The influence of the marsh grasshopper, *Orchelium fidicinium,* on nutrient cycling and productivity of *Spartina alterniflora* in a salt marsh environment

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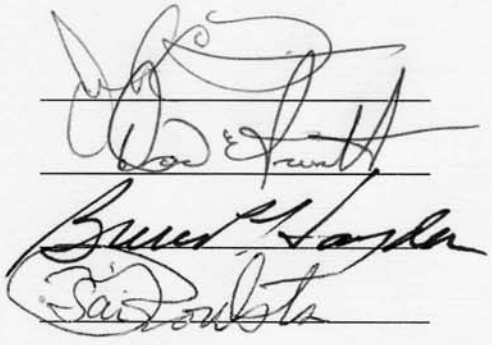

Abstract

Although salt marshes have been studied extensively, in regards to system function and ecological dynamics, little is known about the effects of grazing insect herbivores in these ecosystems. There is evidence of top down control of salt marsh plants by grazing organisms, through consumption of aboveground biomass and through alteration of nutrient cycling. *Orchelium fidicinium,* the marsh grasshopper, feeds exclusively on *Spartina alterniflora,* smooth cordgrass. Grasshoppers feed by scraping the surface of the leaf, hastening its senescence, and increasing litter inputs. *O. fidicinium* assimilates less than a third of the material ingested, resulting in nutrient-rich fecal matter returning to the marsh surface. Understanding the direct and indirect effects of grasshopper grazing, and beginning to quantify them, is necessary in understanding the role of *O. fidicinium* in salt marsh ecosystems.

This experiment tested the hypothesis that grazing will increase the sediment nutrient content through litter and fecal inputs, while simultaneously causing the plant to respond to the aboveground stress by increasing belowground biomass. This corresponding response could result in a positive feedback loop for the grasshoppers, increasing the quantity and quality of their own food source. To investigate the effects of *O. fidicinium* grazing, inclusion and exclusion treatments were established on the Virginia Coast Reserve LTER site. There were four treatments: uncaged controls, exclusion treatments, ambient density inclusions and triple density inclusions. Within each treatment aboveground plant productivity and belowground biomass were measured. Grazer damages and plant morphology were assessed. Sediment organic matter, plant and

sediment nutrient content (C, N, and NH_4), and litter and fecal inputs were measured. Surface chlorophyll was measured as a proxy for microalgal communities. The percentage of plant and leaves grazed were linearly related to grazer density ($R^2 = 0.42$ and 0.52 respectively), significantly increasing with grazer density ($p < 0.0003$). The percent of water in plants increased significantly with grazer density treatments ($p < 0.05$). Surface sediment organic matter increased significantly with grasshopper density ($p = 0.027$). The increased sediment organic matter is due to fecal inputs and litter inputs due to grazers. Live root biomass increased significantly in triple density treatments, and decreased significantly in ambient density treatments ($p < 0.05$). The changes in root biomass are a result of alternate compensation strategies for different grazer densities. Many of the results of the experiment were statistically non-significant. This may be due to low experimental power or the short time scale of the experiment. Within the significant and non-significant results trends were evident to support hypothesized results of the grazer density treatments.

Overall the results of this experiment indicate that small changes in grasshopper density can elicit significant changes in the above and belowground environment of a *S. alterniflora* dominated salt marsh environment. *O. fidicinium* had a significant effect on nutrient recycling in the marsh, which may possibly affect their own food source, the detritus and filter feeding community.

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1 Introduction

" Insects and plants must be viewed as coevolving, competing, interdependent, biochemical systems."

(Mattson and Addy, 1975)

The current theory that herbivores play a relatively minor role in salt marsh ecosystems is questionable. Smalley's (1960) energy budget of a salt marsh concluded that only a relatively small portion of the energy flow was transferred from the primary producers to the herbivorous community, and the detrital food chain processes most of the net primary productivity. Herbivores can influence plant species diversity, abundance, nutrient content, and the chemistry of the host plants (Mattson and Addy 1975). These effects can cascade up through the food chain, allowing species at a given trophic level to change their own resource availability. For example, geese grazing in Arctic salt marshes appear to regulate their own forage (Bazely and Jefferies 1985). The work of Silliman and Zieman (2001) demonstrated a top down control on *S. alterniflora* production by the grazing of the periwinkle *Littoraria irrorata*. If the energy budget developed by Smalley (1960) is reasonably correct, then *S. alterniflora* grazers greatly surpass secondary production attributed to grazers in other grassland systems (Pfeiffer and Wiegert 1981). The overall goal of this research work is to understand the effects of grazing by the marsh grasshopper, *Orchelium fidicinium*, on the salt marsh ecosystem, in regards to nutrient recycling, litter production, and primary productivity.

Salt marshes, the dominant intertidal habitat along the east coast of America, are among the most productive ecosystems in the world (Pennings et al 2001, Mitsch and Gosselink 1993). These biogenic systems, created and maintained by the organisms within them, are often seen as large monocultures of halophytic plants. There are distinct plant zonations resulting from changes in salinity, sediment type, nutrient availability, and elevation. *Spartina alterniflora*, the most common halophyte on the salt marsh, is a stiff leafy grass that can grow up to 3m tall in the mid to lower portions of the marsh (Bertness 1999; Mitsch and Gosselink 1993). Less than 10% of the aboveground primary production of *S. alterniflora* is consumed by herbivores due to the plant's structural defenses, low nutritive quality, and defensive secondary compounds (Bertness 1999). The remaining 90% of the aboveground primary productivity is processed through the detrital food web.

O. fidicinium, the marsh grasshopper, is one of the main grazing insects on *S. alterniflora.* The marsh grasshopper nymphs hatch in early May and remain on the marsh through September/October. Through the summer their numbers decline, while their size and total biomass increases. Bright green or brown in color, fully grown adults reach lengths exceeding 2cm. *O. fidicinium* densities in a Georgia salt marsh range from 5 to 50 individuals m^{-2} over the course of one summer, while the average grasshopper population is 10-20 individuals m^{-2} (Odum and Smalley 1959, Smalley 1960). From personal field observations the density of grasshoppers is very patchy, changing both location and density throughout the summer. In general the average density was about 5 individuals

m^{-2}. This varied, and in some patches grasshopper density was up to 20 m^{-2}. *O. fidicinium*, in adult and nymph stages, feeds exclusively on taller *S. alterniflora*. The grazing habit of *O. fidicinium* consists of scraping material, with chewing mouthparts, from the adaxial surface of the middle portion of the leaf, and chewing the tips and sides. The adaxial surface is the surface of the leaf facing the stem. Grazing wounds can be from 1-15 cm long and 1-2 cm wide.

The severity of the resulting leaf damage depends on the location of the grazing. Leaching of organic and inorganic compounds from scarred leaves may be increased (Pomeroy et al 1981). Often the grasshoppers graze the middle portion of the leaf, resulting in premature senescence of the undamaged leaf tip. This damage may inhibit translocation of leaf fluids back into the plant, resulting in nutrient-enriched litter fall. Continued grazing pressure on plants may stimulate translocation of materials from the aboveground to the belowground biomass. Increased root activity has been noted in studies on blue gramma grass with continued grasshopper grazing. Grazing stimulated increased root respiration and production of organic acids in exudates, particularly in the early season (Dyer and Bokhari 1976, Pfeiffer and Wiegert 1981).

Smalley's energy budget of a salt marsh ecosystem (1960) estimated that *O. fidicinium* ingested 2% of the net primary productivity of *S. alterniflora,* and assimilated it with 27% efficiency. Wastage, material removed from the plant but not ingested, was not accounted for in this budget. Prairie ecosystem research indicates that litter production is the primary role of the grazing insects. Mitchell and Pfast (1974) estimated that prairie grasshoppers could waste a quantity of grass 50-100% of the total amount

ingested. If the figures for *O. fidicinium* were comparable, this would result in approximately 5% of the net primary production of *S. alterniflora* being removed (Pfeiffer and Wiegert 1981). These figures are small when considering the whole ecosystem, but may prove to be significant as the material is processed through the system.

The effects of grazing have been studied in many salt marsh ecosystems (Bazely and Jefferies 1989, Silliman and Zieman 2001, Odum and Smalley 1959, Teal 1962, Vince et al. 1981, Parsons 1980). Grazing affects the primary production of a system, both directly and indirectly. Grazing directly removes leaf material reducing aboveground biomass. At low grazing pressure, plant losses may be offset by stimulated growth, due to the removal of senescent material and nutrient regeneration. As grazing pressure increases plant growth may be out competed by grazing. Decreased aboveground productivity may results as the plants translocate material belowground (Power 1992, Flint and Goldman 1975, McNaughton 1979).

Grazing may indirectly affect nutrient availability through increased litter and fecal matter inputs. The increase in litter fall has two components: wastage, and premature senescence due to increased leaf damage. Grasshopper grazing is expected to increase the natural rate of large litter input through premature senescence. Wastage can increase the smaller size fraction of litter present on the marsh surface, enhancing nutrient cycling through the sediments. The size fraction of detritus affects the rate of decomposition and bacterial colonization, the smaller the size fraction the faster the decay rate. Increased litter fall should stimulate the activity of decomposers on the marsh

surface. Burkholder and Bornside (1957) found that marsh grass detritus has a stimulating effect on the growth of mud bacteria. Opportunistic dormant bacteria, which are capable of rapid growth in response organic matter inputs, are abundant in the marsh mud. Therefore, bacterial populations in the mud should increase with increased litter inputs. Microbial fungi and bacteria are responsible for processing 75% of the decaying matter on the marsh surface. As *S. alterniflora* undergoes bacterial decomposition, the detritus increases in protein content, and the C:N ratio decreases. The bacterial populations responsible for these nutritional changes are preyed upon by detritus grazers (Gosselink and Kirby 1974).

The unassimilated materials, ingested by herbivores, enter the salt marsh detritus in the form of feces. This material may significantly alter the nutrient availability for detritus feeders (Smalley 1960, Odum and Smalley 1959). Fecal matter nutrient regeneration can be an important trophic link for herbivores. Studies of other grazers have noted the importance of fecal matter input as a nutrient source for the salt marsh ecosystem. Bazely and Jefferies (1985) determined that geese feces increased nitrogen content of plants and enhanced late summer standing crop. In Sterner's phytoplankton study (1986) he found the indirect effects due to nitrogen regeneration were as large as the impact of direct grazing.

Grazing also affects the abiotic portion of the marsh system, through the removal of aboveground biomass, and therefore increased light penetration. Microalgal mats on the surface of the marsh sediments are poorly understood ecologically. The microalgal community of a Georgia salt marsh is composed mostly of several hundred species of

pinnate diatoms (Pomeroy et al 1981). Their net primary production represents a major contribution to the total primary production of the salt marsh ecosystem, secondary only to marsh grass. Although moderately photo inhibited at full sunlight, light is implicated as the most important factor influencing microalgal productivity (Pomeroy et al 1981). Increased light penetration and surface nutrient inputs on the marsh surface may stimulate microalgal growth. Microalgae are heavily consumed by fiddler crabs, snails, herbivorous fish, and other surface feeders. Algal biomass is more readily assimilated and more nutritious than marsh grasses for these surface grazers (Gosselink and Kirby 1974, Pomeroy et al 1981).

In developing an understanding of the role of grasshopper grazing on the salt marsh ecosystem the following specific objectives were assessed. The grazing habits of *O. fidicinium* on lower marsh *S. alterniflora* stands were determined using past literature, field data from 2002, and grazing surveys in 2003. Litter production was assessed through field collection and dry weight. The fecal matter of *O. fidicinium* was collected, dried, weighed, and assessed for nutrient content (C and N). The effect of *O. fidicinium* grazing on *S. alterniflora* productivity was assessed using plant height, stem density, number of flowers, percent plant water, number of leaves, and below ground biomass. Sediment nutrient and organic matter content were measured to assess the impacts of grasshopper grazing on nutrient regeneration. Surface chlorophyll measurements were made to assess the indirect effects of grazing on the surface microalgal community. A conceptual model describing the role grasshoppers in the salt marsh ecosystem was developed using the findings of these previous objectives.

1.1 Study site

The study site was located on the mainland peninsula of the Eastern Shore of Virginia at the Brownsville Marsh. The area is owned and managed by The Nature Conservancy as part of the Virginia Coastal Reserve-Long Term Ecological Research Site (VCR-LTER). [See figure 1.1 for map].

1.2 Sampling layout

Within the low marsh *S. alterniflora* environment four homogenous blocks were haphazardly established. A block design was used to minimize the effect of environmental variability. The four grazer treatments were randomly placed in each block. The four treatments were as follows:

1. Exclusions to assess the effects of grasshoppers
2. Uncaged controls to assess the natural state of the marsh
3. Ambient grazer density treatments containing 2 grasshoppers per cage
4. Triple grazer density treatments containing 6 grasshoppers per cage

The density treatment of 2 grasshopper per cage was called ambient for ease of discussion and represents the lower densities found on the marsh throughout the summer. Triple is three times the ambient density treatments. (See figure 1.2 for experimental design).

All blocks were approximately equal distance from creeks and equal in elevation, judging by tidal inundation. The density of snails was very low, but fiddler crabs were

ubiquitous. Plant densities varied from block to block but were similar across all treatment types (Table 7.3 Appendix A). The cages were 1 m^3 with a front access panel. Six additional cages were established, next to the original plots, with exclusion and inclusion treatments applied to them. These cages were used for destructive harvesting of aboveground biomass, to develop height to dry biomass relationships. The belowground rhizomes and roots of *S. alterniflora*, along the edge of each plot, were severed to a depth of 40 cm using a saw. This was to assure the effects observed on plants within the plot were due to conditions within the plot. The grasshoppers included in the cages were counted, and replaced if necessary, every two weeks. Grasshoppers within the cages showed little interest in escape from the cages. The cage was constructed with 1-2 mm mesh screen during May and June, and 5 mm aluminum screen for July through October. These mesh sizes permitted the maximum amount of light penetration while preventing grasshopper migration into and out of the cages.

Figure 1.1 Map of field sites within the VCR-LTER research site

The map illustrates the exact location of the field sites, within the black box, on the Brownsville marsh area. The lat long of site 1 is 372716N and 754941W. The lat long of site 2 is 372710N and 0754930W. This marsh is located near Nassawadox on the Eastern Shore of Virginia within the VCR-LTER research site.

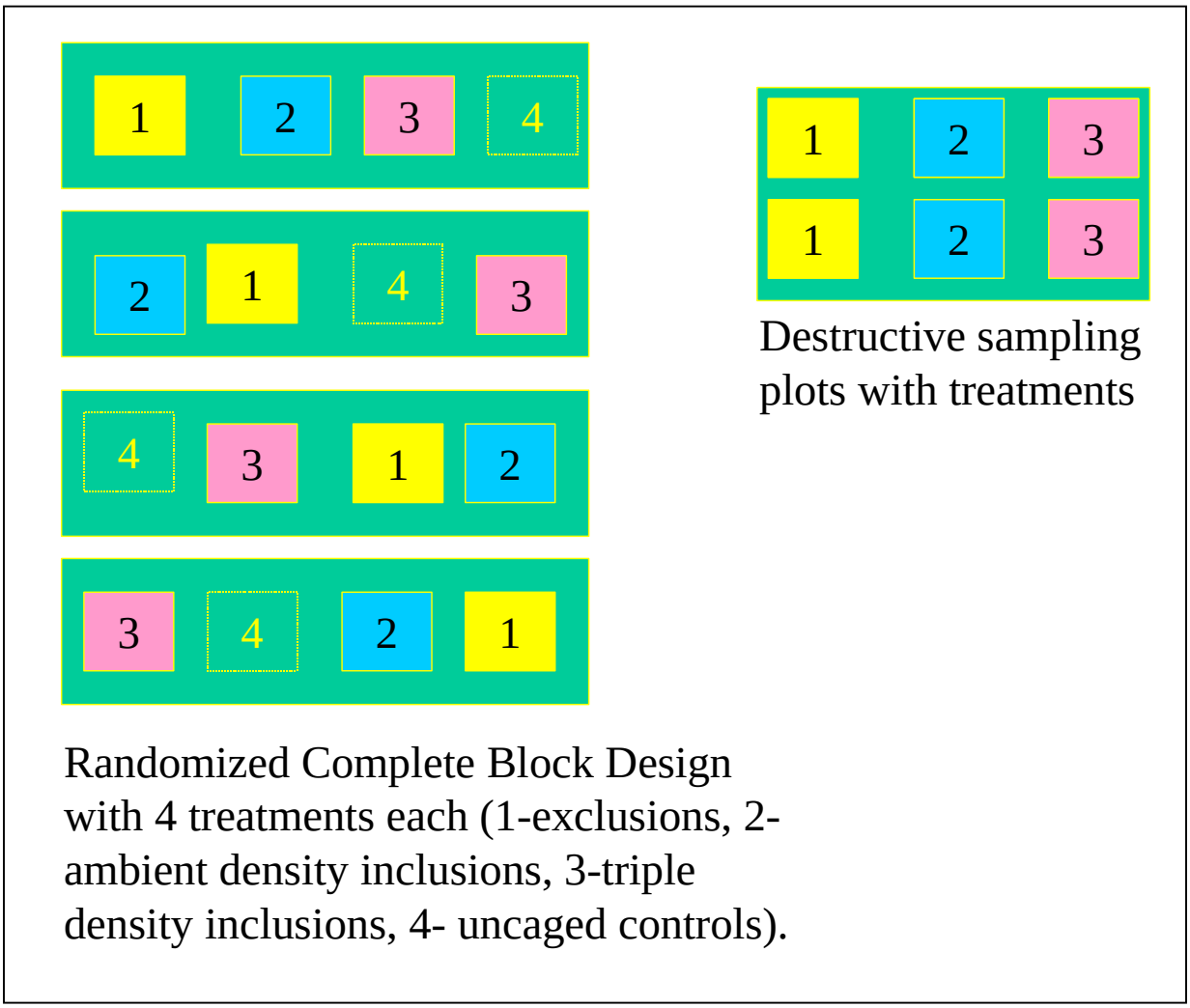

Figure 1.2 Experimental design

This illustrates the design of the experiment. There were 4 blocks, each containing 4 treatments (1-4). There were destructive sampling plots established for sampling of aboveground biomass in July and October, containing inclusion and exclusion treatments 1,2 and 3.

1.3 Significance:

The grasshopper, *O. fidicinium,* is the primary chewing insect grazer of live *S. alterniflora* in this region. Understanding the effects of grasshopper grazing on plant productivity and nutrient cycling, whether that effect is large or small, is an important

aspect of salt marsh ecology that has not yet been addressed. Multiple studies (Smalley 1960, Odum and Smalley 1959, Mitchell and Pfast 1974, Pfeiffer and Wiegert 1981) have previously concluded that the indirect effects of grasshopper grazing are likely the primary effect of grasshoppers in grassland ecosystems and may be ecologically significant. This study assessed the direct and indirect effects of grasshopper grazing, providing a more comprehensive understanding of the role of grasshoppers in salt marsh ecosystems.

Salt marshes are economically significant habitats, as they serve as nursery grounds for many organisms, in particular supporting commercial and sport fisheries. Salt marshes filter nutrients and sediment from terrestrial runoff, protect the land from erosion, and provide natural ecosystem for tourism. Despite the ecological significance of salt marshes, they are one of the shoreline habitats that have been most heavily disturbed by humans. Understanding the role of grazing fauna in salt marsh wetlands could greatly aid in successful restoration projects.

With proposed sea level rise and global warming salt marsh ecosystems are threatened ecosystems. Understanding their form and function to the best of our ability will aid in mitigating changes caused by larger global processes.

2 Effects of grazing on the aboveground environment

2.1 Introduction

Although salt marshes have been studied extensively in regards to system function and ecological dynamics (Teal 1962, Odum and Smalley 1959, Pennings and Bertness 2001, Bertness 1984 and 1985), little is known about the effects of grazing insect herbivores in these ecosystems. There is evidence of top down control of salt marsh plants by grazing organisms through consumption of aboveground biomass (Silliman 2001, Bertness and Shumway 1992) and through alteration of nutrient cycling (Bazely and Jefferies 1985).

Grasshopper grazing may affect the aerial portion of the salt marsh directly by altering plant productivity, leaf turnover, flowering rate, and plant height. Grazing may indirectly affect sediment nutrient content through increased litter and fecal matter inputs. These sediment nutrient changes may in turn alter plant nutrient content. This study aims to identify and quantify the influences of *O. fidicinium* on the aboveground biomass of temperate salt marsh environments.

Plant morphology and productivity are affected by grazing through direct removal of aboveground biomass. Grazed plants may compensate for canopy loss by increasing aboveground production (McNaughton 1983, Power 1992). This compensation may manifest itself as increased plant height, plant biomass, leaf production and flowering rate. A net increase in biomass of the plant may occur when plants overcompensate for current grazer damages (McNaughton 1983). When grazing damages are greater than the compensation mechanism plants may begin redirecting energy belowground into rhizome

and root storage (Dyer and Bokhari 1976, McNaughton 1983), possibly reducing aboveground production (Silliman 1999). Direct grazing of inflorescences by grasshoppers has been noted to greatly reduce the seed production and frequency of male flowers in *S. alterniflora* (Bertness and Shumway 1992), therefore reducing the reproductive success of the grass.

O. fidicinium grazes *S. alterniflora* by scraping the adaxial surface of leaves, resulting in translucent rectangular scars. The grazing patterns within a plant, or group of plants, are not well documented. Such patterns could include grazing specific leaves on every plant, certain parts of leaves at different times in the season, or apparently random choice of plants and leaves within a group.

Grasshoppers' litter making abilities are considered their primary role in short grass prairies (Mitchell and Pfadt 1974). *O. fidicinium* gazing may increase the input of litter to the salt marsh surface due to canopy damage, increased leaf senescence and wastage material. Increased litter inputs may increase nutrient cycling and availability in the sediments.

