated in May 2000 to test the effects of variable N and P subsidies on: (1) the N and P contents of *Spartina* (% dry mass) and both *Prokelisia* species, (2) the biomass and mortality of *Spartina*, and (3) performance (body size and development time) and survival of both planthopper species. Potted *Spartina* seedlings (3–5 per pot and grown from seed) were cultured in a greenhouse in flats (80 pots per flat) exposed to four levels of nitrogen fertilization (0, 10, 30, or 60 g/m²) and four levels of phosphorus addition (0, 2, 6, or 12 g/m²) in a fully crossed design. In all, there were 80 pots per flat, 2 flats per treatment, and 16 treatments for a total of 2,560 pots. To achieve desired treatments, plants in each treatment combination were fertilized every 3 weeks from May to July. Nitrogen was applied as ammonium nitrate (0, 5, 16, or 32 g/flat/application) and phosphorus as triple super phosphate (0, 0.8, 2, or 5 g/flat/application). The macronutrient treatments are hereafter referred to as 0N, 10N, 30N and 60N and 0P, 2P, 6P and 12P for N and P respectively. The range of N and P fertilization rates was chosen to produce a spectrum of *Spartina* nutrient contents that falls within the natural range in the field (Denno et al. 2000).

Effect of nutrient subsidies on Spartina mortality, biomass, and N and P content

Treatment effects on *Spartina* mortality (assessed on 13 July), biomass and nutrient content (N and P) (measured on 26 July) were determined on plants never

exposed to planthoppers. Treatment effects were assessed by measuring plant mortality (number of dead plants per pot / total number of plants per pot) and biomass (gram dry mass per pot) in 30 randomly chosen pots within each of the 16 treatments. Treatment effects on the N and P content (% dry mass) of *Spartina* were determined from 6 randomly chosen pots per treatment. Foliar N content was used as an index of the phloem nitrogen available to planthoppers because the two plant nitrogen variables are related (Youssefi et al. 2000). For biomass and nutrient determination, plants were harvested, oven dried for 48 h at 60°C, and weighed. Subsequently, leaves were ground in a Wiley Mill and analyzed for %N using a Perkin–Elmer 2400 CHN analyzer, and for %P by persulfate digestion (Clesceri et al. 1998). The grand mean of all experimental treatment plants was used to assess the overall N and P content of *Spartina*, a statistic that was used ultimately to assess the mismatch in macronutrient content between plants and planthoppers.

Effect of nutrient subsidies on planthopper survival, performance, and N and P content

Cohorts of 3–5 first instar nymphs of each *Prokelisia* species were placed separately on caged plants (20 initial replicate cohorts per treatment) on 17 July (see Denno et al. 2000 for cage design). Nymphs were obtained from laboratory cultures initiated from ovipositing adults collected from the field site. Severe plant mortality occurred in the 30N and 60N treatments, resulting in the loss of these treatments. Thus, nutrient effects on planthopper performance were assessed using a 2×4 factorial design (0N and 10N, and 0P, 2P, 6P, and 12P). The survival (%), body size (tibia length in millimeter), and development time (days to adult molt), of both *Prokelisia* species were determined at the time of adult emergence. Adult planthoppers of each species were pooled by replicate (all sexes and wing forms) and oven dried prior to analysis for N and P content (% dry mass).

Statistical analyses

Treatment effects on *Spartina* biomass, mortality, %N, and %P were each analyzed as a factorial mixed-model ANOVA with N (four levels) and P (four levels) as fixed effects (SAS 2002). Treatment effects on planthopper survival (arcsin-squareroot transformed proportion) were analyzed for each species using 2×4 mixed-model ANOVA (sexes and wing forms pooled). For each species, treatment effects on body size (tibia length) and development time were each assessed

using a factorial (two levels of N, four levels of P, two wing forms) mixed-model weighted ANOVA. For the analyses of development time and body size, only females were used, because few male brachypters of *P. marginata* emerged. Because multiple insects were placed onto caged plants, pot means for development time and body size were used for analysis, and means were weighted by the number of observations per pot. A mixed-model ANOVA was used to compare the average N and P contents of *Spartina*, *P. dolus*, and *P. marginata* (organisms were pooled across all treatments for this analysis).

Prior to analysis, data were assessed for normality and homogeneity of variances (SAS 2002). If residual variances were heterogeneous, variance partitioning was conducted and the best model was chosen using Bayesian Information Criterion (SAS 2002). Degrees of freedom were calculated using the Kenward–Roger method (SAS 2002). Means comparisons were conducted using a Tukey adjustment for inflated comparison-wise error rates. Means and standard errors are presented as untransformed if data were transformed for analysis.

Field experiment

A 2×2×2 factorial experiment was conducted in May 2000 at Tuckerton to test effects of N fertilization (0, 80 g/m²), P subsidy (0, 80 g/m²), and habitat type (meadow vs tidal creek) on *Spartina* biomass, the population density of both *Prokelisia* species, and the N and P content (% dry mass) of *Spartina* and planthoppers. We employed a randomized complete double-block design with two sites (marsh areas) each containing two habitat types and each of these containing two blocks of the four treatment combinations. Thus, each nutrient treatment combination was replicated 8 times for a total of 32 plots. Fertilizer treatments (Control, +P, +N, +N+P) were randomly assigned to single plots (4 m²) within each block. Nitrogen was applied as ammonium nitrate (0 or 236 g/plot/application) and phosphorus was added as triple super phosphate (0 or 176 g/plot/application) on four dates (9 and 21 May, 4 and 17 June). The range of N and P fertilization rates was selected because it has been shown to produce *Spartina* nutrient contents that occur naturally in the field (Patrick and Delaune 1976; Denno et al. 2000). Treatments were established in both habitat types to ensure the presence of both *Prokelisia* species; *P. marginata* occurs abundantly in low-marsh *Spartina* whereas *P. dolus* predominates in *Spartina* meadows (Denno et al. 1996). Habitat type was included in the design because ambient nutrient availability is greater along tidal creeks than in high-marsh meadows (Ornes and Kaplan 1989).

Effect of nutrient subsidies on Spartina biomass and N and P content

Spartina biomass was determined twice during the course of the experiment, once prior to fertilization (9 May) and again at the end of the experiment (22 July). Live biomass was assessed by clipping all above-ground vegetation within a 0.047-m² wire frame (Denno et al. 2002) and one sample was taken from each plot on each date. *Spartina* leaves were dried at 60°C for 48 h before weighing. The foliar N and P content of *Spartina* (% dry mass) was assessed 6 times (9 and 21 May; 4, 17, and 24 June; and 22 July) during the experiment by taking five snippets (leaves of 5 *Spartina* stems) per plot per date. Samples were oven dried, ground in a Wiley Mill, and the powder analyzed for N and P content. The grand mean of all experimental treatment plants was used to assess the overall N and P content of *Spartina*.

