NUTRIENT SUBSIDIES TO BELOWGROUND MICROBES IMPACT ABOVEGROUND FOOD WEB INTERACTIONS

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Abstract. Historically, terrestrial food web theory has been compartmentalized into interactions among aboveground or belowground communities. In this study we took a more synthetic approach to understanding food web interactions by simultaneously examining four trophic levels and investigating how nutrient (nitrogen and carbon) and detrital subsidies impact the ability of the belowground microbial community to alter the abundance of aboveground arthropods (herbivores and predators) associated with the intertidal cord grass *Spartina alterniflora*. We manipulated carbon, nitrogen, and detrital resources in a field experiment and measured decomposition rate, soil nitrogen pools, plant biomass and quality, herbivore density, and arthropod predator abundance. Because carbon subsidies impact plant growth only indirectly (microbial pathways), whereas nitrogen additions both directly (plant uptake) and indirectly (microbial pathways) impact plant primary productivity, we were able to assess the effect of both belowground soil microbes and nutrient availability on aboveground herbivores and their predators. Herbivore density in the field was suppressed by carbon supplements. Carbon addition altered soil microbial dynamics (net potential ammonification, litter decomposition rate, DON [dissolved organic N] concentration), which limited inorganic soil nitrogen availability and reduced plant size as well as predator abundance. Nitrogen addition enhanced herbivore density by increasing plant size and quality directly by increasing inorganic soil nitrogen pools, and indirectly by enhancing microbial nitrification. Detritus adversely affected aboveground herbivores mainly by promoting predator aggregation. To date, the effects of carbon and nitrogen subsidies on salt marshes have been examined as isolated effects on either the aboveground or the belowground community. Our results emphasize the importance of directly addressing the soil microbial community as a factor that influences aboveground food web structure by affecting plant size and aboveground plant nitrogen.

Key words: aboveground–belowground interactions; detritus; food web dynamics; insect herbivores; intertidal cord grass; nitrogen mineralization; nutrient subsidies; plant–insect interactions; predation; soil microbes; Spartina alterniflora.

INTRODUCTION

There is growing interest in the potential for soil microbial communities to impact aboveground assemblages of herbivorous insects and their arthropod predators (Adams and Wall 2000, Hooper et al. 2000, van der Putten et al. 2001, Bardgett and Wardle 2003). Complex community interactions have been examined separately in belowground microbial populations (Mikola and Setala 1998, Laakso and Setala 1999, Sundareshwar et al. 2003, Blum et al. 2004) and aboveground primary-producer-based communities (Silliman and Bertness 2002, Denno et al. 2003, Pennings and Silliman 2005), but very few empirical studies have examined links between belowground and aboveground multitrophic interactions. In response to this void, ecologists are now asking how microbial processes feed back to affect aboveground plant quality (Hobbie and

Vitousek 2000) and the associated assemblage of herbivores via altered plant nutrition (Bonkowski et al. 2001).

Interactions between plants and the soil microbial community can have beneficial (Goverde et al. 2000, Bonkowski et al. 2001), negative (Chapman 1997*a*), or null effects (Barbosa and Krischik 1991, Setala et al. 1998) on plant productivity. Likewise, microbial activity has a broad range of potential interactions with herbivore populations that could be mediated through changes in plant productivity and nutrition. Heterotrophic microbes mineralize organic matter, thereby releasing macronutrients such as nitrogen to other trophic levels (Newell and Porter 2000) and enhancing plant productivity (Bonkowski et al. 2001). However, microbes can also compete with plants for nutrient resources. Microbial populations can temporarily sequester nutrients in biomass (immobilization; Chapman 1997*b*, Jingguo and Bakken 1997) or produce gaseous N (denitrification; Jordan et al. 1998), making nitrogen and other resources unavailable for plants and, ulti-
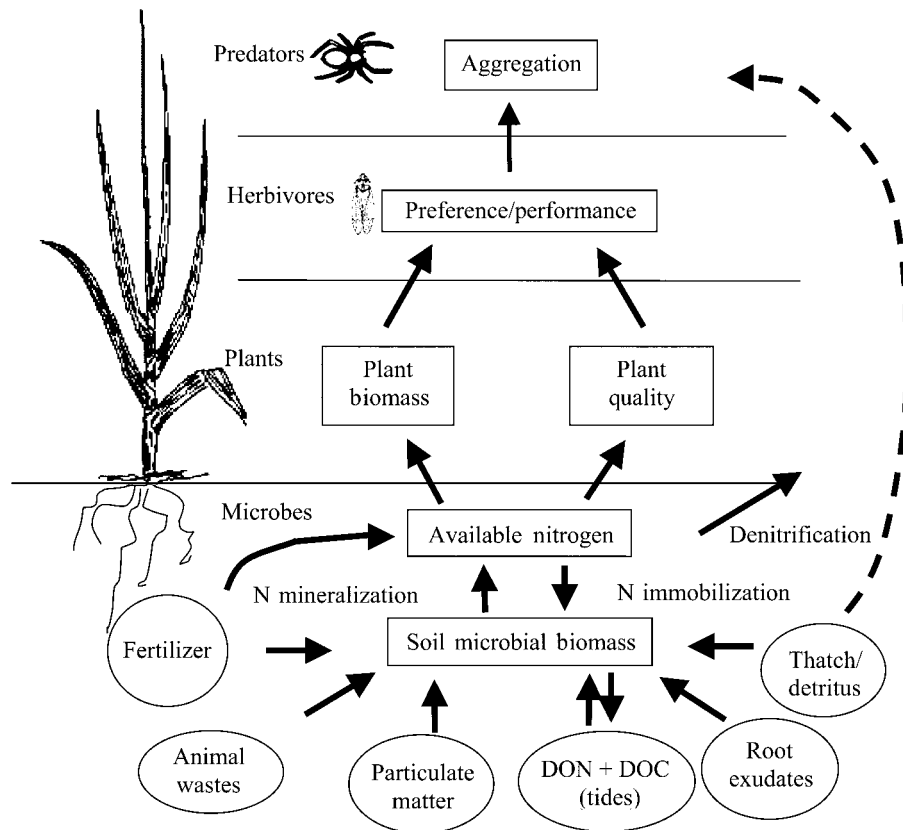
FIG. 1. Conceptual model of microbial mediation of herbivore performance. Solid lines indicate direct effects, and dashed lines specify indirect effects. The addition of carbon and nitrogen subsidies from a variety of sources influences microbial biomass and activity (N mineralization, N immobilization, and denitrification) and therefore affects the availability of nutrients for plant uptake. Nutrient availability influences plant biomass and quality (N content), and thus affects the performance of herbivorous insects. Invertebrate predators such as spiders aggregate in more complex thatchy habitats, where they enhance top-down suppression of insect herbivores.

mately, for the herbivores that consume them (Scheu et al. 1999, Bonkowski et al. 2001).

