

**FINE ROOT BIOMASS DISTRIBUTION AND PRODUCTION ALONG A
BARRIER ISLAND CHRONOSEQUENCE**

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ABSTRACT

FINE ROOT BIOMASS DISTRIBUTION AND PRODUCTION ALONG A BARRIER ISLAND CHRONOSEQUENCE

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Fine roots play an important role in community development on barrier islands. Fine roots can influence nutrient losses from the soil environment along with regulating water loss based on their distribution and concentration (Nobel et al., 1989; Gleeson and Tilman, 1990). A sequential coring method was used to determine fine root biomass and total biomass along a chronosequence of barrier island dunes and swales on the Virginia Coast Reserve - Long Term Ecological Research Site. Fine root production and the effects of nitrogen fertilization were also examined using an ingrowth core method along the chronosequence. Live fine root biomass, total biomass and fine root production patterns were analyzed. These patterns were associated with topographic position and the interaction with nitrogen, phosphorus and water availability along the chronosequence. Patterns between dunes and swales defined them as two very different community types both structurally and functionally. Dune communities were xeric and swales more mesic in community structure due to their interaction with water table position. The swales had significantly larger accumulations of total biomass (live fine roots, dead fine roots and detrital material) ranging from 59 to 1505 g/m² and the dunes ranged from 64 to 229 g/m². The higher biomass quantities were probably due to greater accumulation of detritus resulting from anaerobic conditions in the swales created by a higher water table position. Live fine root biomass changed very little with increases in dune age, 5, 13, 6 and 4 g/m² for the 6, 24, 36 and 120 yr dunes respectively. But swales showed a general decrease with increased swale age, 180, 105 and 122 g/m² for the 24, 36 and 120 yr swales respectively. The 6 yr swale did not follow this pattern and had significantly lower biomass than the other swales. Live fine roots and total biomass were concentrated in the upper 10 cm of soil in dune and swale communities across the chronosequence.

Root nitrogen concentration increased with increased age along the dune and swale

chronosequence. Root phosphorus concentrations increased with age in the dunes but were not different in the swales. Fine root production increased significantly with N-fertilization in the dune communities, 1.5 times to 2.5 times the control sites. The increased nitrogen levels in the N-fertilized sites were reflected in increased nitrogen concentration in live fine root tissues but root nitrogen levels in the fertilized areas did not increase with increased age; 1798, 1334 and 1826 mg/100g dry wt. for 24, 36 and 120 yr dunes respectively.

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INTRODUCTION

Belowground biomass and fine root production represent a large proportion of total biomass and production in most ecosystems (Nadelhoffer, 1992; Neil, 1992). Root production has been studied in various ecosystems including forested wetlands (Powell and Day, 1991), tidal marshes (Valiela et al., 1976; de la Cruz and Hackney, 1977; Gallagher and Plumley, 1979; Smith et al., 1979) and prairies (Dahlman and Kucera, 1965; Knapp and Seastedt, 1986). Changes in belowground biomass and fine root production are important to the analysis of functional relationships of an ecosystem. There are clearly many factors that affect development and growth of root systems in plant communities. Root growth can be affected by pH, Al toxicity, mineral nutrient deficiency and physical factors such as soil moisture, temperature and aeration (Gregory, 1987). Belowground research involving root and rhizome growth has been limited due to the great amount of time and labor required and high sample variability (Schubauer and Hopkinson, 1984). Belowground production is perhaps the most difficult belowground process to study (Santantonio and Grace, 1987). The deficiencies associated with belowground studies are attributed to methodological and logistical problems (Powell and Day, 1991). Methods for measuring fine root production are primarily indirect and subject to uncertainties and possible biases (Nadelhoffer and Raich, 1992).

In this study, a sequential coring method was used to determine total fine root biomass along a chronosequence of barrier island dunes and swales. Fine root production was measured using an ingrowth core method. These methods have been used in previous wetlands research to determine biomass and production rates (Lund et al., 1970; Persson, 1983; Roman and Daiber, 1984; Schubauer and Hopkins, 1984; Howes et al., 1985; Ellison et al., 1986; Symbula and Day, 1988; Bertness, 1991; and Powell and Day, 1991). These techniques are tedious and difficult, involving the separation of live from dead matter (Howes et al., 1985). The coring method is a destructive method although not as destructive as the pit excavation method used for determining general root biomass patterns on Hog Island during the summer of 1989 (Conn and Day, 1993). The pit method is very labor intensive and time consuming.