O. fidicinium assimilates only 27% of the food it ingests (Smalley 1960). Their feces are green pellets, less than 0.5 cm long, which disintegrate on contact with the wet marsh surface (McGoff pers. obs.). The fecal matter is partially broken down plant material, rich in nutrients that are easily recycled. The nutrient content of *O. fidicinium's* feces has not been quantified, and may represent a source of nutrients being recycled into the plants.

Plant nutrient content influences food choice by grazers (Silliman 1999, Valiela and Teal 1974). Grasshopper grazing may increase sediment nutrient content, through increased litter and feces inputs (Bazely and Jefferies 1985). Increased sediment nutrient content may affect plant nutrient content as plants increase their nutrient uptake. It is more likely that the grazed plants will increase their nutrient content through increased leaf growth. Juvenile plant tissues have higher nitrogen content.

The role of grasshoppers in salt marsh ecosystems has been largely ignored due to their short life span, patchy distribution, and small amount of biomass ingestion. The direct effects of grazing, such as biomass consumption and subsequent damage to plants, have previously been noted without quantification. The indirect effects of grazing, such as litter production and nutrient recycling, are not yet understood and could constitute the main role of grasshoppers in these ecosystems. Quantifying the direct effects, and understanding the indirect effects, of grazing is necessary in understanding the overall effect of *O. fidicinium* on the aboveground environment of the salt marsh ecosystem.

2.2 Objectives and working hypothesis

1. *To assess and quantify grasshopper grazing rates on Spartina alterniflora in the low marsh*. The grazing rates of grasshoppers on *S. alterniflora* plants are unknown.
2. *To assess the effects of grasshopper grazing on:*
    a. *Natural production rates of Spartina alterniflora.* Grasshopper grazing is

expected to stimulate growth in *S. alterniflora* within the first stages of grazing, and as grazing continues through the season aboveground production may be reduced in favor of belowground biomass.

b. *Plant morphology and changes*

Grazing at low to moderate levels is expected to increase leaf turnover, plant height and plant biomass, and reduce flowering rate. At higher rates of grazing some morphological characteristics may decrease in favor of increasing belowground biomass.

c. *Litter production*

Grasshopper grazing is expected to increase litter production due to canopy damages and leaf senescence. This litter production may increase the amount of organic matter and nutrient recycling in the surface sediments.

d. *Plant nutrient content*

Increased sediment nutrient content, due to litter and fecal inputs, is expected to increase nutrient availability to plants, possibly increasing the plant tissue nutrient content.

3. *To assess the effects of grasshopper fecal matter inputs on nutrient regeneration*. The nutrient content of *O. fidicinium* feces is unknown. Grasshopper fecal matter inputs to the marsh surface are expected to increase the surface nutrient content.

4. *To develop a diagrammatic model of the role grasshoppers play in temperate salt marsh ecosystems*. The role of grasshoppers in salt marsh ecosystems is

currently understood from a detrital food web perspective. This work should enable a different perspective to be developed on the role of grasshoppers as prominent herbivores in these systems.

2.3 Methods

2.3.1 Grasshopper density

The density of grasshoppers was assessed using two methods: sweep net and drop cage, a modification of Beall (1935) and Smalley (1960). A sweep net survey consisted of the net being passed 5 times back and forth over the grass, while walking swiftly forward. To understand the area covered by this sweep the drop cage, 0.5 x 0.5 x 0.5 meters, was used as a comparison. The cage was small enough to be handled by one person. The person walked across the marsh swiftly placing the cage down over the grass haphazardly. The grasshoppers were then removed from the cage by hand. A comparison of the two methods was intended to clarify the density of grasshoppers per meter and the efficiency of each method.

2.3.2 Grazing rates

The grazing rates of *O. fidicinium* were assessed semi-monthly using the productivity plots in the center of each plot (described below). Fifteen plants were randomly selected within each of the productivity plots in May. Every two weeks all the leaves on these plants were assessed for grazing scars.

2.3.3 Plant productivity and morphology

Plant productivity was assessed monthly from May through September using the Morris and Haskins (1990) census method. Each plot contained a centrally located 25 by 25 cm productivity plot, within which all of the plants were identified with numbered bird bands. The height of each banded plant was measured monthly. Each month, new stems taller than 5 cm were banded, and the death of banded stems was recorded to assess turnover rates. Plant biomass within each plot was calculated by destructively sampling 50 plants from the surrounding area in May, July and September. The plant length was measured from the base of the stem to the top of the leaf, stem, or inflorescence. The wet weight was recorded, the plants were freeze-dried and reweighed for dry biomass. A regression for height to biomass was calculated and used to estimate biomass for the plants within the productivity plots. Due to the unknown effects of grazers on plant biomass in the treatments, the height-to-biomass ratio may not be consistent for all treatments. Additional destructive sampling plots were established in nearby areas containing the same densities of grasshoppers as the experimental inclusion and exclusion treatments. Fifty plants were collected from these also in May, July, and October. The height-to-biomass ratio was calculated separately for all experimental treatments. The water content of plants was calculated as the difference in weight from wet to dry plants divided by the wet weight. This was calculated for the plants destructively sampled for productivity estimates in May, July and October. Productivity was calculated as the rate of biomass change in grams/m^2/day.

To assess plant morphology changes, due to grazing, fifteen plants were randomly selected, by band number, within each of the productivity plots in May. Every two weeks these plants were assessed for plant height, number of dead and live leaves, leaf length and inflorescences.

2.3.4 Litter and feces

Litter was sub-sampled from each quadrant monthly using a 100-cm^2 quadrat. Three replicate quadrats were randomly sampled from each cage. Litter was defined as all visible organic matter collected off the surface of the marsh, including wrack and dead plant material still attached to the plant. Only litter within the quadrat was collected, connections to plants etc. outside of the quadrat were cut. Upon return to the lab the litter was rinsed of debris, and weighed. The litter was then freeze-dried and reweighed.

Small litter and fecal matter inputs were collected together by containing grasshoppers of various sizes in large glass jars in the field through the summer. Moist grass was placed in the jars, and the jars were placed in the longer grass to minimize environmental disturbance to the grasshoppers. The duration of containment was recorded to attain a rate of input. All fecal matter and small litter pieces were collected at the end of containment. Samples were weighed and freeze-dried for further analyses. Fecal samples were assessed for carbon and nitrogen content. Samples were ground to a fine powder using a mortar and pestle and treated with 20% HCl to remove carbonates. Treated samples were analyzed using a Carlo Erba Elemental Analyzer 2500. Two analytical replicates of each sample were run to ensure machine precision.

2.3.5 Tissue composition

The tissue composition of *S. alterniflora* plants within each plot was assessed monthly from May through September. Three whole plants were collected randomly from each treatment. They were wiped free of debris in the field and stored on ice until return to the lab. The samples were freeze-dried and ground to a fine powder using a Wiley Mill. The three plants were combined to represent one monthly sample from each plot. For carbon and nitrogen assessment the powdered samples were treated with 20% HCl to remove carbonates and analyzed using a Carlo Erba Elemental Analyzer 2500. Two analytical replicates of each sample were run to ensure machine precision.

2.4 Data analysis

The use of the randomized complete block design (RCBD) allowed for comparison of the various treatments within each block, and minimized variability due to the environment. Productivity data were taken in the field monthly, and grazing damage was assessed every two weeks. Three replicate plant and litter samples were collected monthly from each cage. The data were analyzed using repeated measures ANOVA. The repeated measures ANOVA accounts for repeated sampling within the same plot for consecutive months. Consecutive samples collected from each cage were treated as replicates for that cage. An autoregressive order-1 covariance structure was used. This assumes that samples in May are more closely related to samples in June than in October. This type of structure was chosen due to a higher Akaike's Information Criterion (AIC) number than other covariance structures. The repeated measures ANOVA analyzed for three fixed factors: month, treatment, and month by treatment interaction. The month

factor assesses the average value per month across all treatments. The treatment factor assesses the average value per treatment across all months. The treatment by month interaction assesses the average value of each treatment within each month. If the p value of any fixed factor was significant ($p < 0.05$) this factor was further analyzed using pair-wise contrast. If contrasts were non-orthogonal the alpha value was adjusted using the Dunn-Sidak method to maintain a 95% confidence limit. Least square means, and associated standard errors, were calculated and plotted for each set of data. All data was assessed for homogeneity of variance using the F-max test. The variables percent plant grazed, percent leaves grazed, percent biomass change, and the number of live leaves was log transformed to meet assumptions of variance needed for ANOVA. All statistics were carried out using SAS.

2.5 Results

2.5.1 Seasonal effects

Throughout the summer months, many of the variables changed significantly. These changes were due to the progression of the summer and not the effects of the grasshopper densities. All the results and figures pertaining to seasonal variation of the measured variables are contained in Appendix B. The standing crop increased significantly through the summer ($p < 0.05$, Figure 8.2), as did plant height ($p = 0.0001$, Figure 8.4). The number of dead leaves generally increased through the summer, and was significantly higher in September and October ($p < 0.003$, Figure 8.5). The number of live leaves varied little through the summer, peaking in August, and declining

significantly in October ($p = 0.003$, Figure 8.5). Litter decreased throughout the summer, and was significantly higher in June than all other months ($p < 0.003$, Figure 8.6). Percent plant nitrogen decreased significantly month to month through the summer ($p < 0.0001$, Figure 8.7). Plant percent carbon increased significantly through the summer ($p < 0.003$, Figure 8.8). The percent of leaves grazed increased to a peak mid-July, and decreased into the fall as grazers shifted from leaves to seed heads. The percent of plants grazed increased to a peak in early August (Figure 8.1).

2.5.2 Cage effects

Establishing cages in the marsh influenced some of the environmental factors associated with these sites. The cages were expected to reduce tidal export of litter on a daily basis, therefore increasing organic matter and nutrient recycling in situ. They were expected to decrease the light reaching the plants, possibly decreasing their productivity as a result. The cages provide a structural buffer for the plants against high winds or currents, possibly affecting the plants growth form. Including a set density of grasshoppers within the cages may exaggerate the effects of these grazers as they are limited in their food choice. The statistical results regarding the influence of cage structures on the experiment are important to remember while interpreting the results. All of the results pertaining to cage structure will be addressed here and considered throughout the remaining results sections.

As expected, the control treatments had slightly lower litter content. This may have affected nutrient recycling, as plant nitrogen was significantly lower in control plots ($p < 0.0001$, Figure 2.10a). The control treatments had slightly higher aboveground

biomass (Figure 2.2a), and significantly shorter grass (Figure 2.55, p = 0.02a) than caged treatments. The control treatments had significantly fewer leaves grazed than inclusion treatments as the grasshoppers grazing the control plots were not limited in their food choice (p = 0.006,

Figure 2.1a). Control plots may also represent disturbed grazing sites due to their proximity to the cages. The cage structure had no noticeable effect on the number of dead or live leaves (Figures 2.8a and 2.7a). In summary, the plants in control treatments were shorter, heavier, changed the most through the season, and were less grazed.

2.5.3 Grasshopper densities and feces

Approximate densities of grasshoppers are given in Appendix A, table 7.4. For the term of the experiment, ambient density was considered 2 grasshoppers, and the triple density was 6 grasshoppers, per meter squared. Only grasshoppers approximately 1 cm, or greater, in length were included, for ease of locating and containing them. The biggest challenge in establishing the treatments came not from enclosing the grasshoppers but from excluding them. Grasshoppers in the cages rarely tried to escape and grasshoppers outside the cage often tried to get in.

Through various containment studies, grasshopper fecal inputs were estimated to be less than 0.01g of dry feces per grasshopper per hour. Although containment studies ranged in length of time from 2 to 48 hours, the fecal input rate varied little after 2 hours. From general observations, the grasshoppers in containment were acting disturbed, including reduced feeding, and therefore decreased fecal inputs. The average nitrogen content of fecal matter varied broadly from 0.12 to 0.71 %. Carbon also varied widely

from 3.19 to 16.95% (Table 7.2, Appendix A). These variances could be due to poor preservation of samples in the field, or could be indicative of the natural variances in grasshopper feces.

2.5.4 Grazing

Percent leaves grazed:

The percent of leaves grazed peaked by mid-July, and decreased thereafter due to the development of seed heads for grazing. The seed heads are an easy food source for grazers. The percent of leaves grazed was directly related to the density of grasshoppers (Appendix A, Figure 7.4). Inclusion treatments had significantly more grazed leaves than exclusion treatments ($p = <0.0001$, Figure 2.1a). Ambient and triple density treatments were not significantly different from each other ($p = 0.232$). By early August triple density treatments had significantly more grazed leaves than exclusion treatments ($p = 0.0004$, Figure 2.1c), and by late August triple and ambient density treatments had significantly more grazed leaves than exclusion treatments ($p<0.0001$).

Percent plants grazed:

The percent of plants grazed peaked in early August, and decreased into the fall. The percent of plants grazed was directly related to presence of grazers. Inclusion treatments had a significantly higher percent of grazed plants than exclusion treatments ($p < 0.0001$, Figure 2.1a). By late August there was a significant difference between exclusion and each of the inclusion treatments ($p = <0.0001$, figure 2.1b).

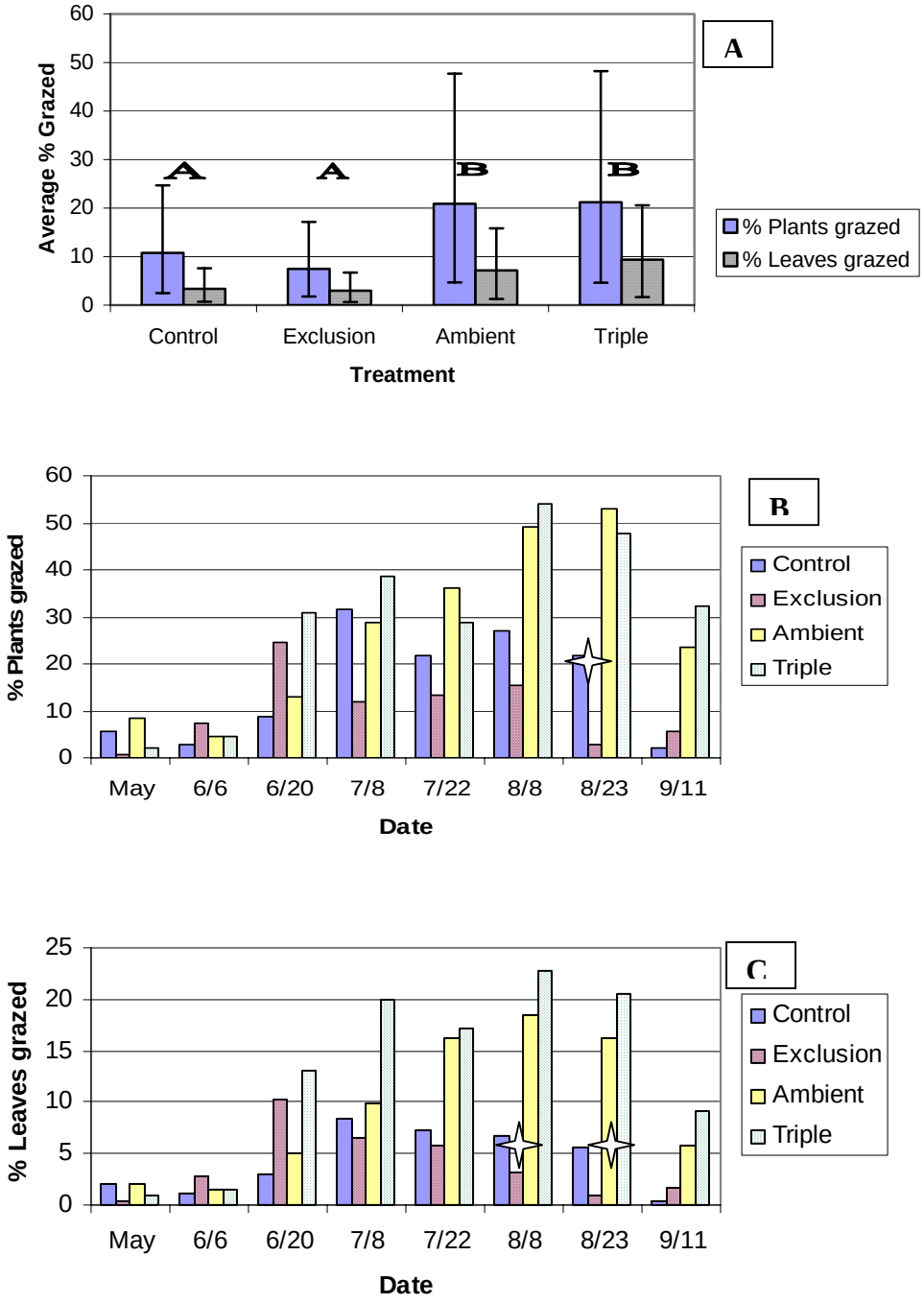

Figure 2.1 Percent plants and leaves grazed

Average percent of plants and leaves grazed per treatment (Graph A, +/- 1 SE), and per treatment each month (Graph B and C). Letters indicate significantly different groups ($p<0.05$). Stars indicate significant differences between groups for that month. For percent of plants grazed the star indicates exclusion vs. both inclusion treatments separately. For percent of leaves grazed the star indicates triple vs. exclusion in August 8, and both inclusions vs. exclusions in August 23 ($p < 0.002$).

Photo 2.1 Comparative canopy damages

A comparison of the canopy damages on plants from triple (left) and ambient (right) plots. See increased leaf folding and reduced plant integrity with triple grazers.

2.5.5 Productivity and morphology

Productivity:

The aboveground biomass polynomial regression equations are given in Appendix A, table 7.1. The equation for May was used to calculate the biomass for May, and had a low R^2 value (0.46). The equations for July were used to calculate the biomass for June, July and August (R^2 = 0.82 to 0.92), as these months were most similar in plant growth. The October equations were used to calculate biomass for September and October (R^2 = 0.79 to 0.91) again as these two months were very similar in growth habits.

Using the differences between treatments on a monthly basis a rate of productivity was generated and is illustrated in figures 2.2 a and b. The treatments had a non-significant trend of decreased productivity with increased grazer density (Figure 2.2a). From May through August ambient density and triple density treatments had the lowest productivity, while control and exclusion treatments were distinctly higher (Figure 2.2b). By October all the treatments returned to a similar biomass per meter crop as the influence of grazers diminished. Grazer inclusion treatments had increased productivity at the end of the season.

Stem density:

The stem density was calculated monthly, using the density found in productivity plots. Stem density was not significantly affected by treatments. The controls had higher stem density than the caged treatments. Ambient density treatments had the lowest stem density (Figure 2.3a).

Water content:

The statistical tests on water content did not pass the F-max test for homogeneity of variances, therefore all results should be interpreted with caution. The amount of water present in the plants generally decreased over the summer (Figure 8.9, Appendix B). The presence of the cages significantly increased plant water content ($p = 0.0001$), as did each of the grazer densities independently ($p = 0.0028$, figure 2.4a).

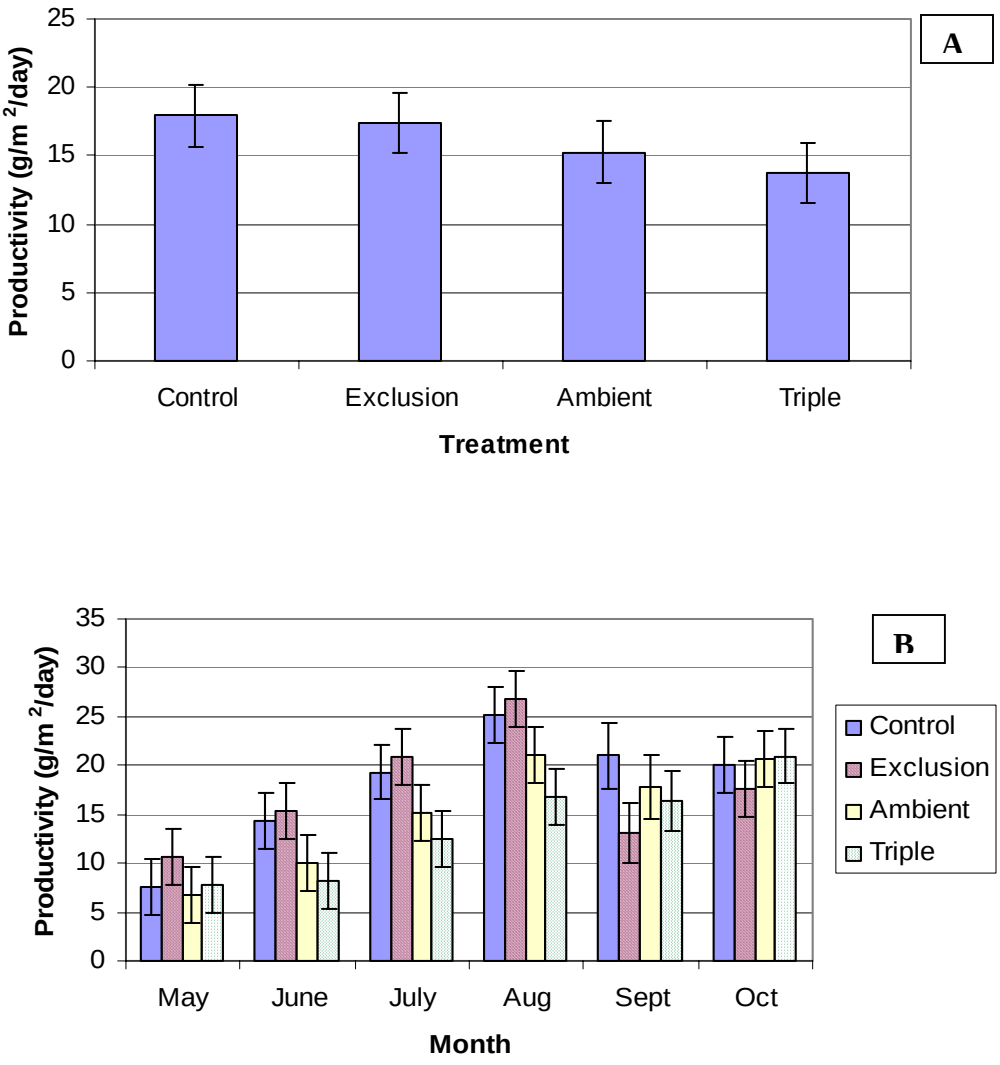

Figure 2.2 Productivity

Average productivity, in grams dry biomass per meter squared per day, for each treatment over the whole summer (Graph A), and for each treatment per month (Graph B). +/- 1 SE.

