# LONG TERM RESIDUAL EFFECTS OF A NUTRIENT ADDITION ON A BARRIER ISLAND DUNE ECOSYSTEM

by

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# ABSTRACT

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In 1991, 150 $m^2$ were fertilized with nitrogen on three dunes on Hog Island, part of the Virginia Coast Reserve Long Term Ecological Research site, to examine plant community response to nitrogen addition. In 2000, the fertilized plots continued to exhibit a positive growth response. This study sampled the aboveground biomass, belowground biomass, and nutrient content of the experimental plots to examine the long- term patterns of nitrogen retention in a nitrogen limited system. Aboveground and belowground biomass was significantly greater in the fertilized plots than in the control plots. Aboveground biomass exhibited was significantly greater in control and fertilized plots in 1991 than 2000, while the belowground portion exhibited increased biomass in both plots over time. Biomass estimates of all plant components were significantly greater in treated plots. Nitrogen standing crop revealed a similar response to treatment in all plant components. Nitrogen concentrations were not affected by fertilization. These data suggest that the retention of nitrogen within the fertilized plots has been partially driven by increased biomass. The conclusion of this study was that increased pools of decomposing litter have altered nutrient processing rates within the fertilized plots to conserve available nitrogen in the system.

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# INTRODUCTION

Gleeson and Tilman (1990) assert that primary production and succession are driven by soil quality (nitrogen availability). Intensive research has been conducted to assess the availability of nutrients within ecosystems in order to determine the relationships among requirements for growth (Willis and Yemm 1961; van der Valk 1975; Chapin 1980; Saterson and Vitousek 1984; Tilman 1986; Ehrenfeld 1990; Gleeson and Tilman 1990; Day 1996).

Previous research on sand dune ecosystems has shown that these systems are nutrient poor (Willis and Yemm 1961; van der Valk 1975), have low water retention capacity, and do not accumulate large amounts of organic matter (Ehrenfeld 1990). Sandy soils are nutrient deprived because nutrients readily leach from the soil especially in young seral stages (Odum 1969; Vitousek and Reiners 1975; Wilson and Tilman 1993). As a system ages, nutrients are retained by storage in organic matter and this decreases the tendency for nutrient leaching (Vitousek 1997).

Coastal systems are dominated by a number of physical factors that alter succession and thereby alter nutrient and energy cycles. Plants endemic to these dynamic systems are subject to loose nutrient cycles, variation in water availability, and changes in the physical landscape due to oceanic influences (Ehrenfeld 1990). Study plots on Hog Island, a barrier island on the Delmarva Peninsula in Virginia, were established in 1991 and fertilized with nitrogen to study plant community response to fertilization. After nine years, the fertilized plots continue to exhibit increased biomass production. In a system

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with highly leachable soils and dynamic physical changes, it is interesting that the evidence of nutrient addition nine years prior has been retained.

Hog Island is comprised of a series of dunes dating to 1871. The dunes on Hog Island are nutrient and water limited (Ehrenfeld 1990; Day 1996; Day et al 2000). The chronosequence of dunes on Hog Island was developed as the shoreline progressed east creating three distinct dune ridges in 1871, 1955, and 1967. Cowles (1899) study of the sand dunes on Lake Michigan was the first to look at succession by using spatially separated dunes as a substitute for time. The dunes on Hog Island do not represent typical succession as assumed by Cowles' landmark study due to free surface changes and anthropogenic influences. Through examining the plant communities on Hog Island, we can examine the mechanisms that aid in nutrient retention and cycling.

Hog Island is a very dynamic system. It has been documented that abiotic disturbances are a major influence of state change on the island (Hayden et al. 1991). Because of the dynamic nature of the system, the dunes do not represent typical seral stages. Inundation by salt water and overwash have strongly influenced the vegetation types on certain parts of the island. The abiotic disturbances such as storms may have caused the succession of these dunes to be slowed or diverted to an alternate successional state; this is termed state change. For example the southern portion of the island supported a maritime forest until a storm in 1930 diminished the freshwater lens and subsequently the forest perished (Hayden et al. 1991). The abiotic and biotic disturbances in these instances dramatically altered the free surfaces of the island. Free surfaces include the soil surface that is influenced by sand deposition and erosion, ground water level as influenced by precipitation and evapotranspiration, and sea level as affected by storm surges and global climate change. Changes of the free surfaces could initiate state change on the island.

Fresh water availability can strongly influence plant communities on the island. It has been documented that the 1871 dune is water limited, a condition believed to be altering succession (Day et al. 2001). It has also been shown that as systems age, water retention increases as a result of increasing organic material (Olff et al. 1993; Foster and Gross 1998).

The dunes on Hog Island are different from one another. Initial studies in the early 1990's showed the 1871 dune has naturally higher soil nitrogen than the other two although it had less aboveground and belowground biomass (Conn and Day 1993; Day 1996; Stevenson and Day 1996: Dilustro and Day 1997). After one year of fertilizer applications, increased aboveground and belowground biomass were observed on the 1955 and 1967 dunes. Also with fertilization, mineralization and root decay rates increased (Conn 1993), thereby increasing nutrient availability.

Fertilization of nitrogen limited systems has been shown to have a greater effect on production in younger successional stages than older (Chapin 1980; Tilman 1987; Day 1996). Young seral stages are composed of plants that are adept at sequestering nutrients and grow better on soils with low nutrient content thus inhibiting the growth of later successional species (Tilman 1986). Berendse et al. (1992) have also proposed that plants that are competitively more advanced in nutrient poor soils have either the ability to maximize nutrient use within the plant or minimize loss of nutrients.

Dead plant biomass plays an important role in nutrient cycling and retention. Litter can act as a source or a sink for nutrients (Jordan et al. 1989). During the first stages of decomposition litter will accumulate nutrients, and as decomposition continues the nutrients are mineralized and returned to the soil chemistry (Jordan et al. 1989; Melillo 1984). The nutrients that remain in plant material and those nutrients accumulated via atmospheric deposition are stored in litter and returned to the system through mineralization.

In infertile soils, root turnover is slower and the ratio of below to aboveground biomass is greater than fertile sites. This is believed to prevent nutrient loss through senescence (Dennis 1977; Chapin 1980; Saterson and Vitousek 1984; Nadelhoffer et al. 1985). In nutrient limited systems, biomass and nutrient allocations are primarily to roots (Saterson and Vitousek 1984). The study performed by Saterson and Vitousek (1984) showed that *Aristida stricta* Fernald. translocates nutrients from senescent leaves to roots before shedding. In a nutrient limited system such as Hog Island, it is quite possible that the root systems (primarily from *Ammophila breviligulata* Fernald and *Spartina patens* (Aiton) Muhl.) are playing a critical role in the retention of nitrogen.

The purpose of this study was to continue the investigation of nitrogen influence on Hog Island initiated by Day in 1991. Previous studies have shown short-term responses aboveground and belowground to nitrogen enrichment (Conn and Day 1993; Conn 1994; Day 1996; Stevenson and Day 1996; Dilustro and Day 1997; Day et al. 2001). This study evaluated the long-term residual plant responses to a nitrogen application that occurred in 1990 and 1991.

The specific objectives of this project were: 1) to assess aboveground and belowground biomass in fertilized and control sites along a chronosequence of dunes, 2) to compare the current biomass estimates with those determined the year of the fertilization (1991), 3) to assess biomass and nitrogen content of soil, belowground plant material, aboveground plant material, and litter in the experimental plots on the 1955 dune, and 4) to compare biomass and nitrogen concentrations of all components.