Barrier island dunes and swales were the focus of this belowground biomass and production study. Barrier islands can be a very harsh environment for plants. The environmental influences on primary productivity include limited freshwater, low nutrient levels, high salinity caused by ocean spray, and encroachment by marine tides. The vegetation faces extreme physical constraints from salt spray, salt water, moving sand and poor soil (Ehrenfeld, 1990; Hayden et al., 1991; Conn and Day, 1993). These factors affect plant growth and fine root production.

Barrier islands are very dynamic systems. They thrive by storm activity and move through changes in their structure, migrating landward as sea level rises. There is a dynamic balance between sea level, sand supply, wave energy and vegetation. As a result ecosystem structure and function are very dynamic. The vegetation on these landscape formations control the shape, size and movement of the islands (Pilkey, 1990).

The present study observed communities located at different topographic positions on a coastal barrier island, in hopes of developing a better understanding of barrier islands in a landscape perspective. Because barrier islands are nutrient limited systems and are subjected to various types of stress (Hayden et al., 1991), dune and swale communities may respond differently to these conditions.

The present study was conducted on Hog Island, a barrier island off the coast of Virginia and part of the National Science Foundation's Virginia Coast Reserve Long Term Ecological Research (LTER) site. The primary objectives of this study were (1) to quantify fine root biomass (FRB) distribution by depth and topographic position (dune vs. swale) along a natural chronosequence, (2) to determine if swales produce more FRB than dunes and what some of the influencing factors may be, (3) to compare the younger and older sites, (4) to compare total nitrogen and total phosphorous content of fine roots across the chronosequence and (5) to compare the response of fine root production to N-fertilization along the chronosequence. Soil nutrients play an important role in fine root development and growth (Gregory, 1987) as well as nutrient uptake (Haynes, 1986). By examining fine root production in controlled and nitrogen enriched sites one may determine responses of different dunes in a nutrient poor system. Other studies have shown that root biomass increases with an increase in community age

(Gleeson and Tilman, 1990; Conn and Day, 1993). This study looked for a similar pattern using sequential cores along a chronosequence of dunes and swales.

SITE DESCRIPTION

This study was conducted on Hog Island, a barrier island of the Virginia Coast Reserve Long Term Ecological Research (LTER) site, located off the eastern shore of the Delmarva Peninsula. The island is approximately 11.3 km long, averages 0.8 km in width, and lies 14 km off the mainland (Fig. 1). Mean annual total precipitation ranges from 81 to 122 cm with mean daily temperatures from -1 to 10°C in winter months and 18 to 30°C during mid-summer (Deuser et al., 1976).

Beach dunes extend slightly more than half way down the island from the northern end. The northern end of Hog Island, which is accreting (5 m/yr), has a widening beach with young dunes and swales to the east near the ocean progressing to the older dunes and swales towards the west. More than 16% of the island has been lost to sea level rise since 1852. The southern end of Hog Island experiences overwash and is eroding (5 m/yr). (Deuser et al., 1976; Hayden et al., 1991).

The soils on Hog Island consist of Duckston, Newhan and Corolla series. The Duckston soils are mainly concentrated in the marshes on the western side of the island and were described as nearly level, very poorly drained to poorly drained, sandy, silty and loamy soils in tidal marshes. The soils are located from the lagoon to the ocean and described as nearly level to sloping, excessively drained, sandy soils and can be found on frontal or interior dunes varying with dune elevation. The soils are located on elongated areas roughly parallel to the ocean. The Corolla soils located in the swales are nearly level or gently sloping and are poorly or moderately well drained with a seasonally high water table (Dueser et al., 1976).

The island increases with age moving westward from the ocean to the lagoon. The study involved eight sites across the island in four age categories. There were four dune and adjacent swales sites, 6 years, 24 years, 36 years, and 120 years of age (Fig. 2).

