ABSTRACT

Title of Thesis: NUTRIENT AND STRUCTURAL EFFECTS OF DETRITUS ON FOOD WEB INTERACTIONS IN AN INTERTIDAL MARSH

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In most systems the majority of plant primary production is not directly consumed by herbivores, but instead dies and enters the system as detritus. This study examines indirect (nutrient) and direct (structural) impacts of detritus on the aboveground community of arthropods associated with the *Spartina alterniflora*. I manipulated carbon, nitrogen, and detrital resources in a field experiment and measured the response of the aboveground and belowground communities. Herbivore density in the field was limited by carbon supplements that also decreased decomposition rates, and limited plant size as well as predator abundance. Nitrogen addition enhanced herbivore density by increasing decomposition rate, inorganic soil nitrogen pools, and plant quality. In the laboratory, thatch directly affected herbivore fitness by decreasing survivorship and male body size. Overall, results suggest that detritus has the potential to adversely affect

aboveground herbivores directly by decreasing fitness and indirectly by reducing plant biomass and enhancing natural enemy abundance.

# NUTRIENT AND STRUCTURAL EFFECTS OF DETRITUS ON FOOD WEB INTERACTIONS IN AN INTERTIDAL MARSH

By

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

# Nutrient Consequences of Detritus on Food Web Dynamics: Linking Belowground and Aboveground Communities

## INTRODUCTION

There is growing interest in the potential for belowground communities to impact aboveground species assemblages (Adams and Wall 2000, Hooper et al. 2000, Van Der Putten et al. 2001, Bardgett and Wardle 2003). Although complex community interactions have been examined in both belowground microbial populations (Mikola and Setala 1998, Laakso and Setala 1999), and aboveground primary producer-based communities (Polis et al. 1997, Silliman and Bertness 2002) very few empirical studies have examined links between belowground and aboveground multi-trophic 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).

Theory suggests that interactions between plants and the belowground microbial community can have beneficial (Goverde et al. 2000, Bonkowski et al. 2001), negative (Chapman 1997a) or no effect (Barbosa and Krischik 1991, Setala et al. 1998) on plant productivity. Therefore, microbial activity has a broad range of potential impacts on

herbivore populations depending on alterations in plant productivity and nutrition. Activity of heterotrophic soil microorganisms such as bacteria and fungi can result in increased nutrient availability for plants. Microbes degrade carbon and nitrogen subsidies allowing for the transfer of mineral resources to other trophic levels (Newell and Porter 2000) that can result in increased plant productivity (Bonkowski et al. 2001). However, plants and microbes can also compete for carbon and nitrogen resources. Microbe populations can temporarily sequester nutrients in their biomass (immobilization) making nitrogen and other resources unavailable for plants (Chapman 1997b, Jingguo and Bakken 1997), and ultimately for the herbivores that consume them (Scheu et al. 1999, Bonkowski et al. 2001) (Figure 1.1).

In most terrestrial systems, the rate of microbial mineralization/immobilization, and subsequent release of nutrients from resource pools such as decomposing leaf litter, is limited by factors that affect microbial metabolism (soil moisture, temperature, pH, and oxygen levels) and resources that affect nutrient availability for microbes such as lignin/cellulose composition, litter quality (C:N:P), and soil nutrient availability (Aber and Melillo 1991). Therefore, in nitrogen-limited systems, there is the potential for a positive feedback loop whereby low-quality litter (high C:N ratio and high lignocellulose content) may lead to microbial immobilization of nitrogen and accumulation of litter due to slow decomposition, ultimately making less nitrogen available for plant uptake (Hobbie 1992). Thus, in nutrient-limited systems where nitrogen is tightly retained, the rate at which microbes decompose and re-mineralize plant leaf litter is an important determinant of plant productivity (Laakso and Setala 1999), and could influence plant nitrogen content as a resource for herbivorous insects (Figure 1.1). Consequently if the

microbial community is not limited by nutrients provided by leaf litter input, the microbial community should be resistant to detritus addition, and it would not act as a link in a feedback loop that would affect nutrient availability for herbivores (Christian et al. 1978).

Herbivorous insects face a fundamental nutritional constraint in that they must utilize plant tissue that has less nitrogen than their own body tissue (Fagan et al. 2002). Thus, host plant quality (percent nitrogen) often limits herbivore growth and fitness (Mattson 1980, Price 1991, White 1993). Insects have many adaptations that allow them to cope with nitrogen-poor host-plant resources. For example, insect herbivores can engage in compensatory feeding (Slansky and Wheeler 1992) or disperse to more nutritious alternatives (Denno et al. 1996) when feeding on nutrient-poor plants. The result is lower overall insect abundance on low-quality host plants (Coley et al. 1985). Therefore, by altering host-plant quality, belowground microbes have the potential to decrease herbivore populations feeding aboveground (White 1993, Hobbie and Vitousek 2000).

The salt marsh ecosystem is ideal for investigating belowground-aboveground interactions because the aboveground food web is well studied (Denno et al. 2002, Moon and Stiling 2002), and because tidal flushing, storm surges (Michener et al. 1997), and agricultural run-off (Valiela and Cole 2002) provide important belowground carbon and nitrogen subsidies. Furthermore, much of the primary productivity remains ungrazed by consumers (Teal 1962, Odum 1980). Thus, most plant biomass dies and enters the system as detritus or thatch (Teal 1962, Odum 1980), which serves as an important

nutrient and structural resource for plants, herbivores, and predators (Döbel and Denno 1994, Finke and Denno 2002).

Atlantic coastal salt marshes are dominated by the cord grass *Spartina alterniflora*. Differences in *Spartina* production and decomposition lead to spatial differences in the autochthonous accumulation and the quality (C:N) of thatch across habitats on the salt marsh (Howes et al. 1986, Boyer and Zedler 1998). Additionally, differences in tidal disturbance contribute further to the patchy deposition of allochthanous thatch/wrack across habitats on the marsh (Pennings and Richards 1998). Because some marsh plants exhibit decreased growth in areas of high thatch/wrack accumulation (Brewer et al. 1998), detritus could play an important role in affecting the structure of *Spartina* and therefore the dynamics of its associated invertebrate community.

Phloem-feeding planthoppers in the genus *Prokelisia* (Hemiptera: Delphacidae) are the principal herbivores of *Spartina* on Atlantic coastal marshes. These monophagous insects show a strong numerical response to increased plant quality, and often aggregate in high densities in patches of nitrogen-rich *Spartina* (Denno et al. 1996, Denno et al. 2002). Additionally, in the *Spartina* system, invertebrate predators such as spiders aggregate in thatch-rich habitats leading to enhanced herbivore suppression in such habitats (Döbel and Denno 1994, Finke and Denno 2002, Langellotto and Denno 2004). Thus, I hypothesize that thatch/detritus has the potential to limit above-ground herbivores both by an adverse bottom-up effect of decreased plant quality via microbial immobilization of nitrogen, and by the top-down effect of enhanced risk of predation (Figure 1.2).

Using a factorial experimental approach in the field, my objectives were: 1) to determine the extent to which carbon (sucrose) and nitrogen (ammonium nitrate) subsidies affect the ability of the belowground microbial community to influence herbivore communities via altered *Spartina* nutrition, and 2) to determine if thatch provides the carbon, nitrogen, and/or structural resources necessary to indirectly limit herbivore communities by decreasing plant quality (% nitrogen) via microbial immobilization or by influencing predator aggregation. By measuring microbial activity, soil nutrient availability, plant quality, and the density and diversity of arthropods in response to carbon, nitrogen, and thatch addition treatments, I aim to investigate the extent that aboveground herbivorous insect populations are influenced by the structural and nutrient resource components of detritus.

## METHODS

### *Study site and system*

This field study was conducted on in a high-marsh meadow of *Spartina alterniflora* located on an intertidal salt marsh in the Great Bay-Mullica River estuarine system in Tuckerton, New Jersey (39° 30.8' N, 74° 19.0' W). Along an elevation gradient from robust-structured *S. alterniflora* growing along tidal creeks in the low marsh to high-marsh meadows of short-form *S. alterniflora*, tidal flooding and disturbance decrease, salinity increases, and more leaf litter (thatch) accumulates (Blum 1968). Thus, both the fraction of nitrogen that is tied up in thatch, and the potential impact of thatch decomposition on plants, herbivores, and their predators vary greatly across habitats on the marsh.

Decomposition of standing dead *S. alterniflora* is promoted largely by ascomycetous fungal decomposers (Phylum: Ascomycota)(Newell and Porter 2000). However, after stems have collapsed onto the marsh surface, bacterial decomposers quickly colonize (Newell and Porter 2000). Because bacteria are diverse and much about their taxonomy remains unknown (Torsvik et al. 1990, Lovell et al. 2000), I will focus mainly on indirect microbial effects on soil nutrient pools rather than on a direct assessment of subsidy effects on microbial diversity and abundance**.**

The phloem feeders, *Prokelisia dolus* and *Prokelisia marginata* (Hemiptera: Delphacidae) are the dominant herbivores on *Spartina*. Adult densities of these monophagous insects regularly reach densities of 1,000-10,000 individuals/$m^2$ (Denno and Roderick 1992). *Prokelisia* planthoppers are trivoltine with peak adult abundances occurring in May, July, and September (Denno et al. 1987). Both species of *Proklesia* planthoppers over-winter in the high marsh meadows as nymphs (Denno et al. 1987). However *P. dolus*, the more sedentary of the two species tends to remain in the high marsh throughout the summer (Denno and Roderick 1992). In contrast, the more migratory and nitrogen-sensitive *P. marginata* moves to the low marsh where it spends the summer developing on nitrogen-rich tall-form *S. alterniflora* plants before returning to the high marsh to over-winter (Denno and Roderick 1992).

The major predators of *Prokelisia* planthoppers are generalist spiders and the specialist egg predator *Tythus vagus* (Hemiptera: Miridae). Wolf spiders, *Pardosa littoralis* (Araneae: Lycosidae), and sheet-web building spiders, *Grammanota trivittata* (Araneae: Lyniphidae) aggregate in more structurally complex thatchy habitat where they regularly reach combined densities of 600 individuals/$m^2$ (Döbel and Denno 1994, Denno

et al. 2002, Langellotto and Denno 2004). Additionally, in thatchy habitats intra-guild predation between the major predators of planthoppers (*Pardosa littoralis* and *Tythus vagus*) is diminished (Finke and Denno 2002). The result is enhanced suppression of planthopper prey in thatchy habitats (Finke and Denno 2002, Langellotto and Denno 2004). Thus, thatch has the potential to impact herbivore fitness both by the top-down effect of enhanced predator populations and by the bottom-up effect of altered plant quality via microbial immobilization and mineralization of nitrogen.

*Experimental Design*

To determine the extent that carbon and nitrogen resources affect the ability of the belowground microbial community to influence herbivore density via altered *Spartina* nutrition, I measured changes in microbial activity, soil nitrogen pools, *Spartina* quality (nitrogen content), and arthropod densities in response to experimental nutrient inputs (carbon, nitrogen, and thatch). Carbon and nitrogen treatments were designed to represent a diversity of nutrient subsidies on a *Spartina* marsh without directly altering the structural complexity of the habitat. I employed a 2X2 factorial design using small field plots ($4m^2$) established in high marsh meadows at the Tuckerton field site. Two levels of labile carbon addition (sucrose at $50g/m^2$ or not) were crossed with two levels of nitrogen addition (ammonium nitrate at $45g/m^2$ or not). The experimental design was a randomized complete block with two blocks (year 2001, year 2002) and with each treatment combination replicated six times (4 treatments x 6 replicates x 2 blocks = 48 field plots). I acknowledge that sucrose and ammonium nitrate fertilizer have priming effects on microbes that may differ from the refractory effects of carbon and nitrogen compounds typically found in leaf litter. Therefore, to meet my second objective, and

determine if thatch has the potential to indirectly limit herbivore populations by decreasing plant quality via microbial immobilization of nitrogen and/or influencing predator aggregation, a fifth thatch-addition treatment ($75g/m^2$) was included as a natural comparison (60 total field plots). In 2001 and 2002, the 5 treatments were applied 7 times bi-weekly from June-August. 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). I measured microbial activity (2002), soil nitrogen pools (2002), plant quality (2001, 2002), herbivore density (2001, 2002), and predator abundance (2001, 2002) to assess the impact of the 5 treatments on the belowground and aboveground communities.

*Microbial activity*

To indirectly assess treatment effects on the level of microbial activity, I conducted a litterbag decomposition study in 2002. Standing dead *S. alterniflora* was collected at the beginning of the growing season and placed in litterbags. On 2 July 2002, five open-ended litterbags (1-$mm^2$ nylon mesh, 15cm length x 5cm diameter), each containing 5.0 g of *Spartina* litter, were pinned 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 2002). At each sampling period I measured remaining mass, ash free dry weight (AFDW), and the C and N content of the litter. I calculated the %AFDW remaining as the difference between the AFDW of litter initially present in the litterbag and the AFDW of the remaining litter on a given harvest date divided by the AFDW of litter initially present. Decay coefficients were calculated according to: $X_t=X_0^{e-kt}$ where $X_t$ is the mass of litter remaining at time *t,* $X_o$ is the amount of litter

initially present, and *k* is the exponential decay coefficient. Because of the short-term nature of the study, treatment effects on *k*, C:N, and %N of both the litter collected throughout the season, and litter exposed to treatments for the longest time (those exposed for 56 days, collected on last sample date 27 Aug 2002), were analyzed using repeated measures ANOVA with treatment, time, and their interaction as fixed effects, or ANOVA with treatment as the fixed effect respectively.

*Mineralization potential*

To assess the extent that microbial N mineralization or the N immobilization potential is limited by soil carbon and nitrogen availability, I measured the net flux of soil N during a 3-week laboratory incubation of soils collected from the field plots. One soil core (12 cm diameter X 20 cm deep) was taken from each experimental plot every four weeks (31 May, 19 June, 20 July, 22 August 2002). The top 10cm was separated from each core, washed with 50 ml of anaerobic salt water (40ppm salt, a typical salinity for the high marsh), and sieved (.5 cm), forming a slurry free of plant material. Excess water was decanted and 3, 15 ml sub-samples of homogenized slurry were taken by syringe during rapid stirring. Inorganic soil N was determined after extraction with 30 ml of 2.0 M KCl from sub-samples that were either incubated or not (Sims et al. 1995).

Microbial activity, measured as the amount of carbon mineralized to $CO_2$ by microbial respiration, was determined by measuring the $CO_2$ concentration in the headspace of the incubation jar using infrared gas analysis (IRGA $CO_2$) in combination with colormetric titration of $CO_2$ captured by a 10ml 1.0 M NaOH trap during the incubation (Cabrera and Beare 1993).

*Soil Nutrient Pools*

To assess the direct and indirect effects (via microbial pathways) of the carbon and nitrogen treatments on the soil nitrogen available for plant uptake, I analyzed the inorganic nitrogen (ammonium, combined nitrite and nitrate), microbial nitrogen, and dissolved organic nitrogen (DON) in sub-samples taken from the soil cores. Microbial biomass N, and DON were determined by chloroform fumigation/ extraction followed by persulfate digestion (Cabrera and Beare 1993) using published $k_{en}$ values (Voneroy et al. 1993). In all cases, inorganic soil N was determined (Sims et al. 1995) after extraction with 30 ml of 2.0 M KCl. (Sims et al. 1995).

*Plant Biomass and Quality*

To measure the response of *Spartina* to belowground microbial activity and soil nutrient availability, I tracked changes in root biomass, aboveground live biomass, and aboveground plant nitrogen content (%N). I assessed changes in belowground plant growth by comparing differences in root biomass among treatments. Roots from soil cores (sampled on 19 June, 20 July, and 22 August 2002) were cleaned and dried to a constant mass. I determined aboveground plant growth and plant nitrogen by comparing differences in grass height (cm), culm density (culms/$m^2$), live aboveground plant biomass ($g/m^2$), and dead aboveground plant biomass ($g/m^2$) 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). Live and dead plant materials from each quadrat were separated, oven dried at 100ºC (VWR forced air oven), weighed, and analyzed for CHN (Perkin Elmer 2400 CHN analyzer). 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. Live plant N content was tracked throughout the experiment by randomly selecting nine *S. alterniflora* culms from each plot, drying them, and analyzing them for C and N on three dates per year (19 June, 10 July, 31 July 2001; 19 June, 11 July, 25 July 2002) (Perkin Elmer 2400 CHN analyzer).

*Habitat Complexity*

Because as the number and complexity of different plant parts (stems, leaves, flowers, thatch) increased, biomass increased, and because many components of architectural complexity such as plant height, culm density, number of leaves per culm, and live biomass were highly auto-correlated, total plant biomass (live + dead + thatch) was used as an indirect measurement of habitat complexity. To determine the effect of habitat complexity on arthropod species assemblages, and control for confounding effects of altered plant quality and increased area associated with increases in live biomass, thatch addition and control plots were contrasted because plant quality ($F_{1,4.58}$=3.68, $p$=0.12) and live plant biomass ($F_{1,54}$=0.01, $p$=0.94) were not significantly different in these two treatments.

*Arthropod Abundance and Diversity*

To determine plant-mediated treatment effects on herbivores and predators, arthropods were sampled using a D-vac vacuum sampler (D-vac Company, Ventura, California). One sample was taken in each plot on 31 May, 19 June, 10 July, 31 July, 20 August 2001; and 24 May, 19 June, 11 July, 25 July, 27 Aug 2002. Each sample consisted of 3, 3-s placements of the D-vac head (20 cm diameter) over the cordgrass in each plot. The density of dominant herbivores (number of *Prokelisia* nymphs, adult *P.*

*dolus,* and adult *P. marginata*/$m^2$), herbivore load (number of adult *P. dolus* and adult *P. marginata* /g live plant biomass·$m^2$), herbivore diversity (Shannon-Weinner H'), herbivore species richness (species/sample), and spider density (individuals/$m^2$) were measured on each sample date.

