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## Nitrogen effects on an interaction chain in a salt marsh community

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**Abstract** Nutrients can structure communities by influencing both plant interactions and plant herbivore interactions, though rarely do studies integrate these processes. In this study we examined how nitrogen fertilization influenced (1) the positive interaction between the marsh elder, *Iva frutescens*, and the black rush, *Juncus gerardi*, and (2) the quality of *Iva* as a host plant for the aphid, *Uroleucon ambrosiae*. Previous studies have shown that by mitigating soil salt accumulation and hypoxia, *Juncus* is essential to the survival of *Iva* and its aphid herbivore at mid-marsh elevations. To address the effects of nitrogen on this interaction, we compared fertilized and unfertilized *Iva* plants subject to *Juncus* removal and control treatments in the field. Additionally, we measured the monthly population growth rates of aphids transplanted onto these *Iva* plants. *Iva* leaf biomass and flower number results indicated that fertilizing *Iva* eliminated its dependence upon *Juncus*, such that fertilized plants grown without *Juncus* were not different from unmanipulated plants. Aphid monthly population growth rates through mid-summer revealed that fertilization also eliminated the indirect dependency of aphids on *Juncus*, so that aphid growth rates on fertilized *Iva* without *Juncus* neighbors were similar to rates on unmanipulated *Iva*. Results also indicated that fertilizing *Iva* grown with *Juncus* increased *Iva* size, potentially enabling these plants to support larger aphid populations. Our results suggest that only

under conditions of nitrogen limitation are the positive effects of *Juncus* essential to the mid-marsh persistence of *Iva* and its aphid herbivore. Furthermore, we found that nitrogen effects on aphid populations may arise not only from a direct effect of nutrients on *Iva* size but also through the indirect effects of nitrogen on the interaction between *Juncus* and *Iva*. We argue that studies integrating processes occurring both within and between trophic levels, are important to fully understanding the community-wide effects of nutrients.

**Key words** Nitrogen · Salt marsh · Positive interaction · Insect herbivory · Trophic interaction

### Introduction

Nutrient availability has gained the attention of terrestrial community ecologists because of its tremendous potential to influence plants and higher trophic levels. Nutrients can affect the patterns of plant community diversity (Huston 1979, 1994; Goldberg and Miller 1990) and succession (Tilman 1988; Berendse and Elberse 1990) through the mediation of both competitive (Wilson and Keddy 1986; Tilman 1988; McGraw and Chapin 1989; Levine et al. 1998) and facilitative (Chapin et al. 1994; Callaway 1995) interactions. In addition, studies have shown that by increasing the nutrient content of host plants, nutrients can have important positive effects on the abundance and distribution of insect herbivores (Southwood 1973; Onuf et al. 1977; Slansky and Feeny 1977; Dixon 1985; Bryant et al. 1987; Bowdish and Stiling 1998).

Though ecologists agree that nutrients can dictate both plant interactions and plant-herbivore interactions, few experimental studies have made a link between nutrients and these intra-trophic and inter-trophic level processes. Specifically, when nutrients mediate plant competitive and facilitative interactions, they influence the physiology, abundance, and diversity of plants (Tilman 1988), all of which are likely to have important

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consequences for herbivores. Understanding the degree to which these indirect effects of nutrients on herbivores operate in conjunction with more direct effects of nutrients on plant quality is important for predicting the community-wide consequences of nutrient availability.

In this paper, we explore the consequences of nitrogen addition to the interactions among members of a salt marsh community. Specifically, we examined the importance of nitrogen to the positive interaction between the black rush, *Juncus gerardi* Loisel. and the marsh elder, *Iva frutescens* L., and to the population growth rate of the aphid *Uroleucon ambrosiae* (Thomas), a common herbivore of *Iva* (Bertness and Hacker 1994; Hacker and Bertness 1995, 1996). This is an ideal system to examine the community-wide consequences of nitrogen limitation, because the interactions among these species are well studied (Bertness and Hacker 1994; Hacker and Bertness 1995, 1996; Hacker and Gaines 1997).