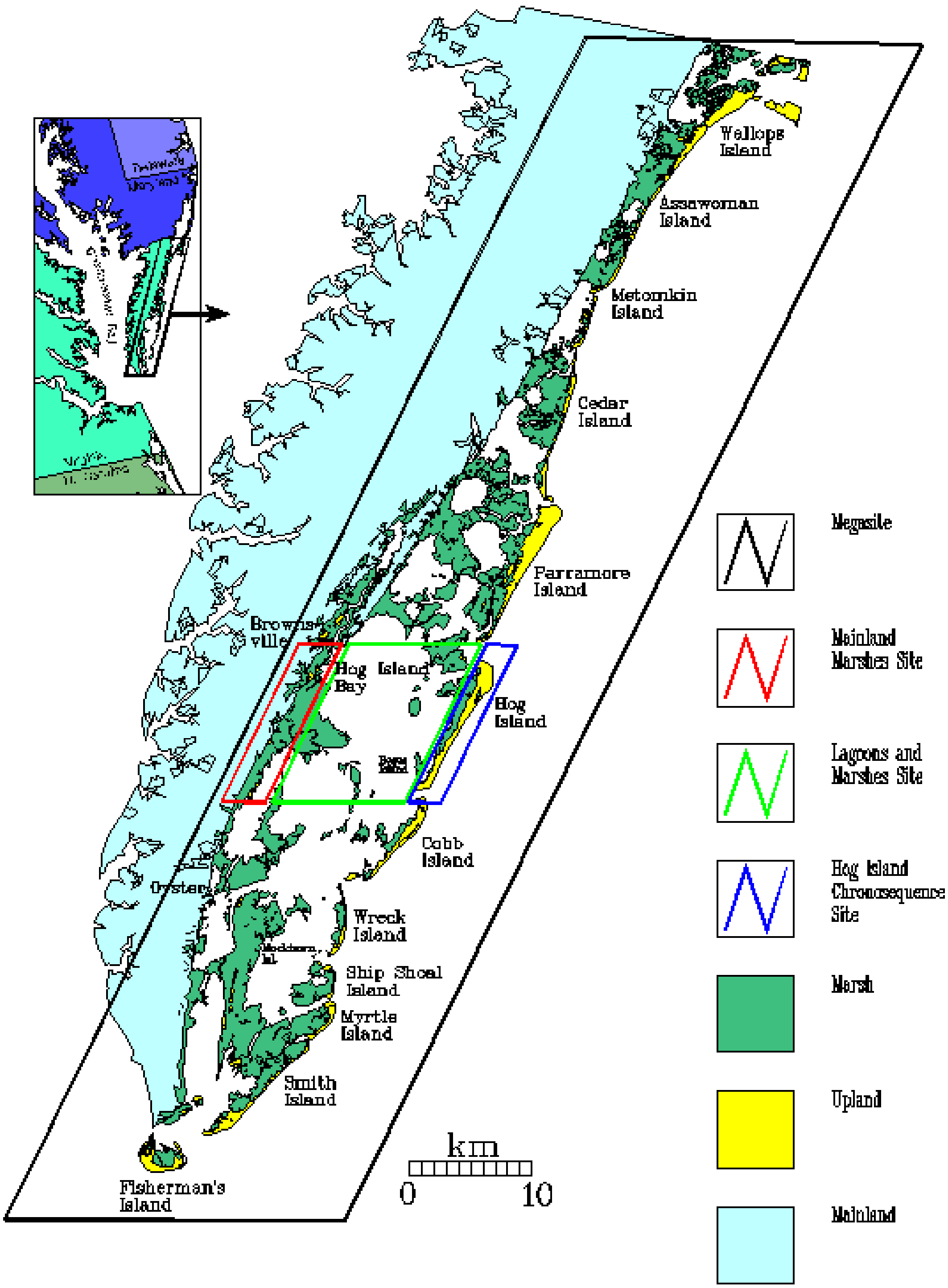
# MATERIALS AND METHODS

## Site description

Hog Island is situated off the Eastern Shore of Virginia in a chain of barrier islands that extends along the coast of the Delmarva Peninsula (Fig. 1). The Virginia Coast Reserve (VCR) is comprised of the islands that extend from Assateague at the north to Fisherman's Island in the south. The VCR is owned and maintained by the Nature Conservancy and research at the VCR has been sponsored by the National Science Foundation as a Long Term Ecological Research Site (LTER) and is also a Man and the Biosphere (MAB) site.

Hog Island lies 48 km north of the mouth of the Chesapeake Bay (37? 40'N, 75? 40'W). It is 11 km long and averages 0.8 km in width. The coastline is constantly renovated by wave action. The southern end of the island experiences overwash and is eroding at a rate of approximately 5 m/year, while the northern end is accreting at roughly the same rate (Hayden et al. 1991). Anthropogenic influences on the island include activities of Native American tribes that used the islands for fishing and hunting as early as the 1600's. English settlers slowly took over the area in the early 1700's and used the islands as graze land. The town of Broadwater was established in 1903 on the southern end of the island. A strong storm in the 1930's influenced the population to move to the mainland. When The Nature Conservancy purchased the islands in 1980, the last feral cows were removed from the island.

**Fig. 1.** Map view depicting the Eastern Shore of Virginia and the Virginia Coast Reserve.



The process of erosion and accretion of sand has created a series of dunes and swales at the northern end of the island running perpendicular to the shoreline. The oldest dune ridge was formed in 1871, and the youngest dune in 1967 (Fig. 2; Hayden et al. 1991).

Main sources of nitrogen to the system include atmospheric deposition and nitrogen fixation by microbes. The estimated atmospheric input at the VCR is 8 to 12 kg N $ha^{-1}$ $yr^{-1}$ (Galloway and Keene 1998).

*Ammophila breviligulata* Fernald and *Spartina patens* (Aiton) Muhl. are the predominant plant species on the three dunes are. The predominant vegetation type in the older swales is the nitrogen fixer, *Myrica cerifera*, while the younger swales are dominated by *Spartina patens* (Hayden et al.1991).

**Collection methods**

In 1990, four plots,10 m by 15 m each, were established on each of three dunes, (1871, 1955, and 1967). Fertilizer (60 g N $m^{-2}$ $yr^{-1}$, 41.8% urea N) was applied in two of the four plots on each dune in four applications over the period of one year (1990-1991). 30% was in the form of quick release pellets and 70% was slow release pellets. Root biomass measurements were made within these plots at the time of fertilization via the in-growth core method (Day 1996; Stevenson and Day 1996). Decomposition rates were also measured within the large plots (Conn 1994).

Biomass was sampled in 1990 from smaller experimental plots on the dune ridges (Day 1996). The biomass sampling in 1990 provided the data for comparison with biomass sampled in 2000 and 2001. Biomass sampling dates for the current study were

July and October 2000 and February and May 2001. The sampling in July of 2000 was across all three dune sites while the subsequent samples were limited to the 1955 dune due to time and resource limitations.

Aboveground biomass harvests were taken from fifteen 0.25 $m^2$ quadrats from each treatment. All standing material was clipped from within each quadrat to the ground level. After standing material was collected, litter was collected and placed in a separate bag. On the 1955 dune, flags were placed in the top left corner of the quadrat to eliminate repetitive harvesting within the same quadrat. The standing material was separated into standing live and standing dead material. The standing live material was further separated by species. All plant material was placed in paper bags and dried in a 70? C drying oven for 48 hours. Dry mass was then obtained on an analytical balance. Final biomass estimates were converted to g $m^{-2}$.

One root core (30 cm depth x 7 cm width) was taken within each quadrat after aboveground material was removed. The cores were placed in Ziploc© bags in the field and stored in a refrigerator at 1- 4? C until processing. Roots were separated from the soil using a hydropneumatic elutriator (Smucker 1982). After washing, the roots were separated into live and dead and placed in labeled paper bags. Live roots were distinguished from dead by the flexibility of the roots and coloration. The root material was dried and weighed in the same manner as aboveground plant material. Masses were calculated to g $m^{-2}$ over a depth of 30 centimeters.

Soil cores (30 cm depth x 2.5 cm width) were taken on the 1955 dune only and also placed in Ziploc© bags. The soil samples were stored in a refrigerator at 1-4? C until processing. The soil cores were placed in paper bags and dried at 50? C for 24 hours (Robertson, et al. 1999). Root and large organic material were sieved from the soil using a 2 mm sieve. A sub-sample for nutrient analysis was taken from each soil sample. The sub-sample was ground to a fine powder using mortar and pestle and stored in a desiccator for nutrient analysis.

All aboveground and belowground plant materials from the 1955 dune were ground in a Wiley mill to 40 mesh size. When vegetation samples were very large, a sub-sample was taken for nitrogen analysis. A Wig-L-Bug grinding mill was used to grind samples to a powder that was then stored in a desiccator until analysis was conducted. It has been shown that ball mill preparation of samples increases precision and the homogeneity of the samples (Schepers et al. 1989).

Nutrient analysis was conducted on a Carlo- Erba 1200 CHNS analyzer. The nutrient values were calculated with Eager 200 software. Protocols were established based on Cutter and Radford-Knoery (1991). Two to three mg samples were used for standing live, standing dead, necromass, and dead and live roots; 15-16 mg samples were used for soil analysis. The standard was sulfanilimide. Soil nutrient content values were converted to grams per cubic centimeter based on soil bulk densities. Soil bulk densities were obtained through a previous study on Hog Island (Day personal communication).

Ground water was continuously monitored using Stevens model 68 type F recorders on each dune. Daily ground water values were averaged based on eight-hour periods.

**Statistical analysis**

All statistical analyses were performed with SPSS version 10.0. A univariate

Analysis of Variance (ANOVA) was used to determine differences in aboveground biomass from July 2000 between treatment and dune sites. Data were natural log transformed in order to meet assumptions of normality and homogeneity. ANOVA was also used to test differences in biomass between collections made in 1991 and those made in July 2000. A natural log transformation was used on the 1991 and 2000 data.

Belowground biomass was tested between treatment and dune sites using a univariate ANOVA. Comparison of belowground biomass between 2000 data and 1991 data were also analyzed using a univariate ANOVA. Both data sets analyzed here violated assumptions of normality and homogeneity. transformations did not improve the data set so the original data was used in analysis. Root shoot ratios were calculated for 1991 and 2000 data. Ratios were arc sin transformed and tested with a univariate ANOVA design.