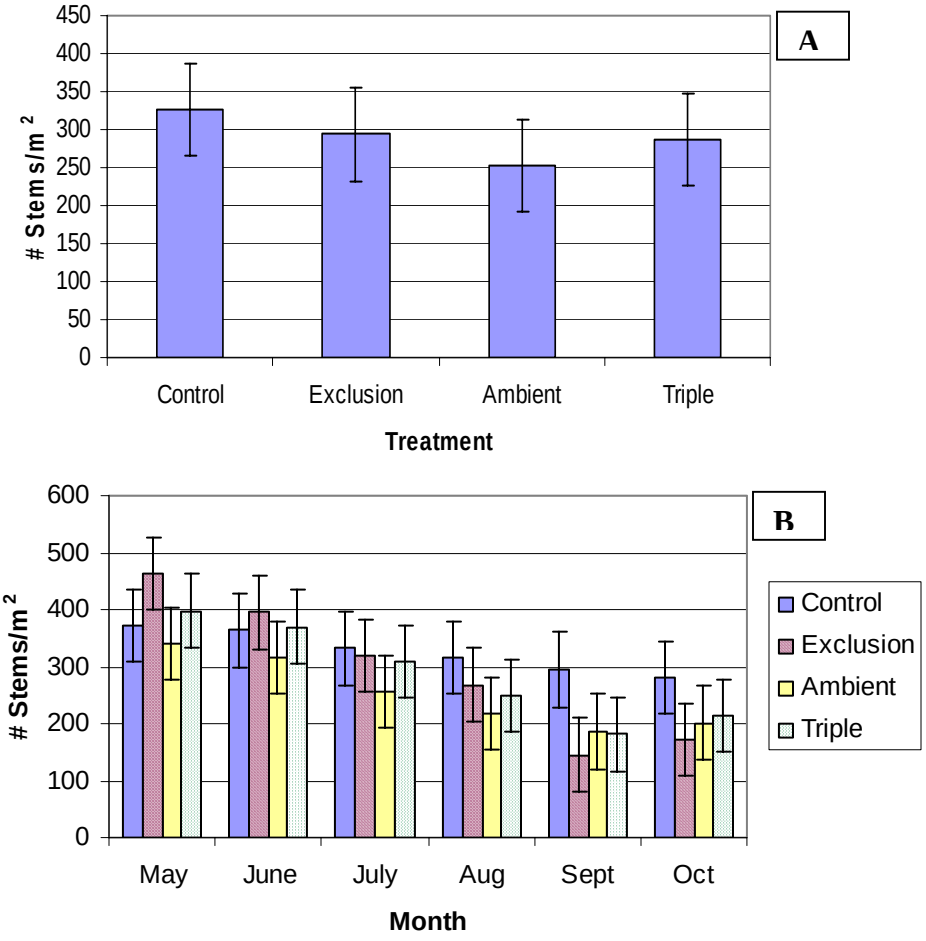

Figure 2.3 Stem density

Average number of stems per meter squared for each treatment (Graph A), average number of stems per treatment each month (Graph B). +/- 1 SE.

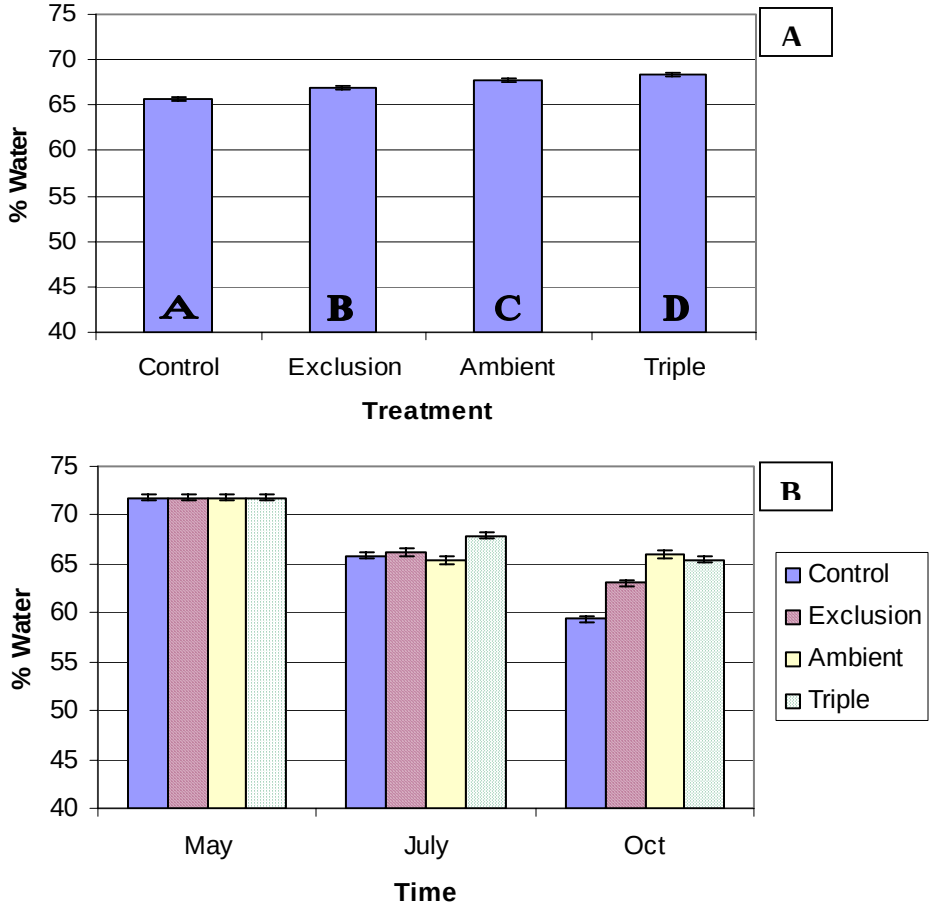

Figure 2.4 Percent plant water

Average percent of water in plants per treatment over the whole summer (Graph A), and per treatment each month (Graph B). +/- 1 SE. May values were all calculated from a single collection and hence are equal in value. P value < 0.05.

Plant Height and Leaf Length:

Plant height increased through the summer. Caged treatments had significantly taller grass than uncaged treatments ($p = 0.02$, Figure 2.55a). Ambient density treatments contain plants that were 2% taller than exclusion treatments, possibly due to grass compensating for grazing. The plants in triple density treatments were 4% shorter than in exclusion treatments, possibly due to grazing out competing the compensatory growth. This 6% height difference between the two inclusion treatments may have significant effects on photosynthesis and other ecosystem functions.

Leaves were significantly longer in caged treatments ($p = 0.02$, figure 2.6a). Ambient density treatments had slightly longer leaves than exclusion treatments, and triple density treatments had shorter leaves. Plant height was measured to the tip of the tallest plant part, most often the leaves. The increase found in plant height is a result of increased leaf length and stem length. Plant height alone will be discussed henceforth with the understanding that it is not independent of leaf length.

Live and Dead Leaves:

Data on the number of live leaves did not conform to the F-max test for homogeneity of variance, thus the results must be interpreted with caution. The data on dead leaves met all statistical assumptions. The absence of grasshoppers significantly decreased the number of live and dead leaves in exclusion treatments ($p = 0.05$ and 0.036, Figures 2.7a and 2.8a resp.). The ambient density treatments had the highest number of live leaves. By the end of the season, triple density treatments had the highest number of

live leaves (Figure 2.7b). This is possibly an end of season pulse of aboveground biomass, as the plants rebound from a summer of heavy grazing.

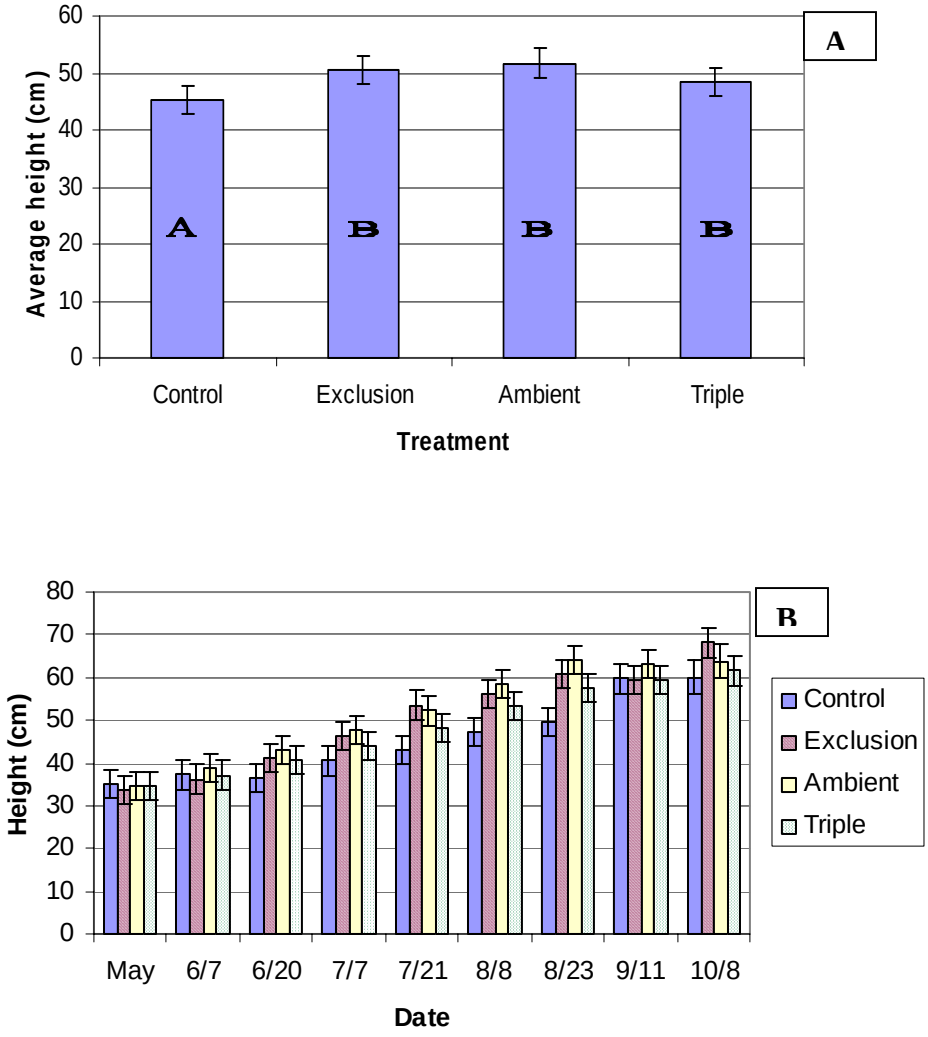

Figure 2.5 Plant height

Average plant height for each treatment for the whole summer (Graph A); and average height for each treatment each month (Graph B). +/- 1 SE. P value < 0.05. The different letters in graph A represent significantly different groups within the treatments.

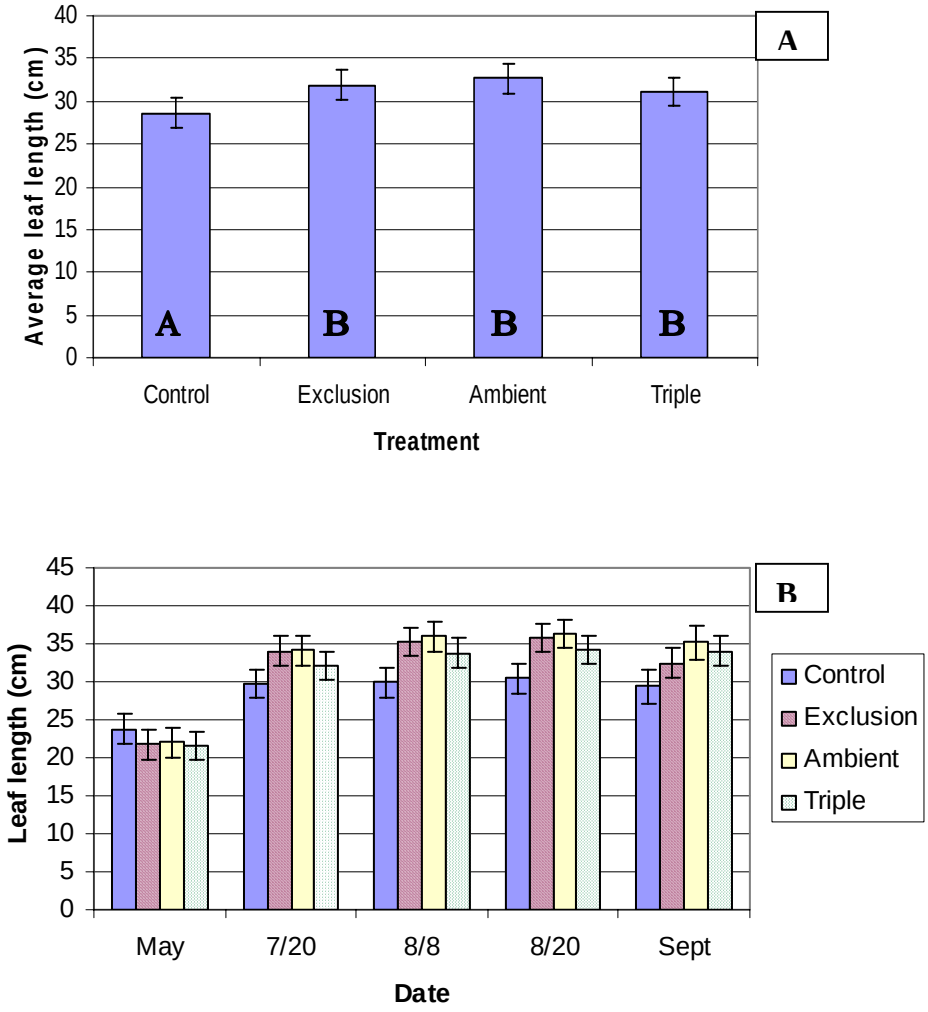

Figure 2.6 Leaf length

Average leaf length per treatment for the whole summer (Graph A), and per treatment each month (Graph B). +/- 1 SE. P value < 0.05. The different letters in graph A represent significantly different groups within the treatments.

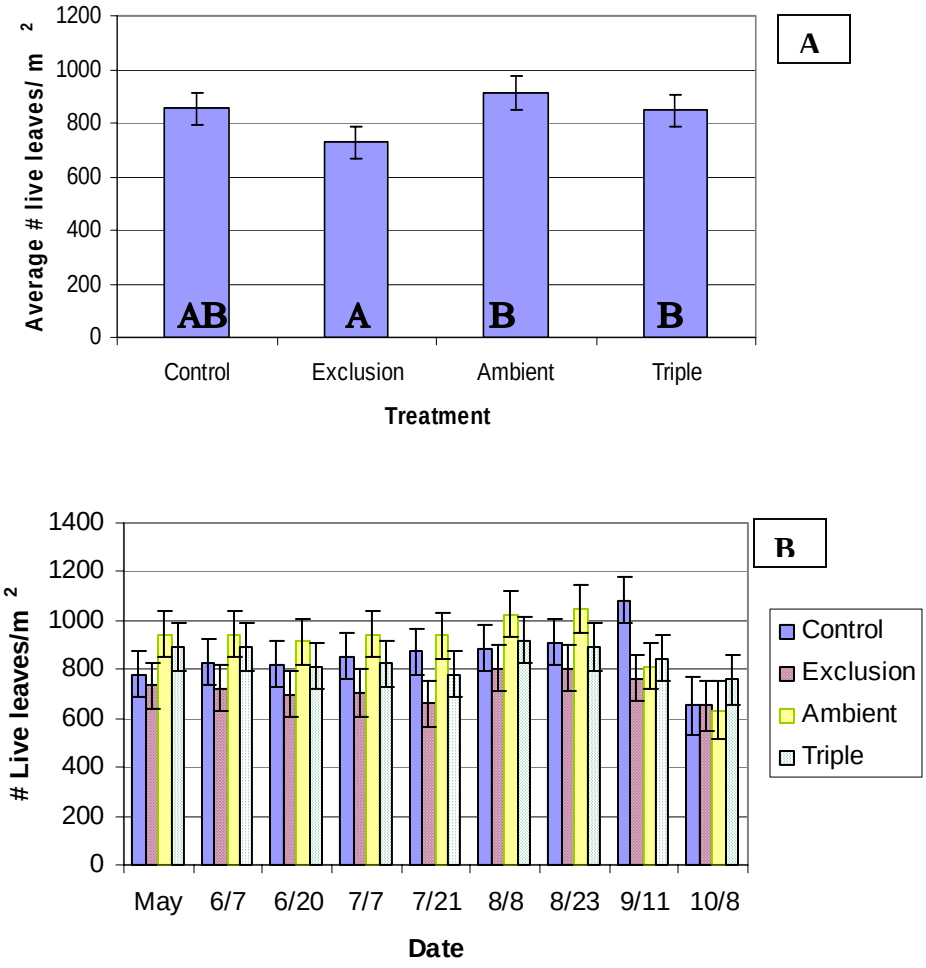

Figure 2.7 Number live leaves

Average number of live leaves per square meter for each treatment over the whole summer (Graph A), and per treatment each date (Graph B). +/- 1 SE. P value < 0.05. The different letters in graph A represent significantly different groups within the treatments.

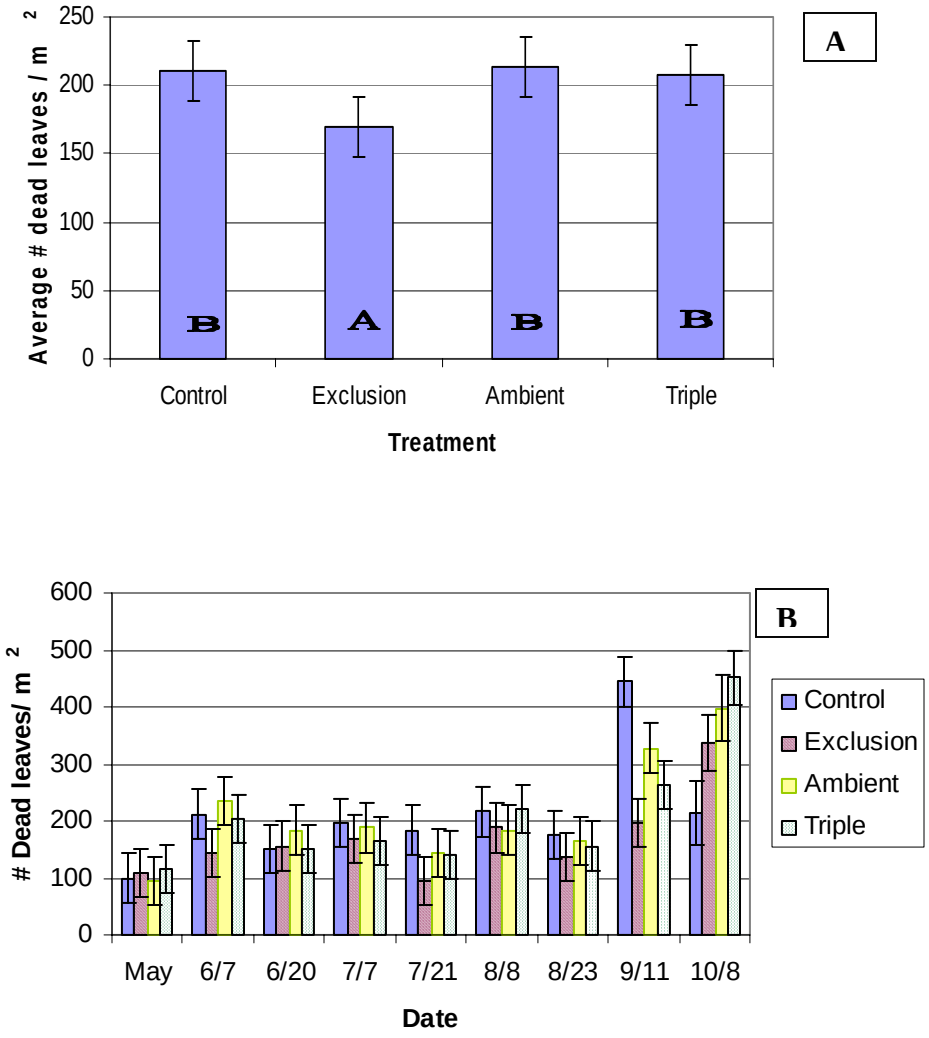

Figure 2.8 Number of dead leaves

The average number of dead leaves, per meter squared, for each treatment over the whole summer (Graph A), and per treatment each date (Graph B). All +/- 1 SE. P value < 0.05. The different letters in graph A represent significantly different groups within the treatments.

2.5.6 Litter

The amount of litter did not vary statistically due to the grazer treatments. Control plots generally had the least litter, due to tidal flushing and export of material (Figure 2.9a). Triple density treatments had the most litter each month. By October, as the influence of grazers diminished, all the caged treatments returned to a similar value (Figure 2.9b).

2.5.7 Tissue composition

Plant % Nitrogen:

Plant nitrogen values increased significantly due to the presence of cages ($p < 0.0001$, Figure 2.10a). Within the caged treatments, plant nitrogen varied very little, but ambient density treatments had a 3% increase in tissue nitrogen.

Plant % Carbon:

There was no significant effect of grazer density on plant carbon content. Exclusion treatments had the lowest tissue carbon (0.5% decrease) values while the other treatments were similar in value (Figure 2.111a).