In New England salt marshes, the composite shrub, *Iva*, ranges from the terrestrial border of the marsh to mid-marsh tidal elevations. Except at the terrestrial edge of the marsh, high soil salinity and low soil oxygen stunt the growth of *Iva* (Bertness and Hacker 1994). In this habitat, the surrounding matrix of the more salt tolerant *Juncus* is critical to the survival of these stunted *Iva*; dense *Juncus* vegetation shades soil surfaces, and thereby prevents severe evaporation of soil porewater and salt accumulation, which is detrimental to *Iva* (further details of the mechanism described in Bertness and Hacker 1994; Hacker and Bertness 1995). Additionally, *Juncus* aerates its rhizosphere with aerenchyma tissue, which indirectly oxygenates the soil surrounding the roots of *Iva* (general mechanism described in Armstrong 1967; Schat 1984; Braendle and Crawford 1987; Hacker and Bertness 1995; Callaway and King 1996; for more detail about the consequences of soil anoxia for marsh plants, see Howes et al. 1981). The aphid, *Uroleucon*, feeds exclusively on *Iva* and is also dependent on *Juncus* for its survival, though the relationship is indirect. Experimental removal of *Juncus* dramatically reduces the quality of *Iva* as a host so that aphid populations are unable to persist on these plants (Hacker and Bertness 1996).

We believe that understanding the importance of nitrogen to the positive interactions among *Juncus*, *Iva*, and aphids is significant for several reasons. First, salt marshes in New England are well known to be severely nitrogen limited (Valiela and Teal 1974; Jefferies et al. 1979; Adam 1993), yet few experimental studies have examined the consequences of this limitation at the community level (but see Jefferies 1977; Vince et al. 1981; Levine et al. 1998). Second, nitrogen has been shown to increase the salinity tolerance of various marsh species (Jefferies 1977, 1980; Jefferies et al. 1979; Cavalieri 1983; Adam 1993). This result suggests that if nitrogen influences the salt tolerance of *Iva*, it could mediate the dependence of *Iva* on *Juncus*. This is intriguing because of the possible importance of nitrogen to the outcome of positive plant interactions, an

unexplored relationship (see Callaway 1995 for review). Our third motivation for exploring the effect of nitrogen on these marsh plants is that the interaction between *Juncus* and *Iva* has known population consequences for the aphid herbivore, *Uroleucon* (Hacker and Bertness 1996). As a result, we suspected that nitrogen could influence *Iva* food quality and aphid population growth. It could do so directly, by increasing the nitrogen content of *Iva* phloem (Dixon 1985; Bowditch and Stiling 1998), or indirectly, by influencing the outcome of the *Juncus/Iva* positive interaction.

In this study, we manipulate *Juncus* cover and nitrogen in the field to examine how nitrogen regulates the positive interaction between *Juncus*, *Iva*, and aphids. We present results that document how aphid populations respond to both (1) the direct effects of nitrogen on *Iva* plant quality and (2) the indirect effects of nitrogen that result from modifications of the *Juncus/Iva* interaction. We show that nitrogen determines the integrity of this salt marsh plant interaction, and that this mediation has important consequences for an insect herbivore.

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## Methods

To address the influence of nitrogen on the positive interaction between *Juncus* and *Iva*, and on the aphid which feeds on *Iva*, we performed a field manipulation experiment. All field work was conducted in the Rumstick Cove salt marsh in Barrington, Rhode Island, United States. The Rumstick Cove salt marsh has plant distributions and species composition typical of southern New England salt marshes (for further description of the study site, see Bertness 1992).

### Experimental manipulations of *Iva*

In early May 1993, we randomly selected 32 stunted *Iva* plants that were no closer than 2 m from each other. All occurred on a 200-m stretch of shoreline, 1.45 m above mean low water. We randomly assigned (1) *Juncus* removal and control treatments, and (2) fertilized and unfertilized treatments to these *Iva* in a fully factorial design. *Juncus* removal involved clipping all *Juncus* stems within 1 meter of *Iva* plants until the *Juncus* failed to regrow and died ( $n = 16$ ). *Iva* assigned to be controls were left unmanipulated ( $n = 16$ ). Half of the *Juncus* removal and half of the control plants were fertilized with Jobes time release fertilizer spikes. One spike (22.3 g nitrogen) was inserted in the soil 50 cm from the base of each fertilized *Iva* plant in early May and again in late July, when the previous spike had dissolved. Spikes also contained several grams of phosphorous and potassium, though these nutrients have been demonstrated by numerous studies to occur in excess in salt marshes and their addition fails to have significant effects on marsh communities (for reviews see Valiela and Teal 1974; Jefferies 1980; Adam 1993).

### Measurements of physical factors

In August, we measured both salinity and redox potential in each of the plots. Salinity was measured with a NaCl refractometer, from soil porewater collected from PVC tubes at 5 cm depth adjacent to the *Iva* plants. Soil redox potential was measured in 1 cm diameter by 5 cm deep soil plugs removed 10 cm from the base of each *Iva*. For more details on this methodology see Hacker and Bertness (1995).