The dune communities were codominated by Spartina patens (Aiton) Muhl. and Ammophila breviligulata Fernald, both rhizomatous perennial grasses. Other dune species

Figure 1. A map of Hog Island, a barrier island in the Nature Conservancy's Virginia Coast Reserve. The map represents a graphical aerial view of the barrier island landscape identifying study site locations. The triangles represent GPS benchmark locations.

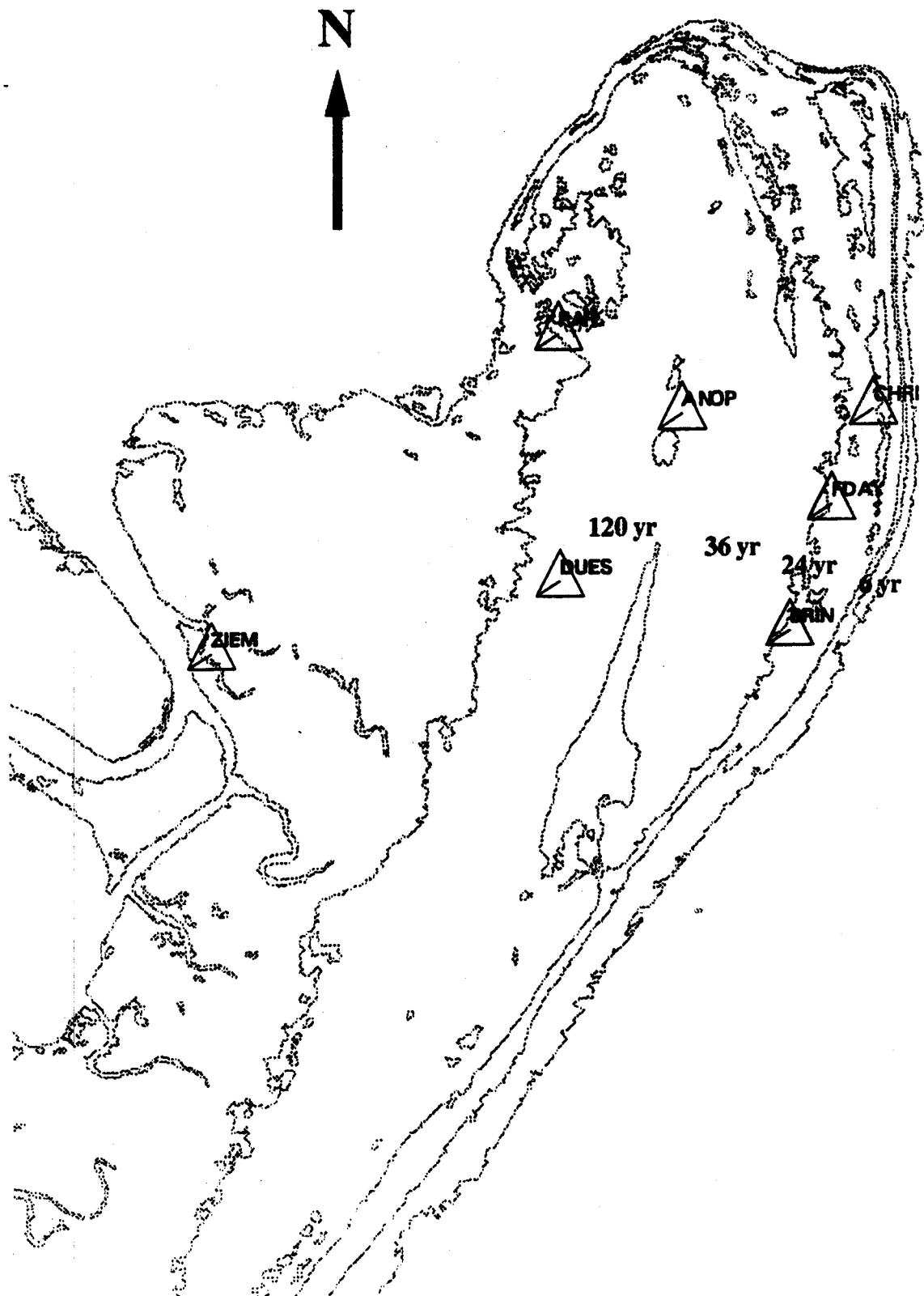
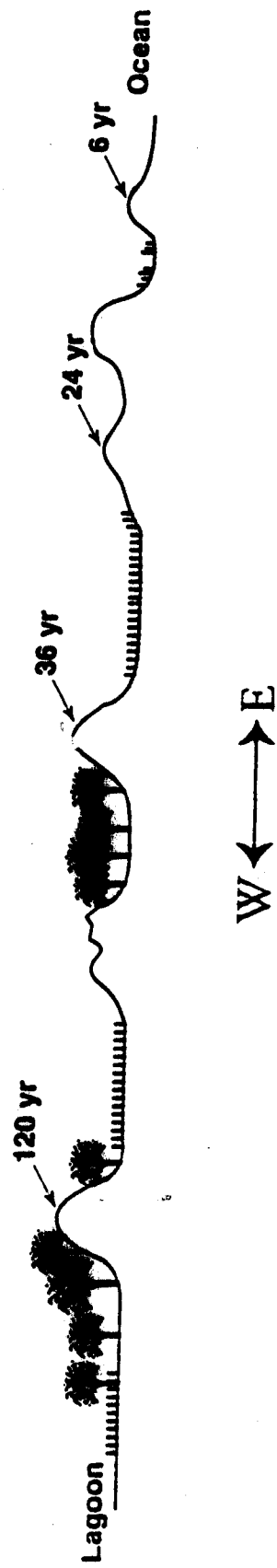