Carbon (organic matter quality; C:N, lignin/cellulose content) and nitrogen availability are important factors regulating heterotrophic microbial metabolism and the subsequent release of nutrients from detritus (Enriquez et al. 1993, Megonigal et al. 2004). Therefore, human impacts that directly or indirectly result in increased organic carbon (atmospheric CO_2 and root exudates [Heath 2005]) and nitrogen (wastewater and fertilizer runoff [Morris and Bradley 1999, Bowen and Valiela 2001, Valiela and Bowen 2002]) in soils will alter microbial metabolism and the subsequent release of nutrients to plants and aboveground food webs (Fig. 1). Subsidies with a high C:N content often result in less nitrogen available for plant uptake (Chapman 1997b, Jingguo and Bakken 1997). For example, additions of simple sugars are often used to experimentally stimulate microbial metabolism, and promote N immobilization as well as mimic natural labile carbon sources such as root exudates, dissolved organic carbon, and end products of decomposition (Schmidt et al. 1997, Jordan et al. 1998, Stiling and Moon 2005). Furthermore, in the

presence of nitrate, additions of labile carbon promote denitrification and nitrogen export from the system (Jordan et al. 1998). Additionally, subsidies of more recalcitrant forms of carbon such as detritus can lead to immobilization of nitrogen (Jingguo and Bakken 1997). Therefore, in nitrogen-limited systems, there is the potential for a positive feedback loop whereby low-quality litter (high C:N ratio, high lignocellulose content) may decompose slowly (Hobbie 1992), ultimately making less nitrogen available for plants (Laakso and Setala 1999) and associated herbivores (Fig. 1). In contrast, nutrient subsidies with a low C:N content (e.g., nitrogen fertilizer [Denno et al. 2002] and animal waste such as urea [Vince and Valiela 1981]) promote microbial mineralization of nutrients (Tobias et al. 2001) as well as provide increased inorganic nitrogen available for plants and their associated herbivores (Vince and Valiela 1981, Denno et al. 2002).

Herbivorous insects face a fundamental nutritional constraint in that they must utilize plant tissue that has much less nitrogen than their own tissue (Fagan et al. 2002). Thus, host plant quality (percentage nitrogen) often limits herbivore growth and fitness (Mattson 1980,

Rossi and Strong 1991, White 1993). Increases in plant quality can promote outbreak dynamics in populations of herbivores with high population growth rates (Cook and Denno 1994). Many studies have examined insect response to increased plant quality as a result of nutrient subsidies (Vince and Valiela 1981, Strong et al. 1984, Rossi and Strong 1991), or they have focused on the relative impact of predation and plant quality (Hunter and Price 1992, Denno et al. 2002) as forces that structure herbivorous insect communities. However, they have ignored the potential for soil microbes to mediate both plant–insect and predator–prey interactions. By altering nutrient availability, plant structure and quality, and litter decomposition rates, soil microorganisms have the potential to impact herbivore populations feeding in a wide variety of habitats.

Predators such as spiders show strong numerical responses to increases in prey density commonly found in patches of high-quality host plants (Döbel and Denno 1994). However, because of differential reproductive rates, herbivores can exhibit outbreak dynamics effectively escaping predation pressure on nitrogen rich plants (Cook and Denno 1994, Denno et al. 2002). In contrast, predators aggregate in structurally complex habitats where antagonistic interactions (cannibalism and intraguild predation) are diminished (Döbel and Denno 1994, Langellotto and Denno 2004). The result is enhanced suppression of prey in patches with increased plant architectural complexity (Fig. 1). By altering nutrient availability and decomposition rate of leaf litter, a key component of plant architectural complexity in grasslands, soil microbes have the potential not only to impact plant resource quality for herbivorous insects, but also to alter abundance of invertebrate predators, namely spiders. Importantly, gradients of nutrient (carbon and nitrogen) availability and plant architectural complexity across habitats may cause the microbe-mediated impacts on herbivore populations to be more dominated by plant quality effects in some habitats (those with abundant labile carbon) and more dominated by predator effects in other habitats (those with abundant leaf litter due to slow decomposition) (Denno et al. 2005).

The salt marsh ecosystem is ideal for investigating the impacts of the soil microbial community on the aboveground arthropod community because most of the primary productivity remains ungrazed by consumers, leaving large amounts of detritus or thatch (Teal 1962, Odum 1980), which serves as an important nutrient resource for soil microbes (Valiela et al. 1985) and a structural resource for invertebrate predators (Döbel and Denno 1994, Langellotto and Denno 2004). Furthermore, although a wide variety of carbon (detritus, root exudates, dissolved organic carbon, atmospheric CO_2) and nitrogen (atmospheric deposition, wastewater surplus, and fertilizer runoff) subsidies have been shown to affect both soil microbial communities and aboveground herbivore communities independ-

ently, there has been little investigation into how nutrient availability affects the strength of the interaction between the communities.

By measuring microbial activity, soil nutrient availability, plant quality, and the density of arthropods in response to refractory carbon (thatch), labile carbon (sucrose), and nitrogen (ammonium nitrate), we aim to investigate the extent to which aboveground herbivorous insect populations are influenced by both structural and nutrient resources subsidies. We predict that herbivores will be limited in thatchy habitats both by increased predator abundance (spiders), and reduced plant quality due to microbial N immobilization. Subsidies of labile carbon should increase microbial N immobilization and denitrification, effectively reducing the N available for plant uptake, thus reducing host plant quality and herbivore abundance. Predators are predicted to be least abundant in habitats subsidized by carbon, where plant size and prey abundance should be most diminished. Furthermore, because Spartina alterniflora-dominated marshes are typically N limited (Mendelssohn 1979b), we predict that subsidies of ammonium nitrate fertilizer will alleviate plant–microbe competition for nitrogen, effectively enhancing plant quality and herbivore abundance. Although a numerical response of predators to increased herbivore density on high-quality plants is predicted, previous work has demonstrated that this response is not strong enough to suppress herbivore populations below levels found on low-quality host plants (Denno et al. 2002). Using a factorial experimental approach in the field, our objectives were: (1) to determine the extent to which organic carbon and mineral nitrogen availability affect the ability of the soil microbial community to influence herbivore communities via altered plant nutrition or biomass, and (2) to determine if thatch indirectly limits herbivore communities by decreasing plant quality (percentage nitrogen) via microbial immobilization of nitrogen and/or by influencing predator aggregation.

METHODS

Study site and system

This study was conducted on a high-marsh Spartina alterniflora meadow on an intertidal salt marsh near Tuckerton, New Jersey, USA (39°30.8′ N, 74°19.0′ W). Due to differences in elevation and tidal inundation, both nutrient subsidies and the fraction of nitrogen that is sequestered in leaf litter (thatch) vary greatly across the marsh, as do their potential impacts on microbes (Tyler et al. 2003, Blum et al. 2004), plants (Mendelssohn 1979b), herbivores (Moon and Stiling 2004), and predators (Finke and Denno 2002).

The dominant herbivores on Spartina are the phloem feeders Prokelisia dolus and Prokelisia marginata (Hemiptera: Delphacidae), which regularly reach densities of 1000–10 000 individuals/m² (Denno et al. 2002; see Plate 1). Among the major predators of Prokelisia planthop-

pers are generalist wolf spiders, *Pardosa littoralis* (Araneae: Lycosidae), and sheet-web building spiders, *Grammanota trivittata* (Araneae: Lyniphidae), which aggregate in structurally complex thatchy habitats where they frequently reach combined densities of 600 individuals/m^2 (Döbel and Denno 1994, Langellotto and Denno 2004). Although there has been recent interest in the contribution of grazing herbivores to reduced primary productivity on salt marshes (Silliman and Bortolus 2003), grazing snails and grasshoppers have restricted geographic influence (Pennings and Silliman 2005), and they do not contribute significantly to herbivory at our study site due to their rarity.

Experimental design

To determine the extent to which the soil microbial community influences herbivore density via altered plant nutrition and biomass, we measured changes in decomposition rate, microbial activity, soil nitrogen pools, plant quality (N content and biomass), and arthropod densities in response to three experimental amendments (carbon, nitrogen, and thatch). Carbon and nitrogen treatments were designed to influence nutrient availability in a *Spartina* marsh without directly altering the structural complexity of the habitat or modifying light availability. We employed a 2 × 2 factorial design using field plots (4 m^2) established in high-marsh meadows. Two levels of labile carbon (50 g/m^2 granular sucrose addition vs. no addition) were crossed with two levels of nitrogen addition (45 g/m^2 granular ammonium nitrate addition vs. no addition). All treatments were added at low tide. The experiment was a randomized complete block design with two blocks (years 2001 and 2002), and each treatment combination was replicated six times (4 treatments × 6 replicates × 2 blocks = 48 field plots). We acknowledge that sucrose and ammonium nitrate fertilizer may affect microbes differently than the relatively more refractory forms of carbon and nitrogen in leaf litter. Therefore, to meet our second objective and to determine if thatch has the potential to influence herbivore populations, we added ~75g/m^2 of thatch as a natural comparison. Thatch was added to the marsh surface at the base of *Spartina* culms (where it occurs naturally) in an effort to minimize potential shading effects. Thatch addition mimicked twice-ambient thatch conditions and was within the range of naturally occurring levels of thatch (Newell et al. 1998, Denno et al. 2002). Altogether there were 60 field plots in total.