After biomass collections were made on the four sampling dates from 2000 to 2001, a 2 x 4 factorial MANOVA was performed on biomass. Date of collection (July, October, February, and May) and treatment (control vs. fertilized) were treated as fixed variables, and standing live, standing dead, litter, live root and dead root biomass were used as response variables. Pillai's Trace value was used to test the significance of the MANOVA. Although Wilk's Lambda is the more commonly used statistic, Pillai's Trace value is more accurate in determining appropriate statistics when the data violate assumptions of normality and homogeneity (Zar 1999). Individual analyses of variance were performed on each dependent variable and the interaction.

A 2 x 4 factorial MANOVA was also used to analyze nitrogen content. Pillai's Trace value was used as a measure of significance. Nitrogen content was also extrapolated to produce gram nitrogen per gram mass for all plant components. These values were also tested with a MANOVA. The data were considered normally distributed and the variance was homogenous.

Soil nitrogen content (g $cm^{-3}$) was analyzed using univariate ANOVA. The independent variables were treatment and date of collection.

# RESULTS

## Comparison of 1991 and 2000 biomass

There was an overall decline in aboveground biomass between 1991 and 2000 in all treatments and all dunes although fertilized plots continued to have higher aboveground biomass than controls (Fig. 3). Aboveground biomass in July 2000 was significantly less than aboveground biomass in 1991 ($F= 89.307$, $P < 0.000$).

The biomass of the fertilized plots was significantly greater than the biomass in the control plots across all three dune sites ($F= 23.069$, $P<0.000$, Fig. 4). There was no significant difference between dune sites ($F=1.292$, $P=0.280$, ?=0.272).

Belowground biomass was significantly greater in fertilized plots than in control plots across all three dune sites ($F= 12.083$, $P= 0.001$) and was significantly different between the 1967 dune and the 1955 and 1871 dunes ($F=6.404$, $P=0.003$; Tukeys HSD 1955 <u>1967 1871</u>; Fig. 5). Belowground biomass was significantly greater in 2000 than in 1991 in control and fertilized plots ($F= 46.492$, $P= 0.000$; Fig. 6). In contrast to the decline of aboveground biomass in the control and fertilized plots, the belowground biomass increased over time.

## Biomass patterns in 2000 and 2001

MANOVA results showed a significant difference in the biomass of plant components by date of collection, treatment, and date x treatment (Table 1). Treatment was a significant factor for all plant components according to individual Analyses of Variance (Table 1). Fig. 7 shows the mean biomass values for each plant component at

**Fig. 3.** Aboveground biomass estimates made in 1991 and 2000 in control and fertilized plots. Error bars represent one standard error.

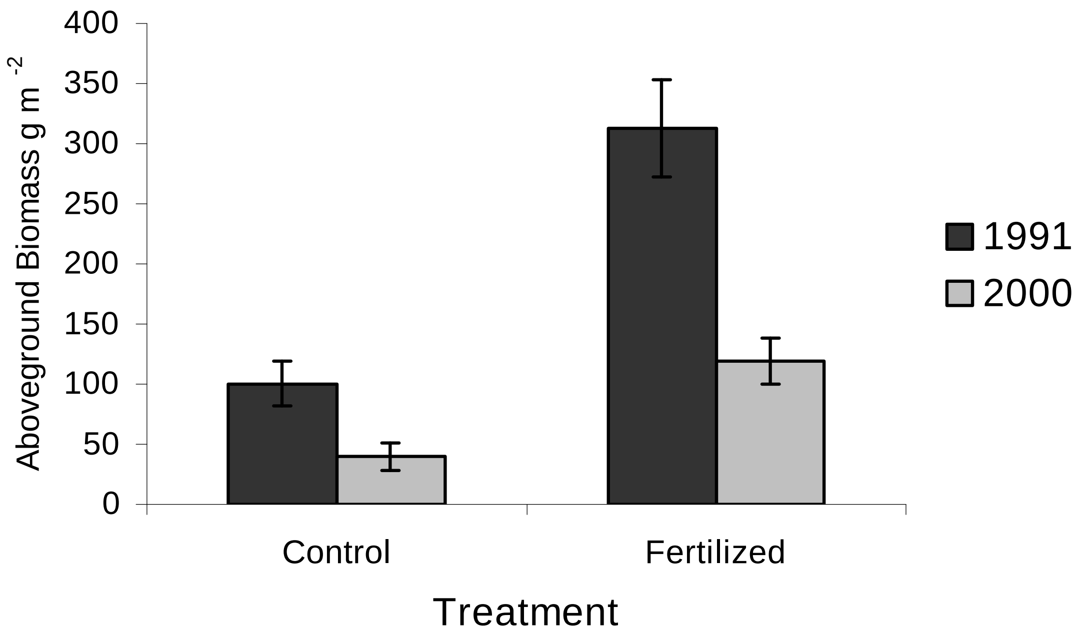


**Fig. 4.** Comparison of aboveground biomass in control and fertilized plots across three dune sites in July 2000. Error bars represent one standard error.