2.5.8 Flowering rate:

There was no significant effect of the grazer treatments on flowering rate of the plants. Plants bloomed in September and October, and Figure 2.122a illustrates the variances within treatments. Triple density treatments had lowest blooming rates and exclusion treatments had the highest.

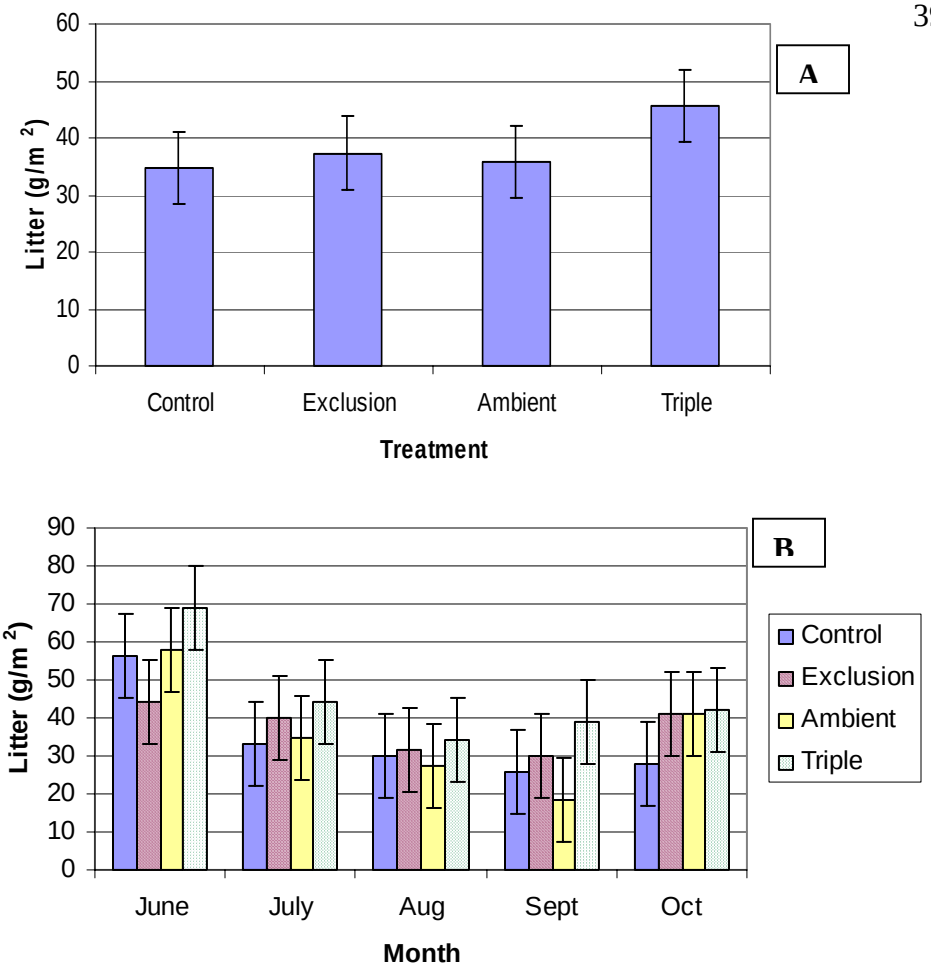

Figure 2.9 Litter by weight.

Average weight of litter, per m^2, per treatment (Graph A), and per treatment each month (Graph B). +/- 1 SE.

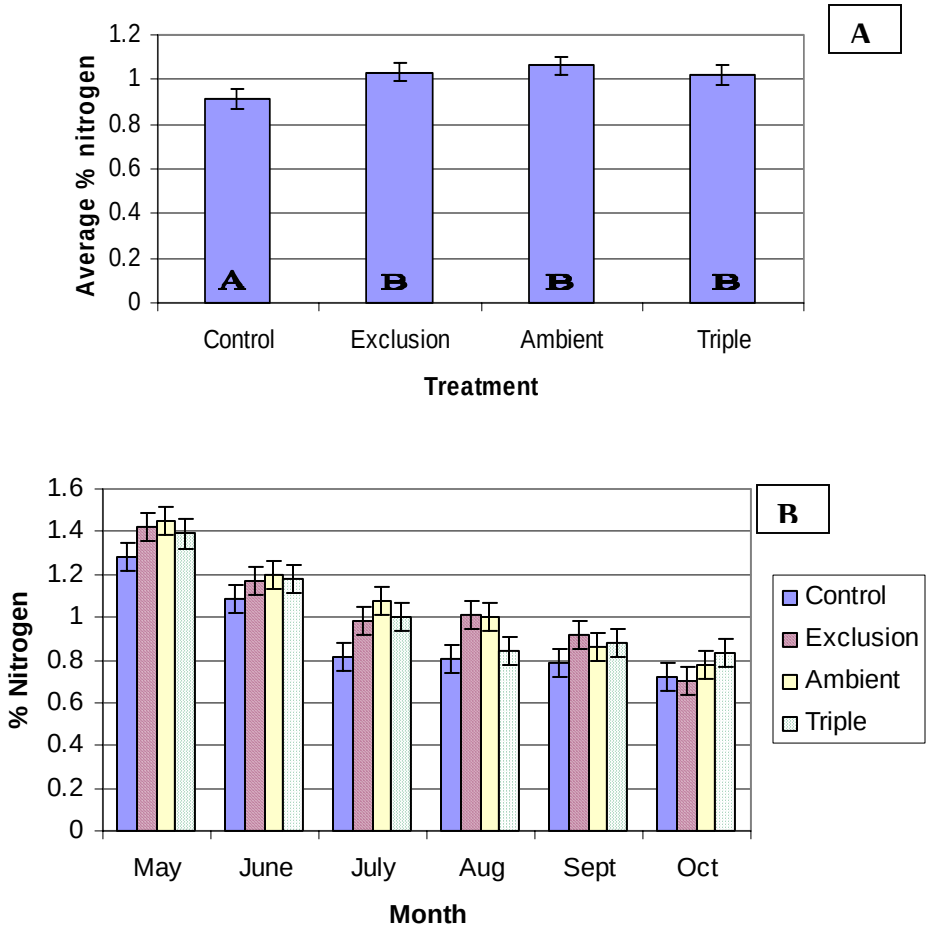

Figure 2.10 Percent plant nitrogen

Average percent plant nitrogen per treatment (Graph A), and per treatment for each month (Graph B). +/- 1 SE. P value < 0.05. The letter in Graph A represent significantly different groups within the treatments.

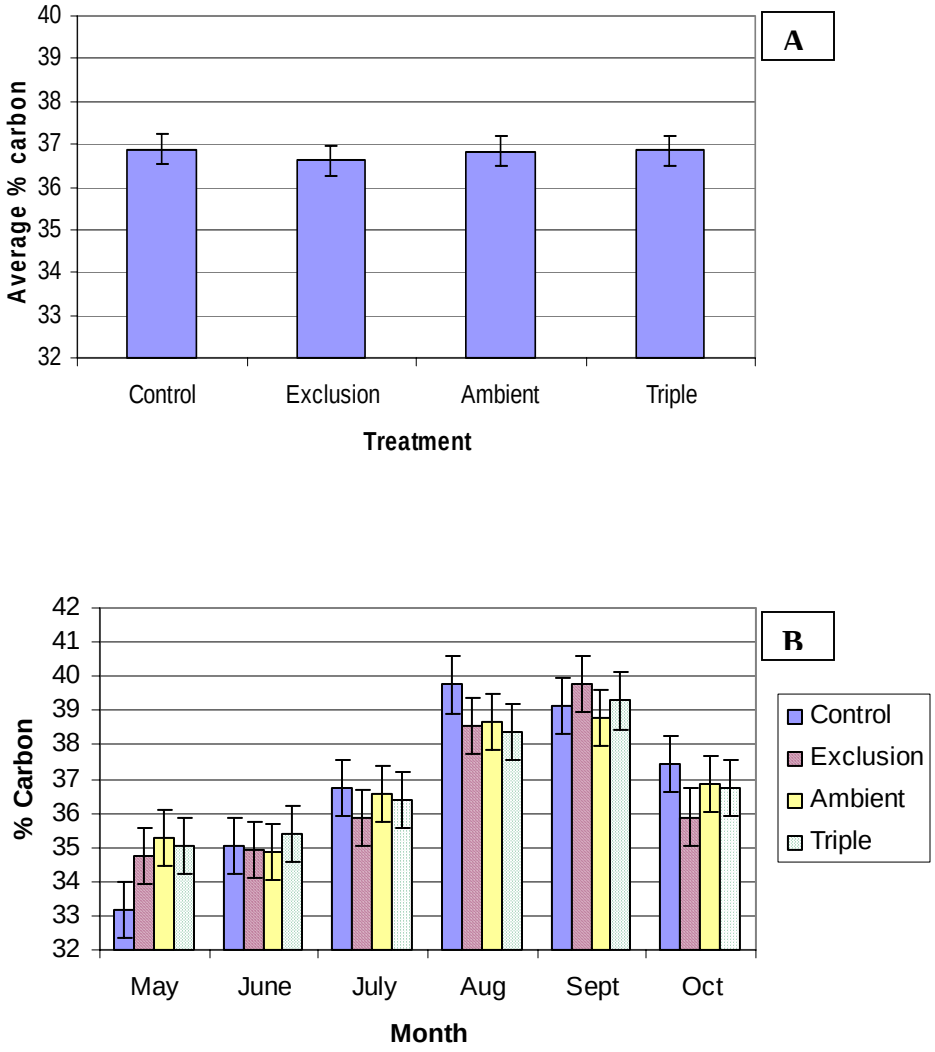

Figure 2.11 Percent plant carbon

Average percent plant carbon per treatment (Graph A), and per treatment for each month (Graph B). +/- 1 SE.

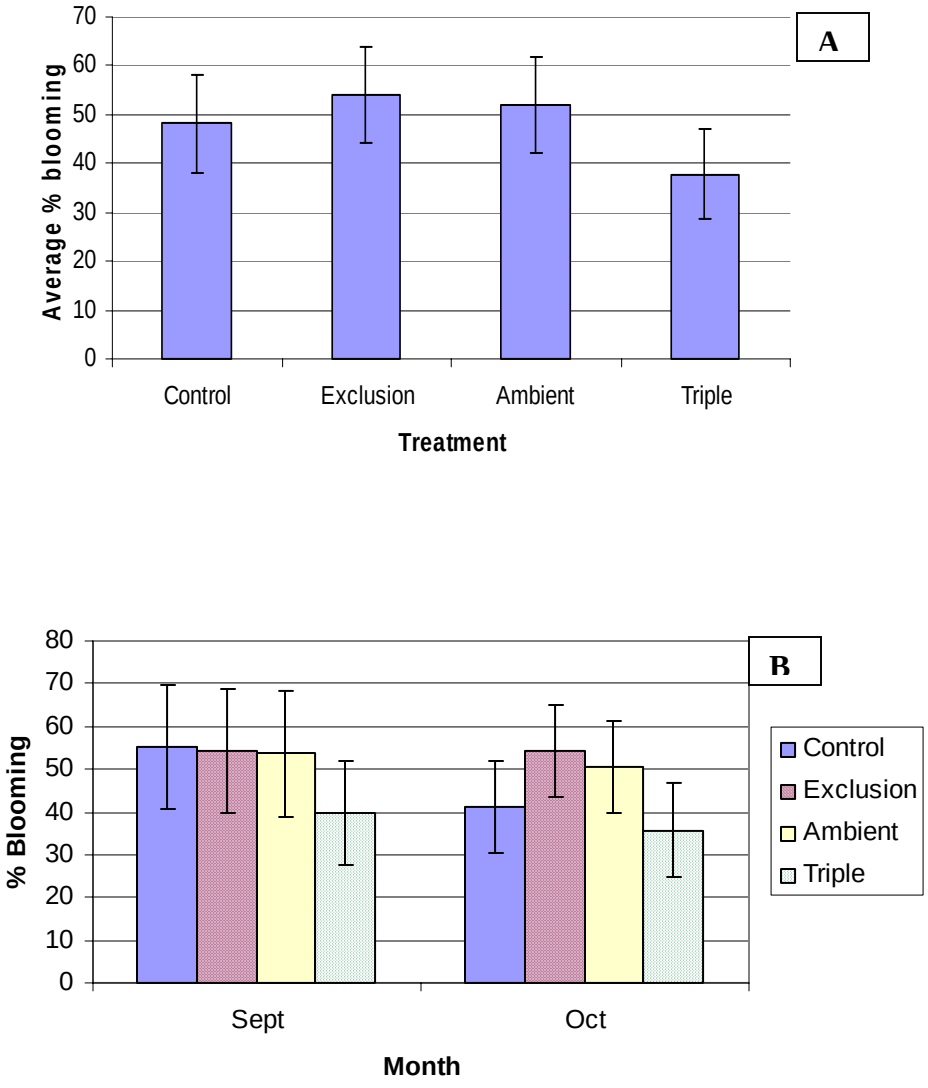

Figure 2.12 Percent plants blooming

The average percent of plants blooming per treatment (Graph A), and average per treatment each month (Graph B). +/- 1 SE.

3 Effects of grazers on belowground environment

3.1 Introduction

Salt marsh ecosystems are viewed as detrital based food webs, with only an estimated 5-10% of carbon fixed by the marsh grasses entering the herbivorous food chain (Pennings and Bertness 2001). Although salt marshes have been studied extensively in regards to system function and ecological dynamics (Teal 1962, Odum and Smalley 1959, Pennings and Bertness 2001, Bertness 1984 and 1985), little is known of the effects of grazing insect herbivores in these ecosystems. Although the grasshoppers, *O. fidicinium,* live and feed in the aerial portion of *S. alterniflora*, they may affect the substratum, directly and indirectly, by altering sediment belowground biomass, sediment organic matter and nutrient content, and benthic microalgal communities. This study aims to identify, and quantify, the influence of *O. fidicinium* on the non-aerial portion of temperate salt marsh environments.

S. alterniflora has substantial belowground biomass, approximately 3.5 times greater than aboveground biomass (Blum 1993). Under lower grazing pressure, plants may increase resource allocation to aboveground material in order to replace damaged material. This could cause a decrease in root biomass (McNaughton 1983, Mattson and Addy 1975, Silliman 1999). As grazing pressure increases, plants may translocate material into the roots. This could cause an increase in root biomass (Dyer and Bokhari 1976) and subsequently asexual reproduction.

Organic matter accumulation is determined by the balance between organic matter inputs and the decomposition rate. Organic matter inputs in salt marshes are primarily from root and rhizome turnover. The predominant fate of roots and rhizomes is in situ microbial decay (Blum 1993). Grasshopper grazing may increase the sediment organic matter by increasing litter inputs, with fecal matter inputs, and by stimulating belowground growth (Mitchell and Pfadt 1974, Dyer and Bokhari 1976).

Sediment nutrient content may increase as a result of increased organic matter. Nutrient regeneration, through fecal inputs, can be an important trophic link for herbivores. The poor digestive assimilation rate of *O. fidicinium* may result in nutrient rich fecal inputs, increasing the nutrient regeneration and availability within the sediments (Odum and Smalley 1959, Smalley 1960). Salt marshes are primarily nitrogen limited, with ammonium (NH_4) as the primary form of nitrogen available to the marsh vegetation. Ammonium is only a small fraction, approximately 1%, of the total nitrogen in salt marsh sediments (Mitsch and Gosselink 1993).

Grazing may reduce the canopy structure, thereby increasing light penetration to the marsh surface. An increase in light, in conjunction with an increase in surface nutrient inputs, could stimulate microalgal growth. Microalgal communities are the second largest primary producers in the salt marsh ecosystem, and are heavily consumed by fiddler crabs, snails, herbivorous fish, and other surface feeders. Algal biomass is more readily assimilated and more nutritious than marsh grasses for these surface grazers (Gosselink and Kirby 1974, Pomeroy et al 1981).

The role of grasshoppers in salt marsh ecosystems has been marginalized due to their short life span, patchy distribution, and small amount of ingestion. The indirect effects of grazing could constitute the grasshoppers' main role in these ecosystems (Mitchell and Pfadt 1974). Understanding these effects, and beginning to quantify them, is necessary in understanding the overall effect of *O. fidicinium* on the system.

3.2 Objectives and hypotheses

1. *To assess the effects of grasshopper grazing on the belowground biomass of Spartina alterniflora*. Grasshopper grazing may stimulate growth in aboveground *S. alterniflora,* thus reducing root biomass, and as grazing continues through the season, aboveground production may be reduced in favor of belowground biomass.
2. *To assess how sediment organic matter and nutrient content is affected by grazing.* Both are expected to increase, with increased litter and fecal matter inputs, due to grasshopper grazing.
3. *To assess the effects of grasshopper grazing on microalgal communities.* Grasshopper grazing may increase light penetration to the marsh surface, through reduction of canopy biomass. This along with additional nutrient inputs, may lead to an increase of microalgal density on the sediment surface.
4. *To develop a diagrammatic model of O. fidicinium's role in temperate salt marsh ecosystem.*

3.3 Methods

3.3.1 Belowground biomass

Large cores, 15 cm diameter and 50 cm deep, were collected to assess belowground biomass. In May, eight representative cores were collected alongside the experimental plots, to avoid damage to the plots. In October, at the completion of the experiment, one core was collected from within each plot. The cores were each divided into five 10 cm layers in the field and stored in plastic bags on ice until return to the lab. The samples were washed free of mud and frozen for sorting at a later date. Within each 10 cm layer, the material was subsequently sorted into obvious live material and all other material, and then rewashed. Distinguishing between live and dead material was subjective based on color and turgor. To minimize sorting errors, and to homogenize distinctions, the root separation was completed within a 96-hour period. The sorted material was freeze-dried and weighed.

3.3.2 Organic matter and sediment nutrients- C, N, NH_4

Three replicate sediment cores, 8 cm deep and 60 cc volume, were collected monthly within each plot. The cores were stored on ice until return to the lab where they were frozen. Once frozen, each core was divided into three layers: 0-2 cm, 2-5 cm and 5-8 cm deep. Each layer was further sub-divided for organic matter and nutrient assessment. These sub-sections remained frozen through the division until further lab analysis.

The percent organic content was determined by weight. The wet sediment sample was weighed, then dried at 60° C for approximately 72 hours. The dry sample was then reweighed. The difference between the two weights represents the water present in the sediment. The dry sample was ashed at 550° C for 4 to 6 hours, and again reweighed. The difference between the dry (DW) and ashed (AFDW) weight represents the organic matter (OM) portion of the sediment. Percent organic matter was calculated as follows: $OM\ \% = 100 * [(DW - AFDW)/DW]$

The freeze-dried sub-sample for carbon and nitrogen analyses was powdered with a mortar and pestle. The sediments were treated with 20% HCl to remove carbonates and analyzed using a Carlo Erba Elemental Analyzer 2500. Two analytical replicates of each sample were run to account for machine accuracy.

Ammonium exists in sediments in an aqueous and a bound form. The bound form is adsorbed onto sediment particles and must be extracted from its adsorption site before being measured in the aqueous form. The sub sample for ammonium was frozen until extraction. A KCl solution was used to extract the bound ammonium into solution, as the K^+ ion replaces the NH_4^+ ion. The solution was treated with alkaline phenol, hypochlorite, and sodium nitroprusside to form indophenol blue. This solution was then read on a spectrophotometer at 635 nm.

3.3.3 Sediment chlorophyll and pheophyton

Benthic chlorophyll and pheophyton concentrations are used as a proxy for microalgal community density. Three replicate syringe cores, 1 cm deep and 5 cc volume, were collected monthly within each plot. All cores were collected at low tide, as some

microalgae are known to migrate vertically relative to the tides, completing the downward migration with the return of the tide (Pomeroy 1959). Cores were kept on ice and in the dark while in the field, and were frozen upon return to the lab. Chlorophyll was extracted from the sediment by adding 90% acetone and sonicating the sample for one minute. The samples were then placed back in the freezer overnight before being read on the spectrophotometer. Four consecutive readings were taken on the spectrophotometer. The first two readings, at 665 nm and 750 nm respectively, were on untreated sample supernatant. The second two readings were treated with 5% HCl and reread at the same wavelengths. Chlorophyll and pheophyton concentrations were calculated from the absorbance readings as follows:

$$CHL = 26.7 * (665o - 665a) * v * A$$

$$PHEO = 26.7 * ((1.7 * 665a) - 665o) * v * A$$

Where 665a = 665 - (750 - blank value) after acidification, 665o = 665 - (750 - blank value) before acidification, v is volume of acetone, and A is area of core.

3.4 Data analysis

The use of the randomized complete block design (RCBD) allowed for comparison of the various treatments within each block, and minimized variability due to the environment. Each month, three replicate samples for each variable were collected, except belowground biomass, which was only collected twice. These samples were analyzed separately in the lab, and the results were pooled to give a mean monthly sample for each cage. By doing this, each mean monthly sample becomes a replicate for that cage. All the data were analyzed using a repeated measures ANOVA. The repeated

measures ANOVA accounts for repeated sampling within the same plot for consecutive months. An autoregressive order-1 covariance structure was used. This assumes that samples in May are more closely related to samples in June than in October. This type of structure was chosen due to a higher Akaike's Information Criterion (AIC) number than other covariance structures. The repeated measures ANOVA analyzed for three fixed factors: month, treatment, and month by treatment interaction. The month factor assesses the average value per month across all treatments. The treatment factor assesses the average per treatment value across all months. The treatment by month interaction assesses the average value of each treatment within each month. If the p value of any fixed factor was significant ($p < 0.05$) this factor was further analyzed using pair-wise contrast. If contrasts were non-orthogonal the alpha value was adjusted, using the Dunn-Sidak method, to maintain a 95% confidence limit. Least square means were calculated and plotted for each set of data. All data was assessed for homogeneity of variance using the F-max test. Sediment carbon and nitrogen at 5-8 cm, and NH_4 at all depths were log transformed to meet this assumption. All statistics were completed using SAS.