In 2001 and 2002, the five treatments were applied seven times biweekly (every two weeks) from June through August. We measured microbial activity (2002), soil nitrogen pools (2002), plant quality and biomass (2001, 2002), herbivore density (2001, 2002), and predator abundance (2001, 2002) to assess the impact of the treatments on soil microbial activity, plant production, and arthropod density.

PLATE 1. Nitrogen and carbon subsidies influence herbivores (*Prokelisia* planthoppers) indirectly via belowground effects on microbial processes that affect plant quality and biomass and by aboveground effects on plant structure that alter predator control. Photo credit: Hartmut Döbel.

Soil microbial processes

Because bacteria are diverse, difficult to exclude, and poorly known taxonomically (Torsvik et al. 1990, Lovell et al. 2000), we focused on the indirect effects of the microbial community on nutrient pools after manipulating nutrient subsidies (carbon, nitrogen, and detritus intended to represent a broad range of soil conditions across the marsh) rather than directly manipulating microbial diversity and abundance. To assess the effect of the treatments on microbial activity and N availability, we took soil cores (12 cm diameter × 10 cm deep) from each experimental plot once every four weeks (31 May, 19 June, 20 July, 22 August 2002). We measured net potential N mineralization (ammonification and nitrification) and carbon mineralization (net potential CO_2 production) during 20-day aerobic incubation intended to represent typical conditions at the detritus–soil interface. Microbial respiration was determined by colorimetric titration of CO_2 captured by a 10-mL 1.0 mol/L NaOH trap during the incubation. To insure that CO_2 mineralization was not in excess of what was

captured in the trap, we measured the CO_2 concentration in the headspace of the incubation jar with an infrared gas analyzer (IRGA CO_2, LICOR 6251, LI-COR, Lincoln, Nebraska, USA). Microbial N and DON [dissolved organic N] were determined by chloroform fumigation/extraction followed by persulfate digestion (Cabrera and Beare 1993). In all cases, inorganic soil N was determined after extraction with 30 mL of 2.0 mol/L KCl (Sims et al. 1995).

To assess the affect of microbial activity on rate of litter decomposition, we pinned five open-ended litterbags (1-mm^2 nylon mesh, 15 cm length $\times$ 5 cm diameter), each containing 5.0 g of *Spartina*, to the marsh surface in each of the 30 plots. Litterbags were serially removed weekly throughout the experiment (2 July, 11 July, 18 July, 25 July, 2 Aug, 27 Aug 2002) and ash free dry mass was measured. Decay coefficients were calculated according to: $X_t = X_0 e^{-kt}$ where X_t is the mass of litter remaining at time t, X_0 is the amount of litter initially present, and k is the exponential decay coefficient (Cebrian and Lartigue 2004).

Plant biomass and quality

To measure the response of *Spartina* to carbon, nitrogen, and thatch amendments, we tracked changes in plant biomass and quality. Belowground plant biomass was assessed by recovering cleaned, dried root biomass from the before-mentioned soil cores. We determined aboveground plant growth by comparing differences in grass height, culm density, live aboveground plant biomass, live plant C:N (Perkin Elmer 2400 CHN analyzer; Perkin Elmer, Norwalk, Connecticut, USA), and dead aboveground plant biomass collected within a 0.047-m^2 quadrat at the beginning and end of each year (31 May, 20 August 2001; 24 May, 27 August 2002). Due to differences in age and structure, autochthonous inputs of dead plant material were easily distinguished and separated from experimentally manipulated thatch supplements in thatch-addition plots.

Arthropod abundance

To determine plant-mediated treatment effects on herbivores and predators, arthropods were sampled using a D-vac vacuum sampler (D-vac, Ventura, California, USA) after one season of population growth and exposure to treatments (20 August 2001, 27 August 2002). Each sample consisted of three 3-s placements of the D-vac head (20 cm diameter) over the cord grass in each plot. On each sample date, we recorded herbivore (*Prokelisia dolus*, *P. marginata*) and spider density (individuals per square meter), and load (individuals per gram live plant biomass per square meter).

Statistical analysis

Net mineralization potential, soil nitrogen pools, and root biomass were analyzed using repeated-measures ANOVA (SAS Institute 2001) with treatment (carbon, nitrogen, carbon and nitrogen, thatch, and control) as a

fixed effect. Unstructured variance–covariance structure was used to achieve best fit using Akaike's Information Criterion (SAS Institute 2001). The effect of the five treatments on end-of-the-season plant parameters (aboveground biomass, height, culm density, dead aboveground biomass, plant quality, aboveground plant nitrogen, and litter decomposition rate) and arthropod abundance (density and load) was examined using ANOVA, with interannual variation (2001, 2002) as a random-block effect. Arthropod abundances were $\log_{10}$-transformed to meet assumptions of normality of residuals and homogeneity of variance. For all ANOVA models, pairwise treatment means comparisons were conducted using t tests when ANOVA results indicated a significant treatment effect ($P < 0.05$). In all figures, different letters illustrate significant ($P < 0.05$) differences between treatment means (nitrogen, carbon and nitrogen, control, carbon, thatch), as indicated by these t tests. A priori contrasts were used to test the main effects of carbon (addition or not), nitrogen (addition or not), the carbon $\times$ nitrogen interaction, and thatch (addition vs. ambient/control) for all ANOVA models (SAS Institute 2001). Statistics represented in tabular format show these a priori contrasts. Main effects can be graphically interpreted in the figures by averaging the two treatment means receiving the supplement (i.e., for the main effect of nitrogen, the nitrogen (N), and carbon plus nitrogen (C + N) addition treatments) and comparing it to the two treatments not receiving the supplement (the control (Cont) and carbon (C) addition treatments). Correlation was used to determine the strength of the association between predator (spider) density and prey (*Prokelisia* planthopper) density sampled throughout the season for both years (2001, 2002; 300 samples), as well as the relationship between predator (spider) density and the abundance of thatch in plots at the end of the growing season each year (SAS Institute 2001).