Measurement of *Iva* leaf biomass, flower number, and leaf thickness

Each *Iva* plant was non-destructively sampled at the end of August. We counted *Iva* leaf number, and measured leaf size (length  $\times$  width) and thickness for three randomly selected leaves. We measured leaf thickness because it is known to increase with salt stress (Steiner 1939; Jennings 1976; Hacker and Bertness 1995). We estimated leaf biomass by multiplying the leaf number for each plant by its average leaf size. We also counted all of the flowers on each plant.

#### Aphid population growth experiments

To evaluate the quality of *Iva* as a host for aphid herbivores, we measured the per capita rate of increase of aphid populations on the experimental plants in predator-free cages in June, July, and August of 1993. In the middle of each month, ten recently born apterous aphid individuals, collected from *Iva* 200 m away, were placed on each of the experimental plants as described in Hacker and Bertness (1996). After the aphids established themselves on the plants, they were enclosed in 36 cm  $\times$  20 cm organza bags to prevent immigration, emigration, and predation, and allowed to grow and reproduce for 12 days. Aphids were enclosed with a standardized amount of leaves (50–75 leaves), which provided an overabundance of space for sap feeding. At the end of the 12 days, we counted the number of aphids produced and calculated the per capita rate of increase as  $[\ln(N_f/N_i)]/\Delta t$  (Hacker and Bertness 1996).  $N_i$  is the initial aphid number placed on each plant,  $N_f$  is the final number after 12 days, and  $\Delta t$  is the duration of the experiment (12 days).

#### Statistical analysis

The effects of removal and fertilization on salinity and redox potential were tested with two factor ANOVAs. The same analysis procedures were applied to *Iva* leaf biomass, leaf thickness, and flower number. For these *Iva* measures, significance was evaluated at the 0.01 level to protect against type I error, the probability of which increases when several ANOVAs are conducted on one experiment. *Iva* flower number data were log transformed to meet the homogeneity of variances assumption of ANOVA. Because aphid population growth was measured on the same experimental *Iva* at three points during the summer, the effects of removal, fertilization, and month on aphid per capita rate of increase were tested with a repeated measures ANOVA. The effects of *Juncus* removal in the unfertilized plots have been published in Hacker and Bertness (1995, 1996), and are included in this paper for statistically comparison with the fertilized plots.

## Results

### Salinity and redox potential

*Juncus* removal significantly decreased soil redox potential ( $F_{1,28} = 51.07$ ,  $P = 0.001$ ) and doubled soil salinity ( $F_{1,28} = 421.08$ ,  $P = 0.001$ ), while fertilization did not significantly affect redox potential ( $F_{1,28} = 0.48$ ,  $P = 0.493$ ) or salinity ( $F_{1,28} = 0.02$ ,  $P = 0.878$ ) (Fig. 1). ANOVA results also indicated nonsignificant removal  $\times$  fertilization interactions for both redox potential ( $F_{1,28} = 1.34$ ,  $P = 0.257$ ) and salinity ( $F_{1,28} = 0.08$ ,  $P = 0.776$ ). These results were comparable to those of Bertness and Hacker (1994).

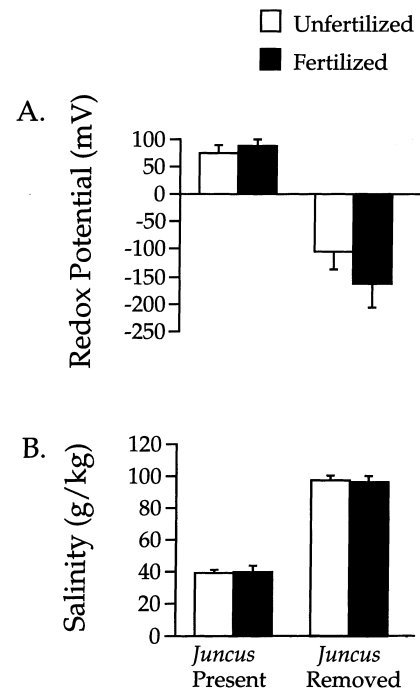


Fig. 1 A Salinity and B redox potential in the experimental plots as measured in August 1993. Bars represent means  $\pm$  1 SE