3.5 Results

3.5.1 Seasonal effects

Throughout the summer months many of the variables changed significantly. These changes were due to the progression of the summer and not the effects of the density treatments. All the results, and figures, pertaining to seasonal variation of the measured variables are contained in Appendix B. Organic matter varied significantly

throughout the summer months at the three depths ($p < 0.0001$, Figure 8.10). Percent sediment carbon in top 2 cm was significantly higher in September than August (Figure 8.12). Microalgal biomass decreased significantly after June ($p < 0.0001$, Figure 8.13).

3.5.2 Cage effect

Establishing cage structures in the marsh influenced some of the environmental factors associated with these sites. The cages were expected to reduce tidal flushing on a daily basis, therefore reducing litter removal, increasing organic matter and nutrient recycling in situ. They were expected to decrease the light reaching the plants, possibly decreasing productivity. The cages provide a structural buffer for the plants against high winds or currents, possibly affecting the plants' growth form. Including grasshoppers in cages will limit their food source, and possibly exaggerate the effects of these grazers. The statistical results regarding the influence of cage structures on the experiment are important to remember while interpreting the results. All the results pertaining to cage structure will be addressed here and considered throughout the remaining results sections. As expected, the percent of organic matter in the surface 2 cm, significantly increased with cages due to reduced tidal flushing ($p = 0.02$, Figure 3.2a). Sediment carbon, nitrogen and ammonium, at 0-2 cm deep, were also significantly increased with the presence of cages (C and N: $p < 0.05$, NH_4: $p < 0.0001$, Figure 3.4a).

3.5.3 Belowground biomass

Due to unforeseen circumstances, half of October's belowground cores were lost while in storage. The remaining cores allowed for comparison of the start and end of the

experiment, within two of the four blocks. The results should be interpreted with caution as replication was very low. Some cores only reached 40 cm deep, so for comparative reasons only material collected to 40 cm depth was considered. Due to the size and decay condition of the dead root matter, sediment remained even after thoroughly washing. This may disproportionately add weight to the dead material. A comparison of the live material by weight is a clearer comparison. The root biomass in May was collected prior to initiation of the grazer treatments. The variation in this biomass, across the four treatments, is the natural variation in *S. alterniflora* roots.

The majority of live material was in the top 20 cm of the sediment, and decreased with depth. Below 20 cm, dead material exceeded live material. In May and October, dead material ranged about 3000-3500 g/m^2, and the range of live material was 1400-2600 g/m^2. Within each core, the live material was analyzed within each layer and as bulk live matter for all depths. The bulk live biomass showed no significant effect of grazer treatments. Ambient density treatments show a decline in bulk live root biomass from May to October (Figure 3.1b). There was no significant effect of grazer treatments within three depth layers, 10-20, 20-30 and 30-40 cm. No treatment was significantly different than the other within either month.

In the surface layer, 0-10 cm deep, there was a significant difference for ambient and triple density treatments between May and October ($p = 0.0147$ and 0.0244 respectively, Figure 3.1a). Ambient density treatments had a significant decrease in live root material. Ambient density treatments may have caused plants to increase aboveground production, thereby reducing root matter. Triple density treatments had a

significant increase in live root biomass. The triple density treatment could be high enough that the plants began to translocate material to the roots, thereby causing an increase in root material. As these effects were only found in the top 10 cm layer it is also possible that they are anomalous, having little to do with the grazer treatments.

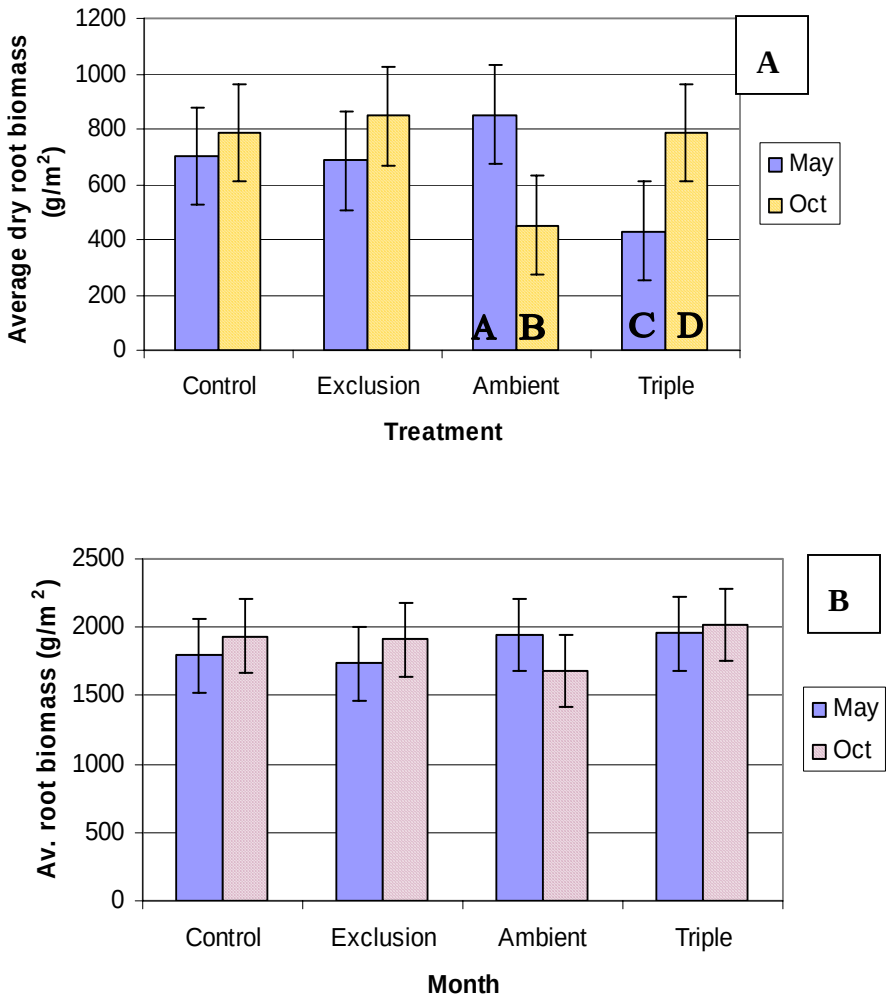

Figure 3.1 Live root biomass

Average dry weight for live belowground biomass, 0-10 cm deep, for each treatment each month (Graph A). Letter designate significant differences within treatments. Significance $p < 0.002$ for both.

Average dry weight of live belowground biomass, from 0-40 cm deep, for each treatment in May and October (Graph B). +/- 1 SE

3.5.4 Sediment organic matter

Sediment organic content was assessed for three different soil depths: 0-2, 2-5 and 5-8 cm. The presence of cages significantly increased organic matter at the 0-2 cm depth ($p < 0.05$, Figure 3.2a). There was also significantly higher sediment organic matter in the inclusion treatments compared to the exclusions ($p = 0.027$). There was no significant difference between the two inclusion treatments. At 2-5 and 5-8 cm deep, there were no significant effect of grazer treatments.

3.5.5 Sediment chlorophyll and pheophyton

Neither chlorophyll nor pheophyton showed a significant effect of grazer treatments (Figure 3.3a). Data was not collected in September, as the tides never fell below the sediment surface. The microalgal communities can be patchy on the marsh surface, and it is possible that the three replicates a month did not capture changes in microalgal biomass.

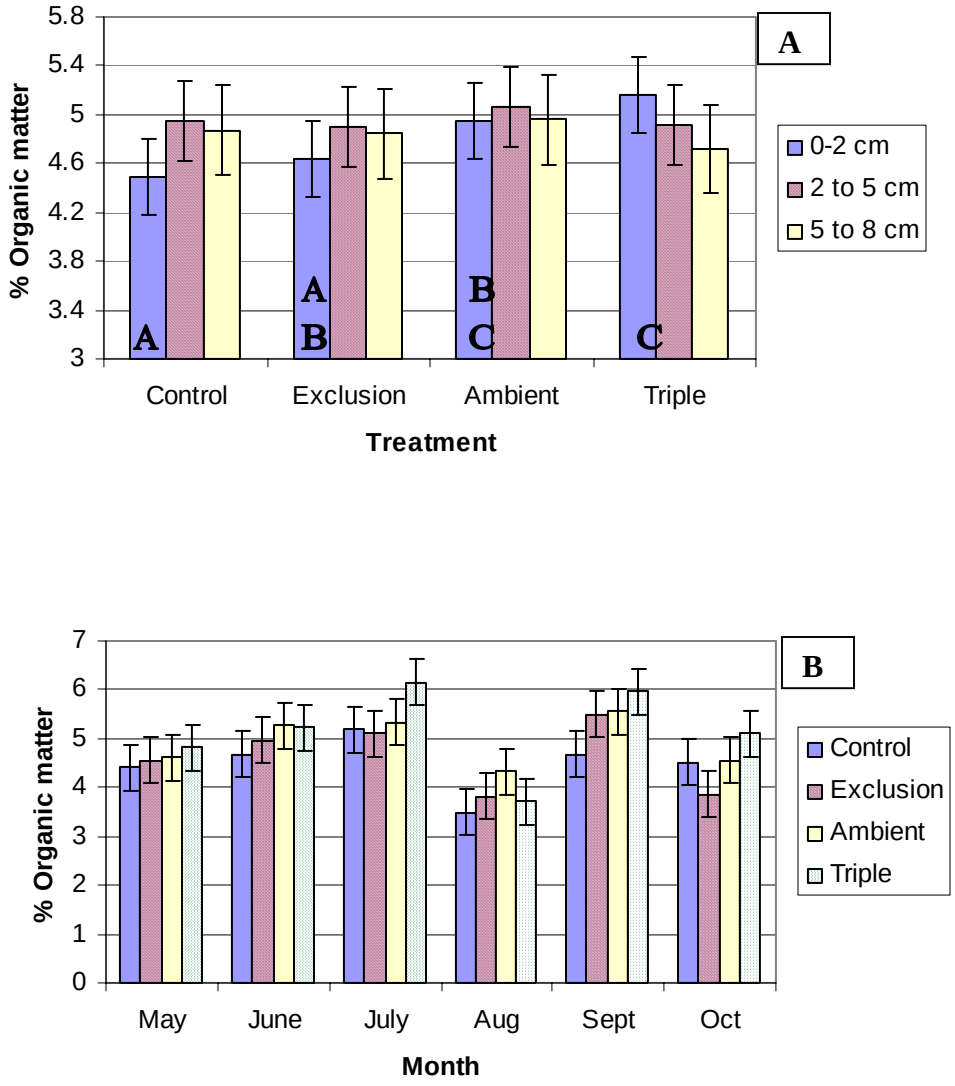

Figure 3.2 Sediment organic matter

Average sediment organic matter content per treatment at three depths (Graph A). The letter designate significantly different groups. +/- 1SE. P value < 0.05.
Average organic matter content at 0-2 cm deep for each treatment monthly (Graph B). +/- 1 SE.

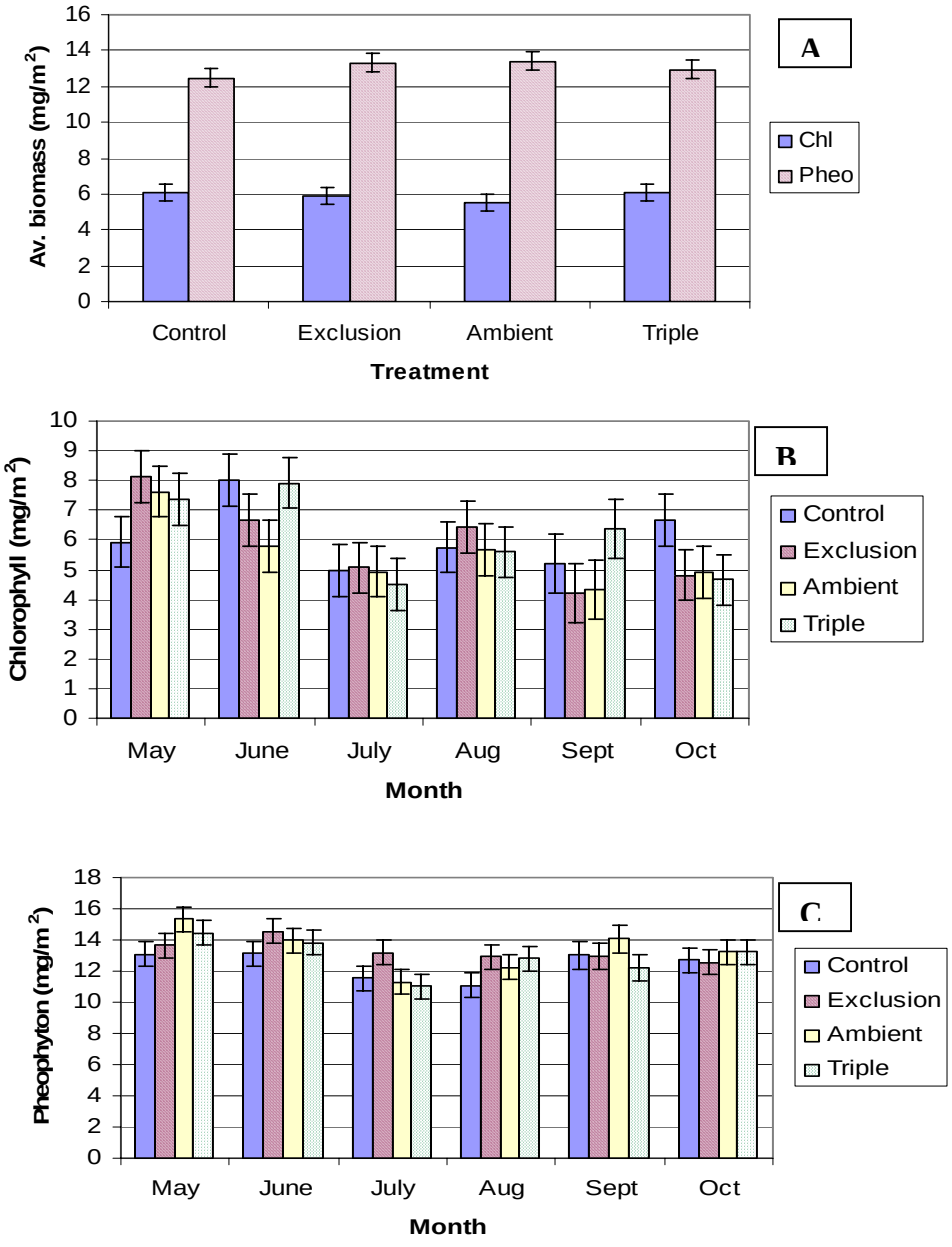

Figure 3.3 Microalgal biomass

Average concentrations of chlorophyll and pheophyton (mg/m^2), as a proxy for microalgal biomass. Graph A is concentration per treatment for the whole summer, Graph B is chlorophyll concentrations per treatment each month, and Graph C is pheophyton concentrations per treatment each month. +/- 1 SE.

3.5.6 Sediment nutrients

3.5.6.1 Sediment carbon and nitrogen

Sediment carbon and nitrogen were assessed for three layers: 0-2 cm, 2-5 cm, and 5-8 cm deep. Carbon showed no general pattern with depth, whereas nitrogen decreased with depth. The magnitude of changes due to grazer densities declined with depth. At 0-2 cm deep, sediment carbon and nitrogen were significantly increased due to the cages ($p < 0.05$, Figure 3.4a and 3.4b). Carbon and nitrogen were also significantly increased in the triple density treatments in September ($p = 0.0219$ and 0.025 respectively, Figure 3.5a and 3.5b). Both carbon and nitrogen data, at the 0-2 cm depth showed a general tendancy of increasing nutrient content with increased density of grasshoppers. At 2-5 and 5-8 cm deep, significant effects of the grazer treatments were not evident. At 2-5 cm deep carbon and nitrogen positively correlated with grasshopper densities (Figure 3.4a and b). At 5-8 cm, the carbon and nitrogen had a slight negative correlation with grazer density.

3.5.6.2 Sediment NH_4

In general the NH_4 values decreased with depth. At 0-2 cm deep, ammonium was significantly lower in controls ($p = 0.0001$, Figure 3.4c). At all depths, there were no significant effects of grazer treatments. Sediment NH_4 generally increased with cages and grazer density, but slightly decreased in the triple density treatments.

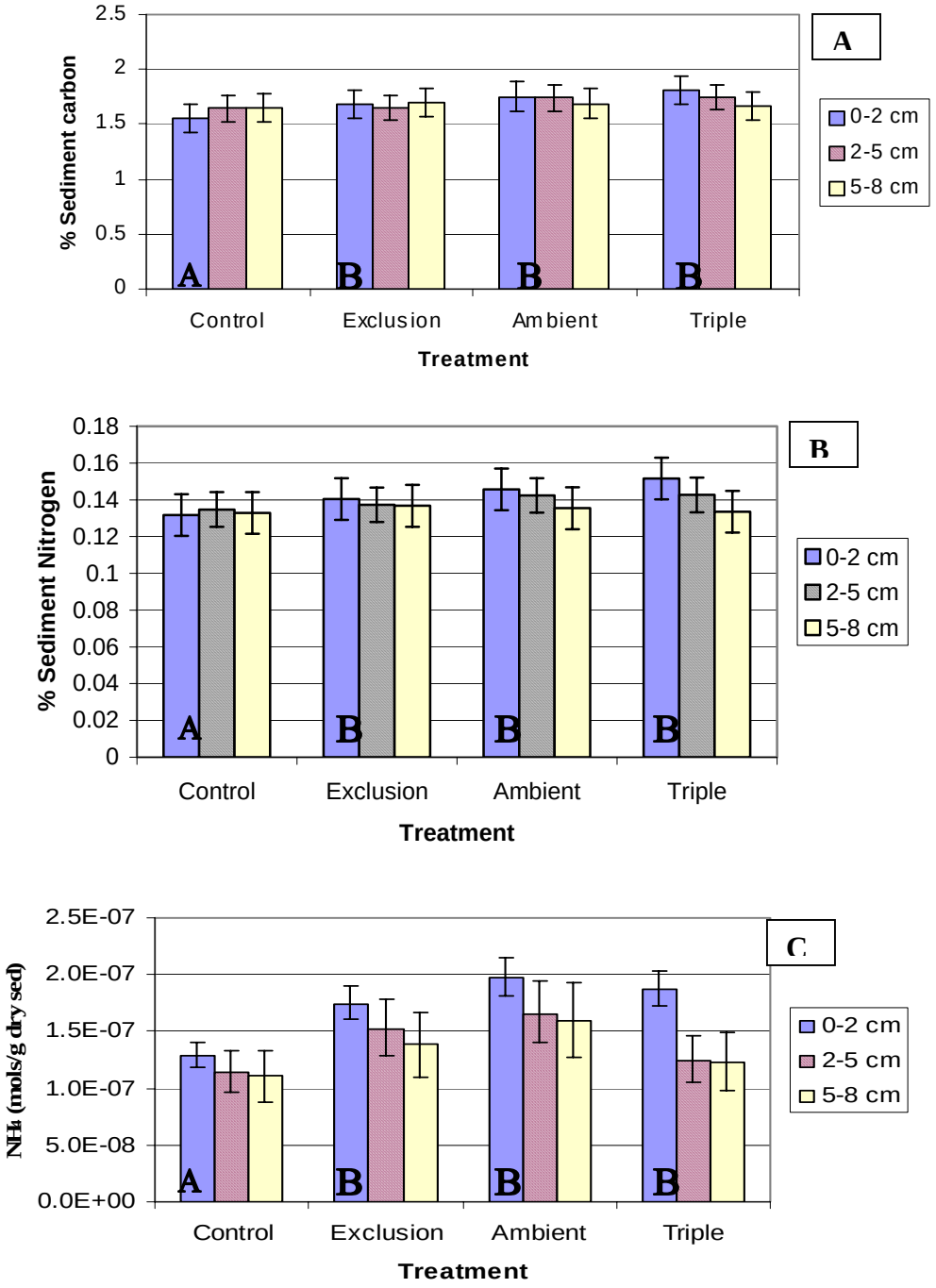

Figure 3.4 Sediment nutrients per treatment

Average sediment nutrients, per treatments for the whole summer, at three depths: 0-2 cm, 2-5 cm, and 5-8 cm deep. +/- 1 SE. Graph A is sediment percent carbon values; Graph B is sediment percent nitrogen values; Graph C is sediment ammonium concentrations. Letters indicate significantly different groups in each graph. P value < 0.05.