RESULTS

Belowground microbial processes

Potential net N mineralization.—The five treatments influenced potential inorganic N mineralization (Fig. 2A–C, Table 1). Soils supplemented with nitrogen had significantly higher potential net nitrification (i.e., accumulation of nitrite + nitrate) than soils not receiving nitrogen ($F_{1,25} = 29.46$, $P < 0.0001$; Fig. 2A, Table 1), whereas soils treated with carbon exhibited significantly higher potential net ammonification (i.e., increase in ammonium) than plots not treated with carbon ($F_{1,25} = 11.99$, $P = 0.002$; Fig. 2B, Table 1). Therefore, net potential microbial N mineralization (nitrification + ammonification) increased when soil was supplemented with both carbon ($F_{1,25} = 17.14$, $P = 0.0003$) and nitrogen ($F_{1,25} = 16.92$, $P = 0.0004$; Fig. 2C, Table 1). There were no significant interactive effects of carbon and nitrogen on potential net N mineralization or any other soil parameters.
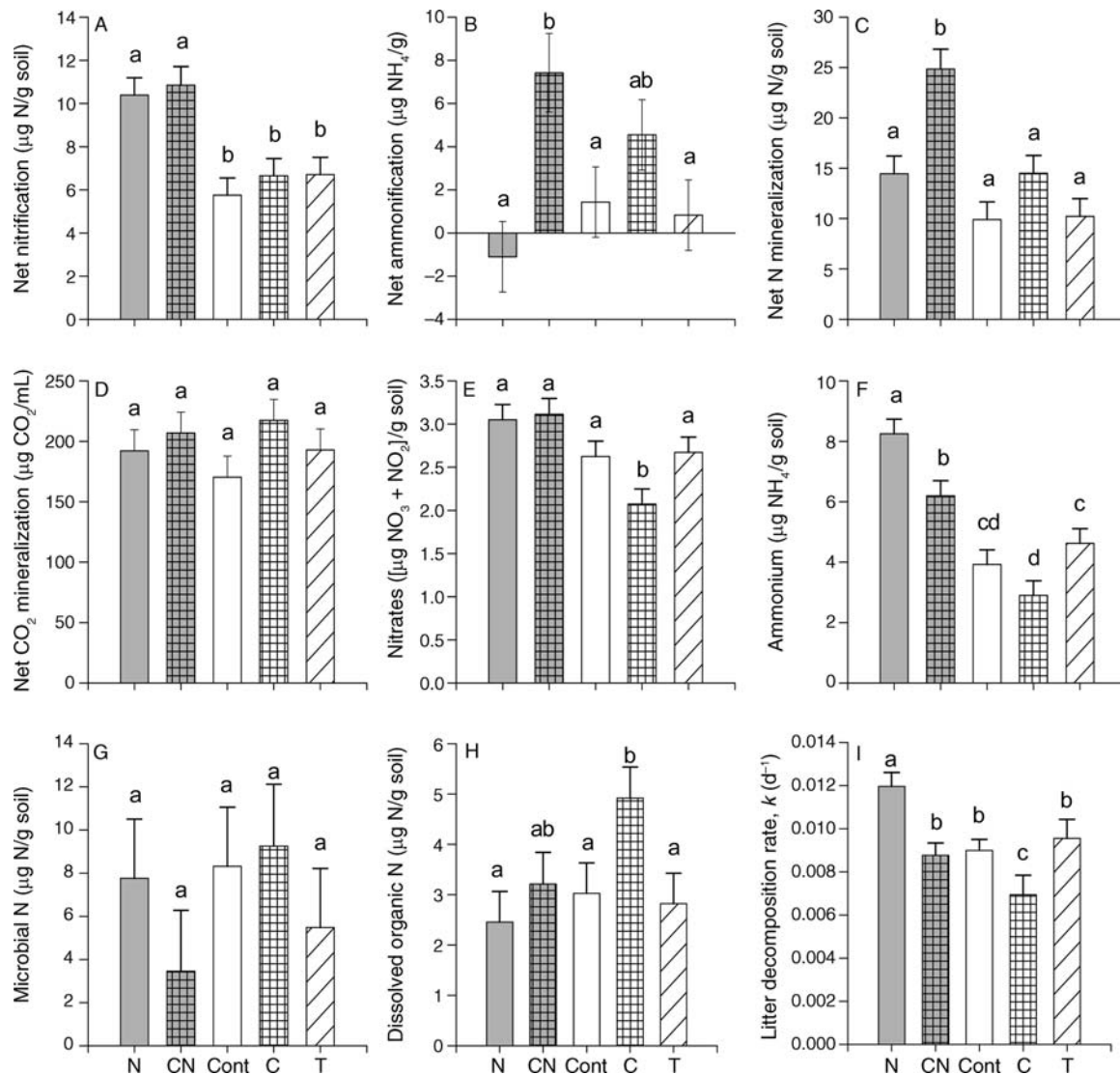
Fig. 2. Microbial activity and soil nitrogen pools (mean + SE, $n = 6$ plot replicates per treatment) measured as change in potential (A) net nitrification, (B) net ammonification, (C) net N mineralization, and (D) net CO_2 mineralization in laboratory incubations; (E) nitrate and nitrite, (F) ammonium, (G) microbial N, and (H) dissolved organic nitrogen from soil cores; and (I) litter decomposition rate in litter bags. All measurements are taken from *Spartina* plots exposed to one of five experimental treatments: nitrogen addition (N), carbon addition (C), carbon and nitrogen addition (CN), thatch addition (T), and unmanipulated control (Cont). Means with different lowercase letters are significantly different ($P < 0.05$).

TABLE 1. ANOVA results for the main effects of carbon, nitrogen, C × N, and thatch on soil parameters.

Soil parameter	All treatments		Carbon (C)		Nitrogen (N)		C × N		Thatch vs. control	
	F	P	F	P	F	P	F	P	F	P
Net potential nitrification	8.34	**0.0002**	0.70	0.41	29.46	**<0.0001**	0.07	0.79	0.72	0.41
Net potential ammonification	3.81	**0.01**	11.99	**0.002**	0.01	0.92	2.59	0.12	0.07	0.80
Net potential N mineralization	10.12	**<0.0001**	17.14	**0.0003**	16.92	**0.0004**	2.55	0.12	0.02	0.90
Net potential CO_2 mineralization	1.03	0.41	3.13	0.08	0.10	0.75	0.85	0.36	0.83	0.37
Extractable nitrate ($NO_2 + NO_3$)	5.41	**0.003**	1.86	0.18	16.71	**0.0004**	2.96	0.10	0.03	0.85
Extractable ammonium (NH_4)	18.55	**<0.0001**	9.84	**0.004**	60.57	**<0.0001**	1.09	0.30	1.05	0.32
Microbial N	0.70	0.60	0.37	0.55	1.29	0.27	0.88	0.36	0.54	0.47
Extractable dissolved organic N	2.50	**0.05**	4.63	**0.04**	3.42	0.08	0.86	0.36	0.06	0.81

Notes: For all treatment effects pooled, df = 4, 25; for individual treatments, df = 1, 25. Significant P values are set boldface for emphasis.

Potential net C mineralization (microbial respiration).—Supplements of carbon showed trends toward increasing microbial respiration ($F_{1,25} = 3.13$, $P = 0.08$). However, neither nitrogen addition ($F_{1,25} = 0.10$, $P = 0.75$) nor thatch addition ($F_{1,25} = 0.83$, $P = 0.37$) affected the potential net CO_2 mineralization (Fig. 2D, Table 1).

Extractable nitrogen.—Nitrogen addition promoted increases in both the nitrate + nitrite pool ($F_{1,25} = 16.71$, $P = 0.0004$; Fig. 1E) and the ammonium pool ($F_{1,25} = 60.57$, $P < 0.0001$; Fig. 2F). Carbon addition caused a larger decrease in the ammonium (for NH_4-N, $F_{1,25} = 9.84$, $P = 0.004$; Fig. 2F) than the nitrate pool (for NO_3-N, $F_{1,25} = 1.86$, $P = 0.18$; Fig. 2E). Although there was no significant interactive affect of carbon and nitrogen addition on ammonium or nitrate availability (Table 1), both ammonium and nitrate availability were reduced in the carbon-only-addition plots, but ammonium availability and not nitrate availability was reduced in the carbon- and nitrogen-addition plots (Fig. 2E, F). Thatch addition (for NO_3-N, $F_{1,25} = 0.03$, $P = 0.85$; for NH_4-N, $F_{1,25} = 1.05$, $P = 0.32$,) did not affect the availability of extractable inorganic N (Fig. 2E, F, Table 1).