Effect of nutrient subsidies on planthopper density and N and P content

Planthopper density was determined by sampling each plot once on 22 July using a D-vac suction sampler (two 8-s placements of the sampling head per plot) (Denno et al. 2002). Planthoppers were placed into 70% alcohol, sorted to species and wing form, and counted. The N and P content (% dry mass) of the two *Prokelisia* species was determined from samples taken in each plot on 24 June. Insect samples were kept on ice until reaching the laboratory where they were stored at –20°C. Planthoppers were then sorted to species, wing form, and sex and then dried. Three individuals of each species, wing form, and sex were taken from each plot and analyzed for their N and P content.

Statistical analyses

Treatment and habitat effects on *Spartina* biomass were analyzed as an ANCOVA (two levels of N, two levels of P, two habitat types) with initial plant biomass (9 May) as the covariate and site, block and site*block as random effects (SAS 2002). The effect of treatment and habitat on the nutrient content (%N and %P) of *Spartina* was analyzed as a repeated measures factorial (two levels of N, two levels of P, two habitats, six dates) mixed-model analysis of variance, with the site, block and site × block as random effects. A separate mixed-model factorial analysis of variance (two levels of N, two levels of P, two habitats) with site, block, and site × block as random effects was run to assess treatment effects on the N and P content of *Spartina* on June 24, the date on which planthoppers were collected for elemental analysis.

Treatment effects on the density of each *Prokelisia* species (log transformed) were analyzed as factorial (two levels of N, two levels of P, two habitats, two wing-forms, and two sexes) mixed-model ANCOVAs, with plant biomass as the covariate and site, block and site × block as the random effects. A mixed-model ANOVA was used to compare average N and P contents of *Spartina*, *P. dolus*, and *P. marginata* (organisms pooled across all treatments). Prior to analysis, residuals were assessed for normality and homogeneity of variances, variance partitioning was conducted and the best model was chosen using Bayesian Information Criterion, degrees of freedom were calculated using the Kenward–Roger method, and means were compared using a Tukey adjustment for inflated comparison-wise error rates (SAS 2002).

Results

Laboratory experiment

Effect of nutrient subsidies on Spartina mortality, biomass and N and P content

Not surprisingly, increasing N fertilization resulted in a remarkable increase in the N content of *Spartina* that ranged from ~1% N in the 0N treatment to ~7% N in the 60N treatment ($F_{3,126}=843.30$, $P<0.0001$) (Fig. 1a). The addition of P also significantly affected the N content of *Spartina* ($F_{3,130}=12.28$, $P=0.0001$). However, this effect was slight and was apparently driven by the higher than expected N content of *Spartina* in the 10N0P treatment. Fertilizing with either P ($F_{3,131}=158.67$; $P<0.0001$) or N ($F_{3,136}=20.65$; $P<0.0001$) significantly increased the P content of *Spartina* (Fig. 1b). Moreover, there was a significant interactive effect of the N and P subsidies on the P content of *Spartina* such that P uptake was positively influenced by N fertilization ($F_{9,132}=12.19$; $P<0.0001$).

Both N and P subsidies resulted in an increase in *Spartina* biomass, but biomass did not increase linearly with application rate (significant N × P interaction, $F_{9,176}=23.3$; $P<0.0001$) (Fig. 1c). For instance, N fertilization at the 10N level resulted in the greatest *Spartina* biomass, followed by the biomass achieved at the 30N, 60N and 0N treatment levels (significant main effect of N; $F_{3,176}=65.04$; $P<0.0001$). Also, *Spartina* exhibited significantly greater biomass when phosphorus fertilizer was added at rates of 2P, 6P, 12P compared with when it was withheld altogether (0P) (significant main effect of P; $F_{3,176}=75.48$, $P<0.0001$), but there was no significant increase in *Spartina* biomass from the 2P to the 12P treatment levels (Fig. 1c).

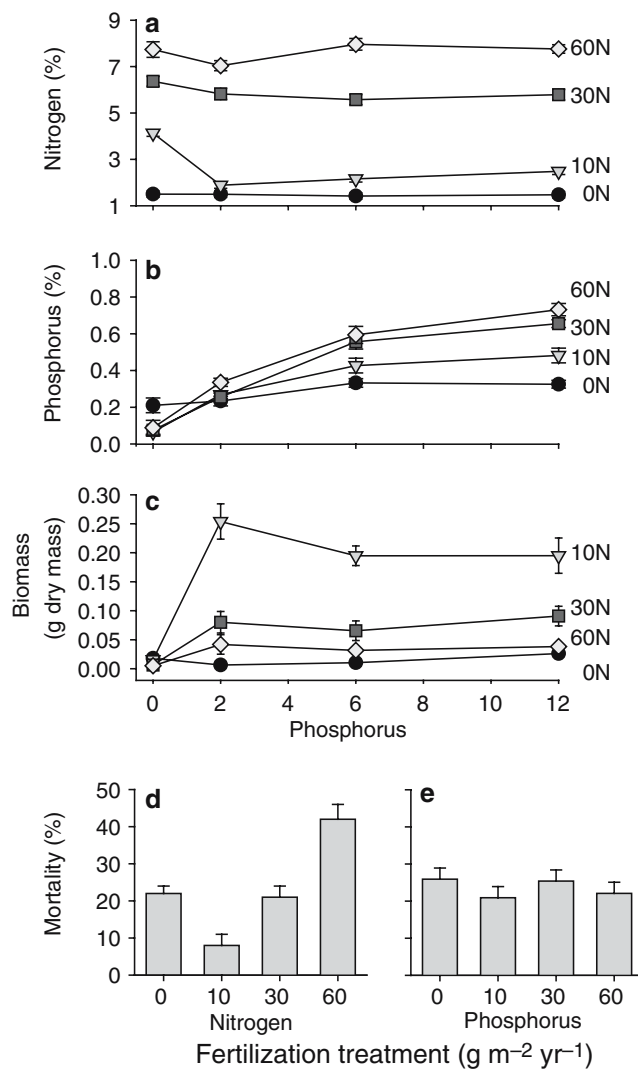


Fig. 1 **a** Nitrogen content (% dry mass), **b** phosphorus content (% dry mass), **c** biomass (g), and **d**, **e** mortality (%) of *Spartina alterniflora* plants grown under laboratory conditions and exposed to four levels of nitrogen (N) fertilization (0N, 10N, 30N, and 60N $\text{g m}^{-2} \text{year}^{-1}$) and four levels of phosphorus (P) addition (0P, 2P, 6P, and 12P $\text{g m}^{-2} \text{year}^{-1}$). Least squares (LS) means \pm SE are shown

Nitrogen addition also resulted in non-linear effects on *Spartina* mortality with the least mortality occurring in the 10N, significantly higher mortality occurring in the 0N and 30N treatments, and the highest mortality arising in the 60N treatment ($F_{3,250}=14.11$; $P<0.0001$) (Fig. 1d). There was no significant effect of P fertilization on *Spartina* mortality ($F_{3,297}=0.57$; $P=0.6$) (Fig. 1e).