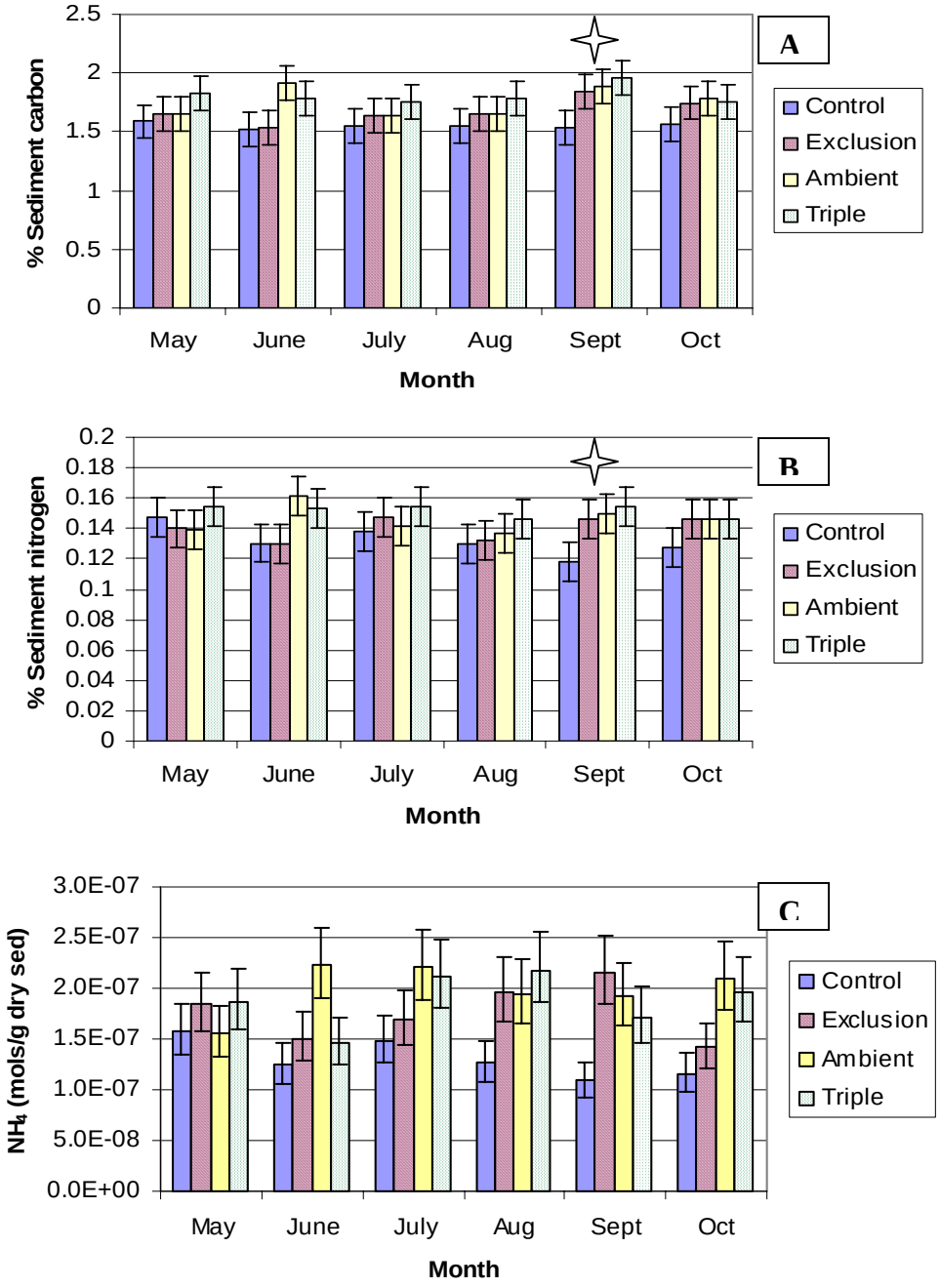

Figure 3.5 Sediment nutrients monthly

Average sediment nutrient values per treatment each month at 0-2 cm deep. +/- 1 SE. Graph A is sediment percent carbon, Graph B is sediment percent nitrogen, and Graph C is sediment ammonium concentrations. Stars indicate significant difference between triple and control treatments.

Variable	Exclusion	Ambient	Triple	Significance
% Leaves grazed	Decreased	Increased	Increased	Inclusion > exclusion
% Plants grazed	Decreased	Increased	Increased	Inclusion > exclusion
Dry Biomass	Decreased	Decreased	Decreased	None
Stem density	Increased	Decreased	Increased	None
Water content	Increased	Increased	Increased	Excl<Ambient<Triple
Plant Height	Increased	Increased	Decreased	None
# Dead Leaves	Decreased	Increased	Increased	Exclusion<Inclusions
# Live leaves	Decreased	Increased	Increased	Exclusion<Inclusions
Litter	---	---	Increased	None
% plant nitrogen	---	Increased	---	None
% plant carbon	Decreased	---	---	none
% Blooming	Increased	Increased	Decreased	None
Root biomass 0-10	Increased	Decreased	Increased	Ambient and triple changes
Sed. Organic matter 0-2	Decreased	Increased	Increased	Exclusions< Inclusions
Microalgal Biomass	---	---	---	None
% sed. Carbon 0-2	Decreased	---	---	None
% sed. Nitrogen 0-2	---	Increased	---	None
Sed NH_4 0-2	---	Increased	Increased	None

Table 3.1 Treatment results summary

A verbal summary of treatment effects and trends, noting if there was significant changes or not. Dashed lines mean the values were not noticeably changed.

4 Discussion

4.1 Grasshopper density

Quantifying the distribution and density of grasshoppers on the salt marsh through the summer was difficult. At the beginning of the summer while working with juvenile grasshoppers both methods for assessing grasshopper densities had problems. The sweep net missed many juveniles as they jumped down into the dense plant canopy. The juveniles were difficult to locate in the drop cage. As summer progressed the sweep net method was progressively better at catching grasshoppers. The larger grasshoppers were

able to avoid the cage. Of the two methods used the sweep net was more efficient and easier to handle. If the sweep radius could be correctly transferred to a per area scale, it would generate good density estimates. The sweep net is not useful for collecting live samples in marshes of high snail density, as the snails in the net squash the other samples.

A confounding factor in understanding the density of grasshoppers is their clumped distribution. They congregate on taller grasses, either in the low marsh or directly beside the creeks, depending on marsh location and time of the season. At the beginning of summer the grasshoppers congregated in medium grasses behind the tall creekside grasses. These congregation sites shifted in mid-July from the medium grasses to tall creekside grasses. Patches of tall creekside grasses contained up to eight times the number of grasshoppers previously surveyed on the marsh. It is possible that tall grasses grow faster than the medium grasses, and are more palatable. The grasshoppers remained dense on the tall grasses until mid-late August, when all the grasses began to flower. From observations the tall grasses did not flower as much as other areas. After mid-August there was a decreased congregation on these tall grasses and the grasshopper density increased in the medium grasses. Grasshopper abundance throughout the marsh increased slightly with flowering of grasses. This increase may be an artifact of altered grazing habits. As grasses flower, the grasshoppers begin to graze on the flowers and seeds, making the grasshoppers quite visible on the grasses. The shifts in grasshopper density, from medium to tall grasses and back, is likely due to the grasshoppers available food sources within the marsh.

In an attempt to generalize grasshoppers' distribution patterns, two other marsh areas were surveyed in June and August. Grasshopper abundance in marshes on north and south Hog Island were lower than at Brownsville marsh. South Hog Island had low grasshopper abundance. In this young marsh, the abundance of snails and crabs may limit grasshopper abundance, due to disturbance and predation respectively. North Hog Island and Brownsville marsh had equally dense grasshopper populations. Their distribution on North Hog Island was not predictable from patterns seen in Brownsville. For example grasshoppers were found in taller and shorter grasses, but not in medium grasses. The short grass showed no signs of grazing.

It appears from these preliminary observations that the grasshoppers are difficult to catch for accurate density measurements, patchy in their initial distribution, and their patchiness is shifting throughout the summer according to grass development stages. The grasshoppers are present in the taller grasses, but may be limited by predators and disturbance.

4.2 Grasshopper demographics

The demographics of the grasshopper population at my sites changed throughout the summer. The juveniles, less than 0.5 cm long, appeared in May in low numbers, and grew rapidly to 1 cm through June. Although the majority of the population grew to 3 and 4 cm lengths by August, juveniles were still present. This may be due to cooler than average weather conditions prolonging the hatching period through the summer. During preliminary fieldwork at Brownsville in 2003 this variance in grasshopper size was not noted. According to Smalley (1960) the number of grasshoppers decrease through the

summer, as the weight of individuals increase. In this study the size and number of grasshoppers increased through the summer. This may result in a grazer biomass peak at the end of the summer.

As the season progressed, the adults became noticeably louder and had attained the ability to fly by early August. The number of grasshoppers began to decline by mid-August. The start of grasshopper decline coincided with an increase in spider numbers, possibly in response to a new easy food source of dying grasshoppers. Spiders are noted as the most important predator upon insects in *S. alterniflora* marshes (Davis and Gray, 1966). There were grasshoppers still present on the marsh, post Hurricane Isabel, in October.

As an aside on two different sampling times, August 22nd and Sept 10th, large dead females were found stuck in the cages while apparently trying to escape. No other grasshoppers ever seemed interested in escaping the cages. These dates coincide with the start of declining numbers of grasshoppers, and may be related to egg laying.

4.3 Patterns in grazing habits

O. fidicinium graze by scraping off the leaf surface without cutting through the leaf blade. The caged inclusions had significantly higher leaf grazer damages than uncaged controls ($p = 0.006$). The inclusion treatments contained a set density of grasshoppers constantly present. The control plots had similar densities of grasshoppers, but they were not as limited in their food choice as caged grasshoppers. Within the caged treatments the percent of plants and leaves grazed were significantly higher with the inclusion of grasshoppers ($p < 0.0001$). Both plants and leaves grazed had positive linear

relationships with grazer density for the second half of the summer, July through September (R^2 = 0.41 and 0.52 respectively, Figures 7.4 and 7.5, Appendix A). Using average values for the whole summer, there was no discernible difference between the percent of plants grazed in the two inclusion treatments, however both were higher than exclusions (7.5%). Triple density treatments had noticeably more leaves grazed (9%) than ambient density treatments (7%). These average values are useful for comparative reasons but to clearly understand patterns of grasshoppers grazing monthly graphs of each treatment are necessary. The percent of plants and leaves grazed reached a maximum in August for both inclusion treatments (triple = plants 54%, leaves 23%; ambient = plants 53%, leaves 18%). Higher density grazer treatments did not graze more plants than ambient density grazers, but did graze more leaves. This may be due to the palatability and location of the plants, territoriality of grasshoppers to certain plants, predation, or other factors. Increased grazing on leaves will decrease the canopy to a greater extent. A decrease in canopy may increase light penetration, change the air temperature, soil salinity, and other abiotic factors. Through field observations, canopy damages were more visible with triple density than ambient density treatments (Photo 2.1).

Knowing that the presence of grazers, and their densities, increased the damages on above ground biomass how does this affect plant standing crop and plant morphology.

4.4 The influence of grazers on aboveground biomass

Biomass increased in all plots throughout the summer. Variation in aboveground production was minimal between treatments, triple being noticeably lower than

exclusions. By the end of the summer all of the treatments had about equal productivity. The grazer inclusion treatments had an end of season increase in productivity. This end of season increase in the highest grazer density may be a result of continued compensation by the plants as the grazing pressure declines.

A decrease in productivity can result from a decrease in the number of plants present per meter, or a decrease in per unit weight of the plants. Stem density was not significantly different in any of the treatments. Ambient density treatments had lower stem density, and triple density treatments increased their stem density at the end of the season. The decreased stem density in ambient density treatments may be influencing the decreased biomass result.

Plant height and leaf length increased slightly with cages, and decreased slightly with triple density treatments. Plant height is equal to leaf length, as the height of the plant was measured from the base of the plant to the tallest part, most often a leaf tip. For the reminder of the discussion only plant height will be discussed knowing that it contains elements of leaf elongation in its results. The increase in plant height within cages could be due to decreased light penetration, and increased sediment nutrients through organic matter retention by the cage. Plant height is slightly decreased in triple density treatments, due to grazer stress.

The number of dead and live leaves is significantly decreased without grazers ($p = 0.006$ and 0.045 respectively). The triple density treatment shows a slight decline compared to ambient treatments.

From these results ambient density treatments have lower productivity and decreased stem density. Triple density treatments had lowest productivity, but stem density was not decreased. Other reasons for lower aboveground biomass may be morphological changes within the plant. Increasing leaf tissue and reducing stem tissue could result in lighter plants even though they have more leaves. Silliman (1999) found with intense snail grazing on *S. alterniflora* the stem mass and diameter decreased significantly. Further study is needed to understand the mechanics responsible for the changes found in aboveground biomass of grazed *S. alterniflora*.

The water content of plants was significantly increased due to cages and grazer density ($p<0.05$). The caged plants have significantly higher water content than uncaged plants, possibly as a result of shading and increased plant height. Taller, and leafier plants tended to have higher water content. This may be due to juvenile plant tissues containing greater water content. As shading and grazing increase leaf growth and elongation water content increases. Each caged treatment was significantly different than the other ($p<0.05$). McNaughton (1982) found grazed plants to have reduced transpiration due to reduced surface area. In the case of grasshoppers the surface area remains the same and the surface tissues are removed. This may lead to increased transpiration through the grazing wound, stimulating the plants to uptake more water than necessary.

To summarize, plants under grazing stress have decreased productivity. This is possibly due to decreased stem density and altered stem morphology in ambient density treatments. In triple density treatments the decreased aboveground biomass is possibly due to decreased plant height, fewer leaves, and altered stem morphology.

4.5 Grazers influence on nutrient cycling and tissue composition

Grazers can influence nutrient cycling by increasing leaf turnover and litter fall, and through fecal inputs. Leaf turnover was significantly higher with grazers ($p<0.05$). Litter increased in triple density treatments (approx. 25%). Increased litter inputs from triple density treatments are expected to increase sediment organic matter and nutrient content.

Grasshoppers were contained to assess the input rate of fecal matter. The input rate is approximately 0.01g/grasshopper/hour. The nitrogen content was less than 1% and carbon content ranged from 3 to 17%. This results in 0.0001g nitrogen, and 0.0003 to 0.0017g carbon per grasshopper an hour. Figuring the grasshoppers are active 8-10 hours a day then a single grasshopper should input approximately 0.0054 to 0.031g carbon/day, and 0.0018g nitrogen/day. These are small values that may not be important to the plants but could influence other surface feeding organisms.

Although plant nitrogen was not significantly affected by treatments, the ambient density treatments had 3% more nitrogen than exclusions, while triple density treatments had 1% less. These are small changes in nitrogen composition but in a nitrogen stressed environment these changes could be noticeable to grazers. From general field observations there were times in the summer when grazers congregated upon taller greener plants right beside the creek. These plants had approximately 8% more nitrogen and 6% more carbon than plants within the study area.

Percent plant nitrogen may be related to plant height as they follow the same pattern with treatments. As the plants grow taller, or elongate their leaves, nitrogen is expected may increase as juvenile plant tissues are richer in nitrogen. Both plant height and nitrogen content are significantly lower in control plots ($p < 0.05$). Triple density treatments had lowered plant height and nitrogen. The tissue nutrient content of the plants needs to be addressed with sediment nutrient content. Correlating these two variables may also illustrate reasons for plant height and nitrogen patterns.

To summarize, the presence of grazers should increase sediment nutrients and organic matter as grasshoppers increased litter inputs, leaf turnover, and have nutrient rich feces. The increased nutrient cycling is not apparent in the tissue nutrient composition of the plants. It is possible that any increase in nutrients results in increased growth not nutrient content.

4.6 Influence of grazers on belowground biomass

The effect of grazer treatments on the belowground biomass is questionable. The live roots showed significant effects of grazers in the top 10 cm. Below this the changes in roots are contradictory. Looking at the bulk root biomass from 0-40 cm deep there is no significant difference between the treatments. The same trend visible in the bulk root data is present with significance in the top 10 cm. The effects in the top 10 cm are discussed herein but may be anomalous to this experiment, simply a cause of marsh belowground variability. Under ambient density treatments the roots showed a significant decline from May to October ($p < 0.006$). As the ambient plants were grazed the plant may have compensated for the damaged material by increased production of leaves. This

type of compensation is reported to often reduce root growth (McNaughton 1979). With triple density treatments there was a significant increase in root biomass ($p < 0.006$). Triple density treatments began with a lower root biomass than the others, increasing in October to similar biomass values as the control and exclusion plots. The significant increase found with triple density grazers may be a result of this lowered starting biomass, or it may be a product of grazing pressure. If grazing pressure is high, or continues for a long time, the grass may not be able to compensate for the damages and may instead begin to translocate material into the roots for storage. This translocation may result in increased root biomass (McNaughton 1979). Root biomass may be somewhat related to sediment nutrient availability. The changes in root biomass may affect asexual reproduction, stem density, and root nutrient uptake.

4.7 Influence of grazers on sedimentary environment

Grazers were hypothesized to increase sediment organic matter, and nutrient content through increased litter and fecal matter inputs. In the sediment surface layer, 0-2 cm, organic matter significantly increased with grazer inclusions ($p < 0.05$). Sediment nitrogen and carbon increased slightly with grazer density in the same pattern as organic matter, increasing 4% with each level of grazer density.

Ammonium, at all three depths, increased slightly with grazers. In the surface sediments ammonium increased 14% with ambient density treatments, but only 8% with triple density treatments. Ammonium is generated through the decomposition of organic matter in the marsh sediments, and is the primary form of nitrogen available to marsh vegetation (Mitsch and Gosselink, 1993). In these results the highest ammonium

concentrations are in ambient density treatments, although organic matter is highest in triple density treatments. There may be some disparity in root uptake between the two inclusion treatments, leaving less ammonium in the sediment in triple density treatments. Triple density treatments have greater root biomass than ambient density treatments, due to aboveground grazer stress. The increased roots in triple density treatments may be taking up greater quantities of ammonium, therefore decreasing the sediment ammonium measured.

To summarize, the presence of grazers caused a non-significant increase in litter and a corresponding significant increase in organic matter. Sediment nutrients increase non-significantly with organics and litter.

4.8 Grazers effects on reproduction

S. alterniflora reproduces sexually, by flowering in late summer, and asexually, by developing clonal runners from the roots. There is a noteworthy decrease in the percent of plants blooming with triple density treatments. In exclusion and ambient density treatments the percent blooming is 54 and 52% respectively. With triple density treatments only 38% of the plants bloomed. The percent of plant flowering may decrease under higher grazing intensity due to reduced assimilation of energy through reduced vegetative tissues (McNaughton 1979). This decrease in sexual reproduction correlates with a significant increased root biomass in higher grazing treatments. Increased root biomass may indicate an increase in asexual reproduction via clones. Stem density is not significantly different across the treatments, but is lower in ambient density treatments. Ambient density treatments had decreased belowground biomass. It appears from these

results that under higher grazing treatments *S. alterniflora* has increased clonal reproduction and decreased sexual reproduction.

4.9 Sediment nutrients effects on aboveground biomass

In the top 2 cm of the sediment organic matter is significantly higher in inclusion treatments than exclusion treatments ($p<0.05$). The carbon and nitrogen increase slightly following the same pattern as organic matter. Ammonium is increased in inclusion treatments, but is slightly decreased in triple density treatments. The belowground biomass, of ambient and triple density treatments, change significantly in opposite directions through the summer ($p<0.006$).

The decrease in ammonium values in triple density treatments is likely due to increased root biomass and uptake. With increased root biomass, and uptake, in triple density treatments the aboveground biomass does not increase. In fact aboveground biomass in triple density treatments had the lowest aboveground biomass, decreased rate of flowering, and decreased nitrogen content. Grasses in triple density treatments appear to be sustaining belowground biomass while aboveground biomass begins to decrease under grazer stresses. At the end of the summer triple density treatments increase their biomass while all other treatments are decreasing biomass. This end of season pulse may come as the stressed plants are released from grazer pressure, and have sufficient belowground reserves to continue growth.

Ambient density treatments have elevated sediment nutrients and organic matter, and reduced belowground biomass. The plants may be compensating for aboveground grazer stress by increasing aboveground production. The root biomass declines to sustain

aboveground biomass. Root uptake per unit area of root may increase to maintain nutrient requirements.

To summarize although the sediment nutrient content presumably had an influence on aboveground biomass the influence of compensation for grazing stress was more apparent. The changes in sedimentary nutrient content may not have been large enough to affect the plants more than the grazers had.

4.10 Diagrammatic model

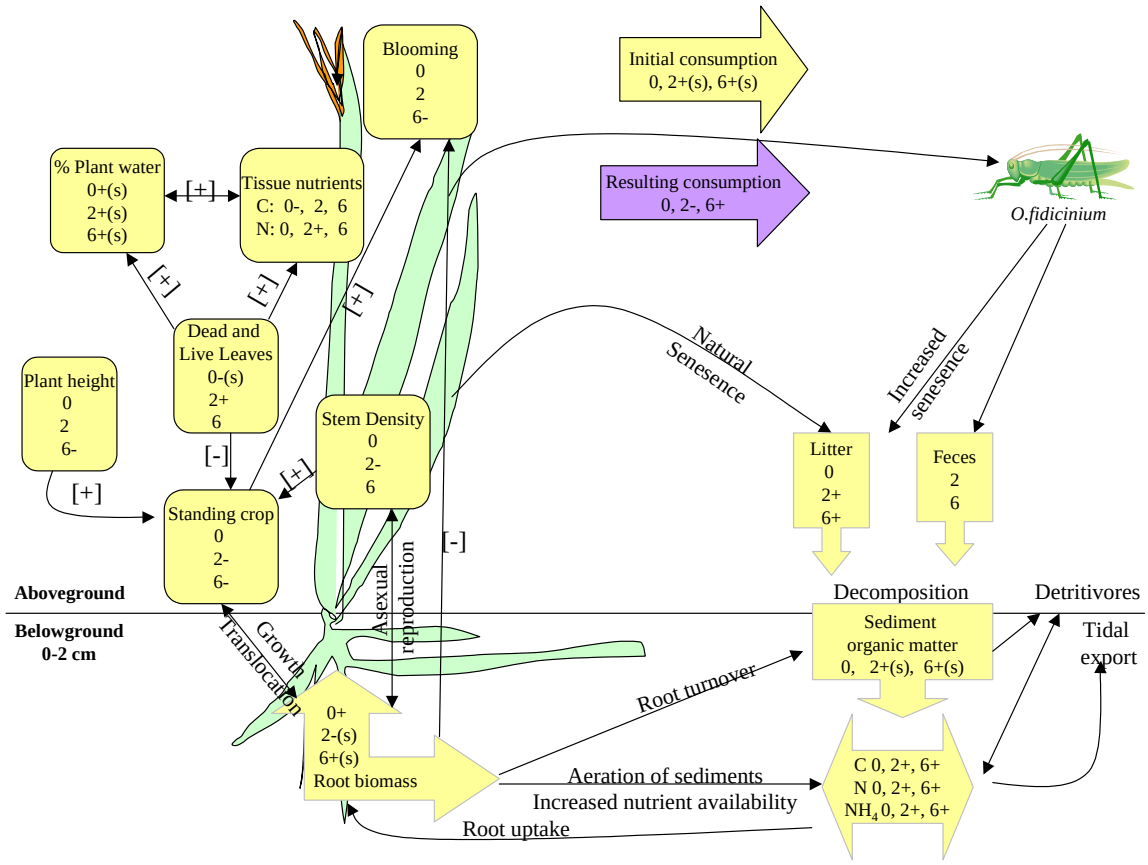

Figure 4.1 Conceptual model

This is a diagrammatic model of the salt marsh ecosystem as affected by grasshoppers. The black arrows are mechanics of the system. The boxes/arrows are compartments measured in this study. The numbers within the compartments are the grazer densities 0, 2, and 6 grasshoppers per meter^2. The +/- signs indicate if the effect was an increase or a decrease. The (s) indicates the change was statistically significant.