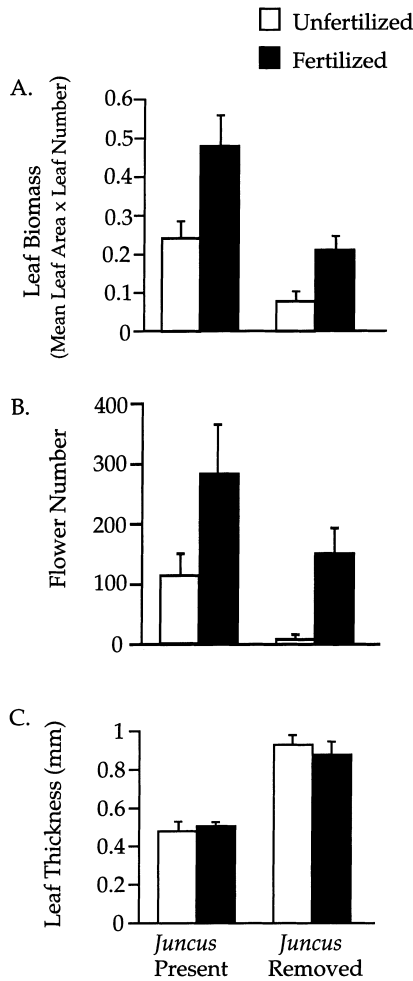
### *Iva* leaf biomass, flower number, and leaf thickness

Results indicated that fertilizing *Iva* plants grown without *Juncus* neighbors more than doubled leaf biomass and increased flower number over 20-fold (Fig. 2A, B). Furthermore, these plants without *Juncus* neighbors were highly similar to unmanipulated *Iva* grown with the surrounding *Juncus*. *Iva* grown with *Juncus* also benefited from fertilization which doubled both leaf biomass and flower number (Fig. 2A, B). ANOVA results indicated that the main effects of removal and fertilization significantly affected both leaf biomass (removal  $F_{1,28} = 20.24$ ,  $P = 0.001$ , fertilization  $F_{1,28} = 14.39$ ,  $P = 0.001$ , removal  $\times$  fertilization  $F_{1,28} = 0.74$ ,  $P = 0.398$ ) and flower number (removal  $F_{1,28} = 10.29$ ,  $P = 0.003$ , fertilization  $F_{1,28} = 21.20$ ,  $P = 0.001$ , removal  $\times$  fertilization  $F_{1,28} = 1.64$ ,  $P = 0.211$ ).

*Iva* leaf thickness in *Juncus* removal treatments was roughly twice that of control *Iva* ( $F_{1,28} = 84.69$ ,  $P = 0.001$ ) (Fig. 2C). In contrast, fertilization did not significantly affect leaf thickness ( $F_{1,28} = 0.09$ ,  $P = 0.770$ ) nor was there a significant removal  $\times$  fertilization interaction ( $F_{1,28} = 1.84$ ,  $P = 0.186$ ).

### Aphid per capita rate of increase

Aphid monthly population growth rates for June and July revealed that fertilization eliminated the indirect dependency of aphids on *Juncus* such that aphid growth rates on fertilized plants grown without *Juncus* neighbors were similar to rates on unmanipulated *Iva*



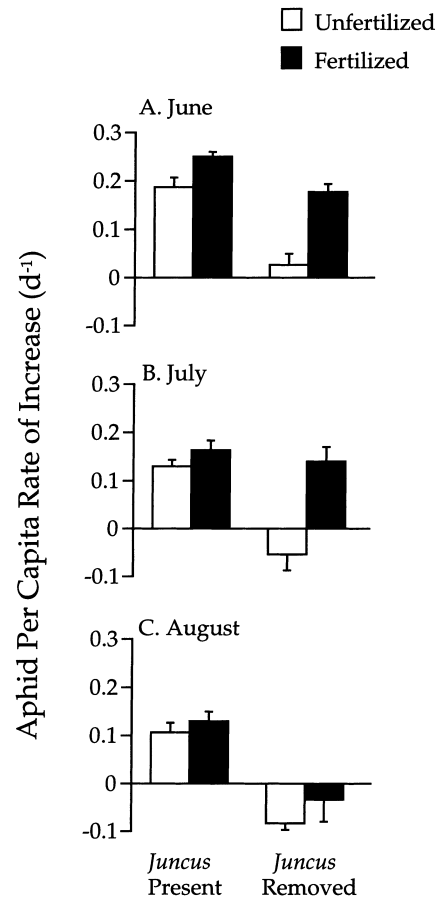
**Fig. 2** Morphological characteristics of *Iva frutescens* at the end of the study in August 1993: **A** leaf biomass, **B** flower number and **C** leaf thickness. Bars represent means  $\pm 1$  SE