Mismatch in N and P content between *Spartina* and *Prokelisia*

There was a striking difference in the N and P content of *Spartina* compared with those for either *Prokelisia*

species. The N content (%) of *Spartina* (2.07 ± 0.09) was 5 times less than that of *P. dolus* (11.87 ± 0.31) and *P. marginata* (12.68 ± 0.34) ($F_{2,110}=304.10$; $P<0.0001$), which did not differ from each other ($P>0.05$). Similarly, the P content (%) of *Spartina* (0.30 ± 0.01) was 3 times less than that of *P. dolus* (0.92 ± 0.02) and *P. marginata* (0.88 ± 0.02) ($F_{2,110}=310.15$; $P<0.0001$), and *P. dolus* had a slightly higher phosphorus content than *P. marginata* ($t_{77,6}=2.1$; $P=0.038$).

Effect of nutrient subsidies on planthopper survival and performance

Overall, data show that both planthopper species are macronutrient limited, that N limitation has greater adverse effects on performance than P limitation, and that *P. dolus* is generally less adversely affected than *P. marginata*. For instance, N fertilization of *Spartina* resulted in enhanced survival ($F_{1,99}=8.31$; $P=0.005$), increased body size ($F_{1,75}=9.37$; $P=0.003$), and reduced development time ($F_{1,75}=10.5$; $P=0.002$) in *P. dolus* (Fig. 2a,c,e). However, for *P. dolus*, P fertilization did not significantly influence its survival ($F_{1,99}=0.71$; $P=0.5$), body size ($F_{3,75}=1.11$; $P=0.3$), or development time ($F_{3,75}=0.19$; $P=0.8$) (Fig. 2b,d,f).

For *P. marginata*, N subsidy also resulted in significant positive effects on survival ($F_{1,90}=15.77$; $P=0.0001$), body size ($F_{1,61}=38.82$; $P<0.0001$), and development time ($F_{1,61}=37.44$; $P<0.0001$) (Fig. 2a,c,e). However, N addition had greater enhancing effects on the survival and performance of *P. marginata* than *P. dolus*. For example, development time was reduced by 8 days for *P. marginata* on N-enriched *Spartina* whereas that for *P. dolus* was reduced by only 4 days. In contrast to *P. dolus*, P fertilization did result in enhanced survival ($F_{3,90}=7.4$; $P=0.002$), increased body size ($F_{3,61}=2.5$; $P=0.06$), and reduced development time ($F_{3,61}=3.64$; $P=0.02$), albeit effects were non-linear for survival and development time (Fig. 2b,d,f). There was no effect of wing form on body size or development time for either species nor was there any interactive effect with either N or P fertilization ($P>0.05$).

Field experiment

Effect of nutrient subsidies on *Spartina* biomass and N and P content

Both N and P fertilization significantly increased the N content of *Spartina* in the field (Fig. 3). Overall, N subsidy increased the N content (%) of *Spartina* from 1.86 ± 0.03 to 2.86 ± 0.30 ($F_{1,124}=472.20$; $P<0.0001$) whereas P fertilization resulted in slight modest

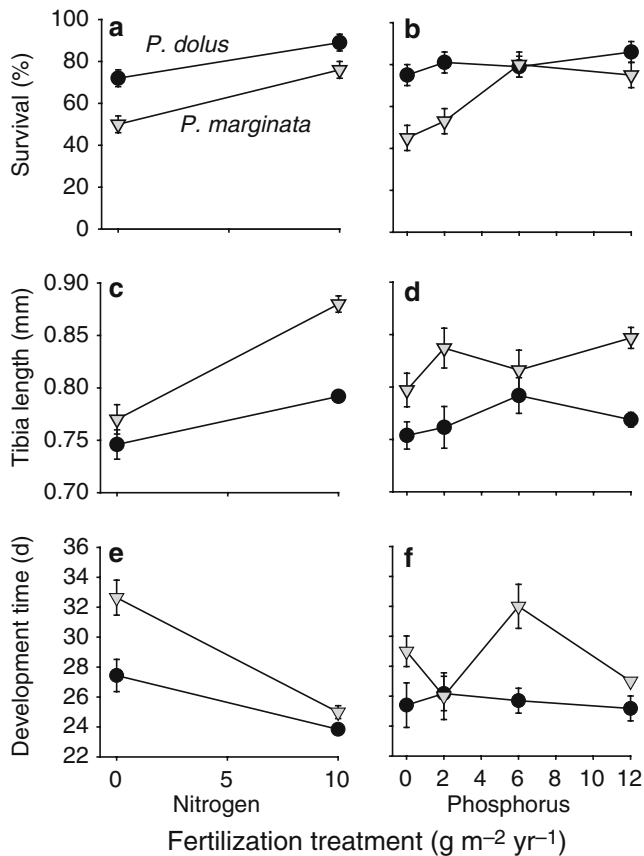


Fig. 2 **a, b** Survival (%), **c, d** body size (tibia length, mm), and **e, f** development time (*d*, days from first instar to adult) of *Prokelisia dolus* (filled circle) and *P. marginata* (filled inverted triangle) raised on plants of *Spartina alterniflora* exposed to (**a, c, e**) two levels of nitrogen fertilization (0N and 10N) and (**b, d, f**) four levels of phosphorus addition (0P, 2P, 6P, and 12P) in the laboratory. LS means \pm SE are shown