*Statistical analysis*

Litter decomposition, mineralization potential, soil nitrogen pools, root biomass, plant nitrogen, and arthropod abundance were analyzed using repeated measures ANOVA with treatment, date, and their interaction as fixed effects. Inter-annual variation was considered as a block effect when measurements were taken for more than one year (2001, 2002). First order autoregressive variance-covariance structure was used because of best-fit using Aikike's Information Criteria (SAS 2001). The effect of treatment on arthropod load (individuals ·g $plant^{-1}$· $m^{-2}$) was assessed only on the last sample date of each year when all arthropods were present and abundant in study plots. Number of culms, dead biomass and arthropod abundance were $\log_{10}$ transformed to meet assumptions of normality of residuals and homogeneity of variance. The main effects of Carbon (addition or not), Nitrogen (addition or not), the Carbon X Nitrogen interaction, the Carbon X time interaction, the Nitrogen X time interaction, and thatch (addition or ambient/control), were assessed using a priori contrasts (SAS 2001).

Correlation was used to determine the strength of the association between predator (spider) density and prey (*Prokelisia* planthopper) density of arthropods sampled throughout the season for both years (2001, 2002), as well as the relationship between predator (spider) density and structural complexity (biomass of *Spartina*) of plots at the end of the growing season each year (SAS 2001).

# RESULTS

## *Microbial Activity*

### *Litterbag decomposition*

Nitrogen addition decreased the C:N ratio of litter in litterbags ($F_{1,25}$=19.73, p<.0002; Table 1.1, Figure 1.3). In contrast, carbon addition did not have an effect on the percent nitrogen of litter ($F_{1,25}$=0.05, $p$=0.83, Table 1.1). Despite the lack of a carbon addition effect on the C:N ratio of the litter, nutrient treatments did apparently affect microbial activity as evidenced by a significant Carbon effect of increased percent AFDW of litter remaining throughout the season ($F_{1,25}$= 7.77, $p$=0.01; Table 1.2, Figure 1.4) and on the last sample date ($F_{1,25}$=12.58, $p$=0.0016 Table 1.2, Figure 1.4). Litter in nitrogen addition plots decomposed more rapidly than litter in plots without the N supplement as evidenced by the amount of litter (AFDW) remaining, and a higher $k$ on the last sample date (27 August 2002) ($F_{1,25}$ 11.16, $p$=0.003; Table 1.2, 1.3**,** Figure 1.4). Furthermore, litter in carbon addition plots decomposed more slowly than litter in plots that did not receive carbon ($F_{1,25}$=13.39, $p$=0.001; Table 1.2, 1.3**,** Figure 1.4). Thatch addition did not effect rate of litter decomposition ($F_{1,25}$= 0.01, $p$=0.92 Table 1.2, 1.3, Figure 1.4).

### *Mineralization Potential (incubation)*

Treatments ($F_{4,25}$=4.57, $p$=0.007) impacted the potential for inorganic N mineralization (Table 1.4). After incubation, soils supplemented with nitrogen had significantly higher potential net nitrification (increase in nitrite + nitrate) than soils not receiving nitrogen ($F_{1,25}$=55.87, $p$<0.0001; Table 1.4, Figure 1.5 A), whereas soils treated

with carbon exhibited significantly higher potential net ammonification (increase in ammonium) than plots not augmented with carbon ($F_{1,25}$=14.44, $p$=0.0008; Table 1.4, Figure 1.5 B). Notably, nitrogen addition did not effect potential N-ammonification ($F_{1,25}$=0.00, $p$=0.97; Table 1.4, Figure 1.5B), and carbon addition did not effect potential N-nitrification ($F_{1,25}$=1.33, $p$=0.26; Table 1.4, Figure 1.5A). Nitrogen addition and time had an interactive effect on potential net nitrification ($F_{2,48}$=6.39, p=.004; Table 1.4) but not on potential net ammonification ($F_{2,48}$=0.03, p=0.97; Table 1.4), whereby nitrogen addition had a larger impact on potential net nitrification earlier (June) in the summer compared to the later dates (July, August, 2002). For both potential net nitrification and ammonification, sample date had a significant effect due to natural seasonal fluctuation (Table 1.4).

*Microbial Respiration*

Supplements of carbon, nitrogen, and thatch did not affect the net $CO_2$ mineralization ($F_{4,25}$=0.95, $p$=0.45; Table 1.4, Figure 1.5 C). There was a seasonal fluctuation in microbial respiration rate ($F_{2,48}$=3.68, $p$=0.03; Table 1.4) whereby the most $CO_2$ was mineralized in carbon addition treatments in August 2002 (Figure 1.5C).

*Soil Nitrogen Pools*

*Inorganic nitrogen*

Treatments significantly affected the availability of inorganic N in the soil ($NH_4$-N: $F_{4,25}$=8.60, $p$=0.002, $NO_3$-N: $F_{4,25}$=5.28, $p$=0.03; Table 1.5). Nitrogen addition promoted increases in both nitrate +nitrite ($F_{1,25}$=5.28, $p$=0.03) and ammonium concentration ($F_{1,25}$=29.92, $p$<0.0001) in the soil (Table 1.5, Figure 1.6A,B). However,

neither carbon addition ($NH_4$-N: $F_{1,25}$=1.16, $p$=0.29, $NO_3$-N: $F_{1.25}$=1.02, $p$=0.32) nor thatch addition ($NH_4$-N: $F_{1,25}$=0.16, $p$=0.69, $NO_3$-N: $F_{1,25}$=0.10, $p$=0.76) affected the availability of inorganic N (Table 1.5, Figure 1.6 A, B). There was a significant effect of time on inorganic N availability ($NH_4$-N: $F_{2,49}$=14.92, $p$<0.0001, $NO_3$-N: $F_{2,49}$=88.07, $p$<0.0001), whereby the highest inorganic N concentrations were found during mid-summer in July (Table 1.5, Figure 1.6 A,B).

*DON*

Both treatment ($F_{4,25}$ =3.12, $p$=0.03) and time ($F_{2,49}$ =46.81, $p$<.0001) had significant effects on DON (Table 1.5). Carbon addition increased DON concentration in the soil ($F_{1,25}$=8.71, $p$=0.005; Table 1.5, Figure 1.6 C). However, DON was not affected by either nitrogen ($F_{1,25}$=2.39, $p$=0.13) or thatch ($F_{1,25}$=0.00, $p$=0.94) addition (Table 1.5, Figure 1.6 C).

*Microbial Nitrogen*

Microbial Nitrogen was affected by both treatments ($F_{4,25}$=4.03, $p$=0.01) and sample date ($F_{2,49}$=19.17, $p$<0.001; Table 1.5). Both nitrogen addition ($F_{1,25}$=5.65, $p$=0.02), and to a lesser extent carbon addition ($F_{1,25}$=3.40, $p$=0.08) increased microbial nitrogen concentration in the soil (Table 1.5, Figure 1.6 D). Thatch supplements did not affect microbial nitrogen ($F_{1,25}$=1.18, $p$=0.19; Table 1.5, Figure 1.6 D).

*Plant Biomass and Quality*

Treatments significantly affected the aboveground biomass of living *Spartina* ($F_{4,54}$=30.79, $p$<0.0001 Table 1.6). *Spartina* in the nitrogen addition plots exhibited increased plant biomass ($F_{1,54}$=68.19, $p$<0.0001), plant height ($F_{1,54}$=41.55, $p$<0.0001), and culm density compared to controls ($F_{1,54}$=11.16, $p$=0.001; Table 1.6, Figure 1.7 A-D).

In contrast, plants in the carbon addition treatment plots obtained significantly less aboveground biomass ($F_{1,54}$=41.95, $p$=0.0001), were shorter in height ($F_{1,54}$=11.43, p=0.001), and exhibited reduced culm density compared to controls ($F_{1,54}$=10.17, $p$=0.002; Table 1.6, Figure 1.7 A-D). Plants in the thatch addition plots were taller than controls ($F_{1,54}$=12.28, $p$=0.0009; Table 1.6, Figure 1.7 B). However, thatch addition 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; Table 1.6, Figure 1.7 A, C). The amount of autochthonous thatch production, or dead aboveground *Spartina* biomass produced by plants within treatment plots, was not affected by the nutrient or thatch addition treatments ($F_{4,4}$=1.01, $p$=0.40; Table 1.6, Figure 1.7 D). At the end of the season (2001, and 2002), there was significantly more total thatch (autochthonous + allochthonous) in thatch addition (495 $\pm$ 26 g/m$^2$ ; mean $\pm$ SEM, n=6) plots compared to control plots (23 $\pm$ 17 g/m$^2$; mean $\pm$ SEM, n=6) due to biweekly treatment additions. Although *Spartina* root biomass increased over time throughout the growing season ($F_{2, 50}$=18.79, $p$<0.0001), it was not affected by nutrient or thatch addition ($F_{4,25}$=1.68, $p$=0.18; Table 1.7).

The nitrogen content (%N) of aboveground *Spartina* was significantly affected by the treatments ($F_{4,4.58}$=32.22, $p$=0.001 Table 1.8). An interactive effect between treatment and time resulted from seasonal variation ($F_{16,221}$=9.35, $p$<0.0001). In general, however, plants in nitrogen addition plots had a higher nitrogen content (%N) than plants in plots not supplemented with nitrogen ($F_{1,4.58}$=118.88, $p$=0.0002; Table 1.8, Figure 1.8). Carbon addition did not affect the nitrogen content of *Spartina* (%N) ($F_{1,4.58}$=0.10, $p$=0.77; Table 1.8, Figure 1.8). However, carbon limited the total aboveground nitrogen (gN/m$^2$) in carbon addition plots ($F_{1,54}$ 51.83 $p$<0.0001) because of the adverse effects of

the carbon subsidy on *Spartina* biomass (Table 1.9, Figure 1.9). Furthermore, plants in the carbon + nitrogen addition plots maintained a nitrogen concentration equal to that of plants in the nitrogen addition plots [2.1 $\pm$ 0.04 (mean $\pm$ SEM) carbon and nitrogen addition, 2.2 $\pm$ 0.04 (mean $\pm$ SEM) nitrogen addition]; however, a significant nitrogen X carbon interaction indicated that the standing crop of total aboveground nitrogen ($g/m^2$) was less in the carbon + nitrogen plots than in plots receiving only nitrogen ($F_{1,54}$=21.76, $p$<0.0001; Table 1.9, Figure 1.9) because of decreased biomass (see Fig 1.7A). Thatch did not significantly effect the nitrogen content of *Spartina* (%N) ($F_{1,4.58}$=3.68, $p$=0.12; Table 1.8, Figure 1.8) or total aboveground plant nitrogen ($g/m^2$) ($F_{1,54}$=0.36, $p$=0.55; Table 1.9, Figure 1.9).

*Arthropod Abundance and Diversity*

*Prokelisia density*

*Prokelisia* planthopper phenology differed between species (*P. dolus*, vs. *P. marginata*) and life-stage (nymph vs. adult), but for each, phenology was similar across all treatment plots (Figure 1.10 A-C). *Prokelisia* nymphs peaked in abundance in early June (2001, 2002), mid July (2002), and again in early September (2001, 2002; Figure 1.10 A). *Prokelisia* nymphs were less abundant in carbon addition plots than in plots where carbon was withheld ($F_{1,4}$=19.79, $p$=0.01), whereas nitrogen addition resulted in increased densities of *Prokelisia* nymphs over the course of the season ($F_{1,4}$=42.87, $p$=0.003; Table 1.10). Thatch addition did not affect the density of nymphs compared to controls ($F_{1,4}$=0.21, $p$=0.67; Table 1.10).

Densities of adult *Prokelisia dolus*, the less migratory of the two congeners, peaked in late May, late July, and late August during both years of the study (Figure 1.10

B). Although *P. dolus* was more abundant in nitrogen addition plots ($F_{1,4}$=12.75, $p$=0.02), neither carbon addition ($F_{1,4}$=5.96, $p$=0.07) nor thatch addition ($F_{1,4}$=0.02, $p$=0.91) affected the density of *P. dolus* density over the course of the season (Table 1.10, Figure 1.10 B). Despite a small population peak in early June, *P. marginata*, the more flight-capable congener, remained relatively rare in all treatment plots until late August and early September when it reached peak density (Figure1.10 C). The 10-fold increase in *P. marginata* density in August and September corresponds with the annual migration of this species from the low marsh habitats to high marsh habitat where over-winter (Denno and Roderick 1992).

Although planthopper phenology was similar across all treatment plots, there were notable differences in planthopper densities across treatments. Because both *Prokelisia* species were abundant in study plots in late August 2001 and early September 2002, and because these dates represented the accumulation of a season's population growth for *P. dolus* as well as colonization for *P. marginata*, I specifically examined *Prokelisia* sp. density (individuals/$m^2$) and load (individuals/g *Spartina*·$m^2$) during this late-season period (Figure 1.11 A-D). Nitrogen addition resulted in a late-season increase in the densities of *Prokelisia* nymphs ($F_{1.25}$=15.16, $p$=0.005) and the adults of both *P. dolus* ($F_{1,25}$=9.36, $p$=0.0008) and *P. marginata* ($F_{1.25}$=13.49, $p$=0.0001; Table 1.10). *P. dolus* was least abundant in the carbon and thatch addition plots, and most abundant in the nitrogen and carbon + nitrogen addition plots (Figure 1.11 A). Herbivore load (insect density/g live plant biomass) adjusts for differences in plant size among treatments. Because there was no significant effect of nutrient addition treatments on the load of *P. dolus* ($F_{4,25}$=1.42, $p$=0.26; Table 1.11, Figure1.11 B), differences in the density of this

planthopper among treatments were more likely attributable to changes in plant biomass and structure than to changes in plant nitrogen content. There was a non-significant trend toward decreased *P. dolus* load in the thatch addition plots ($F_{1,25}$=3.34, $p$=0.08; Table 1.11). In contrast, *P. marginata* showed both increased density ($F_{1,25}$=13.49, $p$=0.001) and increased load ($F_{1,25}$=9.47, $p$=0.0005) in the nitrogen addition plots (Table 1.10, 1.11, Figure 1.11 C, D). Carbon and thatch addition did not affect either the density or load of *P. marginata* compared to controls (Figure 1.11 C, D). Overall, results suggest that *P. marginata* has a greater sensitivity to plant nitrogen content (%N) than *P. dolus.*

*Herbivore Diversity*

Seven herbivore species were collected in d-vac samples: phloem feeding planthoppers, *Prokelisia marginata, P. dolus, Delphacodes penedetecta, Megamelus lobatus,* (Homoptera: Delphacidae), xylem feeding leaf hoppers *Draeculacephala portola, Sanctanus aestuarium* (Homoptera: Cicadellidae), and a mesophyll feeding leaf bug *Trigonotylus uhleri* (Heteroptera: Lygaeidae). Nitrogen addition resulted in an increase in the richness of herbivores on *Spartina* ($F_{1,51.1}$=14.61, $p$=0.0004; Table 1.12, Figure 1.12A), whereas herbivore richness decreased in carbon subsidized plots ($F_{1,51.1}$=5.51, $p$=0.02; Table 1.12, Figure 1.12B). There was a marginal effect of Carbon X nitrogen interaction, whereby carbon was more effective at suppressing herbivore species richness in carbon + nitrogen addition treatments compared to plots supplemented with only carbon ($F_{1,51.1}$=3.28, $p$=0.08; Table 1.12, Figure 12 C). Neither nutrient supplement nor their combination affected insect diversity (H') (Nitrogen - $F_{1, 53.2}$=0.21, $p$=0.65; Carbon – $F_{1, 53.2}$=0.02, $p$=0.88; Carbon and nitrogen addition $F_{1,53.2}$=1.10, $p$=0.29; Table 1.12, Figure 1.13A-C). The addition of thatch resulted in increases in

both herbivore richness ($F_{1,51.1}$=11.65, $p$=0.001 Table 1.12, 1.12D) and diversity (H') ($F_{1,53.2}$=10.98, $p$=0.002; Figure 1.13D).

*Spider Density*

Treatments also significantly affected spider density ($F_{4,329}$=19.46, $p$<0.0001; Table 1.13). In general, treatments had a larger effect on spider density later in the season as evidenced by a significant Time x Treatment interaction (Table 1.13, Figure 1.14). Overall, however, there were more spiders in plots receiving a nitrogen subsidy that those that did not ($F_{1,329}$=40.86, $p$<0.0001), and fewer spiders occurred in carbon addition compared to non-carbon subsidized plots ($F_{1,329}$=12.74, $p$<0.0001; Table 1.13, Figure 1.14). Moreover, thatch supplementation enhanced spider densities compared to controls ($F_{1,329}$=17.45, $p$<0.0001; Table 1.13, Figure 1.14). When I adjusted for the effect of plant size and examined the spider load (individuals · g plant · $m^2$) at the end of the season, I found increased spider load on the nitrogen addition plots, those with the highest prey density, and the thatch addition plots, those with the increased structural complexity (Table 1.13, Figure 1.15). In fact, over the course of all sample dates, spider densities were significantly correlated with the density of *Prokelisia* planthoppers ($r^2$=0.26, $p$<0.0001; Table 1.14) and measurements of habitat complexity (total biomass of plant material: live +dead + thatch addition) ($r^2$=0.53, $p$<0.0001; Table 1.15).