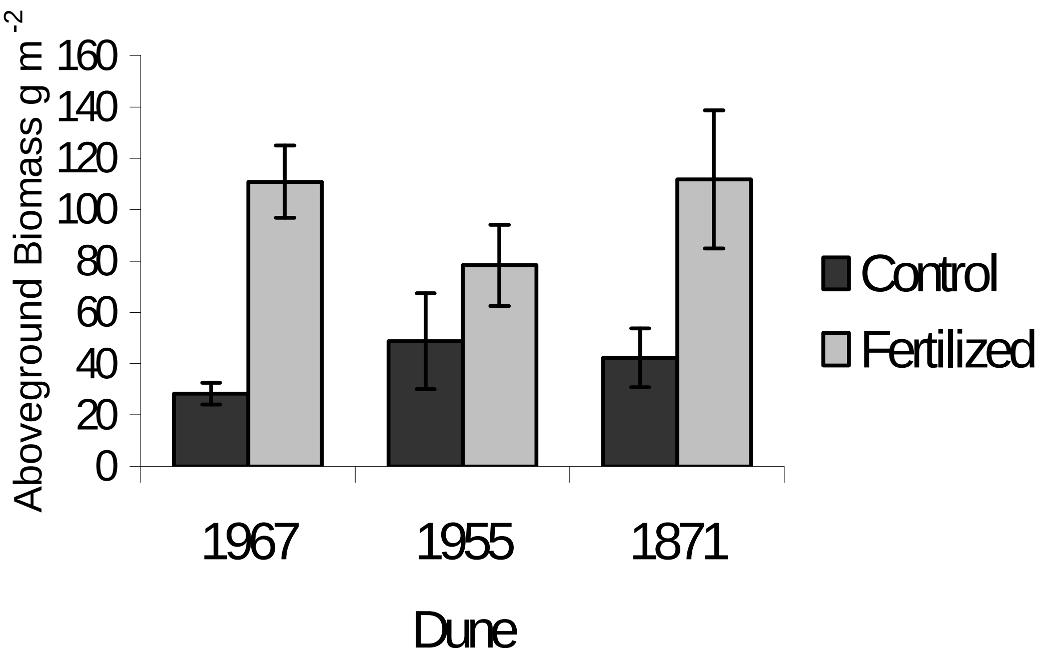


**Fig. 5.** Comparison of 2000 belowground biomass data. Error bars represent one standard error.

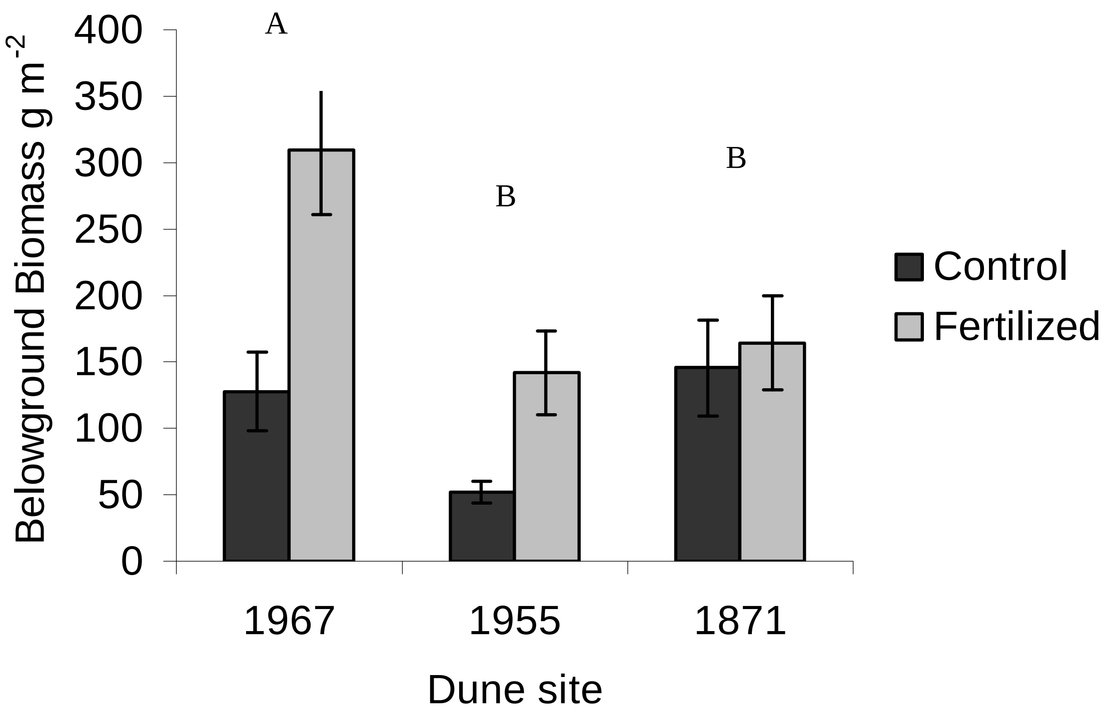
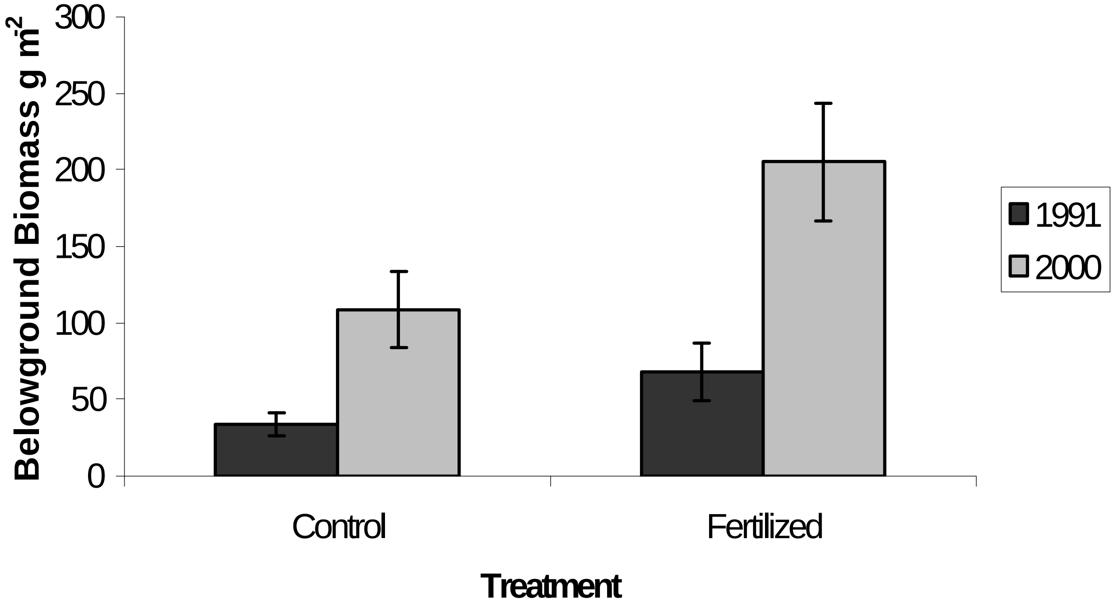


**Fig. 6.** Comparison of belowground biomass from 1991 and 2000. One standard error represented by error bars.



each sampling date. Fertilized plots have a significantly greater biomass in all components.

Comparison of root shoot ratio in control and fertilized plots showed the 1991 root shoot ratios were higher than the 2000 ratios ($F= 6.491$, $P= 0.012$; Fig. 8) and treatment had no significant effect ($F= 1.42$, $P= 0.235$, ?= 0.219). The ratios did not vary on the 1967 and 1955 over time or between treatments. Although, there is an obvious shift in root shoot ratio in the control and fertilized plots on the 1871 dune between 1991 and 2000. The control and fertilized plots had approximately the same ratio in 1991, but there was a dramatic shift in resource allocation in 2000 that is demonstrated by a very high root shoot ratio in control plots and a very low ratio in fertilized plots.

**Analysis of total nitrogen content**

When plant nitrogen concentrations (N mg $g^{-1}$) in control and fertilized plots were compared, date of collection, treatment, and date x treatment interaction were significant in the MANOVA (Table 2). When the individual ANOVA tests were performed, only litter and dead root material had a significant positive response to treatment. N mg $g^{-1}$ of litter and dead root material did not significantly differ based on date of collection (Table 3; Fig. 9).

Variation in nitrogen standing crops (g N $m^{-2}$) was significant based on date of collection, treatment and date x treatment according to MANOVA results (Table 3). The pattern of nutrient allocation followed that of biomass. Individual ANOVA results showed that each plant component had a significant response to fertilization (Table 3).

The plant components from fertilized plots had significantly greater g N $m^{-2}$ than the control groups (Fig. 10).

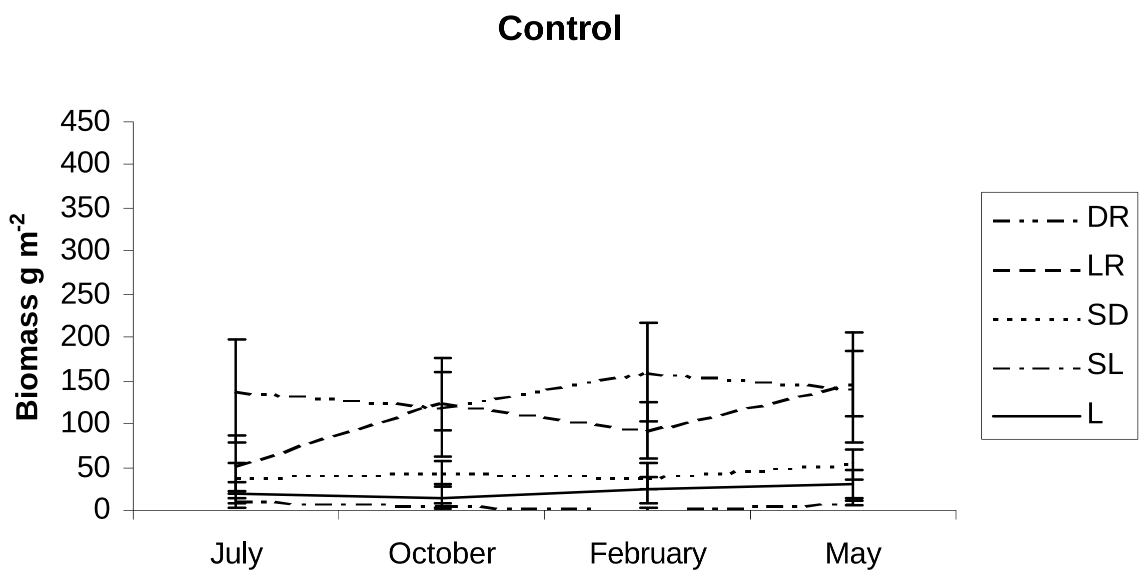
Soil nitrogen (mg $cm^{-3}$) showed greater N content in fertilized plots than control. N content in the fertilized plot peaked in October while control plots exhibited a drop in N content (Fig.11).

**Table 1.** MANOVA results for biomass. Results indicate significance by date, treatment and date x treatment interaction. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots. All P values marked with * are significant (<0.05). Non-significant values, power values are displayed.

| **MANOVA**: Source of Variation | Degrees of Freedom | Pillai's Trace | F | P | Power |
|---|---|---|---|---|---|
| Date | 15 | 0.485 | 4.012 | 0.000* | |
| Treat | 15 | 0.452 | 16.848 | 0.000* | |
| Date* Treat | 15 | 0.285 | 2.169 | 0.007* | |

| **ANOVA:** | Degrees of Freedom | Type III S.S. | F | P | Power |
|---|---|---|---|---|---|
| SL | | | | | |
| Date | 3 | 3317.2 | 11.077 | 0.000* | |
| Treat | 1 | 810.21 | 8.116 | 0.005* | |
| D*T | 3 | 687.29 | 2.295 | 0.082 | 0.564 |
| SD | | | | | |
| Date | 3 | 1811.79 | 0.171 | 0.916 | 0.081 |
| Treat | 1 | 81207.3 | 23.031 | 0.000* | |
| D*T | 3 | 2565.1 | 0.242 | 0.867 | 0.095 |
| L | | | | | |
| Date | 3 | 42515.9 | 4.091 | 0.009* | |
| Treat | 1 | 261850.8 | 75.587 | 0.000* | |
| D*T | 3 | 44546.1 | 4.286 | 0.007* | |
| LR | | | | | |
| Date | 3 | 211389.5 | 4.333 | 0.006* | |
| Treat | 1 | 188489.8 | 11.592 | 0.001* | |
| D*T | 3 | 39246.9 | 0.805 | 0.494 | 0.291 |
| DR | | | | | |
| Date | 3 | 281515.9 | 1.927 | 0.130 | 0.486 |
| Treat | 1 | 222343.8 | 4.566 | 0.035* | |
| D*T | 3 | 437303.1 | 2.993 | 0.034* | |

**Fig. 7.** Mean biomass values (g $m^{-1}$) shown for dead roots (DR), live roots (LR), standing dead (SD), standing live (SL), and litter (L) across four sampling dates. Error bars represent one standard error.