increase in N content from 2.27 ± 0.03 to 2.45 ± 0.03 ($F_{1,124}=14.27$; $P=0.0002$) (Fig. 3a,c). Habitat also significantly influenced the N content of *Spartina* ($F_{1,124}=23.9$; $P=0.0001$). On average, the N content (%) of *Spartina* growing in the meadow habitat (2.50 ± 0.03 , Fig. 3a) was significantly greater than that of *Spartina* growing along tidal creeks (2.25 ± 0.03 ; $F_{1,124}=23.68$; $P<0.0001$) (Fig. 3c). On the date planthoppers were sampled (22 July), the N content (%) of *Spartina* was higher in plots receiving N addition (3.1 ± 0.08) than in control plots (2.1 ± 0.08 ; $F_{1,23}=65.97$; $P<0.0001$) (Fig. 3e). Likewise, the N content (%) of *Spartina* was greater in plots fertilized with P (2.7 ± 0.08) compared with controls (2.4 ± 0.08 ; $F_{1,23}=9.63$; $P=0.005$) (Fig. 3e). On this date there was no difference in the N content of plants growing in meadow and tidal creek habitats ($F_{1,23}=0.37$; $P=0.5$).

We also found a significant interactive effect of fertilization treatment, date, and habitat on the P content

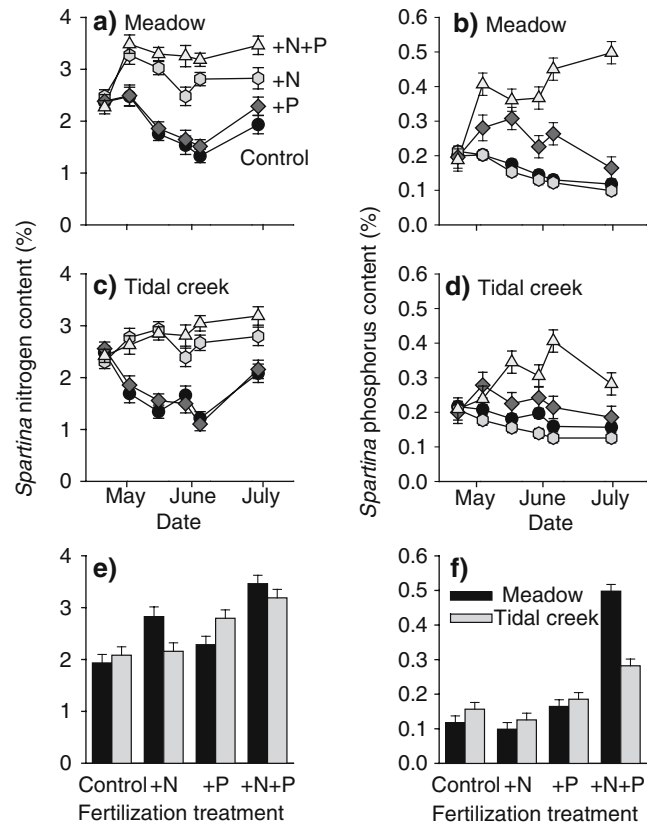


Fig. 3 Effect of nitrogen (N) and phosphorus (P) fertilization treatments (Control, +N, +P, and +N+P) on the N content (% dry mass) of *Spartina alterniflora* growing in **a, b** high-marsh meadow habitat, **c, d** low-marsh tidal creek habitat in May, June and July, and **e, f** in both habitats on 22 July 2002 when planthoppers were sampled at Tuckerton, New Jersey. LS means \pm SE are shown

of *Spartina* ($F_{4,94,3}=2.65$; $P=0.03$) (Fig. 3b,d). In control plots and in N-subsidized plots (+N), the P content of *Spartina* declined from May to July in both habitats, and there was no difference in the P content of *Spartina* in these two treatments. By contrast, in the meadow habitat, there was a significant increase in the P content of *Spartina* in plots receiving a phosphorus subsidy (+P) and a synergistic seasonal increase in P content in plots receiving both N and P subsidies (+N+P) compared with controls (Fig. 3b). In the tidal creek habitat, although phosphorus fertilization resulted in an increase in the P content of *Spartina*, the seasonal increase in P content in response to the +N+P treatment seen in meadow *Spartina* (Fig. 3b) was not as evident in tidal creek plants (Fig. 3d). The difference in the P content of *Spartina* between plants in the meadow and tidal creek habitats that received both N and P subsidies was particularly evident on the date planthoppers were sampled, when meadow plants contained twice as much foliar phosphorus as those along tidal creeks ($F_{1,24}=16.8$; $P=0.0004$) (Fig. 3f).

There was a significant interactive effect of the fertilization treatments and habitat on the aboveground biomass of *Spartina* ($F_{1,17,3}=5.94$; $P=0.03$) (Fig. 4a). Nitrogen fertilization resulted in a significant increase in *Spartina* biomass in the meadow habitat, a response that did not occur in plants growing in the tidal creek. Neither P fertilization nor the application of both N and P significantly altered *Spartina* biomass in the meadow habitats relative to controls. However, the

biomass of plants receiving the P subsidy was significantly less than those fertilized with only N.

Mismatch in N and P content between Spartina and Prokelisia

The N content (%) of *Spartina* growing in the field (2.06 ± 0.16) was approximately 5 times less than that for either *P. dolus* (10.91 ± 0.06) or *P. marginata* (10.79 ± 0.10) ($F_{2,75,4}=1334$; $P<0.0001$), and more than 3 times less in P content (0.23 ± 0.02) than either *P. dolus* (0.71 ± 0.01) or *P. marginata* (0.75 ± 0.01) ($F_{2,77,2}=221$, $P<0.0001$).

Effect of nutrient subsidies on planthopper density

Although both *Prokelisia* species responded with population increases on N-subsidized *Spartina*, *P. marginata* exhibited a relatively stronger response than *P. dolus* (Fig. 4b–e). For example, nitrogen fertilization promoted a significant increase in the density of *P. dolus* ($F_{1,55}=30.47$; $P<0.0001$), and there was a greater increase in the density of macropters than flightless brachypters (N \times wing form; $F_{1,54,9}=6.49$; $P=0.01$) (Fig. 4b, c). The density of *P. dolus* was not affected by P fertilization ($F_{1,55}=0.08$; $P=0.8$). Overall, *P. dolus* was found in greater densities in the meadow habitat than on tidal creek *Spartina* ($F_{1,55}=5.46$; $P=0.02$) (Fig. 4b–c).