**Table 1** Statistical summary of repeated-measures ANOVA performed on aphid per capita increase rate

Source of Variation	df	F	P <sup>a</sup>
Between-subject effects			
Removal	1	55.13	0.001
Fertilization	1	22.60	0.001
Removal $\times$ Fertilization	1	6.35	0.018
Subject	28		
Within-subject effects			
Month	2	32.95	0.001
Month $\times$ Removal	2	2.57	0.086
Month $\times$ Fertilization	2	2.09	0.134
Month $\times$ Removal $\times$ Fertilization	2	3.46	0.038
Subject $\times$ Month	56		

<sup>a</sup> Significance values for the within subject effects are Greenhouse-Geisser corrected *P* values, with epsilon = 0.90; Huynh-Feldt conditions were also met and produced comparable *P* values

(Fig. 3A, B). In August, however, *Juncus* removal resulted in negative population growth rates for aphids on both fertilized and unfertilized plants (Fig. 3C). The



**Fig. 3** Aphid per capita rate of increase on the experimental *Iva* plants for each month of the study (**A** June, **B** July, and **C** August 1993), as determined for a 12-day period in the middle of each month. For the calculation of aphid per capita rate of increase see methods. Bars represent means  $\pm 1$  SE

variation among months in the response of aphid populations to treatments was reflected in the significant month  $\times$  removal  $\times$  fertilization interaction (Table 1). Repeated measures ANOVA results also indicated significant main effects of removal, fertilization, and month, and a significant removal  $\times$  fertilization interaction (Table 1).

## Discussion

Nitrogen substitutes for the facilitating effects of *Juncus*

In this study, we show that nitrogen has important mediating consequences on a positive plant interaction in a New England salt marsh. Previous studies with *Juncus gerardi* and *Iva frutescens* demonstrate that the removal of *Juncus* leads to decreased biomass and eventual mortality of stunted *Iva* plants within two growing seasons (Bertness and Hacker 1994; Hacker and Bertness 1995). This study shows that increasing nitro-

gen availability causes the interaction to switch from a positive dependent interaction to a positive independent interaction. Though nitrogen increased the leaf biomass and flower number of *Iva* independent of the neighbor treatment, fertilized *Iva* grown without *Juncus* neighbors were highly similar to unmanipulated plants with *Juncus* (Fig. 2A, B). This result shows that for at least one growing season, nitrogen can compensate for the effects of *Juncus* removal, by substituting for the facilitating effects of the *Juncus* matrix.

Several mechanisms could explain how nitrogen availability reduced the dependency of *Iva* on *Juncus* (Fig. 2A, B). Fertilization may have directly influenced the physical conditions of our plots, though salinity and redox potential results indicate that there was no change in these conditions with the addition of nitrogen (Fig. 1A, B). A second hypothesis is that the increased leaf biomass and flower production were simply a consequence of increased productivity under nitrogen enhanced conditions. We believe the effect of fertilization on *Iva* grown with *Juncus* neighbors, may reflect this mechanism. We find it unlikely, however, that *Iva*, grown without *Juncus* neighbors at what were lethal levels of soil salinity and hypoxia (Bertness and Hacker 1994), was simply nitrogen limited.

A third hypothesis, and the one we favor, is that nitrogen actually increases the tolerance of *Iva* for the physical stress imposed by *Juncus* removal (Fig. 1). Previous studies with salt marsh plants have shown that nitrogen can be used by these plants for osmotic regulation in the face of high salinity (Shea 1977; Jefferies 1977, 1980; Jefferies et al. 1979; Cavalieri 1983; Adam 1993). Nitrogen addition typically enables increased production of proline, a protein commonly employed by marsh plants, including composite shrubs, to regulate their osmotic balance in the face of hypersaline conditions (Cavalieri and Huang 1979; Cavalieri 1983; Jefferies 1980; Adam 1993). Proline production can be nitrogen limited (Cavalieri 1983; Adam 1993), and we suspect that nitrogen addition increased the production of proline in *Iva*, enabling it to better tolerate marsh physical conditions in the absence of *Juncus*. This “chemical amelioration by nitrogen hypothesis” (Jefferies 1980) seems best supported by our results. Considering that *Juncus* mitigates the physical stress experienced by *Iva* (Bertness and Hacker 1994; Hacker and Bertness 1995), nitrogen addition could increase the tolerance of *Iva* to this stress, and should have similar consequences for plant biomass and flower number as the presence of *Juncus*. The results of our study, where nitrogen addition almost perfectly compensated for effects of *Juncus* removal on *Iva* (Fig. 2A, B), are thus consistent with this mechanism.