Figure 2. A Transect of Hog Island: A graphical representation of the vegetative and topographic characteristics of the island. The transect runs along the chronosequence of barrier island dunes and swales.



included Panicum amarum Ell., Aristida tuberculosa Nuttall and Rumex acetosella L. The younger (6 and 24 yr old) swale communities were dominated by Spartina patens (Aiton) Muhl. The older 36 and 120 yr swales were dominated by woody thickets of Myrica cerifera L. (McCaffrey, 1975; Hayden et al., 1991; Conn and Day 1993; Fahrig et al., 1993).

METHODS

Sequential Core Procedures.— The sequential core method was used to remove soil samples for live fine root biomass and total biomass (live fine roots, dead fine roots and detrital material) extractions. This involved randomly collecting ten soil cores each month (February 1991 to February 1992) from areas that represented each of the dune and swale sites. The 6 yr old dune and swale communities were sampled only four times during the study (February, May, August and November). A plunger style corer (7 cm dia. by 10 cm length bucket) was used to extract the soil cores. The soil cores were extracted in 10 cm increments down to a depth 40 cm. Each increment sample was placed in a plastic bag and labeled by date, site location, and depth interval. The soil samples were refrigerated immediately after each sampling trip.

A hydropneumatic elutriator (root washer) was used to separate the roots from the soil. The roots were then hand sorted into the following four categories, live fine roots (≤ 2 mm diam.) and rhizomes, dead fine roots and rhizomes, big roots (> 2 mm diam.) and rhizomes and detritus. The live roots were identified using the method of Schuurman and Goedewaagen (1971 cited in Bohm, 1979) and Powell and Day (1991), i.e. live roots were resilient, flexible and normally contained lateral branches. Color was used as a secondary test. Live roots were sometimes white externally or white internally. Dead roots were inflexible, fragmented or crumbled easily when bent. Dead roots were normally dark externally as well as internally.

After sorting the roots were dried at 70°C for 48 hrs and then weighed. If the fine roots (live or dead) were numerous and hard to separate from other organics in the sample, aliquots were used to breakdown the sample into a more manageable size. The aliquots were weighed and their mass multiplied by the required ratio to obtain a total biomass estimation for each category.

Fertilization Experiment and Production Estimates.— The fertilization experiment was conducted using the 24, 36 and 120 yr dunes. Each dune site contained control and N-fertilized areas. Fertilized areas were located relative to control areas so surface run-off or ground water transport would not introduce N-fertilizer into control areas. The 6 yr old dune had only a control site as fertilizer was not applied there because of spatial limitations. N-fertilizer was in the form of urea as a mix of coated (70%) and uncoated (30%) granules. The N-fertilizer was applied every three months, yielding a total of $60 \text{ g m}^{-2} \text{ yr}^{-1}$.