Microbial nitrogen.—Carbon addition ($F_{1,25} = 0.37$, $P = 0.55$), nitrogen addition ($F_{1,25} = 1.29$, $P = 0.27$), and thatch addition ($F_{1,25} = 0.54$, $P = 0.47$) did not increase microbial nitrogen in the soil (Fig. 2G, Table 1).

DON.—Carbon addition increased DON concentration in the soil ($F_{1,25} = 4.63$, $P = 0.04$; Fig. 2H). However, DON was not affected by either nitrogen ($F_{1,25} = 3.42$, $P = 0.08$) or thatch ($F_{1,25} = 0.06$, $P = 0.81$) addition (Fig. 2H, Table 1).

Litter decomposition.—Litter decomposed faster in nitrogen-addition plots ($F_{1,25} = 11.16$, $P = 0.003$) and slower in carbon-addition plots ($F_{1,25} = 13.39$, $P = 0.001$), whereas thatch addition did not affect decomposition rate ($F_{1,25} = 0.3$ $P = 0.59$; Fig. 2I, Table 2).

Plant biomass and quality

Spartina in the nitrogen-addition plots exhibited increased biomass ($F_{1,54} = 68.19$, $P < 0.0001$), height ($F_{1,54} = 41.55$, $P < 0.0001$), and culm density ($F_{1,54} = 11.16$, $P = 0.002$) compared to plots that did not receive nitrogen subsidies (Fig. 3A–C, Table 2). In contrast, although carbon additions limited plant growth (lower culm density; $F_{1,54} = 10.17$, $P = 0.002$), there was also a significant carbon × nitrogen interactive effect such that carbon addition limited plant biomass ($F_{1,54} = 8.28$, $P = 0.006$), and height ($F_{1,54} = 4.50$, $P = 0.04$) more when it was added in the presence of nitrogen supplements than when it was added alone (Fig. 3A–C).

Plants in nitrogen-addition plots had a higher nitrogen content (% N) than plants in plots not supplemented with nitrogen ($F_{1,54} = 130.37$, $P < 0.0001$; Fig. 2E). Carbon addition did not affect the nitrogen content (% N) of *Spartina* ($F_{1,54} = 0.00$, $P = 0.97$; Fig. 3E). However, carbon limited the total aboveground nitrogen (Fig. 3F, Table 2) by limiting *Spartina* biomass (Fig. 3A). Therefore, because of its adverse effects on plant size,

carbon limited total aboveground nitrogen more when added in combination with nitrogen than when added alone ($F_{1,54} = 21.81$, $P < 0.0001$; Fig. 3F, Table 2). Plants in thatch-addition plots grew taller ($F_{1,54} = 12.28$, $P = 0.0009$), a potential shading effect, but thatch did not affect aboveground live plant biomass ($F_{1,54} = 0.01$, $P = 0.94$) or culm density ($F_{1,54} = 1.85$, $P = 0.18$; Fig. 3A–C, Table 2). The amount of autochthonous thatch production (dead aboveground biomass produced by senescing plants) within treatment plots was not affected by the nutrient- or thatch-addition treatments (Fig. 3D, Table 2). Notably, at the end of the growing season (2001 and 2002), there was significantly more total thatch (autochthonous + allochthanous) in thatch-addition plots (495 ± 26 g/m^2; mean $\pm$ SE, $n = 6$ plot replicates per treatment) than in control plots (23 ± 17 g/m^2; $n = 6$ replicates) due to biweekly (once every two weeks) thatch additions. Thatch addition led to a slight, but nonsignificant, increase in the nitrogen content of *Spartina* ($F_{1,54} = 3.57$, $P = 0.06$; Fig. 3E), but did not affect total aboveground plant nitrogen ($F_{1,54} = 0.36$, $P = 0.55$; Fig. 3F, Table 2). *Spartina* roots showed a trend toward decreased biomass in nitrogen-addition plots ($F_{1,25} = 3.77$, $P = 0.06$) compared to plots not receiving nitrogen, and root biomass remained unaffected by either carbon ($F_{1,25} = 0.06$, $P = 0.81$) or thatch addition ($F_{1,25} = 0.47$, $P = 0.50$; Fig. 3G, Table 2).

Arthropod abundance

Herbivores.—Consistent with known *Prokelisia* life history (see Denno et al. 2003), *P. dolus* was present in the high-marsh study plots throughout the season, whereas *P. marginata* migrated from the low-marsh into the high-marsh plots in late August in both years (not shown). Results presented here show only sample dates in late August, a time when both dominant species were present and abundant in the high-marsh study area. Nitrogen addition resulted in increased densities of both *P. dolus* ($F_{1,53} = 22.36$, $P < 0.0001$) and *P. marginata* ($F_{1,53} = 32.20$, $P < 0.0001$; Fig. 4, Table 3). *P. dolus* was least abundant in the carbon- and thatch-addition plots and most abundant in the nitrogen- and carbon + nitrogen-addition plots (Fig. 4). To control for differences in plant biomass between study plots, we examined *Prokelisia* load (planthopper density per gram of *Spartina*; see Fig. 4). Because there was no significant effect of nutrient-addition treatments on the load of *P. dolus* (Table 3, Fig. 4), differences in the density of this planthopper among treatments were attributable to changes in plant biomass and structure and not to changes in plant nitrogen content. Notably, there was a decrease in the load of *P. dolus* in thatch-addition plots ($F_{1,53} = 7.81$, $P = 0.007$), a difference that cannot be attributed to plant size or plant quality. In contrast, *P. marginata* showed both increased density ($F_{1,53} = 32.20$, $P < 0.0001$) and increased load ($F_{1,53} = 24.17$, $P < 0.0001$) in the nitrogen-addition plots (Fig. 4). Carbon and thatch addition did not affect either the density or

TABLE 2. ANOVA results for the main effects of carbon, nitrogen, C × N, and thatch on plant (*Spartina*) parameters.

	All treatments		Carbon (C)		Nitrogen (N)		C × N		Thatch vs. control	
Spartina parameter	F	P	F	P	F	P	F	P	F	P
Live aboveground biomass	30.79	<**0.0001**	41.95	<**0.0001**	68.19	<**0.0001**	8.28	**0.006**	0.01	0.94
Plant height	15.49	<**0.0001**	11.43	**0.0014**	41.55	<**0.0001**	4.50	**0.04**	12.28	**0.0009**
Culm density	5.32	**0.001**	10.17	**0.002**	11.16	**0.002**	0.27	0.60	1.85	0.18
Dead aboveground biomass	1.40	0.25	0.53	0.46	1.30	0.26	0.78	0.38	2.01	0.16
Plant quality (% N)	35.61	<**0.0001**	0.00	0.97	130.37	<**0.0001**	1.40	0.24	3.57	0.06
Aboveground plant N	64.31	<**0.0001**	52.10	<**0.0001**	37.22	<**0.0001**	21.81	<**0.0001**	0.36	0.55
Root biomass	1.68	0.18	0.06	0.81	3.77	0.06	0.92	0.35	0.47	0.50
Decomposition rate, k	6.35	**0.001**	13.39	**0.001**	11.16	**0.003**	0.56	0.46	0.3	0.59

Notes: For all treatment effects pooled, df = 4, 54; for individual treatments, df = 1, 54, except for root biomass and decomposition rate, with df = 1, 25. Significant P values are set boldface for emphasis.

load of *P. marginata* compared to controls (Fig. 4). Overall, results suggest that the migratory *P. marginata* has a greater sensitivity to plant nitrogen content (percentage N) than does *P. dolus*.