For *P. marginata*, macropters selectively colonized N-subsidized *Spartina*, a density response not observed for flightless brachypters (N \times wing form; $F_{1,96}=20.06$; $P<0.0001$), and the increase in macropter density on N-subsidized *Spartina* was greater in the tidal creek than the meadow habitat (N \times wing form \times habitat; $F_{1,96}=4.11$; $P=0.046$) (Fig. 4d, e). There was no density response of *P. marginata* to P-subsidized *Spartina* in either habitat ($F_{1,96}=0.19$; $P=0.7$). For both planthopper species, there was no difference in the response of males and females to fertilized plants, and plant biomass was not a significant covariate ($P>0.05$).

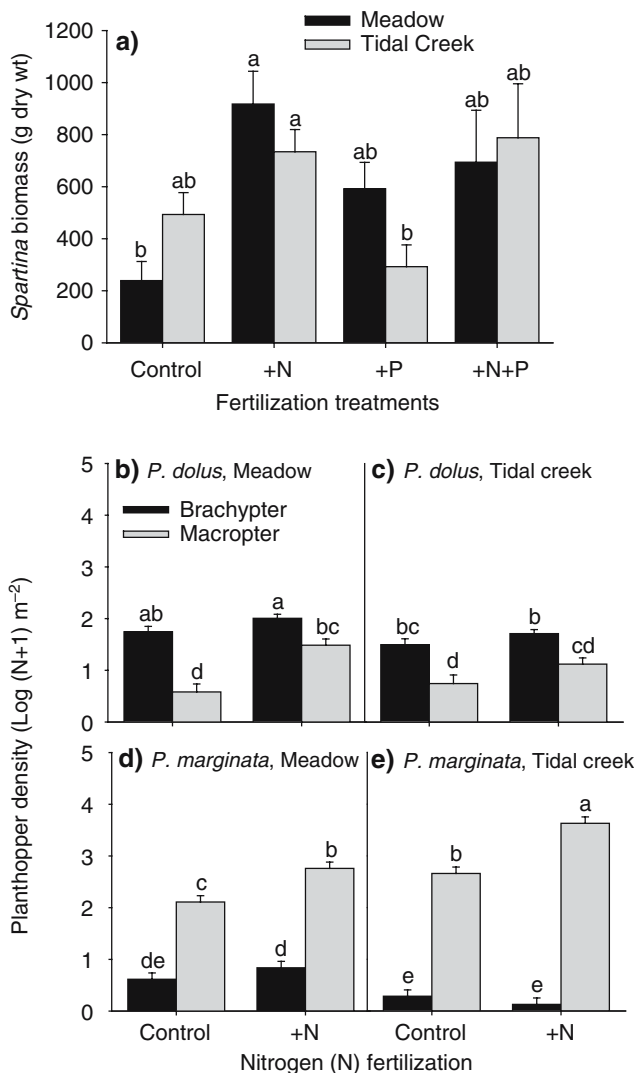


Fig. 4 Effect of nitrogen (N) and phosphorus (P) fertilization treatments (Control, +N, +P, and +N+P) on **a** the biomass (g dry mass m⁻²) of *Spartina alterniflora* growing in high-marsh meadow (black bars) and low-marsh tidal creek (shaded bars) habitats at Tuckerton, New Jersey. Effect of the same nutrient treatments on the density [$\log(N + 1) m^{-2}$] of the adult wing forms: brachypters (black bars) and macropters (shaded bars) of *Prokelisia dolus* in **b** meadow and **c** tidal creek habitats, and *P. marginata* in **d** meadow and **e** tidal creek habitats on a salt marsh at Tuckerton, New Jersey. LS means \pm SE with the same letter are not significantly different

Discussion

Nutrient limitation in *Spartina alterniflora*

Spartina responded vigorously to nitrogen fertilization in both the laboratory and field. In the laboratory, high rates of nitrogen augmentation (30N and 60N) resulted in remarkably high nitrogen content of *Spartina* (~7% N), but also promoted severe plant mortality, suggesting that excess nitrogen has a toxic effect. The mechanism underlying *Spartina* toxicity under high

nitrogen-input conditions may be ammonia accumulation as has been shown in many plant species (Britto et al. 2001). Furthermore, the greatest increase in plant biomass occurred at a moderate level of nitrogen addition and not at the highest fertilization levels, further suggesting the adverse effects of excess nitrogen input. In the field, nitrogen fertilization resulted in increased *Spartina* biomass in the meadow habitat but not along tidal creeks. Moreover, the N content of field plants, particularly those in the meadow habitat, was enhanced by the application of both N and P, suggesting that nitrogen uptake is influenced by ambient levels of phosphorus.

Phosphorus fertilization in the laboratory did not result in dramatic changes in the elemental content or biomass of *Spartina*. Although the P content of *Spartina* increased with P fertilization, a greater response occurred when both N and P were added to growing *Spartina*, suggesting that nitrogen facilitates phosphorus uptake. Plant biomass did increase with P addition, but the increase occurred only when a comparison was made to plants deprived of P altogether. Phosphorus fertilization had only minor effects on *Spartina* plants in the field as well. Phosphorus fertilization alone resulted in a slight increase in the P content of *Spartina* and no increase in plant biomass. Only when phosphorus was applied along with nitrogen did the P content of *Spartina* increase, a response that was more evident in meadow *Spartina*. Notably, P fertilization did not affect the biomass of *Spartina* in either habitat.

Overall, our data suggest that *Spartina* is strongly nitrogen limited and that evidence for phosphorus limitation is weak. Previous research on other Atlantic coastal marshes also demonstrates greater N than P limitation in *Spartina* (Patrick and Delaune 1976; Smart and Barko 1980; Broome et al. 1983; Osgood and Zieman 1993). Phosphorus limitation is much less probable given that salt-marshes have been advocated as long-term phosphorus sinks (Billen et al. 1991; House et al. 1998). That the greatest effects of phosphorus addition on the P content of *Spartina* were seen when both nitrogen and phosphorus were applied compared to when phosphorus was applied alone, suggests that nitrogen demands are more crucial and must be met first (Patrick and Delaune 1976).

In the field, *Spartina* growing in high-marsh habitats exhibited a greater growth response to nitrogen fertilization compared with plants growing in the tidal creek habitat, a response that has been documented previously (Broome et al. 1975, 1983; Mendelsohn 1979; Webb 1983). This result is consistent with reports in the literature that *Spartina* is more nitrogen limited in high marsh habitats that incur less tidal subsidy of nutrients and face problems of nutrient uptake under

salt stressed conditions (Webb 1983; Gallagher et al. 1988; Ornes and Kaplan 1989; House et al. 1998; Osgood and Zieman 1998).