## DISCUSSION

Although interest in complex food web interactions has increased in recent years, few studies have considered the relationship between the belowground nutrient-dynamics and aboveground species interactions in arthropod based communities (Adams and Wall

2000, Hooper et al. 2000, Van Der Putten et al. 2001). My results show that belowground microbe-mediated processes can affect 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 to affect plants, insect herbivores, and ultimately their arthropod predators (Hunter and Price 1992; Wardle et al. 1995; Lill and Marquis 2001). This multi-trophic cascade has broad ramifications for ecosystem function where the composition of organic matter regulates not only decomposition and nutrient availability but also affects forces that structure communities such as competition and predation. However, this study shows that although some carbon and nitrogen inputs have the potential to stimulate microbial activity and alter herbivore communities via changes in plant quality, it is likely that the structure of natural thatch and not any changes in soil nutrient dynamics resulting from decomposition affect aboveground herbivores and their predators.

*Aboveground herbivore response*

There were species-specific responses of herbivorous insects 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 decrease plant/microbe competition for nitrogen (Figure 1.11). Moreover, the lowest densities of both *Prokelisia* species were found in carbon addition plots, treatments intended to enhance microbial activity (Figure 1.11 A and C). However, responses of the two closely related *Prokelisia* species were linked to two very different host-plant characteristics. On the one hand, *P. marginata* selectively

colonized patches of nitrogen-rich plants during its annual migration from the low marsh to the high marsh. In contrast, *P. dolus* showed the greatest population increase on the largest plants independent of plant nitrogen content, as evidenced by the lack of a treatment effect on the load of *P. dolus* (density adjusted for differences in plant size) in experimental field plots (Figure 1.11 B). The responses of herbivores to differences in vegetation texture were not limited to *Prokelisia* planthoppers. For example, species richness and diversity (H') were higher in more structurally complex plots, those supplemented with thatch. These results are consistent with many studies showing that increases in habitat complexity lead to increased diversity of insect herbivores and their predators (Siemann et al. 1998, Haddad et al. 2000).

*Belowground microbial and soil nutrient response*

Although the response of herbivorous insects to nutrient manipulations is clear, it is important to examine the feedback mechanisms underlying their reaction in order to understand the possible extended effects of belowground processes on aboveground herbivores. Rapid microbial decomposition and remineralization of leaf litter may lead to more productive high quality plants (Vitousek et al. 1998, Hobbie 2000). Consistent with the results of many other studies, I found an increased rate of thatch decomposition in nitrogen addition plots, and decreased decomposition rates in plots subsidized with carbon (Figure 1.3, Table 1.2) (Marinucci et al. 1983, Valiela et al. 1984, Enriquez et al. 1993). Notably, because carbon manipulations did not affect the C:N ratio of litter (Table 1.1), it is more likely that the slower decomposition of litter seen in the carbon addition plots was due to sucrose acting as an alternative food source for microbes than to detritus nutrient dynamics. However, the slow decomposition of leaf litter due to external inputs

of labile carbon may lead to a greater proportion of the total nitrogen pool being tied up in detritus, and subsequently less nitrogen available for herbivores and their consumers in the long term (Marinucci et al. 1983, Valiela et al. 1985).

Extractable N and potential net mineralization (ammonification and nitrification) are indicators of N availability in ecosystems (Groffman et al. 1996). I measured changes in soil nitrogen pools and variation in microbial activity in response to carbon and nitrogen nutrient subsides. I found that N addition increased the inorganic N pool (Figure 1.6 A, B). Notably though, carbon addition increased net potential N-ammonification in laboratory incubations indicating that microbial activity was at least partially carbon limited (Figure 1.5B). In contrast, net potential nitrification increased with the addition of nitrogen suggesting that microbial activity may be both carbon and nitrogen limited. Moreover, I found the highest concentration of DON in the carbon addition treatments (Figure 1.5) providing further evidence of increased microbial activity in carbon addition treatments. DON is a heterogeneous nitrogen pool that has been linked to increased microbial turnover and the microbial generation of extracellular enzymes (Aber and Melillo 1991, Neff et al. 2003). My result is similar to the findings of (Stadler et al. 2001) who found increased concentrations of DON on spruce leaves infested with honeydew (labile carbon) producing aphids. These changes in belowground nitrogen pools and microbial activity have the potential to impact both ecosystem function and food web dynamics by altering resource availability for primary producers (Schmidt et al. 1997, Jonasson et al. 1999, Johnson et al. 2003).

*Plant growth and quality*

Historically terrestrial plant productivity has been considered nitrogen limited (Valiela and Teal 1979, Chapin III et al. 1986). Consistent with the results of previous experiments, *Spartina* plants in this study responded quickly to nitrogen treatments by increasing their biomass and nitrogen content (Figure 1.7, 1.8) (Chapin III et al. 1986). Therefore, belowground microbial activity such as mineralization that results in increased N availability to plants will likely increase the size and quality of the aboveground standing crop for herbivores. In contrast, plants in the carbon addition treatments grew more slowly compared to controls as indicated by decreased biomass, height, and culm density (Figure 1.7). While I did not find an effect of thatch addition on plant quality or plant biomass (Figures 1.7 and 1.9), other studies have shown that mulching with high C:N materials that are functionally similar to my thatch/carbon addition treatments such as saw dust (Yeates et al. 1993, Arthur and Wang 1999) and mulch (Lloyd 2001) results in decreased plant quality and growth due to increased microbial immobilization of nitrogen. The absence of a nitrogen treatment effect on *Spartina* root biomass is inconsistent with previous studies that found decreased belowground biomass in nitrogen subsidized *Spartina* (Valiela et al. 1976). This may have occurred in my study because as a result of the extreme density of roots in the soil, I did not distinguish between standing stock, live, dead, and new growth of root tissue. Microbial activity has the potential to alter aboveground primary production as seen in the carbon addition plots; however, because there was no effect of carbon from thatch additions on inorganic N availability, it is unlikely that thatch addition alters plant structure or plant quality via microbial immobilization of nitrogen in this study.

*Predator effects*

Plant structure is known to influence predator aggregation and foraging behavior (Uetz 1991, Denno et al. 2002, Langellotto and Denno 2004). I found increased spider densities in plots with larger plants (nitrogen subsidized) or more complex vegetation (thatch addition) and lower spider densities in smaller and less structurally complex plants (carbon treatments) (Figure 1.14). Notably, nitrogen but not thatch-addition plots also carried higher densities of prey (herbivores such as *Prokelisia*), which was positively correlated with spider abundance (Table 1.14). Therefore it is likely that spiders showed a strong numerical response to increased prey density in nitrogen addition plots, but the extremely high concentration of prey promoted their escape from spider controls. Furthermore, there was a trend toward greater suppression of *P. dolus* by spiders in more complex thatch addition plots, where spiders were more abundant. Thus, my 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, has the potential to be limited by soil microbial activity as seen by the carbon and nitrogen addition treatments (Figure 1.14). However, because thatch addition failed to alter nutrient dynamics or plant quality in this study it more likely that thatch alters food web interactions (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 belowground 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 microbes are exposed to labile carbon, microbes have the potential to alter food web dynamics by inhibiting plant growth and thus affecting the amount of available nitrogen in aboveground plant tissue (Figure 1.9). Associated with increased microbial activity in the carbon addition plots (increased ammonification, increased DON concentration) were decreased plant size and structure, and reduced standing crop of aboveground nitrogen in *Spartina*, which resulted in turn in a diminished herbivore community and fewer predators (figure 1.14). Nitrogen applications in excess of plant and microbial demand resulted in elevated inorganic soil nitrogen, increased plant biomass and nitrogen content, and ultimately higher densities of herbivores, especially nitrogen sensitive species such at *P. marginata*. These results are significant because they indicate that belowground microbial activities that result in increased inorganic nitrogen availability, have the potential to cascade through several trophic levels and affect aboveground herbivores and predators by altering both plant structure and the amount of nitrogen available in aboveground plant tissue. However, because thatch additions did not affect rate of decomposition, soil nitrogen pools, plant biomass, or plant quality, it is likely that the decreased herbivore load, increased herbivore species richness, and increased herbivore species diversity in the thatch addition field plots resulted from its structural effects on predator aggregation rather than altered plant quality via the belowground microbial community. Specifically, this study provides a

framework for examining complex interactions between the belowground and aboveground food web dynamics. In particular, it highlights the importance of including leaf litter, which is commonly considered as a component of the belowground detrital food web, as well as other potential belowground carbon and nitrogen resources, as important contributors to aboveground plant-insect and predator-prey interactions.

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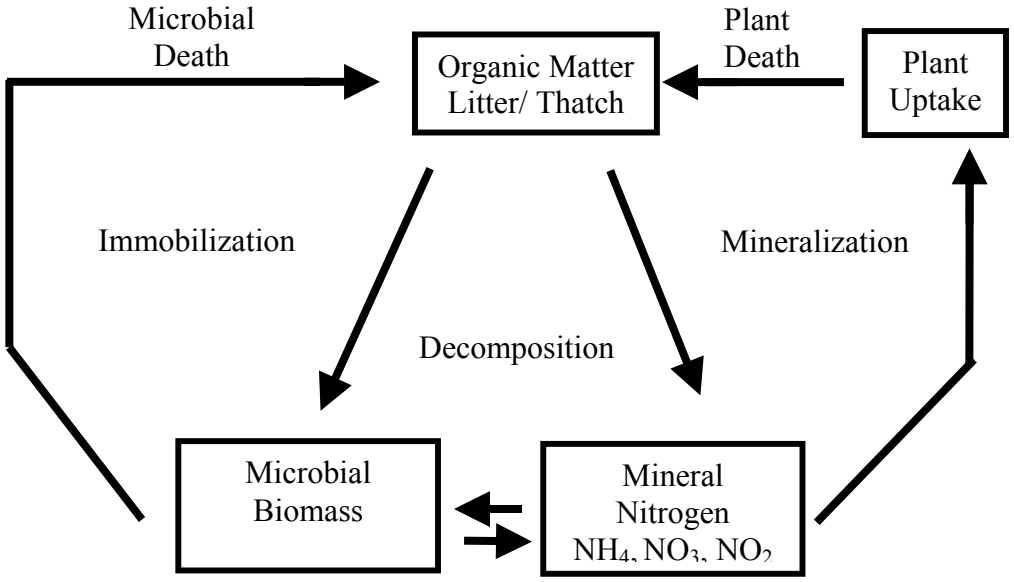


**Figure 1.1.** Conceptual model of nitrogen cycling during the decomposition of leaf litter thatch. Decomposing organic matter releases organic nitrogen that is mineralized into forms available for plant and microbial uptake ($NH_4$, $NO_2$, $NO_3$). Fertilization supplements the mineral nitrogen pool. Nitrogen acquired by microbial biomass is immobilized and thus is unavailable for plant uptake. Carbon addition increases microbial activity. As microbes die and are decomposed, nitrogen is returned to available pools.

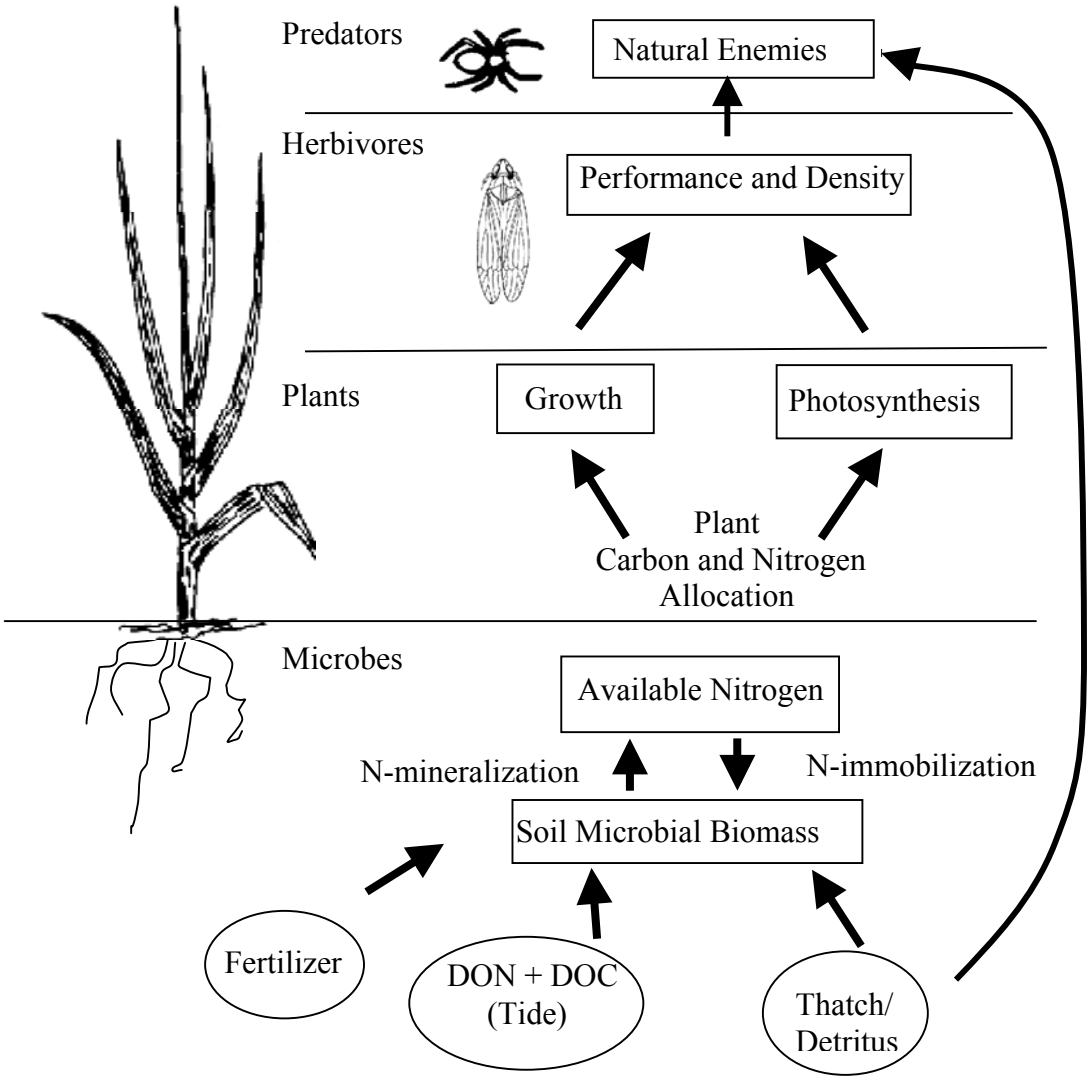


**Figure 1.2.** Conceptual model of herbivore performance mediated by bottom-up microbial impacts and top-down predator effects. The addition of Carbon and Nitrogen resources and/or thatch (leaf litter) stimulates microbial activity, thus influencing mineralization and immobilization of nitrogen, and the availability of nutrients for plant uptake. Nutrient availability influences host quality and therefore herbivorous insect preference, performance and density. Invertebrate predators such as spiders aggregate in more complex thatchy habitats where they assert strong top-down suppression of insect herbivores.

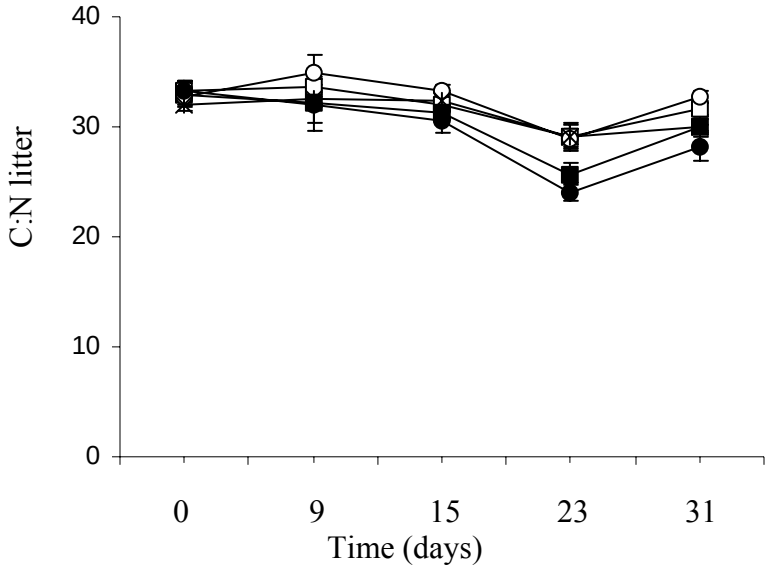


**Figure 1.3** C:N ratio of *Spartina* leaves (mean ± SEM, n=6) in litter bags after two months of decomposition (2 July 2002-27 August 2002) in experimental plots receiving subsidies of Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*). AFDW (%) remaining on 27 August 2002 (mean ± SEM, n=6) is shown in the *right panel*. Means with different letter are significantly different ($P<0.05$).