Predatory spiders.—There were more spiders in plots receiving a nitrogen subsidy than in those that did not

($F_{1,53} = 64.89$, $P < 0.0001$). However, similar to its effect on plant biomass and height, carbon addition in the presence of nitrogen led to larger reductions in spider densities than did the addition of carbon alone ($F_{1,54} = 15.10$, $P = 0.0003$), suggesting that spiders respond positively to plant structure. Moreover, thatch addition,
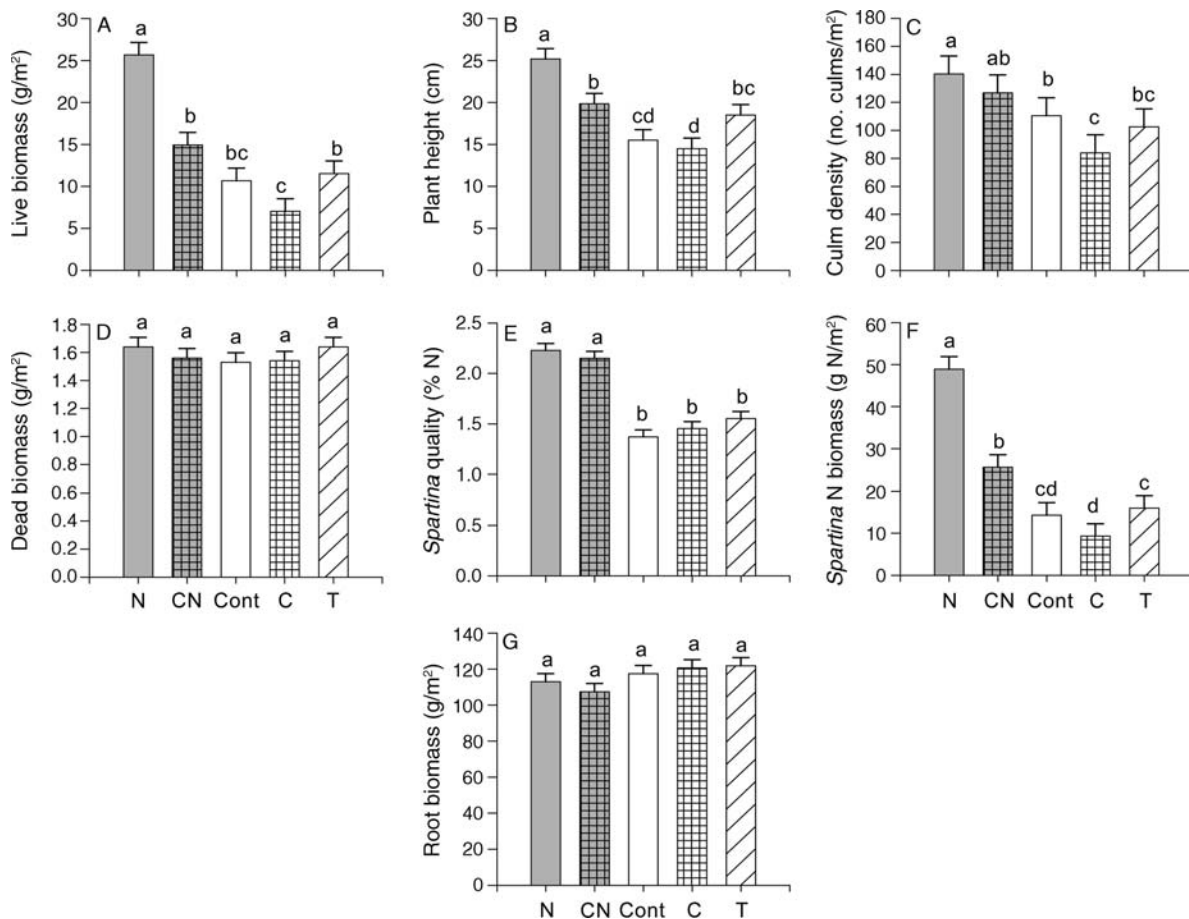

FIG. 3. Effects of nitrogen addition (N), carbon addition (C), carbon and nitrogen addition (CN), thatch addition (T), and unmanipulated control (Cont) on biomass measures, height, density, and nitrogen status of *Spartina* plants in experimental plots in late August on a marsh at Tuckerton, New Jersey, USA. Measurements in panels (A), (D), and (F) are aboveground biomass. If measurements were taken for more than one year, results were blocked by year (2001, 2002). Values are means + SE; means with different lowercase letters are significantly different ($P < 0.05$).
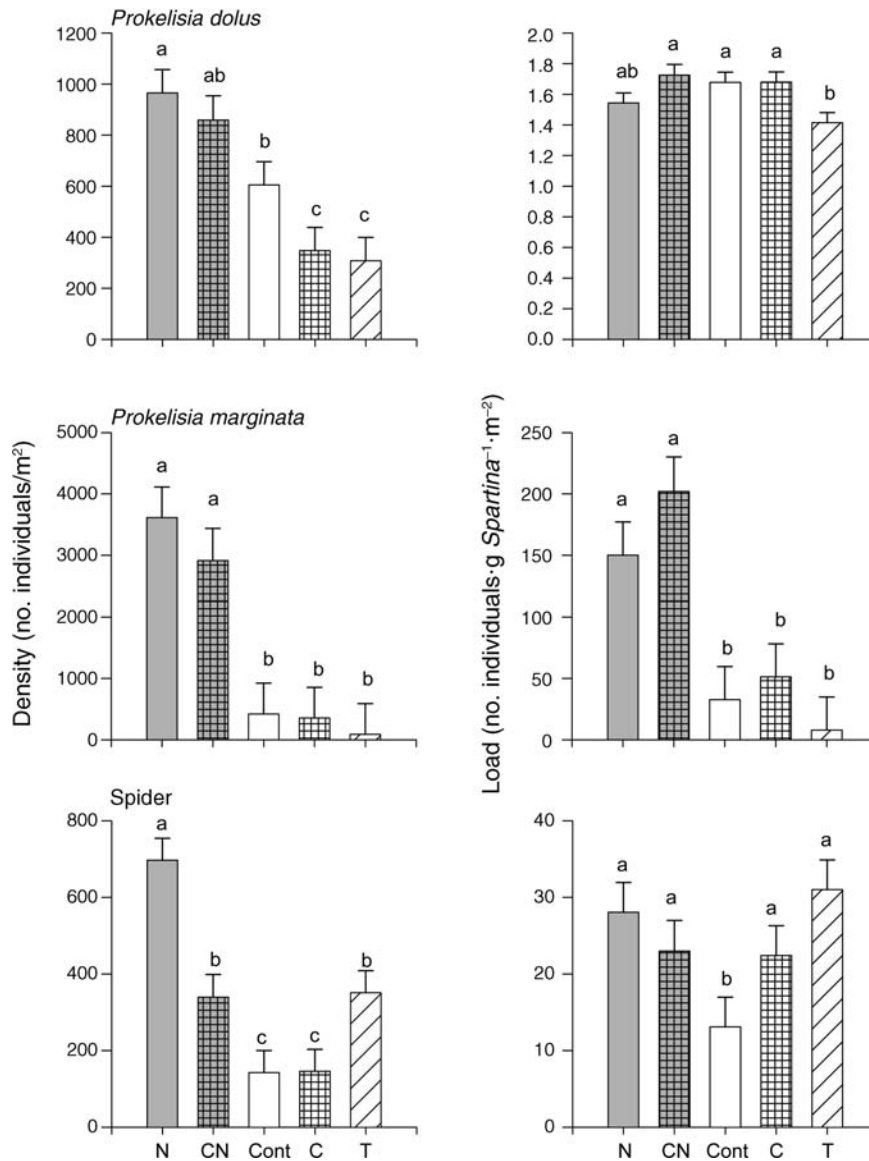
FIG. 4. Effects of nitrogen addition (N), carbon addition (C), carbon and nitrogen addition (CN), thatch addition (T), and unmanipulated control (Cont) on the density (left-hand panels) and load (right-hand panels) of *P. dolus* (top panels), *P. marginata* (middle panels), and spiders (bottom panels) in experimental plots of *Spartina* in late August (blocked by year 2001, 2002) on a marsh at Tuckerton, New Jersey, USA. Values are means + SE ($n = 12$ plot replicates per treatment); means with different lowercase letters are significantly different ($P < 0.05$).