Nutrient limitation and its consequences for *Prokelisia* planthoppers

The N and P content of *S. alterniflora* is remarkably low compared with the body N and P content of both *Prokelisia* species, suggesting that both macronutrients may limit planthopper performance and adversely influence their density. When *P. dolus* and *P. marginata* were raised on plants with an enriched nitrogen signature, they survived better, grew to a larger size, and developed more rapidly than when they developed on nitrogen-deficient plants. Moreover, both species achieved significantly higher densities on nitrogen-subsidized plants in the field. Although both planthopper species responded positively to nitrogen-fertilized *Spartina*, *P. marginata* experienced greater fitness penalties than *P. dolus* on nitrogen-deficient plants. For *P. marginata*, its survival declined by 50%, its body size was reduced 12%, and its development time to adult was extended by 8 days when reared on nitrogen-deficient compared with nitrogen-enriched *Spartina*. In contrast, *P. dolus* suffered only 25% reduction in survival, a 6% decrease in body size, and a 4-day developmental delay when raised on the same nitrogen-poor plants. Notably, migratory aphids, crickets, and corixids are also less tolerant of nutrient stress than their flightless counterparts (Young 1965; Tanaka 1993; Zera and Denno 1997; Dixon 1998).

Phosphorus limitation was not as severe as nitrogen limitation for *P. marginata*, and was not detected at all in *P. dolus*. Nonetheless, *P. marginata* did show a significant increase in survival and body size on P-enhanced plants compared with controls in the laboratory, but like *P. dolus* failed to show a positive density response to P-fertilized *Spartina* in the field. Given the discrepancy in P content between *Spartina* and *Prokelisia*, we fully expected P limitation to have very adverse effects on planthopper performance and growth, as has been observed in other invertebrates (Urabe and Watanabe 1992; DeMott et al. 1998; Sterner and Schulz 1998; Elser et al. 2001; Makino et al. 2002; Urabe et al. 2002; Xenopoulos et al. 2002). However, the relative mismatch in N content between planthoppers and their *Spartina* host plant was greater (5 times greater N content) than that for P (3 times greater P content), suggesting that N may be more inherently limiting than P, at least for these two sap-feeders.

The tempered response of *P. dolus* to N- and P-deficient *Spartina* is probably due to its greater investment

in feeding musculature and hence its ability to compensate for nutrient deficiencies by increasing its ingestion rate of phloem (Denno et al. 2000; Huberty and Denno 2006). 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 (modified esophagus), cell sap is ingested. The cibarial pump is driven by a series of dilator muscles that insert on the interior of the face, and face size is positively related to the cross-sectional mass and thus the power of the cibarial muscles to ingest cell sap (Backus 1985; Huberty and Denno 2006). For *Prokelisia* planthoppers, *P. dolus* has a much broader face and commitment to subtending cibarial musculature than *P. marginata* (Denno et al. 2000; Huberty and Denno 2006). As a consequence, *P. dolus* is more capable than *P. marginata* of increasing food uptake in response to any reductions in plant nitrogen, and this probably underlies its reduced sensitivity to altered plant nutrition. Overall, data suggest that species-specific differences in cibarial pump investment and subsequent ingestion capacity dictate responses to N and P limitation for both planthopper species. Moreover, when both planthopper species feed on the same plant and induce reductions in plant nitrogen (Olmstead et al. 1997), it is *P. dolus* with its greater commitment to cibarial musculature that better tolerates deteriorating plant quality and thus owns the competitive edge (Denno et al. 2000).

The two *Prokelisia* species have evolved very different strategies for coping with nutrient deficiencies in their host plant. Data suggests that *P. dolus* uses compensatory feeding, whereas *P. marginata* has evolved a dispersal strategy that allows it to effectively track spatial changes in host plant quality (Denno et al. 2002, 2003; Huberty and Denno 2006). In fact, all data point to a phenotypic trade-off between the two strategies with a greater commitment to flight musculature in *P. marginata* and a greater investment in the musculature associated with enhanced ingestion in *P. dolus* (Huberty and Denno 2006). When its option of dispersal is eliminated, and *P. marginata* is confined on nutrient-deficient host plants, its performance is drastically affected, far more so than that of *P. dolus*. Thus, despite similar body nitrogen and phosphorus contents, and similar mismatches in N and P composition compared with *Spartina*, the two *Prokelisia* species incur the penalties of depleted host-plant nutrition quite differently. Although compensatory feeding (Raubenheimer and Simpson 1993; Dixon 1998; Kingsolver and Woods 1998; Brodbeck et al. 1996; Lavoie and Oberhauser 2004) and dispersal (McNeill and Southwood 1978; Prestidge and McNeill 1982) have

been discussed as separate mechanisms for meeting nutrient demands in other insect herbivores, possible constraints that one strategy places on the other have only recently emerged (Huberty and Denno 2006). Our research underscores the importance of interfacing an understanding of herbivore life-history strategies with ecological stoichiometry in order to interpret the consequences of macronutrient limitation on herbivore performance and population dynamics.

Acknowledgments Larry Douglass, Irv Forseth, Bill Lamp, Libby Marschall, Charlie Mitter, and two anonymous reviewers provided comments on earlier drafts of this article, and we hope to have incorporated their many insightful suggestions. We would like to thank Jim Elser and Marcia Kyle for providing laboratory space and assistance with the phosphorus analyses and Irv Forseth for assistance with the nitrogen analyses. This research was supported by an EPA STAR Graduate Fellowship to A.F.H. and NSF Grants DEB-9903601 and DEB-0313903 to R.F.D. These experiments comply with the current laws of the USA.