Further support for the “chemical amelioration by nitrogen hypothesis” is provided by *Iva* leaf thickness results. By August, we found that *Iva* leaf thickness had doubled when *Juncus* was removed, independent of nitrogen addition (Fig. 2C). Previous work with *Iva* has shown that this thickening response results from *Iva*

adjusting to the osmotic differential created between the hypersaline soil and its leaves. The osmotic differential favors water uptake, increasing turgor pressure, and ultimately, leaf thickening (Steiner 1939; Jennings 1976; Hacker and Bertness 1995). We would expect this leaf thickening to still occur for fertilized plants without *Juncus* neighbors, even if proline production was enhanced. This is because proline substitutes for salt as leaf osmotica and would thus also favor water uptake and increase leaf turgor pressure and thickness (Adam 1993).

#### Effects of nitrogen availability on aphid population growth

We found that when nitrogen was added to *Iva* without neighbors, these host plants supported normal, viable aphid populations, comparable to those on unmanipulated plants (Fig. 3A, B). This result is in contrast to results obtained for unfertilized plants, where aphids have negative population growth (Fig. 3B) and are predicted to be eliminated from stunted *Iva* hosts when *Juncus* is removed (Hacker and Bertness 1996). These results suggest that nitrogen not only maintains *Iva* populations by substituting for the positive effects of *Juncus* but that these effects are transferred to higher trophic levels resulting in the maintenance of aphid populations as well.

We hypothesize two general pathways through which nitrogen could have influenced *Iva* plant quality for aphids: (1) nitrogen availability could have directly influenced the nitrogen in *Iva* phloem sap (Dixon 1985) and (2) nitrogen could have had an indirect effect on plant quality, by mediating the interaction between *Juncus* and *Iva*, and thereby influencing aphid populations. With regard to the direct effect, though nitrogen addition increased aphid population growth on *Iva* plants with *Juncus* neighbors, this effect was small. A more important direct influence of nitrogen addition may be on *Iva* host quantity, because fertilized plants were roughly twice the size of unfertilized plants (Fig. 2A). We predict that these larger plants may be capable of supporting larger aphid populations. More interestingly, and likely more important to aphid populations, is the effect of nitrogen on the interaction between *Juncus* and *Iva* hosts. These results suggest that nitrogen, by contributing to the growth and survival of *Iva* and aphids without *Juncus* neighbors, mediates the dependency of aphid populations on *Juncus*. This dependency likely occurs only under nitrogen limiting conditions. Overall, our results suggest that effects of nitrogen on aphid populations may arise not only from a direct effect of nitrogen on *Iva* food quantity but also through indirect effects of nitrogen on the interaction between *Juncus* and *Iva*.

In contrast to results from June and July, August results indicated negative aphid population growth in *Juncus* removal plots, regardless of nitrogen availability (Fig. 3). Leaf thickness grew over the duration of this

study (Levine, unpublished data), and we suspect that in August, the leaf thickness of *Iva* grown without *Juncus* hindered aphids from detecting, penetrating, and feeding from the veins of *Iva* leaves (Dixon 1985). Typical leaves were nearly 1 mm thick by August, which is over twice as thick as the leaves on which these aphids characteristically feed (Fig. 2C).

### Community-wide effects of nitrogen availability

To begin to understand the community wide effects of nitrogen in salt marsh communities, we examined the importance of nitrogen to both a plant interaction and a plant-insect interaction in a New England salt marsh. We found that nitrogen availability dictated the importance of the positive plant interaction between *Juncus* and *Iva*, and by influencing this interaction, affected aphid population growth. Interestingly, the effect of nitrogen on aphid populations arose, not only from a direct effect of nitrogen on *Iva*, but also through nitrogen effects on the *Juncus/Iva* interaction. An important point is that a simpler nitrogen addition experiment, ignoring the role of *Juncus*, would not have detected the full importance of nitrogen to aphid populations.

Our study represents a first step toward understanding how nutrients, through their influence on plant interactions, can affect higher trophic levels. It shows how plant and higher trophic level interaction outcomes can be conditional on particular driving forces, such as nutrients. We believe that understanding the community-wide influence of factors such as nitrogen requires integrating the processes occurring both within and between trophic levels.

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