5 Summary and conclusions

The density of grasshoppers on the salt marsh was difficult to determine due to their clumped distribution. The range of grasshopper density was 2-20 individuals per meter squared. The spatial distribution of grasshoppers shifted throughout the season depending on grass developmental stages.

Higher grazer density treatments increased the percent of leaves grazed but not the percentage of plants grazed. With both ambient and triple density treatments 53-54% of the plants were grazed. The triple density treatment had 23% leaves grazed, while ambient density treatments had only 18% of the leaves grazed. The difference in grazed leaves resulted in greater canopy damage (See photo 2.1).

Grazer inclusion treatments had decreased aboveground productivity. In ambient density treatments this was probably due to reduced stem density. For both ambient and triple density treatments there may be changes in the stem morphology also affecting the aboveground productivity.

The presence of grazers increased the turnover of leaves and therefore the amount of litter produced. This increased sediment organic matter in the surface sediments, and slightly increased sediment nutrients. Ammonium increased with the presence of grazer treatments, but was slightly lower in triple density than ambient density treatments. This is possibly due to different root uptake rates for different grazer densities.

Root biomass in the top 10 cm reacted differently depending on the grazer density treatment. In ambient density treatments, the root biomass decreased significantly through the summer. Root biomass may decline as plants sustain the aboveground

biomass under grazing pressure. In triple density treatments the root biomass significantly increased. This is possibly a result of the plants translocating material away from grazers for storage in belowground biomass. The increase in root biomass in triple density treatments may result in increased ammonium uptake. The aboveground changes in plant morphology would indicate that ambient density treatments are maintaining the aboveground biomass, while triple density treatments are showing signs of grazer stress.

Sexual reproduction decreased non-significantly with triple density treatments, while exclusion and ambient treatments had little change. There is a correlated increase in belowground biomass, stem density, and therefore asexual reproduction in triple density treatments. The effects of triple density treatments may be changing the reproductive strategy of the grass.

Further study could improve the density estimates of grasshoppers in these marshes, and their variability from year to year. There is a need to study the effects of grazers on aboveground productivity over consecutive years. With changes in reproductive strategy, there could be further effects on other grazers as the number of seed heads decrease and stem density increases. Within this one summer sediment nutrient changes were barely apparent with increased grazer densities. These sediment changes may become more pronounced over a longer study time. The increased damage to the canopy with higher grazer densities may influence the microclimate of the low marsh. Light penetration may increase resulting in increased temperatures and salinity stress on plants. Changes in light penetration and nutrient recycling may alter microalgal communities.

Although *O. fidicinium* may not be the keystone species of salt marshes, their affects on nutrients cycling and *S. alterniflora* productivity is illustrated by this study. Without grasshoppers these systems would likely have higher aboveground biomass, higher blooming rate, and lower leaf number and litter content. This is turn would lower sediment organic matter and nutrients, thus affecting detritivores in these systems. Increased aboveground biomass may increase shading with resulting effects to microalgae. Ambient grazer treatments had decreased aboveground productivity, and decreased root biomass. There was little increase in litter and organic matter. These plants shall overwinter with reduced root biomass and may be competitively disadvantaged next spring during regrowth due to this. With higher grazer density the aboveground productivity decreased, the litter, organic matter and sediment nutrients increased, and the root biomass was maintained. With a sustained root biomass and richer sedimentary environment the higher grazer treatment plants may have an advantage next spring during regrowth. Using this reasoning it is to the grasshoppers advantage to congregate for grazing, thereby increasing the aboveground production the following spring when the nymphs hatch.

Overall the results of this experiment indicates that even small changes in grasshopper density can elicit significant changes in the above and belowground environment of a *S. alterniflora* dominated salt marsh environment. Grasshoppers have a significant effect on nutrient recycling in the marsh, which may possibly affect their own food source.

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7 Appendix A: Supplementary data

Month	Treatment	Height to biomass equation	R^2 value
May	All	$Y = 0.0004x^2 + 0.0026x$	0.46
July	Control	$Y = 0.0015x^2 – 0.0294x$	0.85
July	Exclusion	$Y = 0.0008x^2 – 0.0124x$	0.92
July	Normal	$Y = 0.0008x^2 – 0.0108x$	0.91
July	Triple	$Y = 0.0008x^2 – 0.0183x$	0.88
Oct	Control	$Y = 0.0004x^2 + 0.0216x$	0.84
Oct	Exclusion	$Y = 0.0006x^2 – 0.0003x$	0.91
Oct	Normal	$Y = 0.0005x^2 + 0.0124x$	0.80
Oct	Triple	$Y = 0.0006x^2 + 0.0059x$	0.79

Table 7.1 Productivity regression equations.

Regression equations developed from destructive sampling of aboveground biomass. These equations develop height to biomass relations for each treatment through the summer.

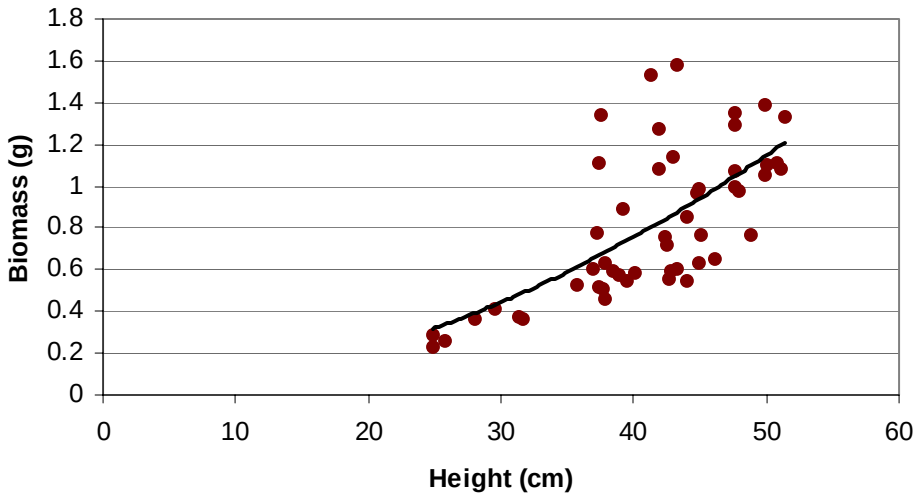

Figure 7.1 Mays height to biomass relations

Graphical representation of the polynomial height to biomass relationship. Equation for the line is in table 6.1 above.

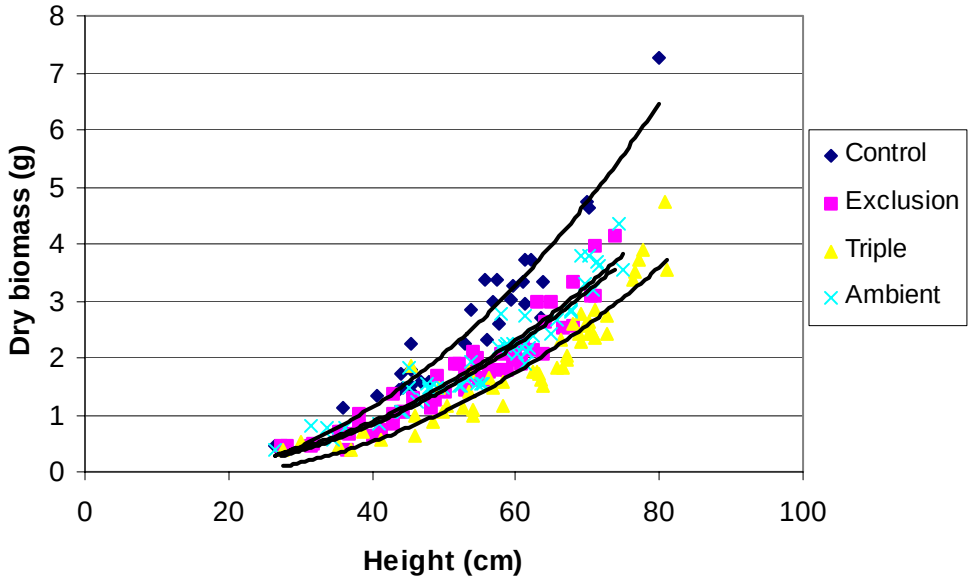

Figure 7.2 July height to biomass relations

Graphical representation of the polynomial height to biomass relationship. Equation for the line is in table 6.1 above.

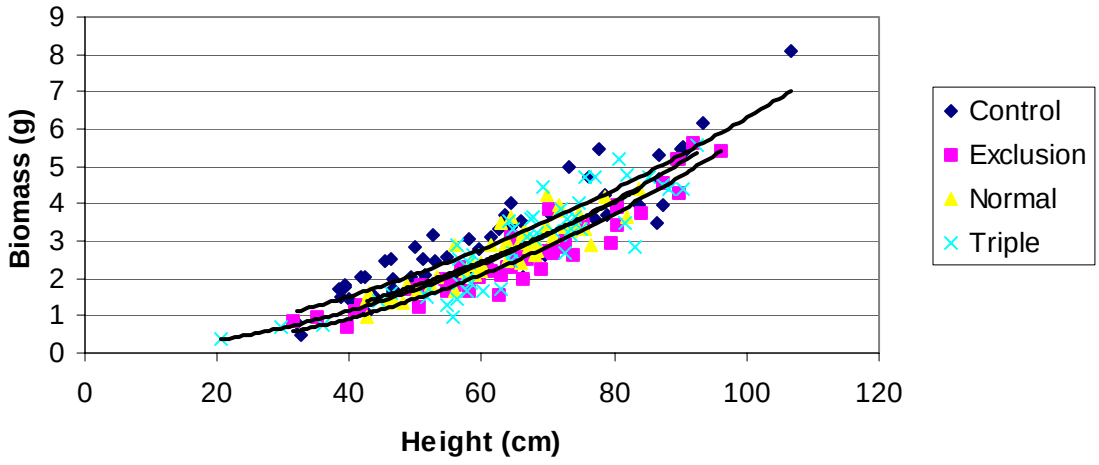

Figure 7.3 October height to biomass relations

Graphical representation of the polynomial height to biomass relationship. Equation for the line is in table 6.1 above.

Date	% N	% C
8/4/03	0.71	16.05
8/4/03	0.68	16.95
8/6/03	0.21	4.93
8/6/03	0.15	4.23
7/13	0.16	4.35
7/13	0.12	3.19

Table 7.2 Grasshopper feces nutrient content

The carbon and nitrogen content of grasshopper feces on three dates during the summer 2003. Feces were collected in containment studies in the field.

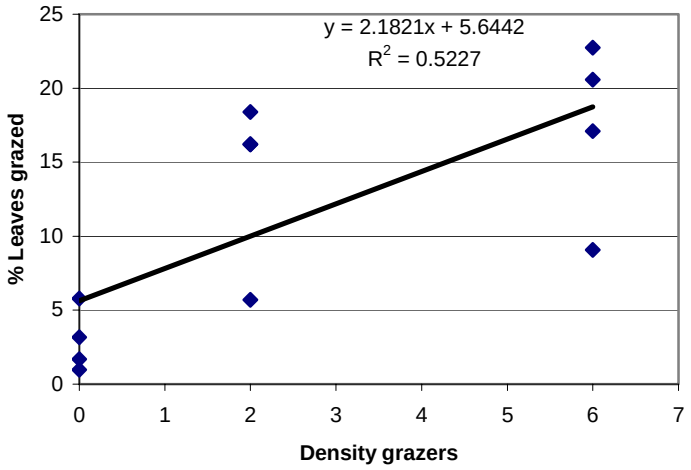

Figure 7.4 Leaves grazed with grazer density

The average monthly value of leaves grazed with the three grazer densities, for the end of July through the start of September. They have a positive linear relationship with an R^2 = 0.52.

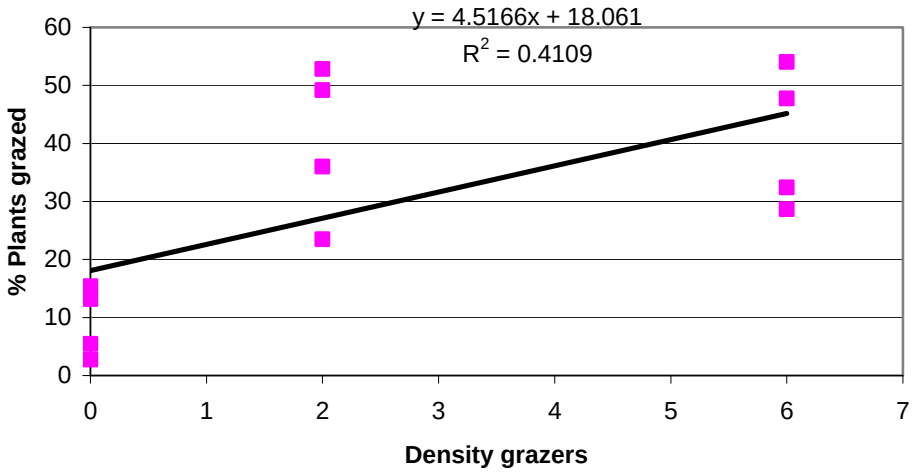

Figure 7.5 Percent plants grazed with grazer density

Graphic illustration of percent plants grazed as density of grazers increases from 0 to 6. It forms a positive linear relationship, $R^2 = 0.41$.

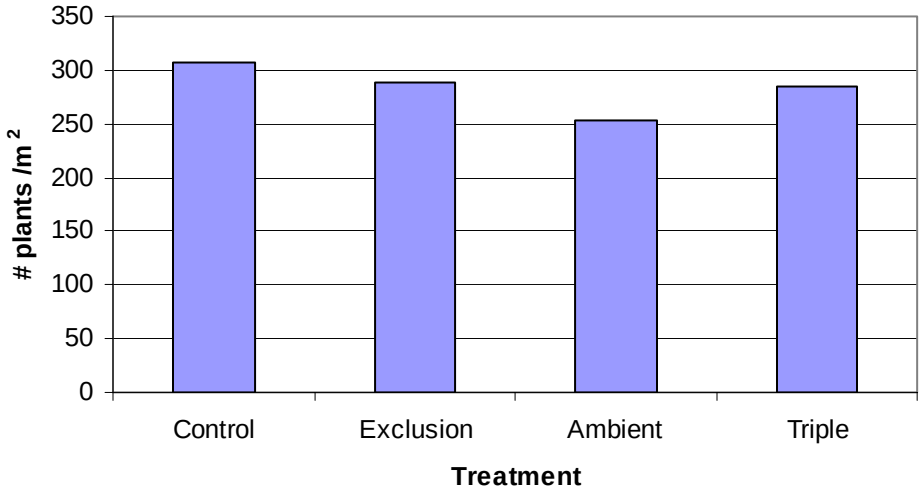

Figure 7.6 Number of plants per meter

The average number of plants per meter squared for each treatment over the whole summer.

	May	June	July	Aug	Sept	Oct	Average
Control	372	364	332	316	176	284	307
Exclusion	460	392	316	264	128	176	289
Ambient	336	312	252	212	200	204	253
Triple	396	368	308	248	176	216	285

Table 7.3 Plant densities

Average plant densities, per meter, for each treatment type- Control, Exclusion, Ambient, and Triple- throughout the summer

Date	Approx density/m^2	Average length (cm)	Inclusion densities
May	<1	<0.5	1 norm, 3 triple
June 3	<1	0.5	1 norm, 3 triple
June 10	<3		2 norm, 6 triple
June 26	<7	>0.5	2 norm, 6 triple
July 7	<5.6	1-1.5	2 norm, 6 triple
July 21	<4		2 norm, 6 triple
Aug 5	<3.5	3-4	2 norm, 6 triple
Aug 22	<5	4	2 norm, 6 triple
Sept 10	<4	3-4	2 norm, 6 triple
Oct 7	<1	3-4	na

Table 7.4 Field density and lengths

Average density results from surveys with a drop cage and sweep net every two weeks.

Date	Site	% N	% C
6/03	N. HOG	1.19	43.25
6/03	N. HOG	1.08	42.07
8/03	Brownsville	1.18	42.35
8/03	Brownsville	1.14	42.31

Table 7.5 Other grass nutrients

Carbon and nitrogen values of grasses collected as grazing densities changes their location and distribution

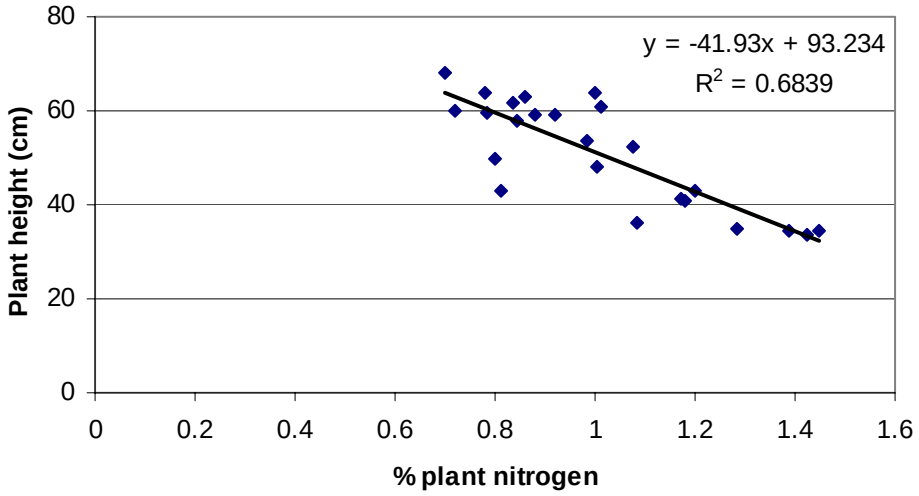

Figure 7.7 Plant height vs. plant nitrogen

Average plant height per treatment each month plotted against the plant nitrogen values for the same treatments each month. There are four treatments and six months of data included. The relationship forms a negative linear relationship, with an R^2 of 0.68.

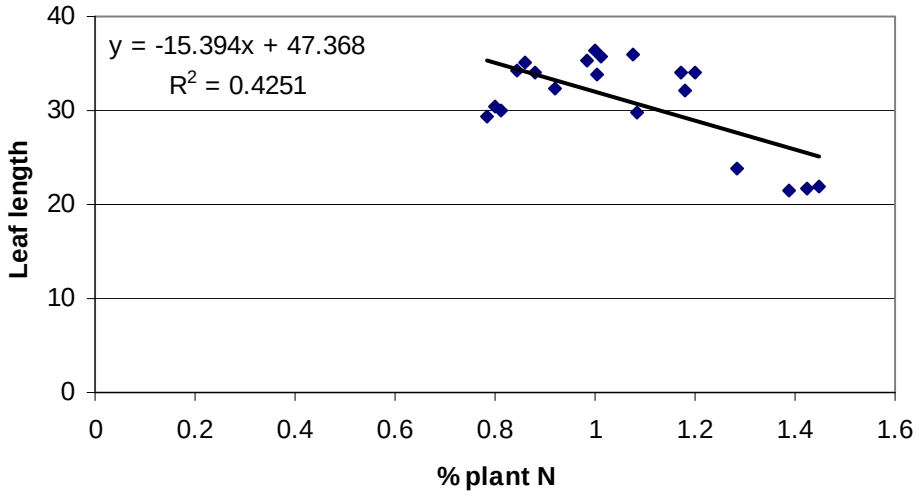

Figure 7.8 Leaf length vs. plant nitrogen

The average leaf length in each plot each month plotted against the percent of plant nitrogen in the same plots each month. They have a negative linear relationship, with R^2 of 0.43.

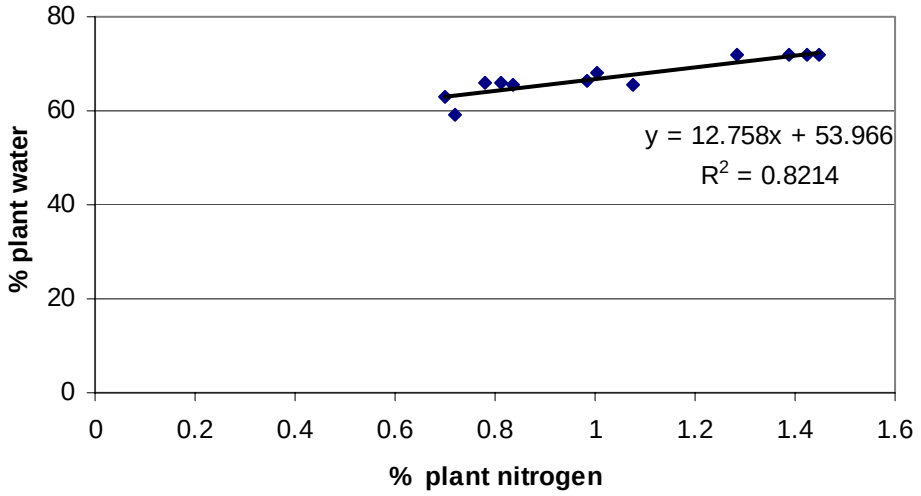

Figure 7.9 Percent plant water vs. plant nitrogen

The average percent plant water values plotted against the average plant nitrogen values. The values are for May, July and October as these are the months when water content was assessed, They have a positive linear relationship with an $R^2 = 0.82$.