Fine root production was determined along the chronosequence of dunes in the controlled and fertilized sites by an ingrowth core method (Persson, 1983). Soil was extracted in February 1991 from twenty 40 cm deep holes at each control and fertilized site using the corer described above. Ten 40 cm deep holes were extracted from the 6 yr control site. The soil from the cores was sieved to remove all organic material (fine roots and rhizomes, both live and dead, big roots, and detritus). The cleaned soil was returned to its original hole and a flag marked the center. The marked areas were recored in October 1991 (after a 260 day period), at 10 cm increments down to a 40 cm depth using the flags as center points for coring. The extracted ingrowth cores were processed in the same manner as described above. Ingrowth was taken as an estimate of production.

Root Nutrient Content.— Nutrient analyses were conducted on live fine roots collected from each adjacent dune and swale community for the period February 1991-July 1991. Live fine roots extracted from August 1991-February 1992 were not analyzed due to the duration of storage. The live fine roots were combined from all depths for each dune and swale community due to small sample sizes. The roots were dried and ground in a Wiley-Mill (No. 40 mesh sieve) and digested by a sulfuric acid, hydrogen peroxide method. The solutions were analyzed colorimetrically for total phosphorus and Kjeldahl nitrogen (TKN) on a Scientific Instruments AP-200 autoanalyzer. TKN was determined by a modified Total Kjeldahl method and phosphorus was determined by the molybdate blue method (Scientific Instruments, 1973). Nutrient analyses were also conducted on live fine roots obtained from the ingrowth cores lumped by treatment across all depths.

Microenvironmental Measurements.— The microenvironmental measurements included soil pH made with a glass electrode and pH meter using a soil solution (1:1) with deionized

water. Hydroperiod was continuously monitored by wells equipped with Stevens' model 68 Type F water level recorders. Soil water was collected from two porous cup lysimeters buried at 15 cm and 50 cm and measured for salinity using a hand held refractometer. Soil redox measurements were obtained with platinum probes (Faulkner et al. 1989) permanently inserted at 5 cm, 15 cm, 25 cm and 35 cm below the soil surface. The soil temperature was measured at each site using a bimetal thermometer inserted at depths of 10 and 30 cm.

Soil cores were extracted from each dune and swale community and analyzed for soil organic matter, NH_4 and $\text{NO}_2 + \text{NO}_3$ (Day and Lakshmi, unpublished). Organic matter was obtained as a percentage of soil as ash dry weight. Nutrients were extracted through a KCl solution and analyzed colorimetrically using the Berthelot Reaction for ammonia and a copper-cadmium reductor column forming a diazo compound determining nitrate and nitrite through nitrate reduction (Scientific Instruments, 1973).