References

- Andersen T (1997) Pelagic nutrient cycles: herbivore as sources and sinks. Springer, Berlin Heidelberg New York
- Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47:817–844
- Ayres MP, Wilkens RT, Ruel JJ, Lombardero MJ, Vallery E (2000) Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi. *Ecology* 81:2198–2210
- Bacheller JD, Romeo JT (1992) Biotic and abiotic stress effects on nitrogen chemistry in the salt marsh cordgrass *Spartina alterniflora* (Poaceae). *Chemoecology* 3:74–80
- Backus EA (1985) Anatomical and sensory mechanisms of leafhopper and planthopper feeding behavior. In: Nault LR, Rodriguez JG (eds) *The leafhoppers and planthoppers*. Wiley, New York, pp 163–194
- Bentz J, Townsend AM (2001) Leaf element content and utilization of maple and elm as hosts by the potato leafhopper (Homoptera: Cicadellidae). *Environ Entomol* 30:533–539
- Billen G, Lancelot C, Meybeck M (1991) Nitrogen, phosphorus, and silica retention along the aquatic continuum from land to ocean. In: Mantoura RFC, Martin JM, Wollast R (eds) *Ocean margin processes in global change*. Wiley, Chichester
- Britto DT, Siddiqi MY, Glass ADM, Kronzucker HJ (2001) Futile transmembrane NH_4^+ cycling: a cellular hypothesis to explain ammonium toxicity in plants. *PNAS* 98:4255–4258
- Brodbeck BV, Andersen PC, Mizell RFI (1996) Utilization of primary nutrients by the polyphagous xylophage, *Homalodisca coagulata*, reared on a single host species. *Arch Insect Biochem Physiol* 32:65–83
- Broome SW, Woodhouse WW Jr, Seneca ED (1975) The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina: II. The effects of N, P, and Fe fertilizers. *Soil Sci Soc Am Proc* 39:301–307
- Broome SW, Seneca ED, Woodhouse WW Jr (1983) The effects of source, rate, and placement of nitrogen and phosphorus fertilizers on growth of *Spartina alterniflora* transplants in North Carolina. *Estuaries* 6:212–226
- Busch JW, Phelan L (1999) Mixture models of soybean growth and herbivore performance in response to nitrogen-

- sulphur–phosphorus nutrient interactions. *Ecol Entomol* 24:132–145
- Cavaleri AJ, Huang AHC (1981) Accumulation of proline and glycinebetaine in *Spartina alterniflora* Loisel. in response to NaCl and nitrogen in the marsh. *Oecologia* 49:224–228
- Chen YH, Welter SC (2002) Abundance of a native moth *Homoiosoma electellum* (Lepidoptera: Pyralidae) and activity of indigenous parasitoids in native and agricultural sunflower habitats. *Environ Entomol* 31:626–636
- Clancy KM, King RM (1993) Defining the western spruce budworm's nutritional niche with response surface methodology. *Ecology* 74:442–454
- Clesceri LS, Greenberg AE, Eaton AD (1998) Standard methods for the examination of water and wastewater. American Public Health Association, New York
- Coll M, Guershon M (2002) Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annu Rev Entomol* 47:267–297
- Cook A, Denno RF (1994) Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense, and host plant specialization. In: Denno RF, Prefect TJ (eds) *Planthoppers: their ecology and management*. Chapman and Hall, New York, pp 114–139
- De Bruyn L, Scheirs J, Verhagen R (2002) Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia* 130:594–599
- DeMott WR, Gulati RD, Siewertsen K (1998) Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnol Oceanogr* 43:1147–1161
- Denno RF, Fagan WF (2003) Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84:2522–2531
- Denno RF, Peterson MA (2000) Caught between the devil and the deep blue sea; mobile planthoppers elude natural enemies and deteriorating host plants. *Am Entomol* 46:95–109
- Denno RF, Roderick GK, Peterson MA, Huberty AF, Doebel HG, Eubanks MD, Losey JE, Langellotto GA (1996) Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecol Monog* 66:389–408
- Denno RF, Peterson MA, Gratton C, Cheng J, Langellotto GA, Huberty AF, Finke DL (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* 81:1814–1827
- Denno RF, Gratton C, Peterson MA, Langellotto GA, Finke DL, Huberty AF (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458
- Denno RF, Gratton C, Dobel H, Finke DL (2003) Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84:1032–1044
- Denno RF, Lewis D, Gratton C (2005) Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Ann Zool Fenn* 42:295–311
- Dixon AFG (1998) *Aphid ecology*. Chapman & Hall, London
- Downing JA (1997) Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. *Biogeochem* 37:237–252
- Drake BG, Gallagher JL (1984) Osmotic potential and turgor maintenance in *Spartina alterniflora* Loisel. *Oecologia* 62:368–375
- Elser JJ, Dobberfuhr DR, MacKay NA, Schampel JH (1996) Organism size, life history, and N:P stoichiometry. *Bioscience* 46:674–684
- Elser JJ, Fagan WF, Denno RF, Dobberfuhr DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, Siemann EH, Sterner RW (2000a) Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–580
- Elser JJ, Sterner RW, Gorokhova E, Fagan WF, Markow TA, Cotner JB, Harrison JF, Hobbie SE, Odell GM, Weider LJ (2000b) Biological stoichiometry from genes to ecosystems. *Ecol Lett* 3:540–550
- Elser JJ, Hayakawa K, Urabe J (2001) Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. *Ecology* 82:898–903
- van Emden HF (1966) Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* (Hemiptera: Aphididae) on brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomol Exper Appl* 9:444–460
- Fagan WF, Seimann E, Mitter C, Denno RF, Huberty AF, Woods HA, Elser JJ (2002) Nitrogen in insects: implications for trophic complexity and species diversification. *Am Nat* 160:784–802
- Gallagher JL, Somers GF, Grant DM, Seliskar DM (1988) Persistent differences in two forms of *Spartina alterniflora*: a common garden experiment. *Ecology* 69:1005–1008
- Hassett RP, Cardinale B, Stabler LB, Elser JJ (1997) Ecological stoichiometry of N and P in pelagic ecosystems: comparison of lakes and oceans with emphasis on the zooplankton–phytoplankton interaction. *Limnol Oceanogr* 41:648–662
- Hessen DO, Lyche A (1991) Inter- and intraspecific variations in zooplankton element composition. *Arch Hydrobiol* 121:343–353
- House WA, Jickells TD, Edwards AC, Praska KE, Denison EH (1998) Reactions of phosphorus with sediments in fresh and marine waters. *Soil Use Manage* 14:139–146
- Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85:1383–1398
- Huberty AF, Denno RF (2006) Trade-off in investment between dispersal and ingestion capability in phytophagous insects and its ecological implications. *Oecologia*. DOI 10.1007/s00442-006-0371-x
- Janssen JAM (1994) Impact of the mineral composition and water content of excised maize leaf sections on fitness of the African armyworm, *Spodoptera exempta* (Lepidoptera: Noctuidae). *Bull Entomol Res* 84:233–245
- Kainulainen P, Holopainen J, Palomaki V, Holopainen T (1996) Effects of nitrogen fertilization on secondary chemistry and ectomycorrhizal state of Scots pine seedlings and on growth of grey pine aphid. *J Chem Ecol* 22:617–636
- Kerslake JE, Woodin SJ, Hartely SE (1998) Effects of carbon dioxide and nitrogen enrichment on a plant–insect interaction: the quality of *Calluna vulgaris* as a host for *Operophtera brumata*. *New Phytol* 140:43–53
- Kingsolver JG, Woods HA (1998) Interactions of temperature and dietary protein concentration in growth and feeding of *Manduca sexta* caterpillars. *Physiol Entomol* 23:354–359
- Lavoie B, Oberhauser KS (2004) Compensatory feeding in *Danaus plexippus* (Lepidoptera:Nymphalidae) in response to variation in host plant quality. *Environ Entom* 33:1062–1069
- Makino W, Urabe J, Elser JJ, Yoshimizu C (2002) Evidence of phosphorus-limited individual and population growth of *Daphnia* in a Canadian Shield lake. *Oikos* 96:197–205
- Mattson WJ (1980) Herbivory in relation to plant nitrogen content. *Annu Rev Ecol Syst* 11:119–161
- McNeill S, Southwood TRE (1978) The role of nitrogen in the development of insect/plant relationships. In: Harborne JB (ed) *Biochemical aspects of plant and animal coevolution*. Academic, New York, pp 77–98
- Mendelssohn IA (1979) Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. *Ecology* 60:574–584