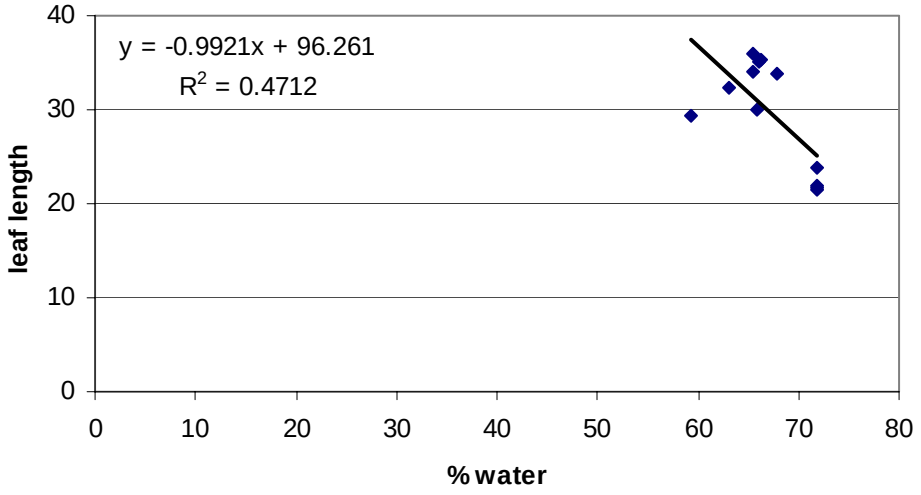

Figure 7.10 Leaf length vs. percent water content

The average length of leaves in each treatment plotted against percent of water in plants. This data is from May, July, and October as these are the months when water content was assessed. They have a negative linear relationship with an $R^2 = 0.47$.

8 Appedix B: Seasonal data

Aboveground:

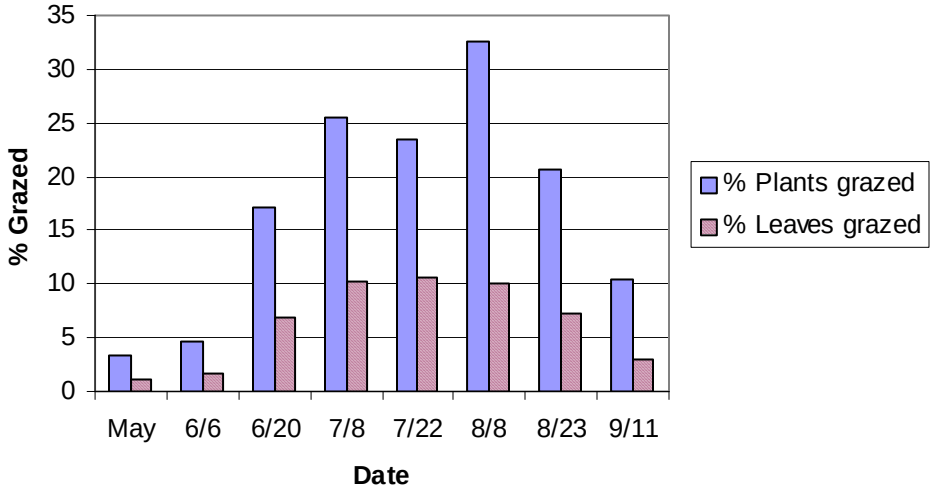

Figure 8.1 Grazing over time

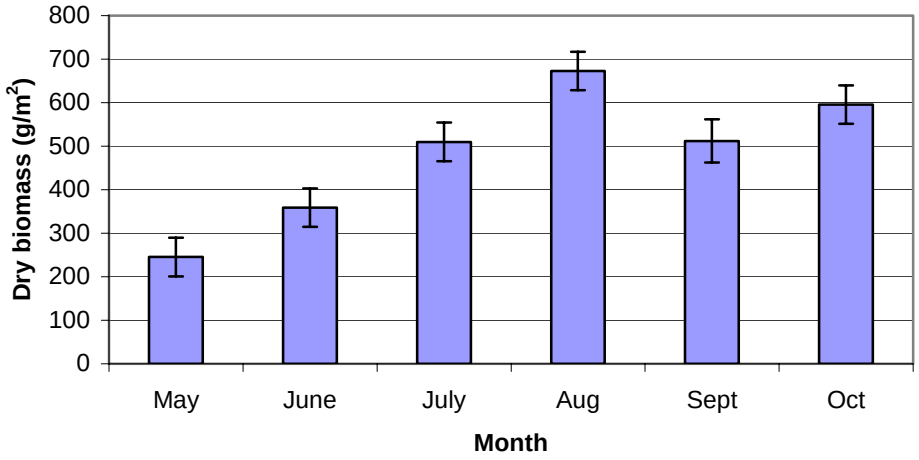

Figure 8.2 Monthly dry biomass

Average monthly dry biomass, per meter squared, including all treatments. +/- 1SE.

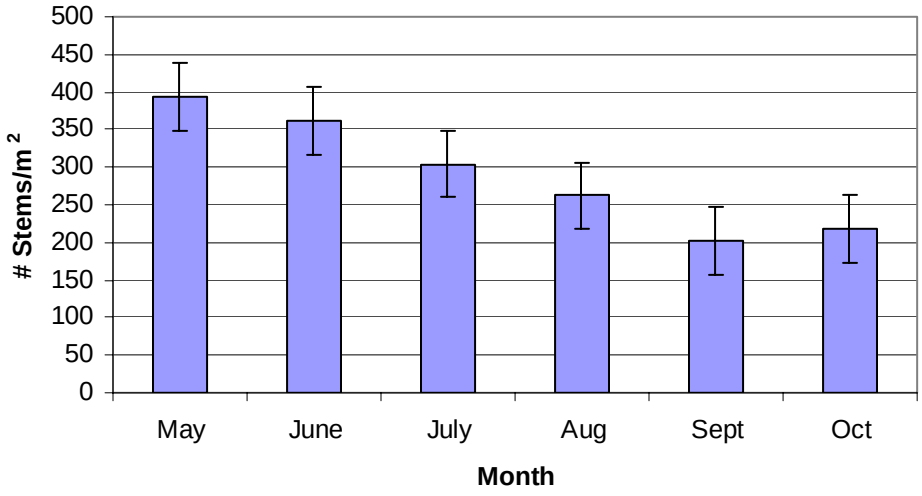

Figure 8.3 Stem density

Average stem density per meter squared each month, averaged across all treatments. +/- 1 SE.

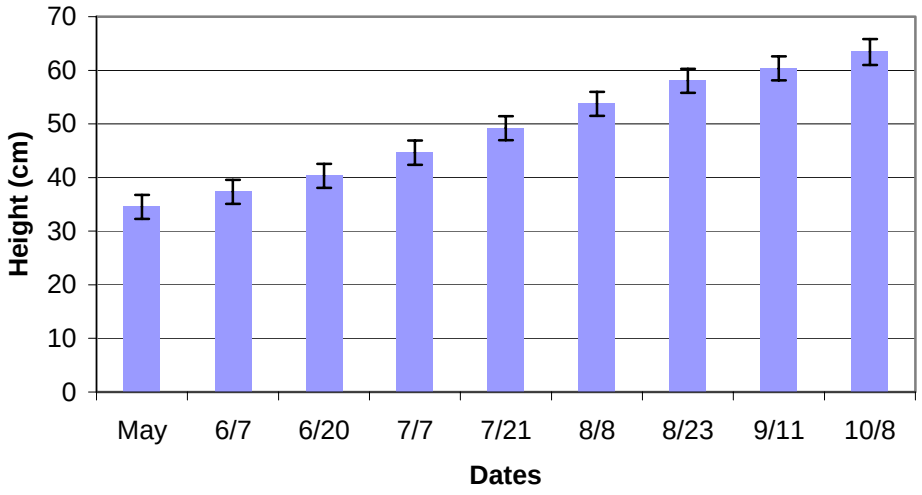

Figure 8.4 Average height per date

Average plant height (cm) at each date, averaging all treatments. +/- 1 SE.

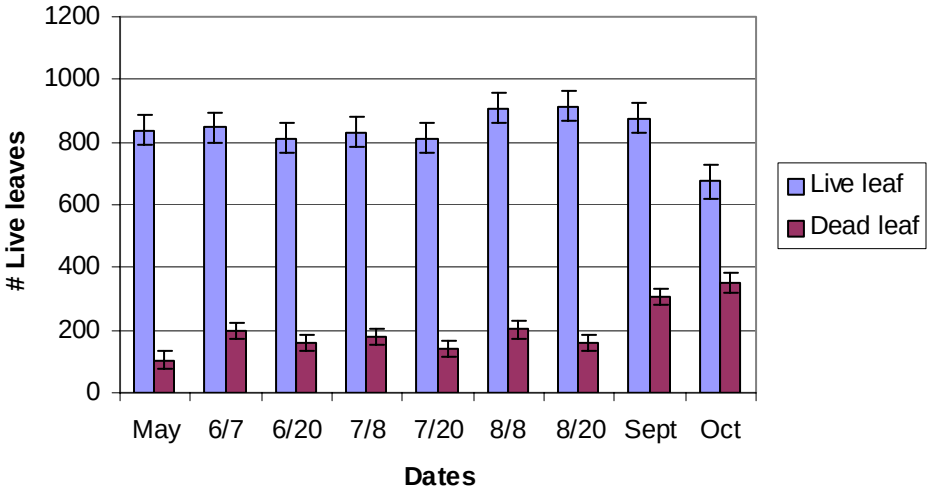

Figure 8.5 Number of leaves over time

The average number of dead and live leaves for each date across all treatments. +/- 1 SE.

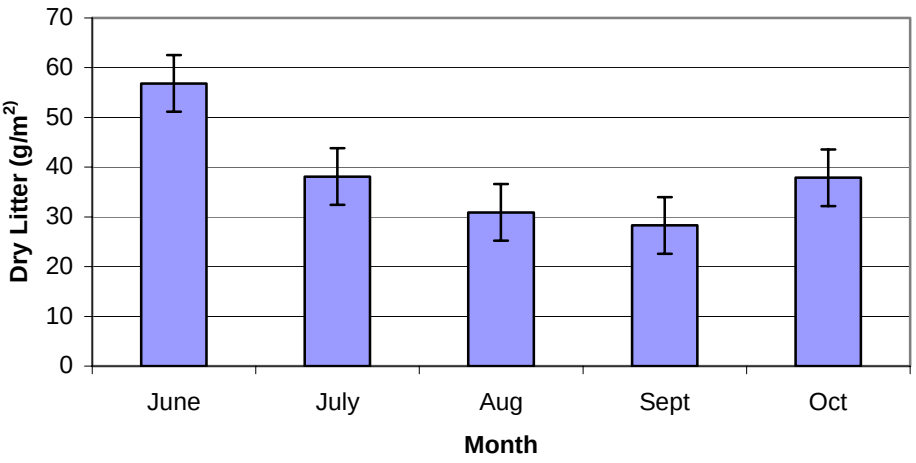

Figure 8.6 Litter per meter over time

Average dry weight of litter, per meter squared, over time. Average value is of all treatment plots for each month. +/- 1 SE.

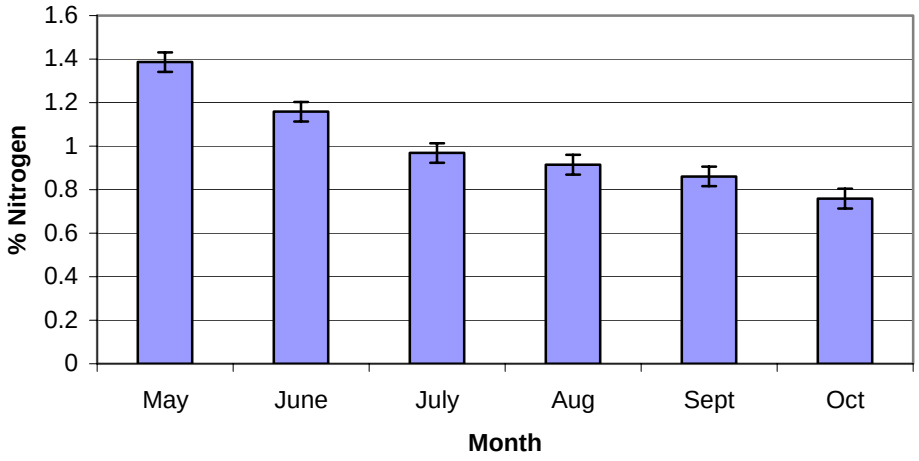

Figure 8.7 Percent tissue nitrogen over time

Average percent nitrogen in plant tissue, each month, including all treatments. +/- 1 SE.

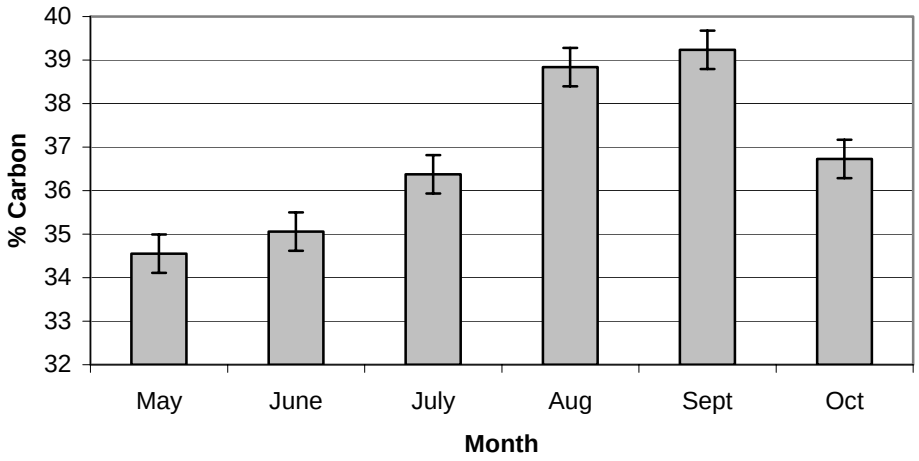

Figure 8.8 Percent tissue carbon over time

Average percent carbon in plant tissue, each month, across all treatments. +/- 1 SE.

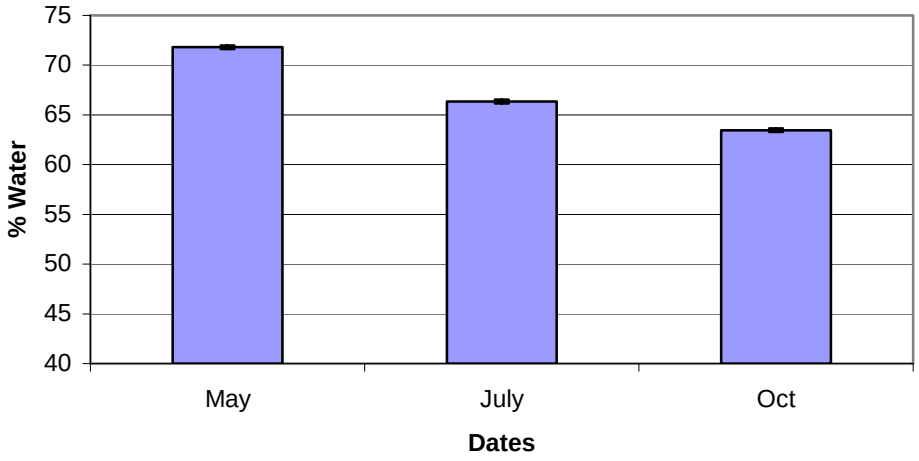

Figure 8.9 Percent water over time

Average water content in all plants for each month. +/- 1 SE.

Belowground :

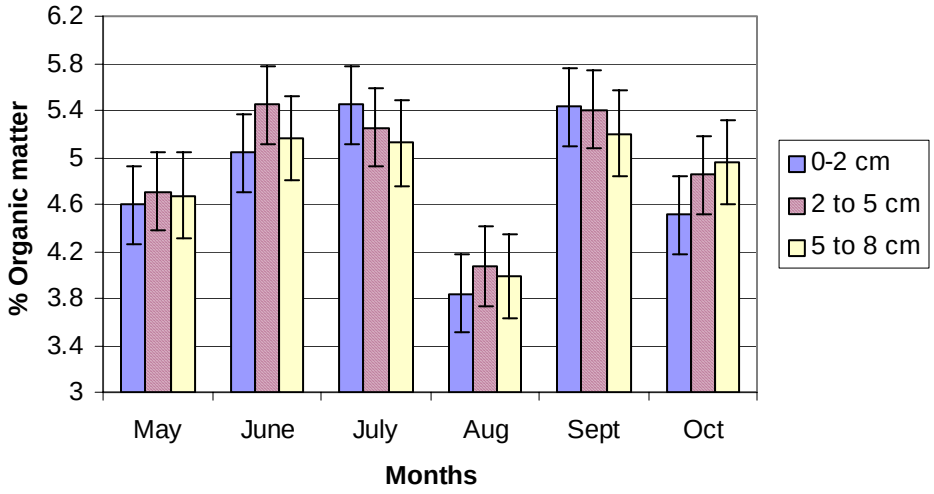

Figure 8.10 Organic matter over time

Average organic matter content each month for the three depths. +/- 1 SE.

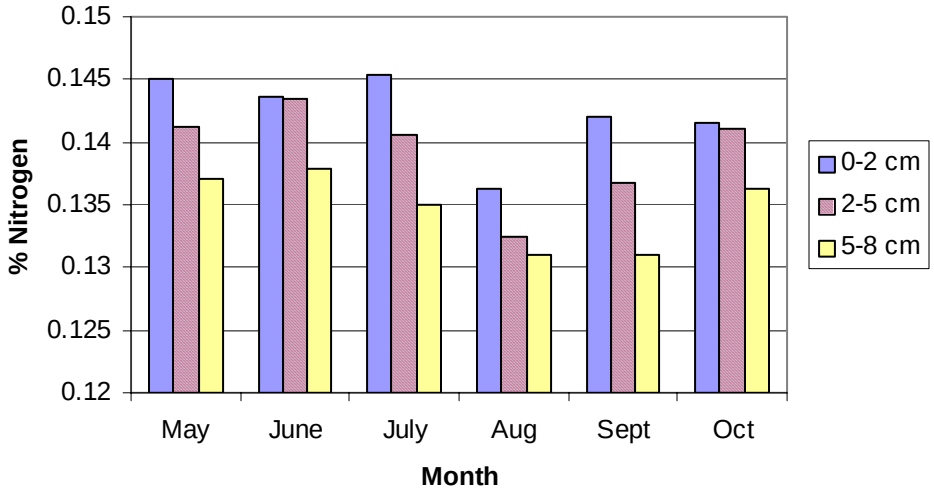

Figure 8.11 Percent sediment nitrogen

Average sediment nitrogen values at the three depths through the summer.

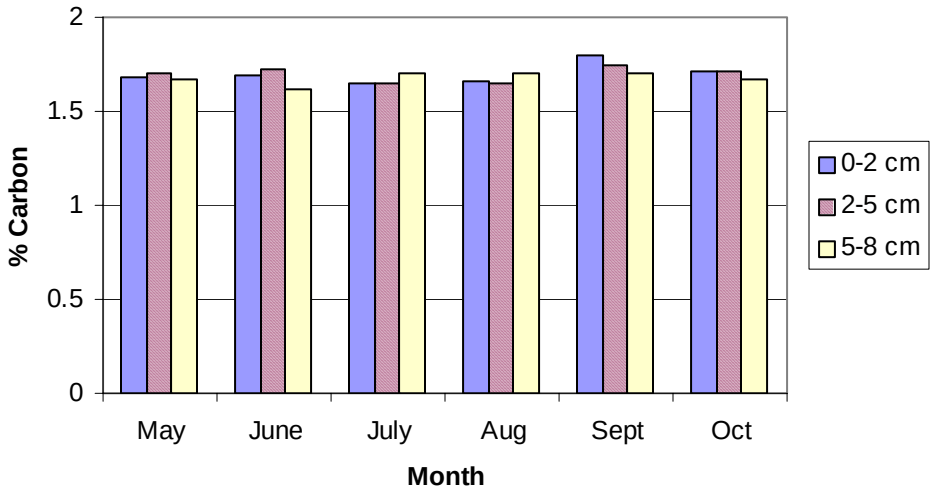

Figure 8.12 Sediment carbon over time

Average sediment percent carbon for the three depths, over the summer.

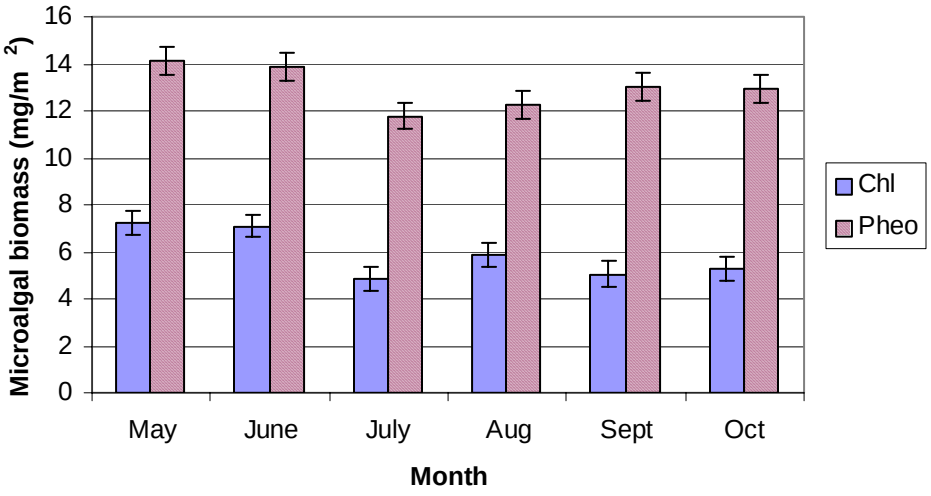

Figure 8.13 Microalgal biomass over time

The average microalgal biomass, represented by Chlorophyll and Pheophyton, each month. +/- 1 SE.