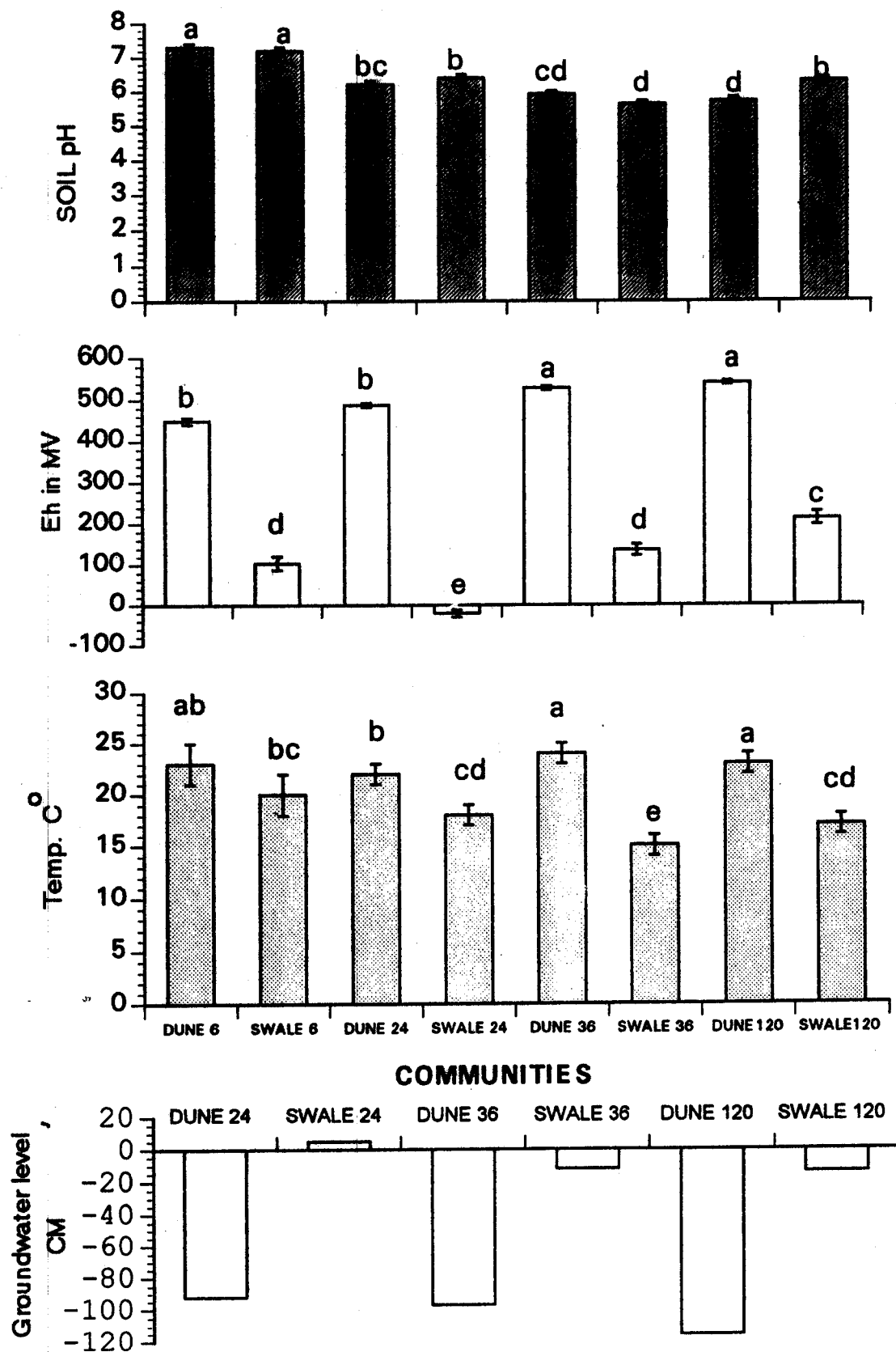
Statistical Analyses.— Tests for significant differences in mean live fine root biomass (LFRB) and total biomass (TB) among dune and swale communities were conducted using a split plot ANOVA. Site and community type (dune or swale) were main factors and depth was the split-plot factor (Statistical Analysis System (SAS) version 4 and 5). Differences among means were analyzed using a Tukey studentized range test ($\alpha = .05$). Dune age was not replicated in this study so only site differences can be tested. Effects of site age can only be inferred.

RESULTS

Microenvironmental Measurements.— During the study, annual mean pH levels decreased with increasing age along the chronosequence on Hog Island. The differences between dunes and swales were generally not significant. Soil pH was highest at the younger (6 yr old) dune (7.3) and swale (7.2) and generally decreased moving west towards the older (120 yr) dune (5.7). The 120 yr swale exhibited a soil pH (6.3), similar to the 24 yr dune (6.2) and swale (6.4) (Fig. 3).

Annual mean soil redox potential (Eh), which measures the degree of reduction in soils, was correlated with topographic position. The lowest readings (more reduced soils) were measured in the swales and the highest (less reduced or more oxidized soils) occurred in

Figure 3. Microenvironmental data representing annual means for the period February 1991 - 92. Samples for pH determinations were collected from depths of 10, 20, 30 and 40 cm. Eh measurements were collected from depths of 5, 15, 25 and 35 cm. Temperature measurements were collected from depths of 15 and 30 cm. The water levels were measured continuously throughout the year. Different lower case letters indicate significant differences (Tukey, $P < .05$). Vertical bars are \pm one SE.



the dunes. The lowest annual mean for soil redox was located in the 24 yr swale (-22 mv).