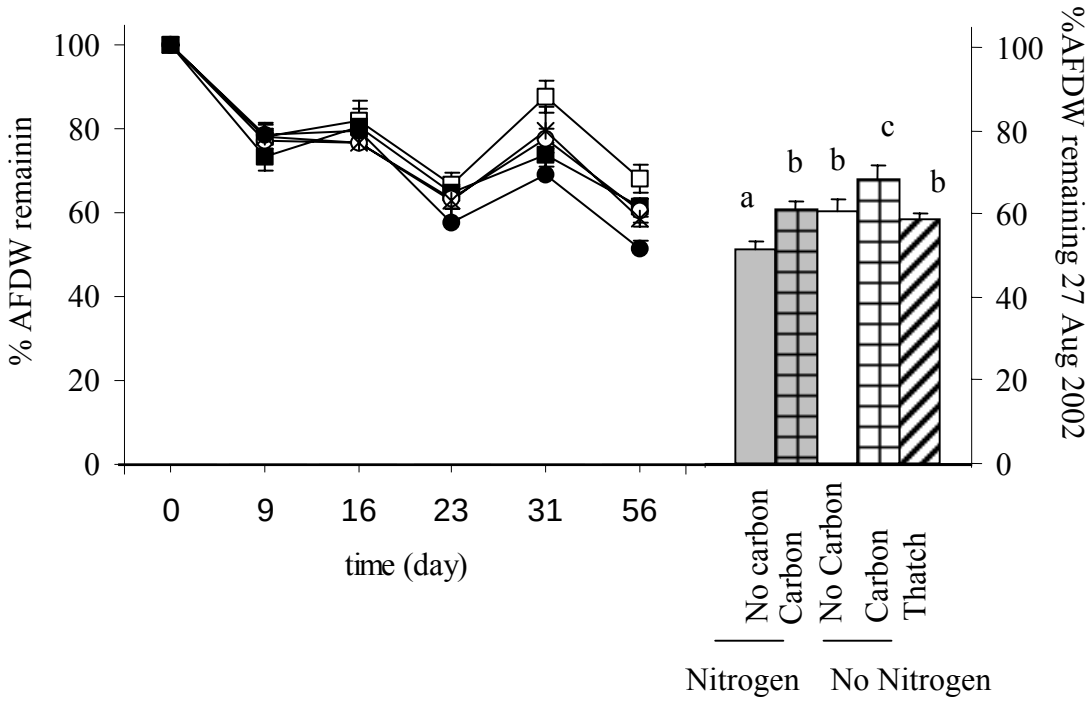


**Figure 1.4** Ash Free Dry Weight (AFDW, %) of *Spartina* leaves (mean ± SEM, n=6) in litter bags after two months of decomposition (2 July 2002-27 August 2002) in experimental plots receiving subsidies of Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*). AFDW (%) remaining on 27 August 2002 (mean ± SEM, n=6) is shown in the *right panel* where shaded bars represent nitrogen addition, square checkered bars represent carbon addition, hatched bars represent thatch addition and open bars are unmanipulated controls. Means with different letter are significantly different ($P<0.05$).

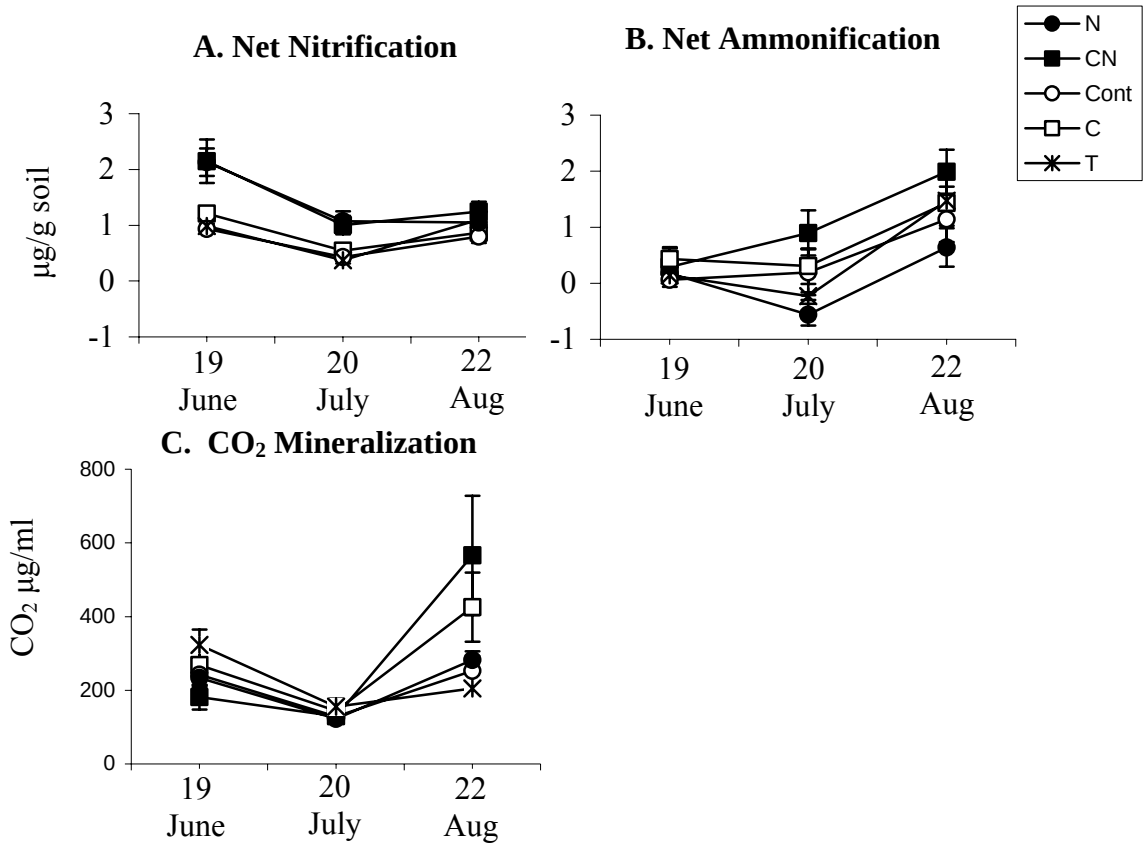


**Figure 1.5** Microbial activity measured as change in soil nitrogen concentration (µg/g, mean ± SEM, n=6) and $CO_2$ production (µg/ml, mean ± SEM, n=6) in laboratory incubations of soil from *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*). Microbial activity is shown as **A**. Net N-nitrification, **B**. Net N-mineralization, **C**. Net C-mineralization.

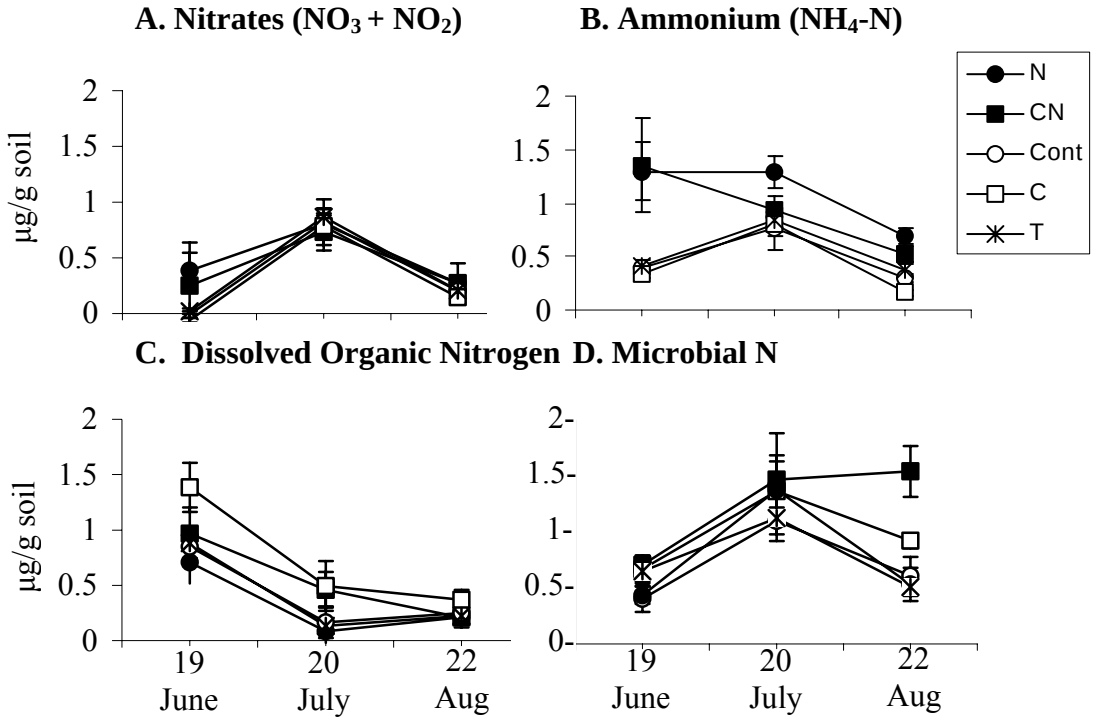


**Figure 1.6** Soil nitrogen pools (µg/g soil, mean ± SEM, n=6) in *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*). Nitrogen pools are **A**. Inorganic nitrogen (nitrate and nitrite), **B**. Inorganic nitrogen (ammonium), **C**. Dissolved organic nitrogen (DON), **D**. Microbial N.

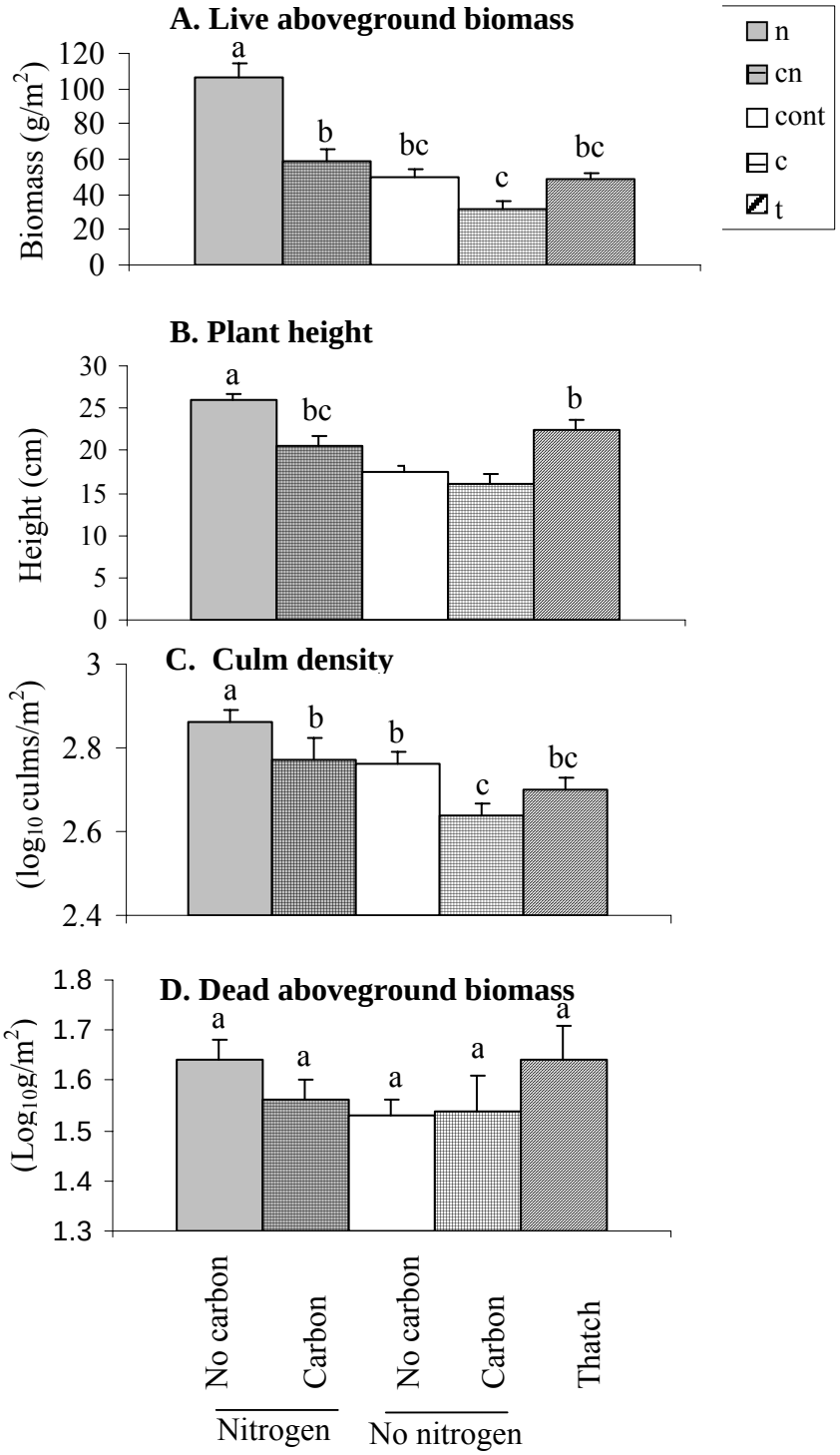


**Figure 1.7**. Effects of nitrogen addition (*shaded bars*), no nitrogen addition (*open bars*), carbon addition (*checkered bars*), no carbon addition (*open bars*), and thatch addition (*hatched bars*) on the (**A)** live aboveground biomass, (**B)** height, (**C) c**ulm density, and (**D)** dead aboveground biomass of *Spartina* plants measured at the end of the season (late August; blocked by year 2001, 2002). Means (mean $\pm$ SEM, n=12) with different letters are significantly different ($P<0.05$).

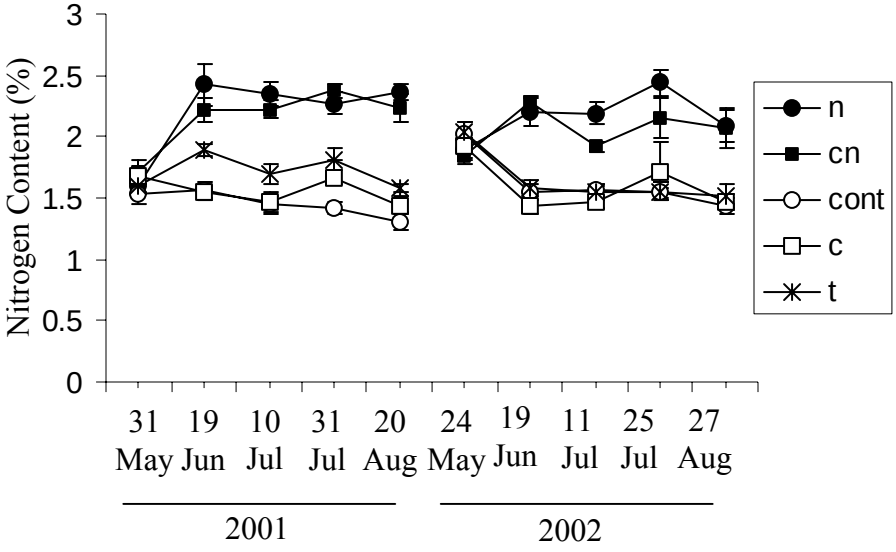


**Figure 1.8.** Nitrogen content of *Spartina* (%N) (mean ± SEM, n=6) throughout the season in 2001 and 2002 in plots receiving one of five treatments: Nitrogen addition (●), Carbon and nitrogen addition (■), Control-no nutrient addition (○), Carbon addition (□), and Thatch addition (*).

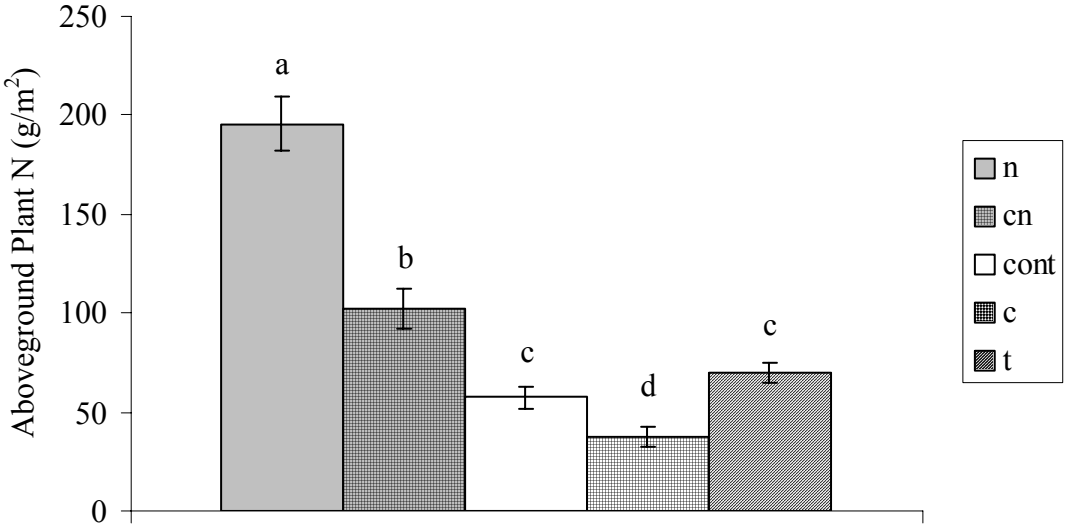


**Figure 1.9.** Effects of nitrogen addition (*shaded bars*), no nitrogen addition (*open bars*), carbon addition (*checkered bars*), no carbon addition (*open bars*), and thatch addition (*hatched bars*) on the nitrogen content (%) of aboveground *Spartina* measured at the end of the season (late August; blocked by year 2001, 2002). Means (mean $\pm$ SEM, n=12) with different letters are significantly different ($P<0.05$).