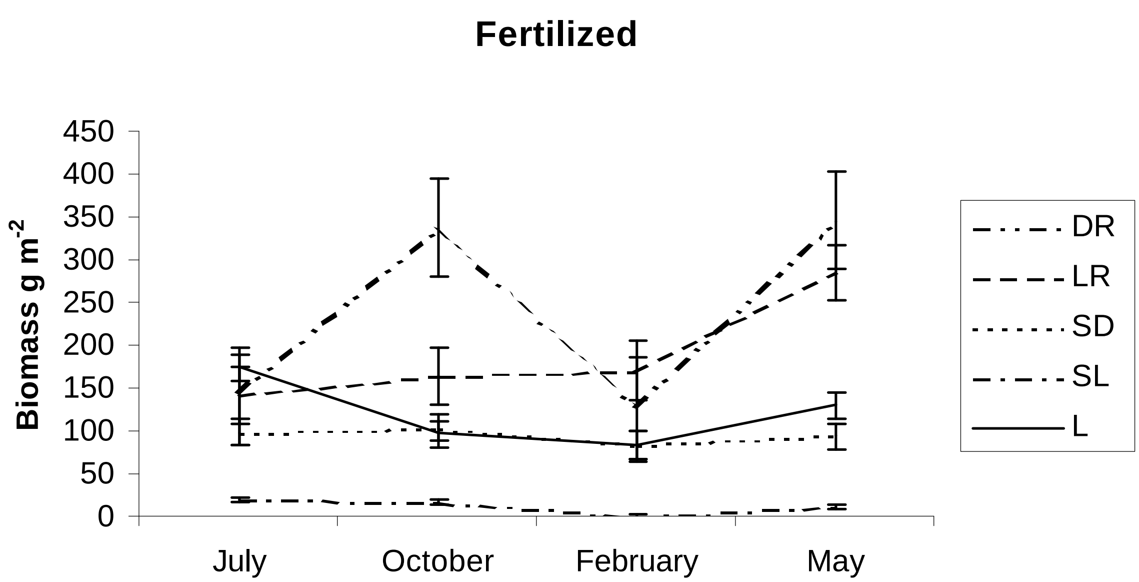
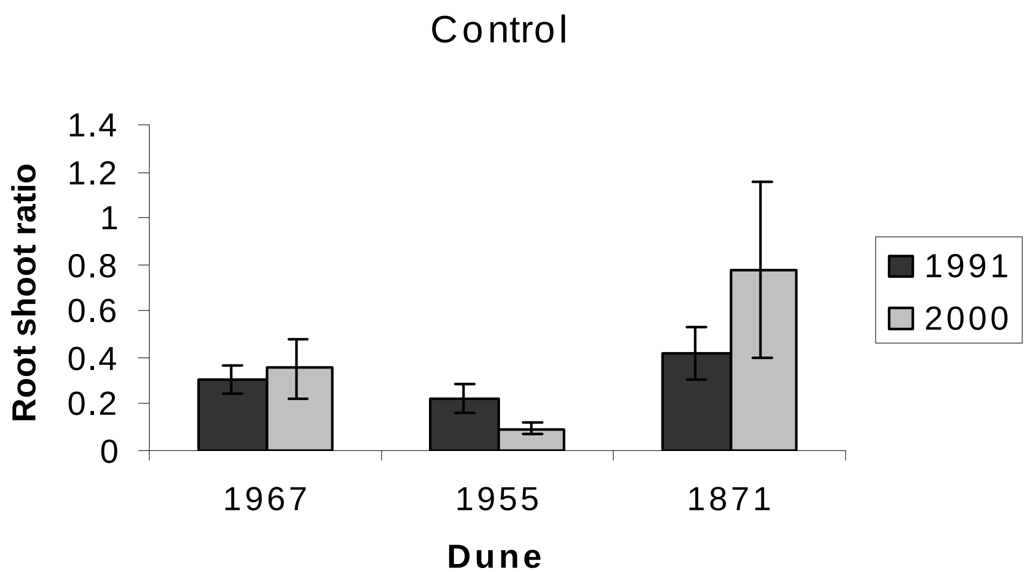



**Fig. 8.** Root shoot ratios compared among dune sites and the 1991 and 2000 sampling dates. Error bars represent one standard error.



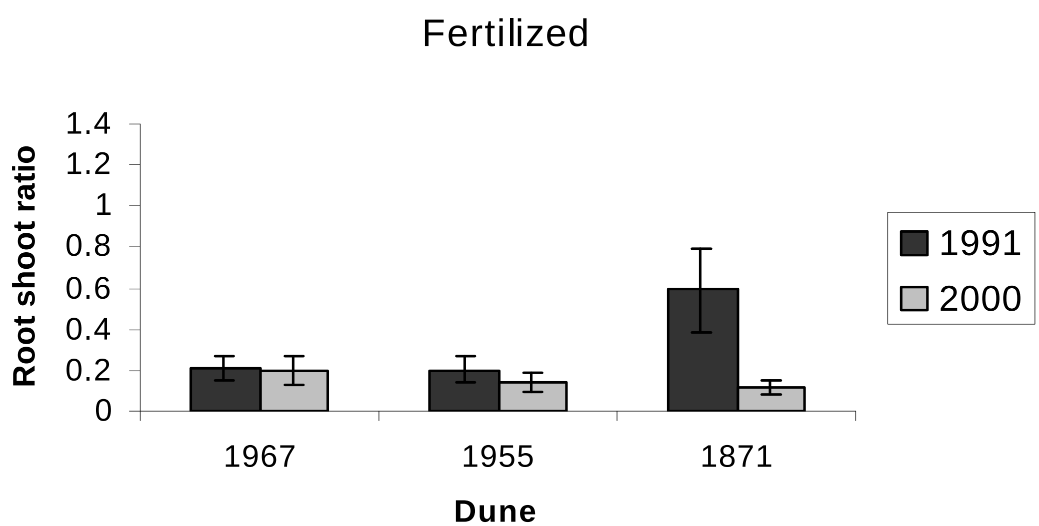
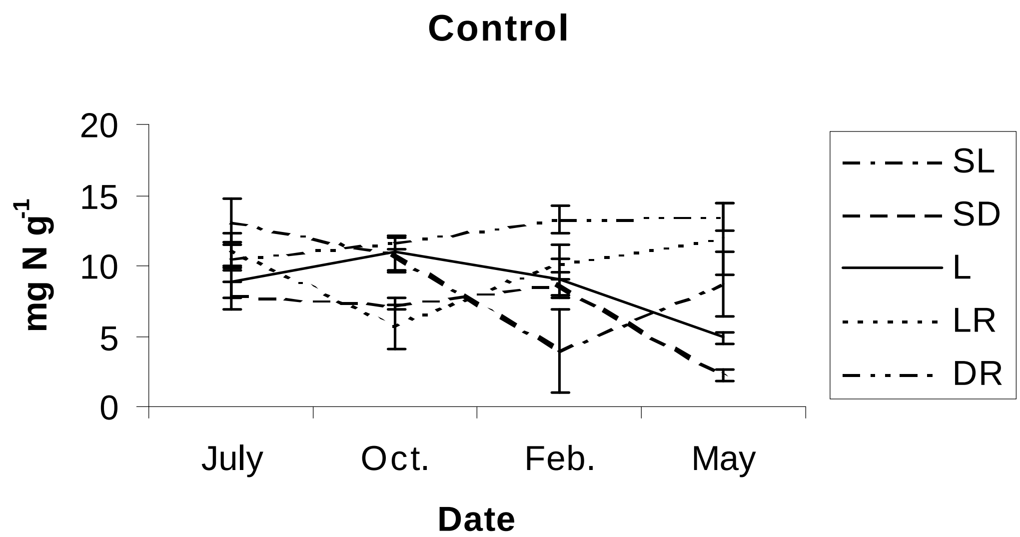



**Table 2.** MANOVA results for nitrogen concentrations. * represents significant values, power values are given for nonsignificant results. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots.

| **MANOVA**: Source of Variation | Degrees of Freedom | Pillai's Trace | F | P | Power |
|---|---|---|---|---|---|
| Date | 15 | 1.360 | 4.972 | 0.000* | |
| Treat | 5 | 0.366 | 3.233 | 0.020* | |
| Date* Treat | 15 | 0.794 | 2.161 | 0.013* | |

| **ANOVA:** | Degrees of Freedom | Type III S.S. | F | P | Power |
|---|---|---|---|---|---|
| SL | | | | | |
| Date | 3 | 5.9 E-4 | 11.619 | 0.000* | |
| Treat | 1 | 1.6 E-8 | 0.001 | 0.976 | 0.999 |
| D*T | 3 | 1.8 E-4 | 3.563 | 0.025* | |
| SD | | | | | |
| Date | 3 | 7.3 E-5 | 6.163 | 0.002* | |
| Treat | 1 | 1.2 E-5 | 3.112 | 0.087 | 0.939 |
| D*T | 3 | 1.3 E-4 | 11.185 | 0.000* | |
| L | | | | | |
| Date | 3 | 1.1 E-5 | 0.629 | 0.602 | 0.166 |
| Treat | 1 | 4.3 E-5 | 7.435 | 0.010* | |
| D*T | 3 | 1.6 E-4 | 9.368 | 0.000* | |
| LR | | | | | |
| Date | 3 | 1.5 E-4 | 4.874 | 0.007* | |
| Treat | 1 | 4.4 E-6 | 0.402 | 0.530 | 0.094 |
| D*T | 3 | 7.5 E-6 | 0.230 | 0.875 | 0.089 |
| DR | | | | | |
| Date | 3 | 5.9 E-5 | 2.493 | 0.078 | 0.563 |
| Treat | 1 | 4.2 E-5 | 5.339 | 0.027* | |
| D*T | 3 | 1.9 E-5 | 0.803 | 0.501 | 0.203 |

**Fig. 9.** Plant nitrogen concentrations (N mg $g^{-1}$) in control and fertilized plots over four sampling dates. One standard error is represented by error bars. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots.