- Mendelssohn IA, Morris JT (2000) Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer, Boston, pp 59–80
- Naidoo G, McKee KL, Mendelssohn IA (1992) Anatomical and metabolic responses to waterlogging and salinity in *Spartina alterniflora* and *S. patens* (Poaceae). *Am J Bot* 79:765–770
- Olmstead KL, Denno RF, Morton TC, Romeo JT (1997) Influence of *Prokelisia* planthoppers on amino acid composition and growth of *Spartina alterniflora*. *J Chem Ecol* 23:303–321
- Ornes WH, Kaplan DI (1989) Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. *Mar Ecol Prog Ser* 55:63–72
- Osgood DT, Zieman JC (1993) Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. *Estuaries* 16:815–826
- Osgood DT, Zieman JC (1998) The influence of subsurface hydrology on nutrient supply and smooth cordgrass (*Spartina alterniflora*) production in a developing barrier island marsh. *Estuaries* 21:767–783
- Patrick WH Jr, Delaune RD (1976) Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Est Coast Mar Sci* 4:59–64
- Perkins MC, Woods HA, Harrison JF, Elser JJ (2004) Dietary phosphorus affects the growth of larval *Manduca sexta*. *Arch Insect Biochem Phys* 55:153–168
- Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3–15
- Popp MC, Wilkinson RC, Jokela EJ, Hardin RB, Phillips TW (1989) Effects of slash pine phloem nutrition on the reproductive performance of *Ips calligraphus* (Coleoptera: Scolytidae). *Environ Entomol* 18:795–799
- Prestidge RA, McNeill S (1982) The role of nitrogen in the ecology of grassland Auchenorrhyncha (Homoptera). *Symp Br Ecol Soc* 22:257–281
- Raubenheimer D, Simpson SJ (1993) The geometry of compensatory feeding in the locust. *Anim Behav* 45:953–964
- Richardson SJ, Press MC, Parsons AN, Hartely SE (2002) How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath. *J Ecol* 90:544–556
- Rossi AM, Strong DR (1991) Effects of host-plant nutrition on the preference and performance of laboratory populations of *Carneocephala floridana* (Homoptera: Cicadellidae). *Environ Entomol* 20:1349–1355
- Rossi AM, Brodbeck BV, Strong DR (1996) Response of xylem-feeding leafhopper to host plant species and plant quality. *J Chem Ecol* 22:653–671
- Salim M, Saxena RC (1991) Nutritional stresses and varietal resistance in rice: effects on whitebacked planthopper. *Crop Sci* 31:797–805
- SAS (2002) SAS/STAT users guide, release 8.2. SAS Institute, Cary, NC
- Schade JD, Kyle M, Hobbie SE, Fagan WF, Elser JJ (2003) Stoichiometric tracking of soil nutrients by a desert insect herbivore. *Ecol Lett* 6:96–101
- Skinner RH, Cohen AC (1994) Phosphorus nutrition and leaf age effects on sweetpotato whitefly (Homoptera: Aleyrodidae) host selection. *Environ Entomol* 23:693–698
- Slansky F, Feeny P (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecol Monog* 47:209–228
- Smart RM, Barko JW (1980) Nitrogen nutrition and salinity tolerance of *Distichlis spicata* and *Spartina alterniflora*. *Ecology* 61:630–638
- Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton
- Sterner RW, Schulz KL (1998) Zooplankton nutrition: recent progress and reality check. *Aquat Ecol* 33:1–19
- Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge
- Tanaka S (1993) Allocation of resources to egg production and flight muscles in a wing dimorphic cricket, *Modicogryllus confirmatus*. *J Insect Physiol* 39:493–498
- Urabe J, Watanabe Y (1992) Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnol Oceanog* 37:244–251
- Urabe J, Clasen J, Sterner RW (1997) Phosphorus limitation of *Daphnia*: is it real?. *Limnol Oceanog* 42:1436–1443
- Urabe J, Kyle M, Makino W, Yoshida T, Andersen T, Elser JJ (2002) Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. *Ecology* 83:619–627
- Vanni MJ, Flecker AS, Hood JM, Headworth JL (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecol Lett* 5:285–293
- Waring GL, Cobb NS (1992) The impact of plant stress on herbivore population dynamics. In: Bernays EA (eds) Insect-plant interactions. CRC Press, Boca Raton, pp 167–226
- Webb JW (1983) Soil water salinity variations and their effects on *Spartina alterniflora*. *Contrib Mar Sci* 26:1–13
- White TCR (1993) The inadequate environment: nitrogen and the abundance of animals. Springer, Berlin Heidelberg New York
- Xenopoulos MA, Frost PC, Elser JJ (2002) Joint effects of UV radiation and phosphorus supply on algal growth rate and elemental composition. *Ecology* 83:423–435
- Young EC (1965) Flight muscle polymorphism in British Corixidae: ecological observations. *J Anim Ecol* 34:353–390
- Youssefi F, Brown PH, Weinbaum SA (2000) Relationship between tree nitrogen status, xylem, and phloem sap amino acid concentrations, and apparent soil nitrogen uptake by almond trees (*Prunus dulcis*). *J Hortic Sci Biotechnol* 75:62–68
- Zera AJ, Denno RF (1997) Physiology and ecology of dispersal polymorphism in insects. *Annu Rev Entomol* 42:207–231