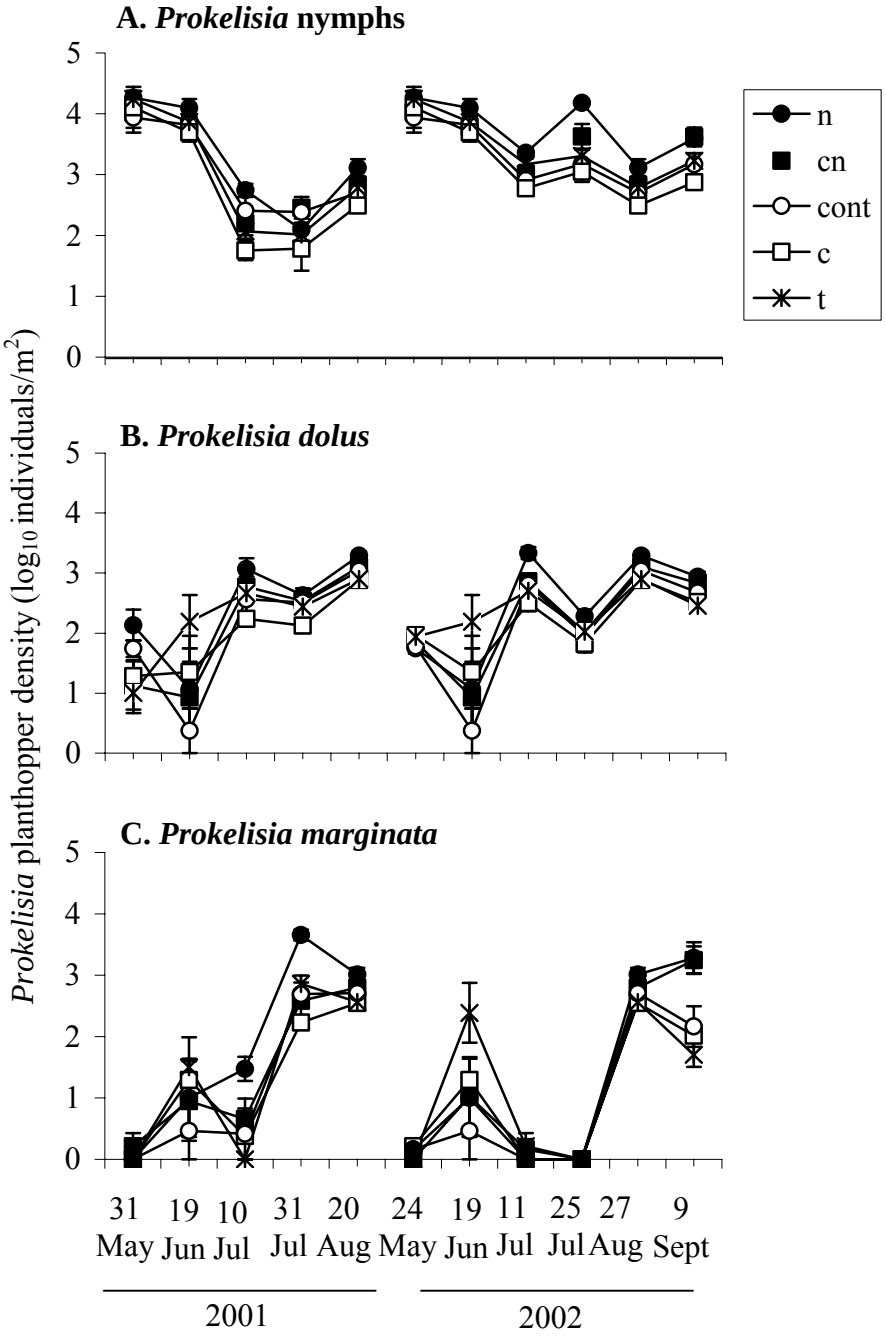


**Figure 1.10**. *Prokelisia* planthopper density (individuals/$m^2$, mean $\pm$ SEM, n=6) throughout the season in 2001 and 2002 in *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*). **A** *Prokelisia* nymphs, **B** adults of *P. dolus*, **C** adults of *P. marginata*.

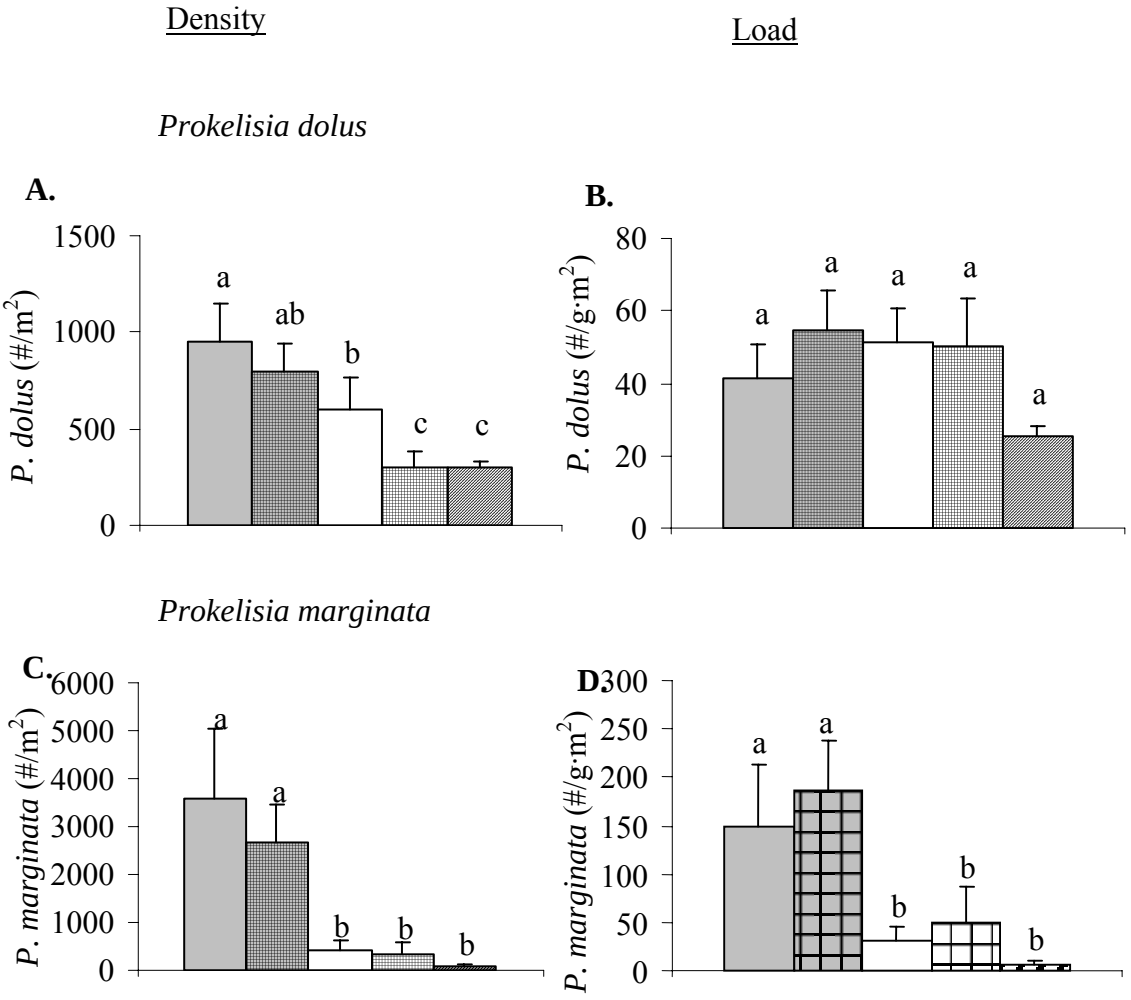


**Figure 1.11**. Effects of nitrogen addition (*shaded bars*), no nitrogen addition (*open bars*), carbon addition (*checkered bars*), no carbon addition (*open bars*), and thatch addition (*hatched bars*) on density (individuals/$m^2$ on the left) and load (individuals/g *Spartina*/$m^2$ on the right) of *Prokelisia dolus* (**A, B**) and *P. marginata* (**C, D**) measured at the end of the season (late August; blocked by year 2001, 2002) in plots of *Spartina*. Means (mean $\pm$ SEM, n=12) with different letters are significantly different ($P<0.05$).

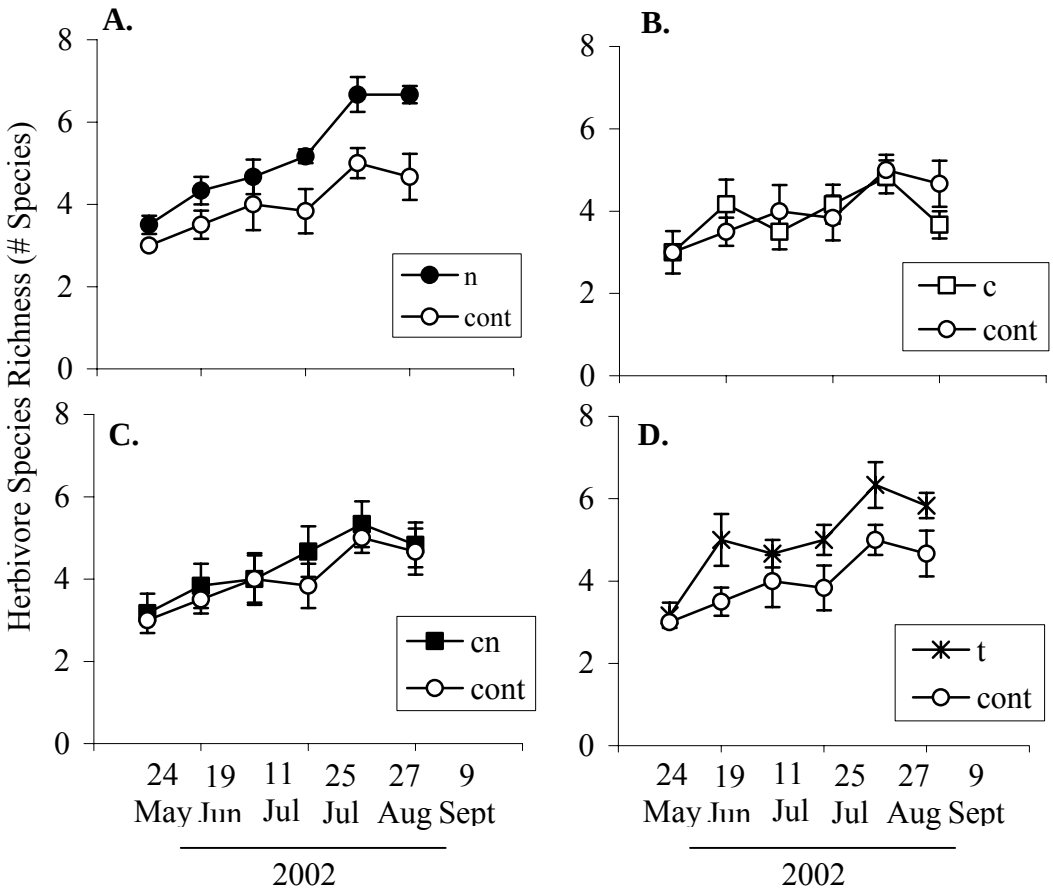


**Figure 1.12**. Species richness of herbivores (mean ± SEM, n=6) throughout the season (2002) in *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*).

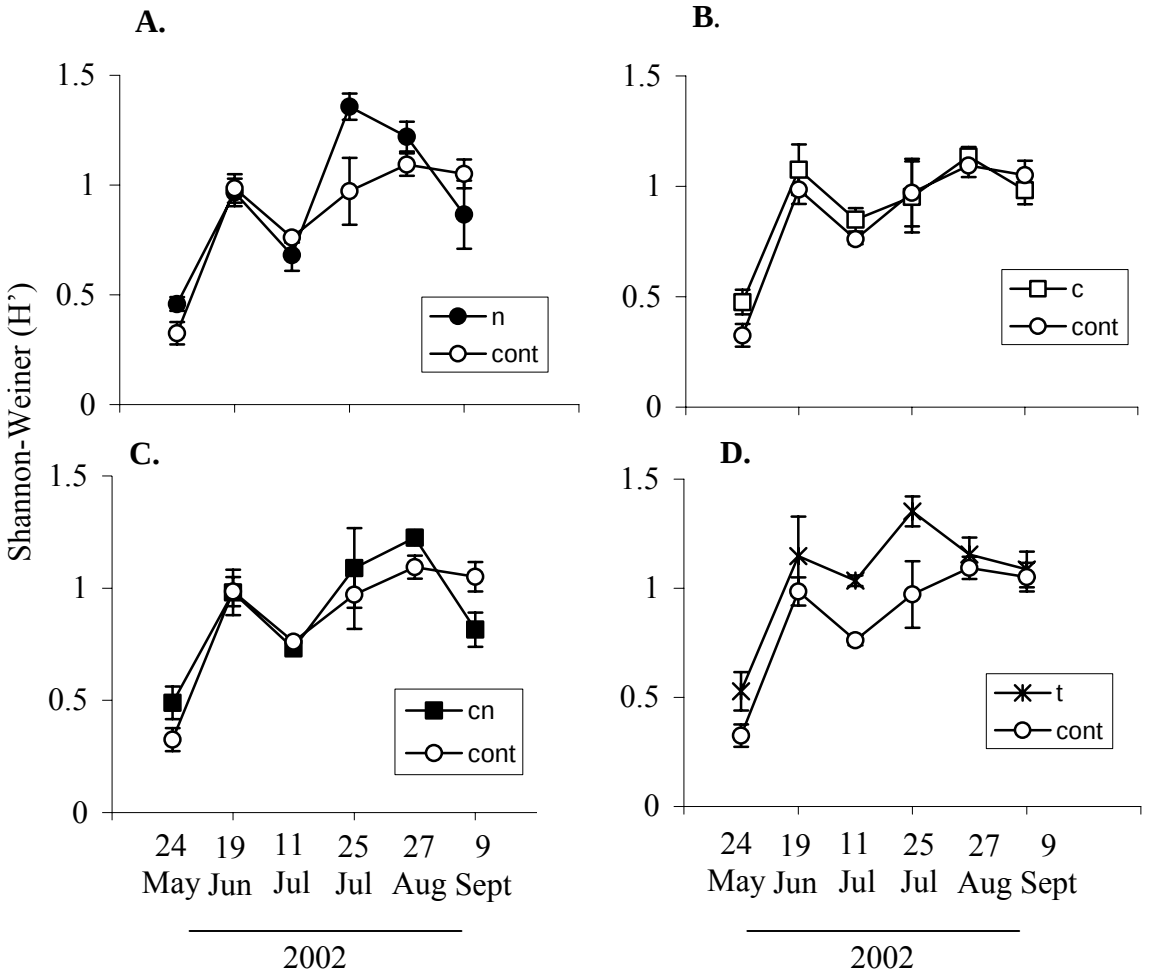


**Figure 1.13**. Diversity (H') of herbivores (mean ± SEM, n=6) throughout the season (2002) in *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*).

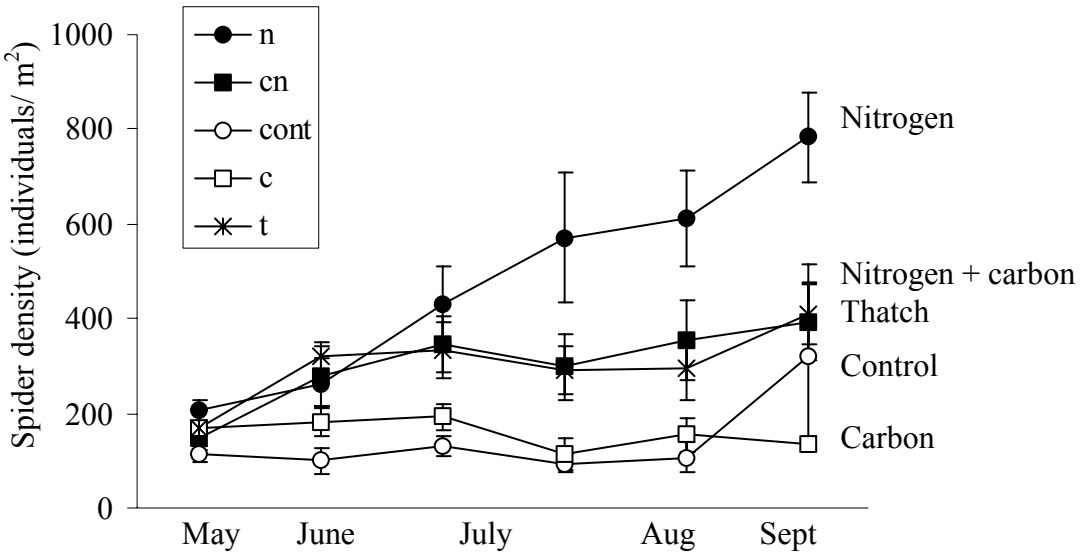


**Figure 1.14**. Spider density (individuals/$m^2$, mean $\pm$ SEM, n=12) throughout the season in 2001 and 2002 in *Spartina* plots exposed to one of five experimental treatments: Nitrogen (●), Carbon and nitrogen (■), Control-no nutrient addition (○), Carbon (□), and Thatch (*).