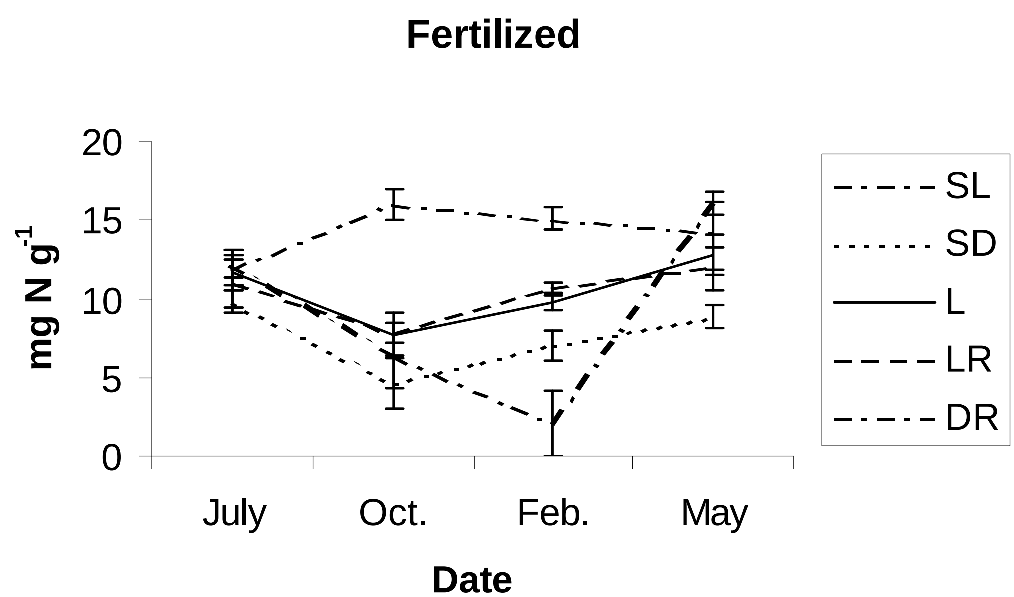
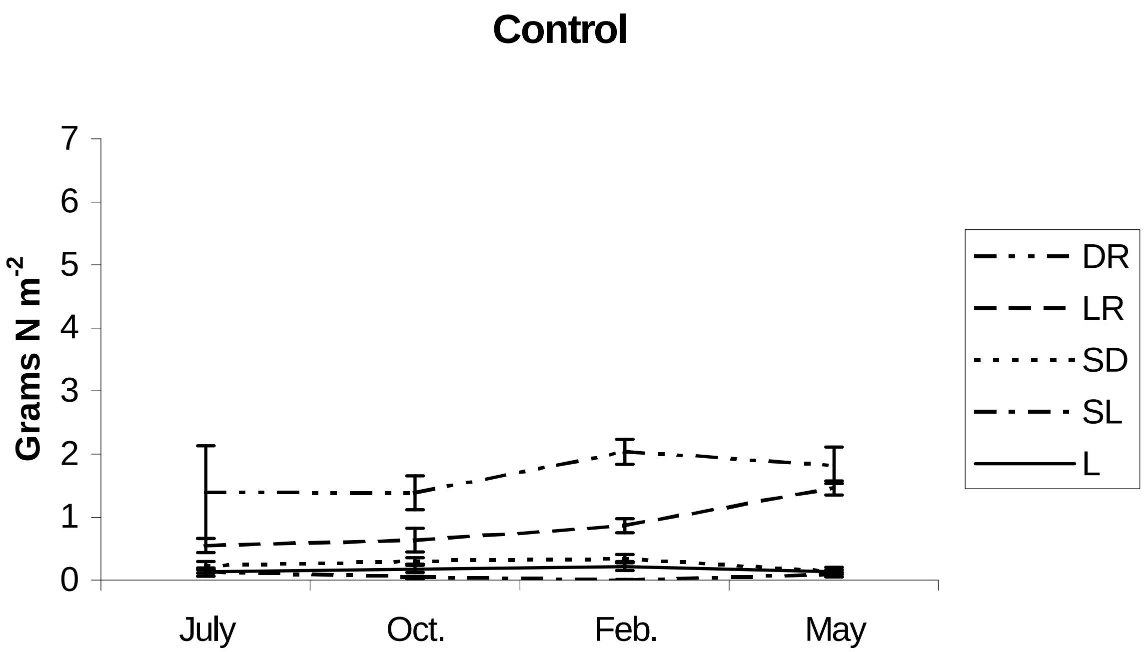



**Table 3.** MANOVA results for nitrogen standing crop. Nitrogen content is different from date to date, control vs fertilized plots, and the interaction of treatment and date. * represents significance <0.05. Power values are displayed for non- significant values. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots.

| **MANOVA**: Source of Variation | Degrees of Freedom | Pillai's Trace | F | P | Power |
|---|---|---|---|---|---|
| Date | 15 | 0.121 | 5.951 | 0.000* | |
| Treat | 5 | 0.312 | 12.364 | 0.000* | |
| Date* Treat | 15 | 0.426 | 1.876 | 0.031* | |

| **ANOVA:** | Degrees of Freedom | Type III S.S. | F | P | Power |
|---|---|---|---|---|---|
| SL | | | | | |
| Date | 3 | .181 | 11.376 | 0.000* | |
| Treat | 1 | 0.048 | 9.063 | 0.005* | |
| D*T | 3 | 0.018 | 1.153 | 0.343 | 0.280 |
| SD | | | | | |
| Date | 3 | 0.354 | 1.435 | 0.251 | 0.343 |
| Treat | 1 | 1.942 | 23.63 | 0.000* | |
| D*T | 3 | 0.850 | 3.446 | 0.028* | |
| L | | | | | |
| Date | 3 | 3.787 | 2.507 | 0.077 | 0.566 |
| Treat | 1 | 13.521 | 26.853 | 0.000* | |
| D*T | 3 | 4.633 | 3.067 | 0.042* | |
| LR | | | | | |
| Date | 3 | 13.462 | 14.581 | 0.000* | |
| Treat | 1 | 10.808 | 35.119 | 0.000* | |
| D*T | 3 | 2.152 | 2.331 | 0.093 | 0.532 |
| DR | | | | | |
| Date | 3 | 21.168 | 2.996 | 0.047* | |
| Treat | 1 | 24.326 | 10.227 | 0.003* | |
| D*T | 3 | 25.307 | 3.547 | 0.025* | |

**Fig. 10.** Nitrogen content (grams N $m^{-2}$) of all components in control and fertilized plots. Error bars represent one standard error. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots.