TABLE 3. ANOVA results for the main effects of carbon, nitrogen, C × N, and thatch on arthropod parameters.

Arthropod parameter	All treatments		Carbon (C)		Nitrogen (N)		C × N		Thatch vs. control	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Prokelisia dolus density	10.31	**<0.0001**	3.89	**0.05**	22.36	**<0.0001**	0.67	0.42	5.29	**0.03**
Prokelisia dolus load	3.63	**0.01**	1.88	0.18	0.43	0.51	1.79	0.18	7.81	**0.007**
Prokelisia marginata density	10.71	**<0.0001**	0.57	0.45	32.20	**<0.0001**	0.39	0.54	0.22	0.64
Prokelisia marginata load	9.14	**<0.0001**	1.66	0.20	24.17	**<0.0001**	0.43	0.52	0.38	0.54
Spider density	24.22	**<0.0001**	14.57	**0.0004**	64.89	**<0.0001**	15.10	**0.0003**	10.33	**0.002**
Spider load	4.58	**0.003**	0.43	0.51	5.80	**0.02**	4.97	**0.03**	15.71	**0.0002**

Notes: For all treatment effects pooled, df = 4, 53; for individual treatments, df = 1, 53. Significant *P* values are set boldface for emphasis.

which increased the structural complexity of *Spartina*, enhanced spider densities compared to controls ($F_{1,54} = 10.33$, $P < 0.002$; Fig. 4), an effect that probably led to the reduced load of *P. dolus* in thatch-addition plots (Fig. 4). Similarly, across all treatment plots, there was a positive relationship between spider density and the amount of thatch ($r^2 = 0.53$, $P < 0.001$). Spider density was also positively correlated with the combined density of both species of *Prokelisia* planthopper prey ($r^2 = 0.26$, $P < 0.0001$).

DISCUSSION

Although interest in complex food web interactions has increased in recent years, few studies have considered the relationship between belowground nutrient dynamics and aboveground interactions among plants, insect herbivores, and their arthropod predators (Adams and Wall 2000, Hooper et al. 2000, van der Putten et al. 2001). Our results show that soil microbial processes can affect both aboveground herbivores and their natural enemies. By integrating theories of nutrient cycling and herbivore community dynamics, a framework is evolving for considering how the effects of belowground inputs of carbon and nitrogen cascade from the bottom up, starting with soil microbes, which affect plants, insect herbivores, and, ultimately, their arthropod predators (Bonkowski et al. 2001, Emery et al. 2001, Bardgett and Wardle 2003) (Fig. 1). This multitrophic interaction has broad ramifications for ecosystem function because it suggests that the composition of organic matter (i.e., carbon quality) not only regulates decomposition and nutrient availability, but also affects the ecological processes, such as competition and predation, that structure consumer communities. This study shows that labile carbon and nitrogen inputs can alter herbivore communities indirectly through changes in microbial activity, which subsequently affect plant quality and structure. In addition, it is likely that the structure provided by relatively recalcitrant natural thatch has particularly strong effects on aboveground predators and a comparatively reduced effect on soils in the salt marsh system.

Aboveground herbivore response

Herbivorous insects showed species-specific responses to nutrient manipulations designed to alter belowground microbial activity. For instance, the numerically dominant *Prokelisia* herbivores were found in highest densities in nitrogen-addition plots, a treatment designed to reduce plant–microbe competition for nitrogen (Fig. 4). Moreover, the lowest densities of *P. dolus* were found in carbon-addition plots, treatments intended to enhance microbial activity (Fig. 4). However, responses of the two closely related *Prokelisia* species were linked to two very different host plant characteristics. *P. marginata* showed a dramatic population increase with nitrogen addition, and it selectively colonized patches of nitro-gen-rich plants. In contrast, the more sedentary *P. dolus* was limited more by plant structure, such that its density was lowest on the smallest plants, independent of plant nitrogen content, as evidenced by the lack of a treatment effect on the load of *P. dolus* in experimental field plots (Fig. 4). The reduced populations on smaller plants probably resulted from a smaller number of suitable oviposition and feeding sites. Other studies have examined the response of herbivores to nitrogen subsidies on the marsh and have found increased densities of grazers (Vince and Valiela 1981), aphids (Levine et al. 1998), and planthoppers (Denno et al. 2000, Stiling and Moon 2005) on plants with increased nitrogen content. However this study provides a more mechanistic understanding of how different components of plant quality (plant biomass and nitrogen content) can affect even closely related herbivores with different life history strategies (e.g., the migratory *P. marginata* and the sedentary *P. dolus*). The differential response of these two abundant herbivores demonstrates the importance of including soil microbial activity as a factor that can broadly impact the composition and diversity of aboveground herbivore communities.

Belowground microbial and soil nutrient response

Because *Spartina* herbivores are limited by the growth and nitrogen content of their host plant (Cook and Denno 1994, Denno et al. 2002), and because *Spartina* takes up N as ammonium and, to a lesser extent, as nitrate (Mendelssohn 1979a), it is important to consider how nutrient subsidies affect the ability of soil microbes to mineralize organic matter into ammonium and oxidize ammonium to nitrate. Extractable N and potential net mineralization (ammonification and nitrification) are indicators of N availability in ecosystems (Groffman et al. 1996). Nitrogen addition directly increased the extractable inorganic N pool, as expected (Fig. 2E,F). Furthermore, net potential nitrification increased with the addition of ammonium nitrate, indicating that microbial processes also influenced the increase in nitrogen content of *Spartina* in our nitrogen-addition plots. Notably, carbon addition increased net potential ammonification in laboratory incubations (in the absence of plant N uptake), and decreased the standing stock of ammonium in the field (in the presence of plant N uptake) (Fig. 2B, F). This suggests that sucrose addition significantly increased microbial N demand, which was satisfied partly through increased mineralization of soil organic matter (sensu a priming effect [Kuzyakov et al. 2000]). Furthermore, potential net mineralization was highest in the carbon and nitrogen (C + N)-addition treatment (Fig. 2C), where plant biomass was relatively most reduced compared to either the carbon (C) or nitrogen (N) treatments alone (Fig. 3A). This provides a strong indication that nutrient availability mediates the strength of the microbial impact on plant productivity.

Although neither microbial biomass N nor soil respiration increased in response to carbon subsidies as hypothesized, our observation that the extractable ammonium pool available for plant uptake decreased in response to carbon addition suggests that microbes denitrified available N or transformed it into other forms unavailable for plant uptake (Jordan et al. 1998, Hamersley and Howes 2003). For example, we found the highest concentration of dissolved organic nitrogen (DON) in the carbon-addition treatments (Fig. 2H). DON is a heterogeneous nitrogen pool that has been linked to increased microbial turnover and the generation of microbial extracellular enzymes (Aber and Melillo 1991, Neff et al. 2003). This result is similar to that of (Stadler et al. 2001), who found increased concentrations of DON on spruce leaves infested with honeydew (labile carbon)-producing aphids. Thus, our results suggest that relieving carbon limitation in salt marsh soils, as evidenced by increased microbial activity (net potential mineralization and DON; Fig. 2A–C, H) in carbon-addition plots, can lead to reduced plant biomass (Fig. 3A) and a lower density of the dominant herbivore *P. dolus* (Fig. 4A).