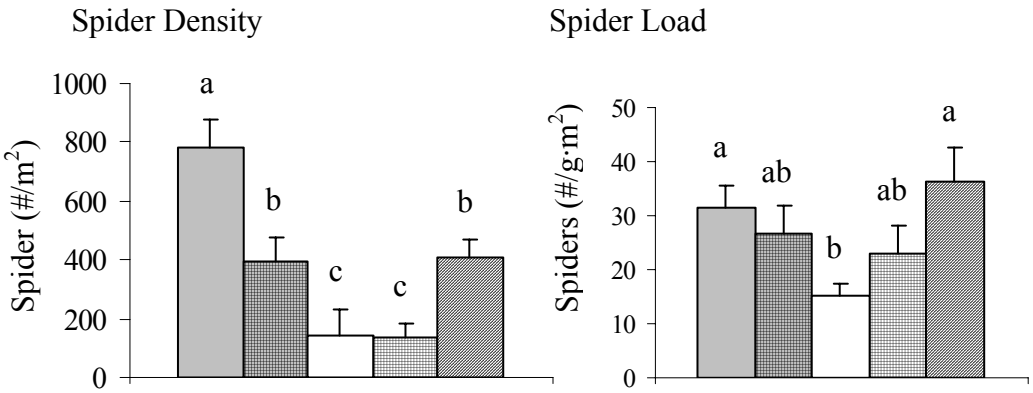


**Figure 1.15** Spider Density and Load. Effects of nitrogen addition (shaded bars), no nitrogen addition (open bars), carbon addition (checkered bars), no carbon addition (open bars), and thatch addition (hatched bars) on density (individuals/$m^2$ on the left) and load (individuals/g *Spartina*/$m^2$ on the right) of spiders measured at the end of the season (late August; blocked by year 2001, 2002) in plots of *Spartina*. Means (mean + SEM, n=12) with different letters are significantly different ($P<0.05$).

**Table 1.1.** Litter decomposition. Repeated measures ANOVA results for the effects of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time and their interaction on the nitrogen content (% dry mass) and C:N ratio of *Spartina* litter remaining in litterbags in 2 July-27 August 2002 on a marsh near Tuckerton, New Jersey. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction with time, and thatch. First order autoregressive variance covariance structure was used. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | | *Percent N* | | *C:N* | |
|---|---|---|---|---|---|
| | df[a] | F | p | F | p |
| Treatment | 4, 25 | 13.96 | **<.0001** | 5.44 | **0.003** |
| Nitrogen (N) | 1, 25 | 52.38 | **<.0001** | 19.73 | **0.0002** |
| Carbon (C) | 1, 25 | 3.33 | 0.08 | 0.05 | 0.83 |
| Thatch | 1,25 | 2.58 | 0.12 | 3.73 | 0.06 |
| N x C | 1, 25 | 0.00 | 0.99 | 1.99 | 0.17 |
| Time | 4, 100 | 36.28 | **<.0001** | 25.20 | **<.0001** |
| Trt x Time | 16, 100 | 1.92 | **0.02** | 1.09 | 0.38 |
| N x Time | 4, 100 | 4.64 | **0.001** | 2.31 | 0.06 |
| C x Time | 4, 100 | 0.48 | 0.75 | 0.31 | 0.87 |

a Degrees of freedom numerator, denominator

**Table 1.2.** Litter decomposition. Repeated measures ANOVA results for the effects of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time, and their interaction on the percent Ash Free Dry Weight (AFDW) and decomposition rate (*k*) of litter remaining in litterbags throughout the season and at the end of the season (27 August 2002). Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction with time, and thatch addition. First order autoregressive variance covariance structure was used. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| | **Source** | | **% AFDW** | | **k (day$^{-1}$)** | |
|---|---|---|---|---|---|---|
| | | df[a] | F | p | F | P |
| **Season** | Treatment | 4, 25 | 4.36 | **0.008** | 1.57 | .21 |
| | Nitrogen (N) | 1, 25 | 9.37 | **0.005** | 3.94 | 0.06 |
| | Carbon (C) | 1, 25 | 7.77 | **0.01** | 1.73 | 0.20 |
| | Thatch | 1, 25 | 0.00 | 0.96 | 0.01 | 0.92 |
| | C x N | 1, 25 | 0.31 | 0.58 | 0.59 | 0.44 |
| | Time | 4, 100 | 54.34 | **<.0001** | 66.47 | **<.0001** |
| | Treatment x Time | 16, 100 | 1.34 | 0.19 | 0.91 | 0.56 |
| | N x Time | 4, 100 | 2.30 | 0.06 | 0.73 | 0.57 |
| | C x Time | 4, 100 | 1.83 | 0.13 | 1.47 | 0.21 |
| **27 Aug 2002** | Treatment | 4, 25 | 6.07 | **0.0015** | 6.35 | **0.001** |
| | Nitrogen | 1, 25 | 11.00 | **0.0028** | 11.16 | **0.003** |
| | Carbon | 1, 25 | 12.58 | **0.0016** | 13.39 | **0.001** |
| | Thatch | 1, 25 | 0.37 | 0.55 | 0. 3 | 0.59 |
| | N x C | 1, 25 | 0.28 | 0.60 | 0.56 | 0.46 |

a Numerator, denominator degrees of freedom

**Table 1.3** Decomposition rate constants (mean $k \pm$ SEM, n=6) of litter remaining in litter bags after 56 days (27 August 2002) in *Spartina* plots treated with nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control field plots. Means with different letters are significantly different ($p<0.05$).

| Treatment | *k* mean | Standard error |
|---|---|---|
| Nitrogen | 0.011956[a] | 0.000648 |
| Carbon and Nitrogen | 0.008765[b] | 0.000566 |
| Thatch | 0.009549[b] | 0.000503 |
| Control | 0.008993[b] | 0.000897 |
| Carbon | 0.006943[c] | 0.000875 |

**Table 1.4.** Microbial activity. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time and their interaction on the net rate of N nitrification and mineralization and net $CO_2$ production in laboratory soil incubations in 2002. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction with time, and thatch. First order autoregressive variance covariance structure was used. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| Source | | Net nitrification (µg/g soil ·14 d) | | Net ammonification (µg/g soil ·14 d) | | Net C-mineralization ($CO_2$ g/ml) | |
|---|---|---|---|---|---|---|---|
| | *df*[a] | F | p | F | p | F | P |
| Treatment | 4, 25 | 16.62 | **<.0001** | 4.57 | **0.007** | 0.95 | 0.45 |
| Nitrogen (N) | 1, 25 | 55.87 | **<.0001** | 0.00 | 0.97 | 1.58 | 0.22 |
| Carbon (C) | 1, 25 | 1.33 | 0.26 | 14.44 | **0.0008** | 0.42 | 0.52 |
| Thatch | 1, 25 | 0.70 | 0.41 | 0.03 | 0.87 | 0.01 | 0.92 |
| N x C | 1, 25 | 0.35 | 0.56 | 4.12 | **0.05** | 1.36 | 0.25 |
| Time | 2, 48 | **33.82** | **<.0001** | 21.72 | **<.0001** | 3.68 | **0.03** |
| Trt x Time | 8, 48 | **2.99** | **0.008** | 0.85 | 0.57 | 1.14 | .35 |
| N x Time | 2, 48 | **6.39** | **0.004** | 0.03 | 0.97 | 1.23 | .37 |
| C x Time | 2, 48 | 0.18 | 0.83 | 0.79 | 0.46 | 1.31 | .32 |

Note: The soils were sampled on 19 June, 20 July, 22 August 2002
a. Numerator, denominator degrees of freedom

**Table 1.5.** Soil nitrogen pools. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time and their interaction on ammonium ($NH_4$-N), nitrate + nitrite ($NO_3$-N), Dissolved Organic Nitrogen (DON), and Microbial Nitrogen (Microbial N). Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction with time, and thatch. First order autoregressive variance covariance structure was used. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | | *$NH_4$-N* | | *$NO_3$-N* | | *DON* | | *Microbial N* | |
|---|---|---|---|---|---|---|---|---|---|
| | df[a] | F | *p* | F | *p* | F | *p* | F | *p* |
| Trt | 4, 25 | 8.60 | .0002 | 1.62 | 0.20 | 3.12 | **0.03** | 4.03 | **0.01** |
| Nitrogen (N) | 1, 25 | 29.92 | **<0.001** | 5.28 | **0.03** | 2.39 | 0.13 | 5.65 | **0.02** |
| Carbon (C) | 1, 25 | 1.16 | 0.29 | 1.02 | 0.32 | 8.71 | **.007** | 3.40 | 0.08 |
| Thatch | 1, 25 | 0.16 | 0.69 | 0.10 | 0.76 | 0.00 | 0.94 | 1.81 | 0.19 |
| N x C | 1, 25 | 0.28 | 0.60 | 0.04 | 0.85 | 0.38 | 0.54 | 5.65 | **0.03** |
| Time | 2, 49 | 14.92 | **<.0001** | 88.07 | **<.0001** | 46.81 | **<.0001** | 19.17 | **<.0001** |
| Trt x Time | 8, 49 | 1.88 | 0.08 | 1.52 | 0.17 | 0.82 | 0.59 | 1.33 | 0.25 |
| N x Time | 2, 49 | 5.11 | **0.01** | 4.79 | **0.01** | 0.78 | 0.46 | 2.78 | 0.07 |
| C x Time | 2, 49 | 0.33 | 0.72 | 0.12 | 0.89 | 2.04 | 0.14 | 1.40 | 0.26 |

Note: The soils were sampled on 19 June, 20 July, 22 August 2002
a degrees of freedom numerator, denominator

**Table 1.6.** Aboveground plant biomass. ANOVA results for the effects of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control) blocked by year (2001,2002) on aboveground plant biomass ($g/m^2$), plant height (cm) culm density ($culms/m^2$), and dead aboveground biomass ($g/m^2$). Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| Source | df[a] | Live aboveground biomass | | Plant Height | | Culm density | | Dead aboveground biomass | |
|---|---|---|---|---|---|---|---|---|---|
| | | F | *p* | F | *p* | F | *P* | F | *p* |
| Treatment | 4, 54 | 30.79 | **<.0001** | 15.49 | **<.0001** | 6.01 | **.0005** | 1.01 | 0.40 |
| Nitrogen | 1, 54 | 68.19 | **<.0001** | 41.55 | **<.0001** | 11.16 | **.001** | 1.30 | 0.26 |
| Carbon | 1, 54 | 41.95 | **<.0001** | 11.43 | **0.001** | 10.17 | **.002** | 0.53 | 0.47 |
| Thatch | 1, 54 | 0.01 | 0.94 | 12.28 | **0.0009** | 1.85 | 0.18 | 2.01 | 0.16 |
| N x C | 1, 54 | 8.28 | **0.006** | 4.47 | **0.04** | 0.27 | 0.60 | 0.90 | 0.34 |

a Numerator, denominator degrees of freedom.

**Table 1.7.** Belowground plant biomass. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time and their interaction on *Spartina* root biomass. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction with time, and thatch. First order autoregressive variance covariance structure was used. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | *df*[a] | *Root biomass* | |
|---|---|---|---|
| | | F | p |
| Treatment | 4, 25 | 1.68 | 0.18 |
| Nitrogen (N) | 1, 25 | 3.77 | 0.06 |
| Carbon (C) | 1, 25 | 0.06 | 0.81 |
| Thatch | 1, 25 | 0.47 | 0.50 |
| C x N | 1, 25 | 0.85 | 0.36 |
| Time | 2, 50 | 18.79 | **<.0001** |
| Treatment x Time | 8, 50 | 1.73 | 0.11 |
| N x Time | 2, 50 | 3.22 | **0.05** |
| C x Time | 2, 50 | 0.66 | 0.52 |

Note: Root Biomass was measured on 19 June, 20 July, 22 August 2002.
a degrees of freedom numerator, denominator

**Table 1.8.** Plant nitrogen content. Repeated measures ANOVA results for the effects of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time, and their interaction blocked by year (2001, 2002) on plant nitrogen content (%). First order autoregressive variance/covariance structure was used. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded p-values highlight significant treatment effects ($p<0.05$).

| Source | **df**[a] | % Nitrogen | |
|---|---|---|---|
| | | F | p |
| Treatment | 4, 4.58 | 32.22 | **0.001** |
| Nitrogen (N) | 1, 4.58 | 118.88 | **0.0002** |
| Carbon (C) | 1, 4.58 | 0.10 | 0.77 |
| Thatch | 1, 4.58 | 3.68 | 0.12 |
| N x C | 1, 4.58 | 1.18 | 0.33 |
| Time | 4, 4.93 | 0.57 | 0.70 |
| Treatment x Time | **16, 221** | **9.35** | <.0001 |
| C x Time | 4, 207 | 1.39 | 0.24 |
| N x Time | 4, 207 | 32.26 | **<.0001** |

Note: Plant nitrogen (%N) was sampled on 31 May, 19 June, 10 July, 31 July, 21 August 2001, and on 24 May, 19 June, 11 July, 25 July, 27 August 2002.
a. degrees of freedom numerator, denominator

**Table 1.9** Aboveground plant nitrogen. ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control) blocked by year (2001, 2002) on the total aboveground plant nitrogen ($g/m^2$). Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | *df*[a] | *Aboveground plant N* | |
|---|---|---|---|
| | | F | *p* |
| Treatment | 4, 54 | 64.19 | **<.0001** |
| Nitrogen (N) | 1, 54 | 167.86 | **<.0001** |
| Carbon (C) | 1, 54 | 51.83 | **<.0001** |
| Thatch | 1, 54 | 0.36 | 0.55 |
| N x C | 1, 54 | 21.76 | **<.0001** |

a. degrees of freedom numerator, denominator

**Table 1.10.** Herbivore density. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time, and their interaction on *Prokelisia* nymphs, *P. dolus*, and *P. marginata* (individuals/$m^2$) throughout the season, and one-way ANOVA results for the last sample date. First order autoregressive variance/covariance structure was used for the repeated measures analysis. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| | *Source* | *df*[a] | *Prokelisia nymphs*[b] | | *P. dolus*[b] | | *P. marginata*[b] | |
|---|---|---|---|---|---|---|---|---|
| | | | F | p | F | p | F | p |
| **Season** | Treatment | 4, 4 | 15.87 | **0.01** | 5.02 | 0.07 | 4.96 | 0.07 |
| | Nitrogen (N) | 1, 4 | 42.87 | **0.003** | 12.75 | **0.02** | 15.88 | **0.02** |
| | Carbon (C) | 1, 4 | 19.79 | **0.01** | 5.96 | 0.07 | 1.58 | 0.28 |
| | Thatch | 1, 4 | 0.21 | 0.67 | 0.02 | 0.91 | 0.02 | 0.88 |
| | N x C | 1, 4 | 0.09 | 0.78 | 0.75 | 0.43 | 0.50 | 0.52 |
| | Time | 5, 5 | 4.54 | 0.06 | 2.41 | 0.18 | 3.83 | 0.08 |
| | Trt x Time | 20, 320 | 1.67 | **0.04** | 1.64 | **0.04** | 5.11 | **<.0001** |
| | N x Time | 5, 320 | 2.23 | **0.05** | 1.52 | 0.18 | 9.33 | **<.0001** |
| | C x Time | 5, 320 | 20.6 | 0.07 | 0.98 | 0.43 | 1.26 | 0.28 |
| **End**[c] | Treatment | 4, 25 | 4.84 | **0.005** | 4.44 | **0.008** | 4.56 | **0.007** |
| | Nitrogen | 1, 25 | 15.16 | **0.0007** | 9.36 | **0.005** | 13.49 | **0.001** |
| | Carbon | 1, 25 | 0.00 | 0.99 | 2.68 | 0.11 | 0.44 | 0.51 |
| | Thatch | 1, 25 | 0.02 | 0.89 | 2.29 | 0.14 | 0.10 | 0.76 |
| | N x C | 1, 25 | 2.84 | 0.10 | 0.21 | 0.65 | 0.33 | 0.57 |

a. Degrees of freedom numerator, denominator
b. Number of individuals/$m^2$, log x + 1 transformed, for the season ANOVA
c. Sampled on 22 August 2001, and 9 Sept 2002