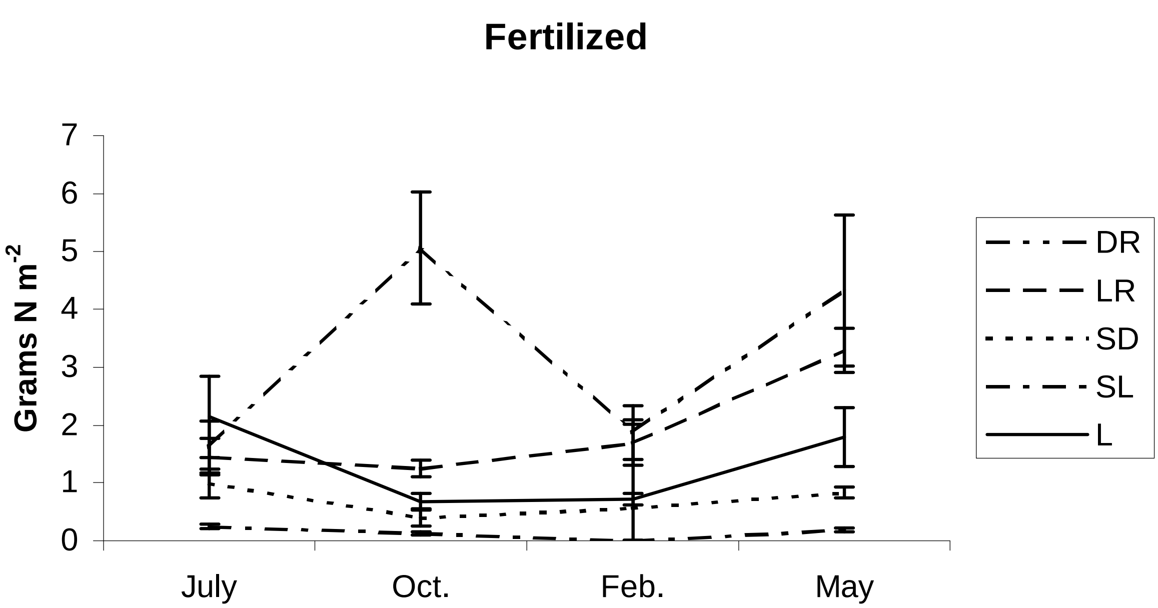
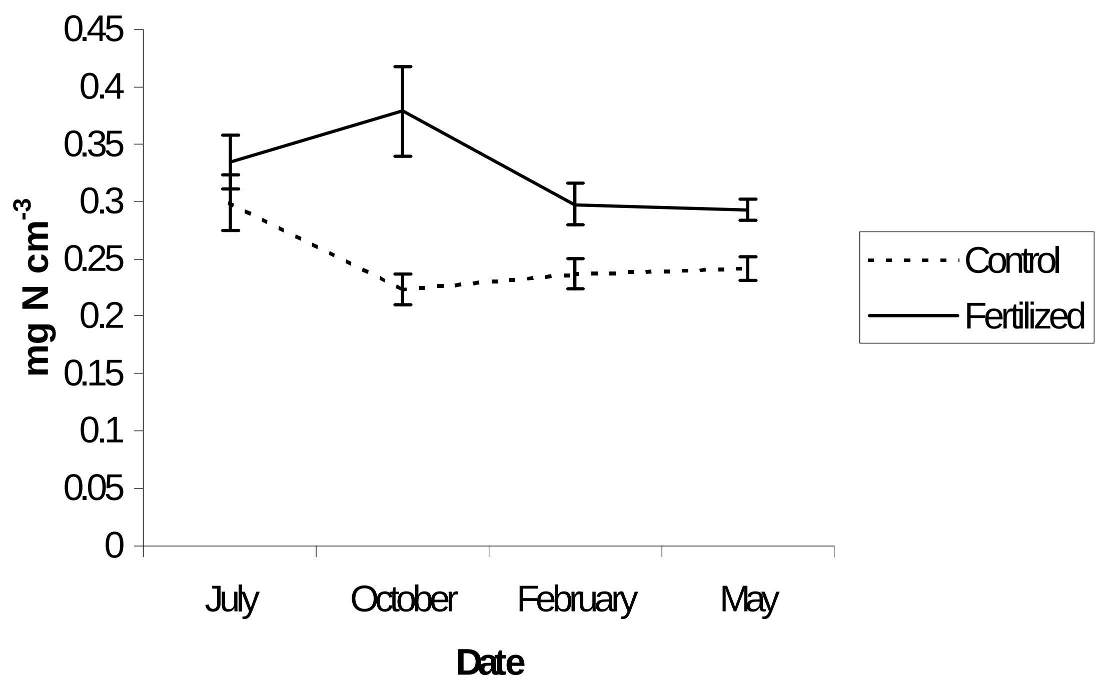



**Fig. 11.** Soil nitrogen content (N mg $cm^{-3}$) in control and fertilized plots over four sampling dates July 2000 to May 2001.



# DISCUSSION

## Long term response to fertilization

Biomass on the 1967, 1955, and 1871 dunes showed a significant positive response to nutrient addition that was applied from 1990 to 1991. The ability for this system to adapt very rapidly to a nutrient addition and retain it for nine years warrants further investigation of the mechanisms at work. It is believed that there may be two mechanisms for nutrient retention within nutrient limited systems, either the plant must maximize the assimilation of nutrients or minimize loss of nutrients (Berendse et al. 1992; Tilman 1986). Perhaps when nitrogen was added to this nitrogen poor system, the ability of plants endemic to low nutrient systems to maximize assimilation and minimize nutrient loss aided in the retention of nitrogen over a long period of time.

The data presented here show that the additional available nitrogen in the system was used efficiently by the plants for increasing biomass, effectively maximizing assimilation. Results show a dramatic difference in biomass between control and fertilized plots that has been sustained for nine years. The analysis of various plant components show that a large sink for retaining nitrogen in the system is the pool of litter accumulated in fertilized plots.

## Changes in biomass over nine years

Aboveground biomass decreased in both treatments from 1991 to 2000 while root biomass increased significantly. Similar responses have been found in aboveground biomass to fertilizer treatment in a six-year vegetation survey conducted on the dunes (Day et al. 2001). Plants that are stressed by poor nutrient availability increase root biomass in order to increase nutrient retention (Chapin 1980; Chapin 1991). If the increase in belowground biomass was only in control plots, this may provide a sufficient explanation. Considering biomass allocation shifted in both control and fertilized plots indicates another mechanism other than nitrogen availability is affecting the dune system.

Hog Island is a very dynamic system and many of the ecosystem processes are strongly affected by changes in free surfaces (Ehrenfeld 1990; Day 2001). Although nitrogen additions increased biomass on the dunes, it is not the only factor limiting aboveground growth. Water availability has been linked to a decline in aboveground biomass on the Hog Island dunes (Day 1996; Day et al. 2001). The results here show that aboveground biomass decreased in both control and fertilized plots and belowground biomass increased. An assumption can be made that the plants have allocated more production to belowground portions of the plant in order to increase root surface area for water absorption.

Day (1996) reported that of the total biomass in control and fertilized plots, the percent biomass allocated to belowground production decreased with fertilization. Similarly, analysis of root shoot ratios in this study show a dramatic increase on the 1871 dune control plots, while the fertilized plots on 1871 exhibit a dramatic decline. Increased aboveground biomass can increase soil moisture by increasing the soil organic matter (Olff et al. 1993). Perhaps the fertilized plots on the 1871 dune are less affected by changes in free surfaces, like ground water availability, and therefore do not need to increase root production as dramatically as the control plots.

According to Tilman's Resource Ratio Hypothesis (1985), when growth is limited due to lack of a resource and that resource limitation is fulfilled, continued growth will ultimately be limited by a different resource. In this instance, if nitrogen availability and water availability are no longer limiting in the fertilized plots, the plants may be competing for light and are allocating greater resources aboveground to accommodate that limiting factor.

**Nitrogen concentrations in plant components**

Analysis of nitrogen concentration in plant components determined that fertilization only had a significant effect on N content in dead roots and litter. Nitrogen concentration did not vary greatly among plant components or between control and fertilized plots. Litter is often a sink for immobilizing nitrogen during decomposition (Jordan et al. 1989) and increasing available nitrogen can increase immobilization rates (Melillo et al. 1984), thus increasing the N content of the litter. Fertilization increases decomposition of litter making nutrients more readily available (Foster and Gross 1998; Hunt et al. 1988). Conn and Day (1993) found increased mineralization rates in these fertilized plots on Hog Island, making nitrogen more available in soils highly susceptible to leaching. Van der Valk (1975) demonstrated that increased production of *Ammophila breviligulata* on sand dunes reduced sand movement thus stabilizing dune sands. When substrate is allowed to build on sand, organic material begins to accumulate and organic soils can be formed.

The intial response to nutrient addition showed a significant response in aboveground and belowground plant components (Conn and Day 1993; Stevenson and Day 1996; Dilustro and Day 1997). Chapin (1980) stated that structural tissues in nutrient limited systems would increase tissue nitrogen with increased nutrient availability.

However, the results presented agree with Nadelhoffer et al. (1985), who concluded the relative allocation of nitrogen in aboveground and belowground plant components did not vary with increasing nitrogen availability.

**Current biomass and nutrient allocation**

Analysis of plots over the four sampling dates, July, October, February, and May of 2000 and 2001 showed that there was a positive treatment response by all plant components. Aboveground and belowground biomass exhibited increases to fertilization (Fig. 7). A biomass budget (Fig. 12) shows the average plant biomass values for July 2000 are greater in fertilized plots than control plots.