Recent studies have demonstrated that soil microbial communities and plant communities can be limited by different elements (Morris and Bradley 1999, Sundareshwar et al. 2003). *Spartina* in the present study was N limited, but the lack of an increase in microbial biomass N following N addition (Fig. 2G) suggests that the soil microbial community is not N limited. However, carbon subsidies had a greater impact on nitrogen pools when added in combination with nitrogen than when added alone (Fig. 2C, F), suggesting that soil microbes may be co-limited by both carbon and nitrogen. Furthermore, recent studies have demonstrated that soil microbes are primarily limited by phosphorous and secondarily limited by carbon and nitrogen in estuarine marshes (Sundareshwar et al. 2003). Thus, carbon and nitrogen limitation of salt marsh soils can be induced by the addition of phosphorous (Sundareshwar et al. 2003). Experimental additions of phosphorous at our study site actually enhanced nitrogen in plant tissue slightly (Huberty 2005). Therefore, although much attention is focused on nitrogen limitation in terrestrial systems, it is likely that complex interactions among the carbon, nitrogen, and phosphorous cycles determine microbial metabolism (Morris and Bradley 1999, Sundareshwar et al. 2003), and can alter resource availability for plants, herbivores, and the predators that consume them. In light of increased nitrogen loading in coastal ecosystems due to increased atmospheric deposition, wastewater inputs, and fertilizer runoff (Bowen and Valiela 2001, Valiela and Bowen 2002), it is increasingly important to consider how interactions among nutrient cycles (C:N:P) will effect multiple trophic levels, both above and below ground.

Plant growth and quality

Consistent with the results of previous experiments, *Spartina* plants in this study responded quickly to additions of inorganic nitrogen by increasing biomass and nitrogen content (Mendelssohn 1979a, b, Denno et al. 2002) (Fig. 3). However, *Spartina* was sensitive to the form of nitrogen addition, such that total aboveground N in *Spartina* leaf tissue (Fig. 3F) was most consistent with patterns of ammonium availability (Fig. 2F) and was not sensitive to availability of nitrate (Fig. 2E). Although recent studies suggest that plants may be able to take up organic nitrogen (Neff et al. 2003), neither *Spartina* biomass (Fig. 2A) nor nitrogen content (Fig. 2E) was consistent with patterns of DON (Fig. 2H), indicating that organic nitrogen was not a dominant nutrient resource for *Spartina*. In itself, this is not surprising, because *Spartina* has long been known to be ammonium limited (Mendelssohn 1979a, b). However, these results demonstrate the complex interplay between the carbon and nitrogen cycles, whereby stimulation of the microbial community with additions of labile carbon can reduce soil ammonium availability and limit plant growth even in the presence of inorganic N in the form of nitrate (Figs. 2E, 3F). Therefore, in the context of our objectives, our results suggest that primary productivity was limited both directly by ammonium availability (enhanced production in N-subsidized plots) and indirectly by microbial activity (reduced aboveground N in carbon-subsidized plots). Furthermore, although neither microbial N nor microbial respiration (CO_2 mineralization) increased in the carbon-subsidized plots, other by-products of microbial metabolism may have contributed to a decrease in plant size. For example, microbial activity may have caused a drop in redox potential and increased hydrogen sulfide in the soil (Feng and Hsieh 1998, Tobias et al. 2001), which have been shown to limit plant productivity. Our carbon-addition treatment illustrates that by decreasing plant biomass, height, and culm density, soil microbial communities can have a particularly strong effect on aboveground arthropods such as *P. dolus* and spiders that are sensitive to changes in plant size and structure.

Although we did not find an effect of thatch addition on plant biomass or aboveground plant nitrogen (Fig. 3), other studies have shown that mulching with high C:N resources such as sawdust (Yeates et al. 1993, Arthur and Wang 1999) and wood chips (Lloyd 2001), which are functionally similar to our thatch-addition and carbon-addition treatments, result in decreased plant quality and growth. Thus, thatch addition had the potential to alter aboveground primary production via changes in microbial N immobilization, as seen in the carbon-addition plots. However, because there was no effect of thatch additions on inorganic N availability, it is unlikely that thatch addition influenced plant structure or plant quality via microbial immobilization of nitrogen.

Predator effects

Plant structure is known to influence predator aggregation and foraging behavior (Uetz 1991, Denno et al. 2002, Langellotto and Denno 2004). We found elevated spider densities in plots with larger plants (nitrogen subsidized) or more complex vegetation (thatch amended) and lower spider densities in plots with smaller and less structurally complex plants (carbon subsidized) (Fig. 4). Notably, nitrogen-addition but not thatch-addition *Spartina* plots also carried a higher density of herbivores (*Prokelisia* planthoppers), which was positively correlated with spider abundance. In fact, thatch-addition plots carried the lowest densities and loads of planthoppers of all the treatments (Fig. 4). Spiders showed a numerical response to increased herbivore load (corrected for differences in plant size) in the nitrogen-addition plots. However, because we did not exclude predators from our treatment plots, only the net effects of increased spider abundance and changes in plant quality on herbivore density can be examined. For an investigation of the relative effects of these two factors on herbivore density, see Denno et al. (2002, 2005). Nonetheless, prey density remained high in nitrogen-subsidized plots where spiders were also abundant, indicating that spiders were unable to limit herbivore populations in these plots. However, there was a reduced load of *P. dolus* in thatch-addition plots, which supported much higher densities of spiders (Fig. 4) and where the N content of *Spartina* was no higher than in thatch-withheld control plots (Fig. 3E). Thus, our results are consistent with those of previous studies that found a close linkage between spider abundance and both habitat complexity (Bultman and Uetz 1984, Uetz 1991) and prey abundance (Halaj et al. 1998, Denno et al. 2003). Consequently, predator abundance, which is strongly linked to plant structure, can be influenced by soil microbial activity, which can suppress plant biomass (Fig. 3A) and alter decomposition rate of thatch (Fig. 2I). However, because thatch addition failed to alter soil nutrient dynamics in this study, it is more likely that the more recalcitrant thatch alters food web interactions (i.e., increases predator abundance and mildly suppresses the concentration of herbivores) by adding a component of structural complexity to habitats that promotes the aggregation of invertebrate predators.

Conclusions

Although examples of both negative and positive effects of soil microbes on aboveground primary productivity exist (Adams and Wall 2000, Hooper et al. 2000, van der Putten et al. 2001, Bardgett and Wardle 2003), results of this study suggest that when salt marsh soils are exposed to labile carbon, microbial responses alter food web dynamics by inhibiting plant growth and the amount of total nitrogen in aboveground plant tissue (Fig. 3). Associated with increased microbial activity (decreased ammonium availability, increased N mineralization, increased DON concentration) in the carbon-amended plots were decreased plant size and structure, and reduced standing crop of aboveground nitrogen in *Spartina*. This resulted, in turn, in a lower density of herbivores (*P. dolus*) and fewer spider predators (Fig. 4). Nitrogen subsidies resulted in elevated inorganic soil nitrogen, increased plant biomass and nitrogen content, and ultimately higher densities of herbivores, especially nitrogen-sensitive species such as *P. marginata*. These results are noteworthy because they indicate that belowground microbial activity that results in increased inorganic nitrogen availability has the potential to cascade through several trophic levels and affect aboveground herbivores and predators. The mechanism for these effects involves changes in both plant structure and the amount of nitrogen available in aboveground plant tissue. However, because thatch additions did not affect soil nitrogen pools, plant biomass, or plant quality, it is likely that the decreased load of herbivores seen in thatch-amended plots was due to the structural role of thatch in promoting predator aggregation. Thus, thatch addition altered vegetation texture and predator abundance rather than altering nutrient resources. Specifically, this study provides a framework for examining complex interactions between belowground and aboveground food web dynamics. In particular, it highlights the importance of considering interactions between elemental nutrient cycling (C:N:P) and decomposition of leaf litter as factors that contribute to aboveground plant–insect and predator–prey interactions.

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