**Table 1.11** *Prokelisia* load. ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control) on *Prokelisia* planthopper load (number of *Prokelisia* nymphs, adults of *P. dolus*, and adults of *P. marginata*/g *Spartina*) at the end of the season (9 Sept 2002). Contrasts show the effect of nitrogen (addition, or not), carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| Source | df[a] | Nymph load | | P. dolus load | | P. marginata load | |
|---|---|---|---|---|---|---|---|
| | | F | p | F | p | F | p |
| Treatment | 4, 25 | 2.95 | **0.04** | 1.42 | 0.26 | 3.61 | **0.02** |
| Nitrogen (N) | 1, 25 | 4.27 | **0.05** | 0.13 | 0.73 | 9.47 | **0.0005** |
| Carbon (C) | 1, 25 | 1.33 | 0.26 | 0.46 | 0.50 | 0.44 | 0.51 |
| Thatch | 1, 25 | 0.01 | 0.91 | 3.34 | 0.08 | 0.18 | 0.67 |
| N x C | 1, 25 | 5.97 | **0.02** | 0.50 | 0.49 | 0.05 | 0.83 |

a degrees of freedom numerator, denominator

**Table 1.12.** Herbivore diversity. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time, and their interaction on the diversity (H') and richness (# species/sample) of herbivorous insects in *Spartina* plots during 2002. First order autoregressive variance/covariance structure was used. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interactions, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| Source | $df^a$ | Shannon-Weiner (H') | | $df^a$ | Species richness | |
|---|---|---|---|---|---|---|
| | | F | *p* | | F | *P* |
| Treatment (Trt) | 4, 53.2 | 3.31 | **0.02** | 4, 51.1 | 7.88 | **<.0001** |
| Nitrogen (N) | 1, 53.2 | 0.21 | 0.65 | 1, 51.1 | 14.61 | **0.0004** |
| Carbon (C) | 1, 53.2 | 0.02 | 0.88 | 1, 51.1 | 5.51 | **0.02** |
| Thatch | 1, 53.2 | 10.98 | **0.002** | 1, 51.1 | 11.65 | **0.001** |
| N x C | 1, 53.2 | 1.10 | 0.29 | 1, 51.1 | 3.28 | 0.08 |
| Time | 5, 98.6 | 44.51 | **<.0001** | 5, 119 | 16.53 | **<.0001** |
| Trt x Time | 20, 98.6 | 1.45 | 0.12 | 20, 125 | 0.86 | 0.64 |
| N x Time | 1, 53.2 | 0.21 | 0.65 | 5, 119 | 1.10 | 0.36 |
| C x Time | 1, 53.2 | 0.02 | 0.89 | 5, 119 | 1.47 | 0.21 |

a degrees of freedom numerator, denominator

**Table 1.13** Spider density. Repeated measures ANOVA results for the effect of treatment (nitrogen, carbon, carbon and nitrogen, thatch, or unmanipulated control), time, and their interaction, blocked by year (2001, 2002) on spider density (individuals/$m^2$). First order autoregressive variance/covariance structure was used. Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | *df*[a] | Spider density | |
|---|---|---|---|
| | | F | *p* |
| Treatment | 4, 329 | 19.46 | **<.0001** |
| Nitrogen (N) | 1, 329 | 40.86 | **<.0001** |
| Carbon (C) | 1, 329 | 12.74 | **<.0001** |
| Thatch | 1, 329 | 17.45 | **<.0001** |
| C x N | 1, 329 | 19.35 | **<.0001** |
| Time | 5, 329 | 7.40 | 0.18 |
| Time x Treatment | 20, 329 | 2.45 | **0.0006** |
| Time x N | 5, 329 | 2.89 | **.01** |
| Time x C | 5, 329 | 2.93 | **0.01** |

a degrees of freedom numerator, denominator

**Table 1.14** Spider load. ANOVA results for the effect of treatment blocked by year (2001, 2002) on the end of the season spider load (individuals ·g *Spartina*$^{-1}$·m$^{-2}$). Contrasts show the main effects of Nitrogen (addition or not), Carbon (addition or not), their interaction, and thatch. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| *Source* | df[a] | Spider Load | |
|---|---|---|---|
| | | F | *p* |
| Treatment | 4, 25 | 3.69 | **0.01** |
| Nitrogen (N) | 1, 25 | 5.72 | **0.02** |
| Carbon (C) | 1, 25 | 0.38 | 0.54 |
| Thatch | 1, 25 | 12.82 | **0.001** |
| C x N | 1, 25 | 2.63 | 0.12 |

a degrees of freedom numerator, denominator

**Table 1.15.** Correlation matrix showing the relationship between spider density, *Prokelisia* density, and *Spartina* biomass on samples taken from treatment plots in 2001, and 2002.

| Spider | ***P. dolus*** | ***P. marginata*** | **Vegetation complexity** |
|---|---|---|---|
| $r^r$ | 0.26 | 0.21 | 0.53 |
| *p* | **<.0001** | **<.0001** | **<.0001** |
| N | 360 | 360 | 121 |

CHAPTER 2

## Direct effects of leaf-litter complexity on herbivore survival and performance

### INTRODUCTION

Understanding variation in the abundance of herbivorous insects on plants, and which plant traits contribute to variation in the density of insect herbivores, has been a central focus in population ecology for decades (White 1993, Jonsen and Fahrig 1997, Dixon and Kundu 1998, Agrawal 2000). Traditionally researchers have focused on characteristics of living plants such as plant nutrition (Mattson 1980, Awmack and Leather 2002), allelochemistry (Zangerl and Bazzaz 1992), plant density (Bach 1980, Solomon 1981, Shea et al. 2000), and patch size (Kareiva 1985, Bach 1988), as they affect the distribution and abundance of insect herbivores. In contrast, there has been very little focus on how the presence of dead plant material or leaf litter might directly impact herbivore fitness (Denno and Roderick 1991, Long et al. 2003). When it accumulates at the base of plants in grassland systems, leaf litter forms a complex lattice of thatch, which alters the structure of the environment for invertebrate arthropods associated with the living parts of plants and thus adds a component of habitat complexity (Brewer et al. 1998, Emery et al. 2001, Bertness and Ewanchuk 2002). Leaf litter has the potential to suppress herbivore populations directly by pre-empting feeding or oviposition sites and by intensifying competitive interactions for these limited sites. Although it is well known that herbivores compete for limiting resources (McClure 1980, Whitham 1986, Denno and Peterson 1995), and that live plant structural defenses such as trichomes (Traw and Dawson 2002, Dalin and Bjorkman 2003) and thorns (Gomez and Zamora 2002) can deny herbivores access to feeding and oviposition sites on plant stems and

leaves, there has been little investigation of leaf litter as a structural deterrent to herbivory, or how competitive interactions for remaining feeding and oviposition sites are affected by high amounts of leaf litter. For example, many herbivores show strong oviposition preference for basal plant stems where they are more concealed from predators and parasites (Raatikainen 1967, Whitham 1986, Ferrenberg and Denno 2003). However in areas with high herbivore densities and intense competition for oviposition sites, herbivores are forced to oviposit in less preferred apical leaves where they have lower survivorship rates due to competition, predation, and parasitism (Raatikainen 1967, Whitham 1986). If thatch envelopes basal resources on host plant stems, crowds herbivores, or denies them access to preferred oviposition sites, they may oviposit fewer eggs or place eggs on leaves in areas of the plant that will be more susceptible to parasitism and predation. Coupled with the fact that invertebrate predators such as spiders aggregate in complex habitats rich in leaf litter (Langellotto and Denno 2004), dead plant material has the potential to limit herbivores via restricted resource availability and increased predator aggregation.

Enhanced habitat complexity, characteristic of increases in leaf litter, often results in greater variation in microclimate due to differences in temperature (Andow 1991), and light exposure (Risch 1981). Ambient temperature surrounding host plants can be a strong determinant of insect abundance, development time, and body size (Stamp and Bowers 1990, Trumbule and Denno 1995, Shrewsbury and Raupp 2000). Abundance of leaf litter thatch could provide pockets of microhabitat that are cooler and shadier and may increase the development time and decrease the body size of herbivores living in such habitats.

Not only does leaf litter have the potential to directly impact herbivores by serving as an element of habitat complexity that influences access to resources and alters microclimate, but it can also indirectly affect herbivores by altering the nutrient resources of their host plants during decomposition (Valiela et al. 1984, Valiela et al. 1985, Chapter 1). Although, microbial decomposition can release nitrogen resources from leaf litter for plant uptake (Hobbie and Vitousek 2000), slow decomposition and microbial nutrient immobilization can result in lower nitrogen availability for plants and ultimately the herbivores that consume them (Jingguo and Bakken 1997, Hooper et al. 2000). Although it is not considered as part of a plant's defensive repertoire, detritus has strong potential to negatively impact aboveground herbivores by denying access to resources, intensifying competitive interactions, supporting increased aggregations of predators, unfavorably altering microclimate, and decreasing plant quality via microbial immobilization of nitrogen.

I investigated a plant-herbivore-detritus interaction involving a native wetland cord grass, *Spartina alterniflora*, and one of the abundant herbivores, the planthopper *Prokelisia marginata,* that feeds exclusively on this host plant. In a laboratory mesocosm experiment I isolated the direct structural effect of detritus from potential indirect (microbial or predator) effects by excluding predators and comparing the addition of natural thatch to a non-decomposing artificial thatch supplement, and measuring their impact on (1) planthopper fitness and performance, and (2) on the vertical distribution of planthopper eggs on their host plant. Temperature was also assessed across treatments to elucidate whether or not any effects of thatch on planthopper distribution or fitness were mediated by changes in microclimate. I hypothesized that by surrounding the basal

portion of plants, both natural and artificial detritus would limit herbivore fitness by restricting available feeding and oviposition space. Thus, I predicted adverse affects on survivorship, development time, and body size of herbivores feeding on plants surrounded by a basal latticework of thatch

## METHODS

### *Study system*

The mid-Atlantic salt marsh is an ideal study system for investigating the direct effect of detritus (thatch) on insect herbivores because there is variation in the distribution and abundance of detritus and thus habitat complexity across the marsh. *Spartina alterniflora*, a perennial cordgrass is the dominant vegetation in mid-Atlantic intertidal salt marshes (Blum 1968, Emery et al. 2001, Bertness and Ewanchuk 2002). Although it can be found growing in expansive monotypic stands, the structural complexity of these habitats varies across the marsh due to differences in *S. alterniflora* height and the abundance its leaf litter (Brewer et al. 1998, Pennings and Richards 1998). Larger more complex tall-form plants are found at lower elevation near tidal creaks, whereas smaller, less complex short-form plants grow in high marsh meadows (Blum 1968, Denno et al. 2002). Habitat complexity is also altered by the differential accumulation and deposition of *S. alterniflora* leaf litter thatch, which creates a patchy lattice of detritus at the base of cord grass plants (Pennings and Richards 1998, Denno et al. 2002). Mud flat habitats in the high marsh are characterized by structurally simple *S. alterniflora* plants that are devoid of thatch (Denno et al. 2002). However in high marsh meadows thatch can accumulate up to 20 cm above the top of the living shoot canopy for the majority of the winter and early spring (Newell et al. 1998). Although normal tides

wet thatch and compress it into a dense lattice at the base of plants, tidal surges during storms commonly burry large patches of *S. alterniflora* with wrack, or large mats of thatch (Brewer et al. 1998). Thus, change in plant structure and tidal flushing across the marsh result in variation from both autochthonous and allochthonous inputs of leaf litter (Teal 1962, Pennings and Richards 1998).

*S. alterniflora* is the only local host-plant of the planthopper *Prokelisia marginata*, one of the dominant salt marsh herbivores (Denno et al. 2003). These monophagous phloem-feeding insects are sensitive to crowding and host plant nutrition (Denno et al. 2000). They over-winter as nymphs in high marsh *S. alterniflora* meadows before they migrate to the larger creek-side plants where they develop during the summer months. When they migrate between low marsh and high marsh habitats, *P. marginata* selectively colonize patches of high quality host plants (Denno et al. 1996).

*Herbivore performance and fitness*

The direct effects of thatch on the fitness and performance of planthoppers (*Prokelisia marginata*) were assessed using a manipulative experiment in which thatch, both natural (300 g/$m^2$, or 15 g/mesocosm) and artificial (400g/$m^2$, or 20 g/mesocosm), was either added or not to the base of plants in laboratory mesocosms. The amount of natural thatch added to mesocosms was within the range of ambient levels of thatch occurring in the early summer on the marsh (Döbel and Denno 1994, Newell et al. 1998). To control for any potential indirect effects of thatch decomposition on herbivores via altered host-plant quality, an artificial-thatch treatment (20cm long x 0.2 cm wide synthetic fiber) was included in order to mimic the structural complexity of thatch without any potential nutritional effects (carbon or nitrogen inputs).

Each mesocosm consisted of 8 *Spartina alterniflora* plants (30 cm tall) grown from seed in a pot (24 cm diameter) filled with autoclaved sand. The plants in each pot were enclosed in a plastic tube cage (21.5 cm diameter X 30 cm high) and capped with an organdy mesh cover. Pots were maintained in plastic wading pools filled with water in the laboratory at 23ºC on a 16:8 (light:dark) daily cycle. The experimental design was a randomized complete block, blocked by year (2001, 2002) and by wading pool (1-4), with three treatments (natural thatch addition, artificial thatch addition, and no thatch addition) replicated 3 times (3 treatments x 3 replicates x 4 pools x 2 years= 72 pots).

I added 25 second instar *P. marginata* nymphs to each pot, and measured thatch treatment effects on their survivorship, development time (days), and body size as indexed by hind-tibia length (mm). The effects of thatch on planthopper fitness (survivorship, development time, body size) were tested using ANOVA with treatment as a fixed effect, and year, pool, and their interaction as random effects (Proc Mixed, SAS 1998).

*Number and distribution of eggs*

To determine if thatch alters the number or vertical distribution of planthopper eggs on living *Spartina* plants, I conducted another randomized complete block experiment in laboratory mesocosms. I placed 15 field-collected adult females and 5 adult males of *P. marginata* in mesocosms to which natural thatch (8 g/mesocosm) was either added to the base of the plants or withheld. The amount and arrangement of thatch was designed to mimic early summer, high-thatch conditions on the marsh (Döbel and Denno 1994, Newell et al. 1998). Each mesocosm contained 3 *Spartina* plants (30 cm

tall) grown from seed in 10.15 X 10.15 cm square pots filled with autoclaved sand. Plastic tube cages (7.5 cm diameter X 30 cm high) covered in organdy mesh enclosed the salt marsh mesocosms. Plant roots were kept inundated by placing the pots in plastic tubs filled with water. After female planthoppers were allowed to oviposit on their host plants for 15 days, plants were harvested and stained with Acid Fuchsin (J.T. Baker Inc.), which highlighted the presence and location of planthopper eggs. Planthopper eggs were counted, and their location on the plant (height aboveground in cm) was scored. A t-test was used to compare the total number of eggs laid when thatch was present and absent (SAS, 1998). To compare the distribution of eggs laid at different heights on the plants in the presence and absence of thatch, I divided the *Spartina* plants (30 cm in height) into 4 quarters (0-7.5cm, 7.5-15cm, 15-22.5cm, and 22.5-30cm) and counted the number of eggs laid in each successive plant quarter. I used a two-way ANOVA with thatch treatment (addition or not) and location of eggs (4 plant height quarters) as fixed factors to determine the effect of thatch on number and location of eggs laid (SAS, 1998).

*Microclimate*

To determine if thatch addition altered the microclimate within the mesocosms, which in turn might alter herbivore fitness or performance, I assessed the temperature in areas either shaded or not shaded by thatch. For both of the above experiments, temperature was measured once at a height of 5 cm above the ground (below the level of thatch in thatch addition mesocosms) and once at 20 cm above the ground (above the level of thatch in thatch addition mesocosms) in all mesocosms. Analysis of variance of the differences between temperature above and below the level of thatch among treatments tested the effect of thatch treatments on mesocosm temperature.

## RESULTS

### *Herbivore performance and fitness*

Both natural and artificial thatch treatments had a general negative effect on several measures of planthopper performance (Figures 2.1-3). For example, the addition of thatch adversely affected planthopper survivorship (pooled males and females; $F_{2,65}$=3.37, $p$=0.04; Table 2.1), whereby fewer planthoppers survived in both natural and artificial thatch addition treatments (Figure 2.1). Moreover, males were significantly smaller in both thatch addition treatments compared to controls ($F_{2,65}$=4.04, $p$=0.01; Table 2.1, Figure 2.2A). Neither natural nor artificial thatch addition affected female body size ($F_{2,65}$= 0.46, $p$=0.64; Table 2.1, Figure 2.2 B), although females were significantly larger than males (1.54 $\pm$ 0.008 males vs. 1.60 $\pm$ 0.001, mean $\pm$ SEM, n=72; Figure 2.2). Last, there was a non-significant trend toward prolonged development time in the thatch addition treatments (Table 2.1, Figure 2.3). Regardless, variation in mean development time across treatments spanned only one day and was therefore not likely to be biologically relevant.

### *Number and distribution of eggs*

Thatch addition did not affect the total number of eggs laid in *Spartina* plants ($T_{1,18}$=1.24, $p$=0.28; Table 2.2, Figure 2.4). Although the presence of thatch did not effect the vertical distribution of *P. marginata* eggs laid in *Spartina* ($F_{1,68}$=0.01, $p$=0.91; Table 2.3, Figure 2.5), planthoppers did selectively oviposit in basal portions of the plant compared to the more apical plant quarters independent of the thatch addition treatment

($F_{3,68}$=11.39, $p$<.001; Table 2.3, Figure 2.5). As expected, *P. marginata* selectively oviposited in leaf blades close to the central stem (personal observation).

*Microclimate*

There was no overall effect of the thatch treatments on temperature either in the performance experiment ( $F_{2,69}$=0.87, $p$=0.42; Table 2.4, Figure 2.6 A) or the oviposition experiment ($F_{1,19}$=0.93, $p$=0 34; Table 2.4, Figure 2.6 B).

## DISCUSSION

The performance and population dynamics of insect herbivores have been linked to a variety of aspects of plant quality including nutrition (Awmack and Leather 2002, Fagan et al. 2002), allelochemistry (Sagers and Coley 1995), and the architecture and spacing of living plants (Rausher 1981, Kareiva 1983, Bach 1988, Shea et al. 2000). In most of these studies, plants directly affected herbivores by altering either the quality or abundance of their food resource (Shea et al. 2000, Awmack and Leather 2002). Although the influence of background matrix vegetation on herbivore search and oviposition has received noteworthy attention (Rausher 1981, Kareiva 1983, Haddad et al. 2001), the direct effects of vegetation structure on herbivore performance have been less well investigated. Better known are the indirect effects of vegetation structure on herbivores via its mediating effects on natural enemies (Denno et al. 2002, Lewis and Eby 2002, Cronin 2003). One inherent component of vegetation texture that has the potential to influence herbivore fitness is the structure of the detrital layer (leaf litter thatch) that accumulates underneath plants. In some plant communities the litter layer

can be extensive (Bultman and Uetz 1984, Long et al. 2003), and it is a predominant structural component of many intertidal habitats where allochthonous inputs of wrack occur (Brewer et al. 1998, Pennings and Richards 1998). This is particularly true in mid-Atlantic coastal salt marshes where tidal effects on delivery and decomposition result in extreme variation in the amount of accumulated thatch across habitats (Pennings and Richards 1998, Denno et al. 2002). Thus, this system provided an ideal opportunity to explore the direct effects of thatch on herbivore survival and performance beyond those involving the mediating effects of thatch on natural-enemy impacts (see (Döbel and Denno 1994, Denno et al. 2002, Langellotto and Denno 2004).