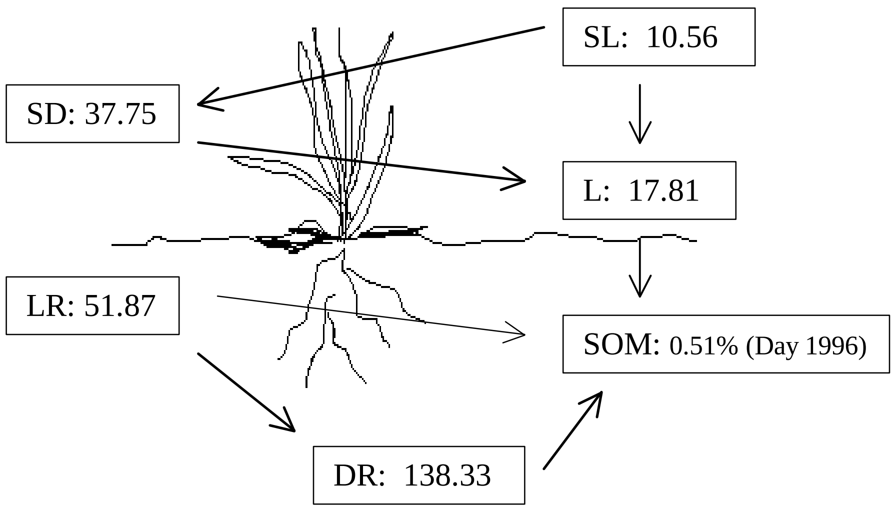
The budget demonstrates the dramatic differences between control and fertilized plots. The greatest difference is the litter pool in the fertilized plots is approximately ten times that of the control. The large portion of litter on the soil surface can dramatically alter the microclimate making the ground cooler and more moist (Jordan et al.1989; Olff et al.1993). Theoretically the decay rate of the litter is thereby altered creating different conditions than the control plots.

Nitrogen standing crop showed a significant positive response to treatment during all dates and in all plant components (Fig. 9). The budget of nitrogen standing crop (Fig. 13) shows the pool of litter contains a large sink of nitrogen that can be made available through mineralization to the plant community.

Analysis of plant nitrogen concentrations, biomass, and nitrogen standing crop have shown that increased biomass and not increased N in plant tissues partly drive the retention of nitrogen in this system. I am suggesting that the initial increase in biomass

**Fig 12.** A budget showing pools of plant biomass depicted at peak biomass in July 2000. Values represent g $m^{-2}$. SL= standing live, SD= standing dead, L= litter, LR= live roots, DR= dead roots, SOM= soil organic matter.

Control




Fertilized

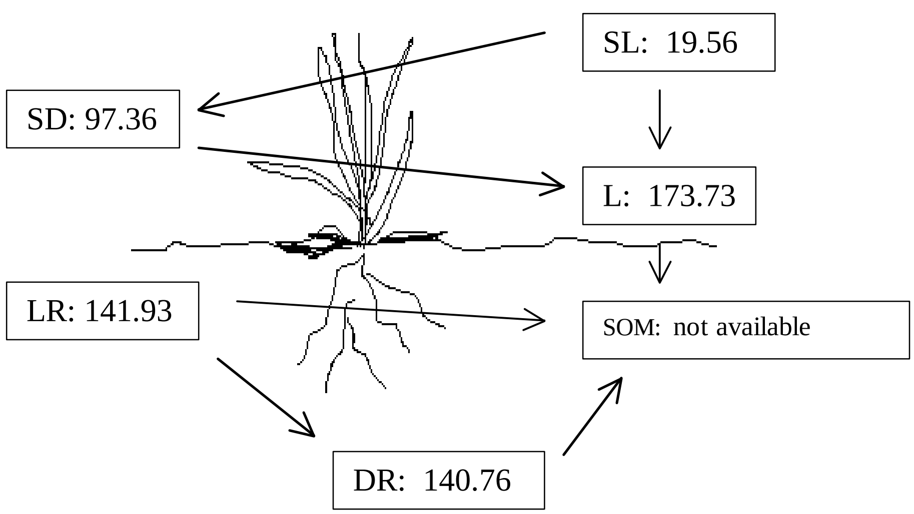
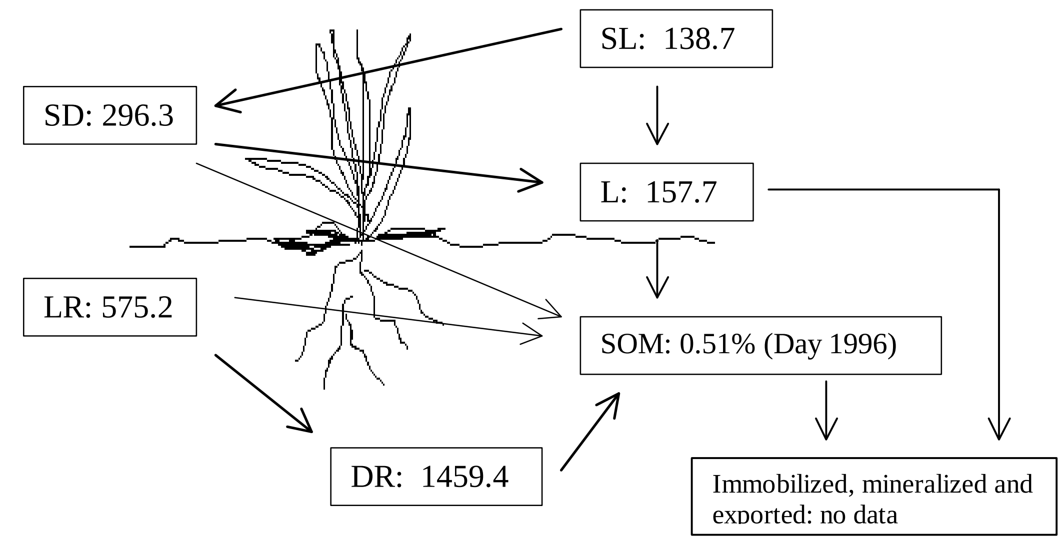
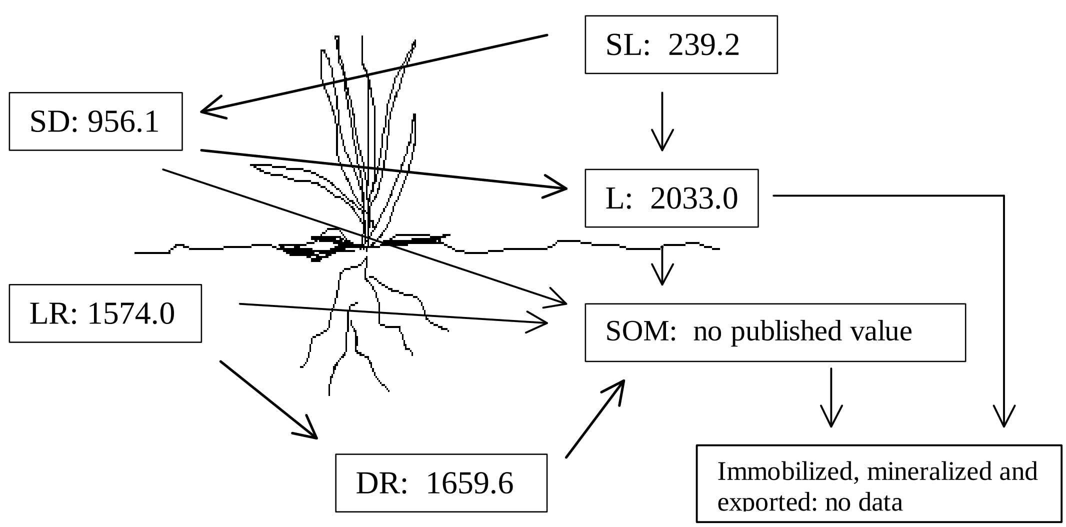


**Fig 13.** A budget depicting nitrogen standing crop (mg $m^{-2}$) at peak biomass in July 2000. Pools are standing live (SL), standing dead (SD), litter (L), live roots (LR), dead roots (DR) and soil organic matter (SOM).

Control




Fertilized



created a pool of litter which has perpetuated the availability of excess nitrogen in the system. What is evident is that the initial increase in biomass production has led to greater nitrogen availability in the treated plots over a nine-year period.

# CONCLUSIONS

Fertilization has played a significant role on the sand dune communities of Hog Island from 1991 to 2000. There remains a marked difference in biomass between the control and the fertilized plots. Both control and fertilized plots were also affected by changes in ground water availability demonstrating how the changes in free surfaces on Hog Island can change the structure of the communities present.

Allocation of resources to belowground or aboveground tissues varied between the control and fertilized plots. Root shoot analysis revealed that the fertilized plots, specifically on the 1871 dune, were allocating greater resources aboveground and less belowground than the control plots. This indicates that the fertilized plots on 1871 dune are less affected by changes in ground water availability. The increased litter layer retains greater amounts of moisture thereby minimizing stress due to low water availability on that dune. The other two dunes are less water limited and subsequently showed little variation in root shoot ratios.

Nutrient concentration of plant components revealed little difference between control and fertilized plots. The plants are able to adapt to increased nutrients by increasing their biomass, in effect diluting the available nitrogen in normal tissue concentrations. The initial increased biomass response to fertilization is part of the mechanism by which increased nutrient availability is perpetuated in the experimental plots. The live biomass then dies and becomes a thick litter layer. Biomass estimations show that the fertilized plots had approximately ten times greater litter masses than control plots. Now these fertilized plots are established to retain available nitrogen within the system through increased immobilization and mineralization due to higher nitrogen levels. An interesting addition to this study would be to measure decomposition, mineralization, and immobilization rates within the control and fertilized plots to determine how these processes directly affect decomposition and nutrient retention within the fertilized plots on Hog Island.

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