Because thatch surrounds the basal portion of living plants, often extensively (Pennings and Richards 1998), it has the potential to indirectly influence conditions for the feeding and oviposition of herbivores. This may occur because it restricts optimal feeding and oviposition space eliminating some sites altogether, by concentrating herbivores and intensifying competitive effects, or by altering microclimate. Alternatively, thatch as it decays provides resources for microbes that may affect soil nitrogen pools and ultimately the nutritional quality of plants growing in those soils (Jingguo and Bakken 1997, Bardgett et al. 2003). Using both natural and artificial thatch in laboratory mesocosms and measuring its effects on herbivore performance and oviposition, my experiments were designed to isolate the potential structural effects of thatch from those involving decomposition.

I found that thatch does indeed impose adverse consequences for the survival and performance of *Prokelisia marginata*, an abundant herbivore that typically encounters a range of habitats that vary in structural complexity and the amount of thatch (Denno et al.

2000, Denno et al. 2002). Specifically, overall survivorship and male body size (not female body size) were adversely affected by the presence of leaf litter thatch. There was no evidence that thatch affected either the number (Figure 2.4) or distribution (Figure 2.5) of eggs laid by female *P. marginata.* Previous studies examining competitive interactions between planthoppers on the salt marsh have shown that males and females partition their host plant resources differently; females remain relatively sessile in leaf junctions, whereas males of some species (including *Prokelisia*) distribute themselves more evenly and forage on the entire plant (Ferrenberg and Denno 2003). I found that females were overall larger than males (Figure 2.2). When resources such as feeding sites are limited, body size often dictates the outcome of competition. Larger aphids were more likely to win in intraspecific competitive interactions, and gain access to preferred basal positions on narrowleaf cottonwood, *Populus angustifolia,* leaves (Whitham 1986). Therefore factors such as thatch, that have the potential to limit access to optimal feeding sites and increase competitive interactions between herbivores, can limit herbivore populations and place a strong selective pressure on herbivore body size. Thus, it is possible that thatch 1) impeded movement of male planthoppers on their host plant resulting in less time spent feeding in optimal sites, and 2) intensified competitive interactions between planthoppers such that larger females were able to dominate males and gain access to preferred feeding and oviposition sites.

Most notable was the finding that both natural and artificial thatch imposed similar negative effects on planthopper survival and male body size (Figures 2.1, 2.2). This result suggests that it is the structural aspect of thatch and not any indirect effect of its decomposition on *Spartina* quality that affected planthopper performance in this

experiment. Previous studies have found that *P. marginata* is highly sensitive to both intra and interspecific competition, whereby it showed decreased survivorship, increased development time, and decreased body size when reared under crowded conditions (Denno and Roderick 1992, Denno et al. 2000). This study showed that increasing vegetation complexity (detritus addition) had similar effects on planthopper performance suggesting an underlying competitive mechanism (Sogawa 1982, Denno and Roderick 1992). Previous studies have attributed adverse affects of competition on planthopper performance to feeding induced changes in plant physiology at high insect density or density-related modifications of insect feeding behavior (Sogawa 1982, Denno and Roderick 1992). However, because insect density was not manipulated in this study my results suggest that induced changes in plant physiology due to high insect density was not likely responsible for decreased survival and body size. Moreover, microclimate was not affected by addition of thatch (Figure 2.6). Therefore, it is more likely that the presence of thatch adversely affected *P. marginata* by preempting feeding sites and thus intensifying competition for the remaining sites.

Although detritus has more often been considered a nutrient resource for the belowground food web (Vitousek et al. 1998, Hobbie 2000), my study suggests that it can mediate aboveground plant-herbivore interactions in even more complex ways. Feedback loops from the belowground food web can limit herbivores by altering host plant quality after immobilizing nutrients in the soil microbial biomass (Hodge et al. 2000, Hooper et al. 2000, Bardgett et al. 2003). Furthermore, previous studies have found that thatch increases the aggregative behavior of predators and limits intraguild predation leading to the enhanced suppression of herbivores (Finke and Denno 2002,

Langellotto and Denno 2004). Specifically, my results show that thatch has the potential to adversely affect aboveground herbivores directly by decreasing survivorship and male body size by pre-empting feeding sites and thus intensifying competition.

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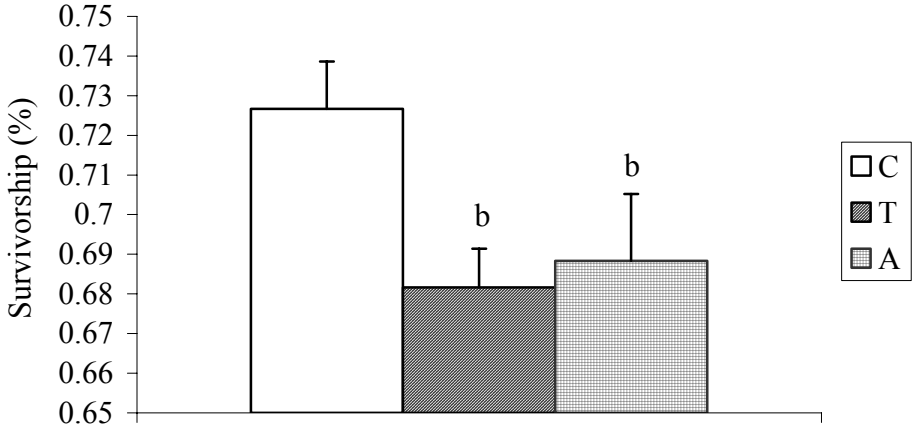


**Figure 2.1.** Survivorship (nymph to adult) of *Prokelisia marginata* nymphs reared on *Spartina alterniflora* under conditions of no thatch addition (open bar), natural thatch addition (hatched bar), and artificial thatch addition (square checkered bar) in laboratory mesocosms. Means with different letters are significantly different ($p<0.05$).

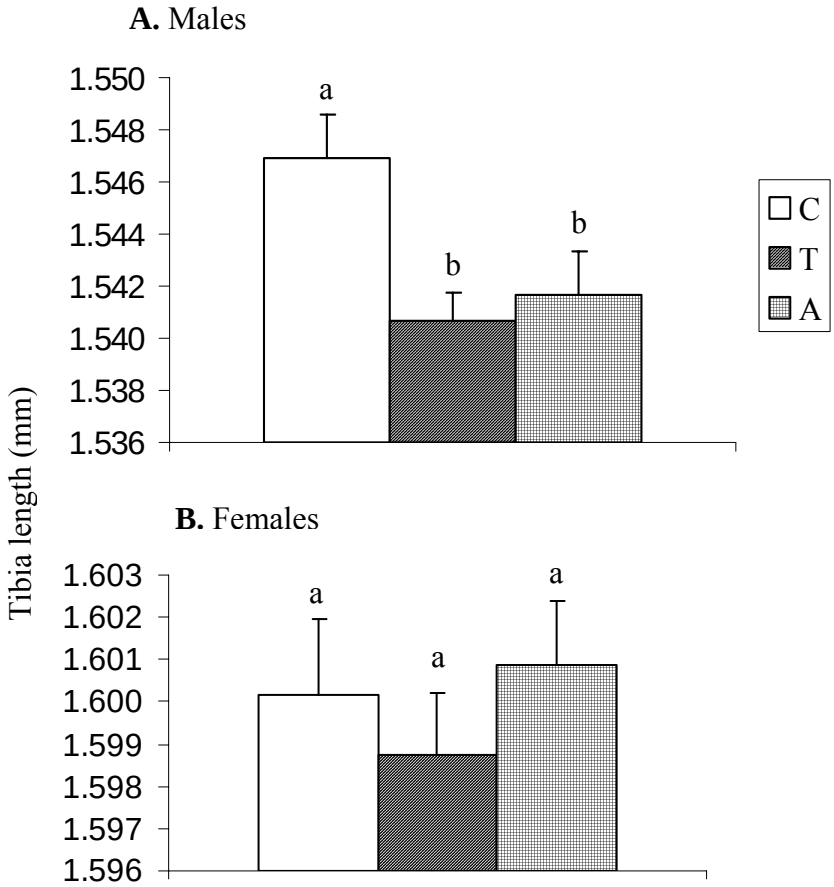


**Figure 2.2**. Body size (mean ± SEM, n=24) of the males (**A**) and females (**B**) of *Prokelisia marginata* raised on *Spartina alterniflora* in laboratory mesocosms under conditions of no thatch addition (open bar), natural thatch addition (hatched bar), and artificial thatch addition (square checkered bar) in laboratory mesocosms. Means with different letters are significantly different ($p<0.05$).

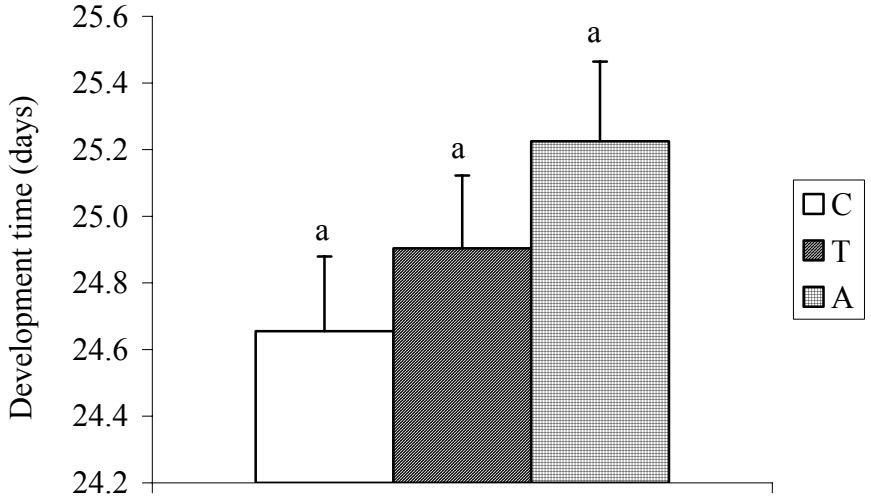


**Figure 2.3.** Development time in days of *Prokelisia marginata* planthoppers reared on *S. alterniflora* in laboratory mesocosms under conditions of no thatch addition (open bar), natural thatch addition (hatched bar), and artificial thatch addition (square checkered bar) in laboratory mesocosms. Means marked with the same letter are not significantly different ($p$>0.05).

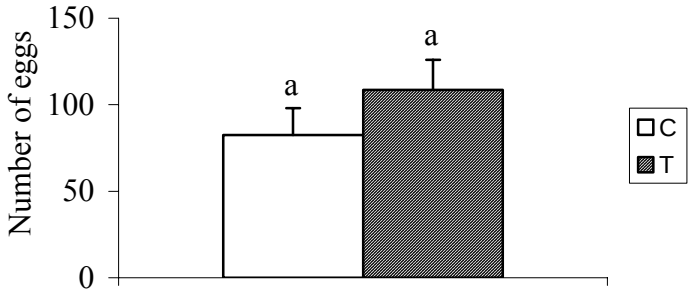


**Figure 2.4.** Total number of eggs laid by *P. marginata* in *Spartina alterniflora* plants under conditions of no thatch (open bar) and natural thatch addition (hatched bar) in laboratory mesocosms. Means marked with the same letter are not significantly different ($p$>0.05).

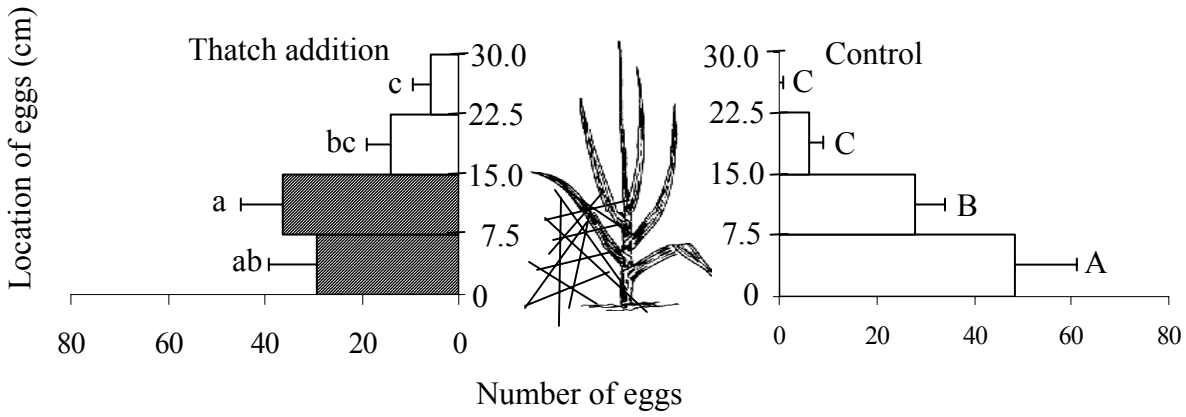


**Figure 2.5.** Distribution of *Prokelisia marginata* eggs on *Spartina alterniflora* plants (30 cm height) when thatch was present or absent in laboratory mesocosms. Each plant was divided into 4 quarters, and each bar represents the number of eggs laid on successive 7.5 cm sections of plant. Hatched bars indicate eggs laid below the level of thatch in the thatch addition treatment. Open bars indicate no thatch addition, or eggs laid above the level of the thatch. Means with different letters (control-CAPITAL, thatch addition-lower case) are significantly different ($p<0.05$).

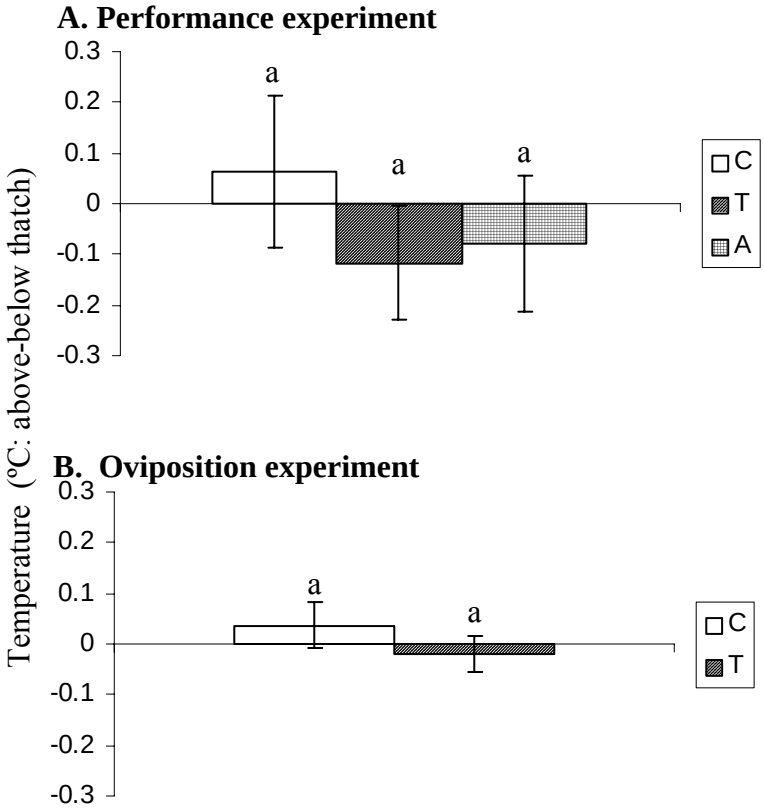


**Figure 2.6** Difference in temperature (mean ºC ± SEM, **A.** n=24, **B.** n=10) between measurements taken at 5 cm above the sediment (below the level of thatch in thatch addition treatments) and 20 cm above the sediment (above the level of thatch in thatch addition treatments) in laboratory mesocosms. Open bars indicate control no thatch addition, hatched bars indicate natural thatch addition, and square checkered bars indicate artificial thatch addition. Same letters indicate no significant difference between treatments ($p$>0.05).

**Table 2.1** ANOVA results for the effect of thatch treatment (no thatch, natural thatch, artificial thatch) on the survivorship, development time (pooled males and females), and body size as indexed by tibia length (reported separately for males and females) of *Prokelisia marginata*. Bolded *p*-values highlight significant treatment effects ($p<0.05$).

| Source | *Df*[1] | Survivorship | | Development Time | | Tibia Length (males) | | Tibia Length (females) | |
|---|---|---|---|---|---|---|---|---|---|
| | | F | *p* | F | *p* | F | *p* | F | |
| Treatment | 2, 65 | 3.37 | **0.04** | 1.57 | 0.21 | 4.94 | **0.01** | 0.46 | 0.63 |
| Year | 1, 65 | 0.76 | 0.38 | 0.28 | 0.59 | 0.51 | 0.47 | 0.11 | 0.74 |
| Pool | 3, 65 | 0.97 | 0.41 | 1.17 | 0.32 | 1.15 | 0.33 | 0.95 | 0.42 |

1. degrees of freedom numerator, denominator.

**Table 2.2.** T-test results showing the effect of thatch addition (present or absent) on the total number of *P. marginata* eggs laid in *Spartina* plants in laboratory mesocosms.

| *Source* | *df* | T | *p* |
|---|---|---|---|
| Treatment | 1, 18 | 1.24 | 0.28 |

**Table 2.3.** ANOVA results showing the effect of thatch (present or absent) and height along the plant (plants were divided into four quarters from bottom to top) on the number of eggs laid by *Prokelisia marginata* in *Spartina* plants caged inlaboratory mesocosms. Bolded *p*-values indicate significant difference ($p<0.05$).

| Source | *df*[a] | F | *p* |
|---|---|---|---|
| Treatment (Trt) | 1, 68 | 0.01 | 0.91 |
| Quarter | 3, 68 | 11.39 | **<.0001** |
| Trt x Quarter | 3, 68 | 1.75 | 0.165 |

a. degrees of freedom numerator, denominator