Higher soil temperatures were recorded on the dunes and lower soil temperatures were found in the swales. The highest annual mean soil temperatures were in the 36 yr dune (24°C) and the lowest were in the 36 yr swale (15°C) (Fig. 3).

Water table was lowest in dunes and highest in swales. The highest annual mean water table was in the 24 yr swale (5 cm above the soil profile) and lowest in the 120 yr dune (-116 cm). Among dunes, water table was highest in the 24 yr dune (-92 cm). All sites exhibited a drop in water table starting in the second week in May 1991 and increasing in severity till the second week in July 1991. This period was the driest period during the study. A second dry period was identified during October 1991 and lasted a little over a week (Fig. 4)

Soil organic matter among dunes and swales increased significantly (Tukey, $P < .05$) with increased age. The youngest (6 yr) swale was significantly lower in organic matter (Tukey, $P < .05$) content than the 36 yr and 120 yr old swales. The 24 yr old swale was not significantly different from the 6 yr or the 36 yr old swales but was significantly different from the oldest swale (Tukey, $P < .05$) (Fig. 5).

Soil ammonium was significantly lower (Tukey, $P < .05$) in the 6 yr old dune in comparison to all the other dunes. The 24 yr, 36 yr and 120 yr dunes were not significantly different from one another but there was a slight increase with age. Soil ammonium in swales increased with age. The two younger swales showed significantly lower percentages of soil ammonium (Tukey, $P < .05$) than the 36 yr and 120 yr swales.

Nitrite+nitrate did not have as strong a pattern as ammonium. The dunes were not significantly different from one another. In swales, there were slight increases with age. The 6 yr swale was significantly lower in $\text{NO}_2 + \text{NO}_3$ (Tukey, $P < .05$) than the 120 yr swale but was not significantly different from the other swales (Fig. 6).

Biomass. Dune Sites. --- The six yr old dune was expected to have the lowest accumulation of total biomass (live fine roots, dead fine roots and detrital material) and the lowest live fine root biomass. However, the annual mean total biomass for the six yr old dune was not significantly different from the 36 yr or 120 yr old dunes. These three dunes were all significantly lower than the 24 yr dune (Tukey, $P < .05$). This pattern was not as dramatic for annual mean live fine root biomass (LFRB). The 24 yr old

dune was significantly higher in LFRB (Tukey, $P < .05$) than the 6 yr and the 120 yr dunes but not significantly higher than the 36 yr old dune (Table 1). The patterns for live fine roots as a percentage of total biomass changed. The 120 yr dune contained a higher percentage of LFRB, 16%, than the 6 yr, 24 yr and 36 yr dunes containing 5%, 6% and 5% respectively (Table 1).

On the 24 yr dune monthly mean total biomass (live fine roots, dead fine roots and detrital material) was significantly higher during April 1991 than July 1991-December 1991 (Tukey, $P < .05$) (Fig. 7). The 24 yr old dune showed the most dramatic increase during April 1991 in contrast to the other months. A pattern of increasing TB in the early spring months followed by TB decreasing during the summer and fall months was present for the 24 yr dune. This pattern was not as obvious in the other dune communities and there was no significant difference in TB between months. The 24 yr dune was significantly different from all the other dunes during the most months (Tukey, $P < .05$) (Fig. 8). The highest quantity of TB (589 g/m^2) was obtained on the 24 yr dune during April 1991. The lowest quantity of TB (18 g/m^2) was measured on the 120 yr dune during July 1991.

On all dunes monthly mean live fine root ($\leq 2 \text{ mm diam.}$) biomass was not significantly different between months from February 1991-February 1992. There was a lot of variability among the individual dunes month to month and this may mask true LFRB increases and decreases. The 24 yr dune showed the largest variability. It followed a pattern of alternating highs and lows from February 1991-January 1992. The standard error per month was so large it was hard to say if there was a true alternating high-low pattern (Fig. 8). The 24 yr dune monthly mean LFRB's were significantly different (Tukey, $P < .05$) than those measured on the 6 yr or 120 yr old dunes (Fig. 8).

There were significant differences in the distribution of annual mean total biomass and annual mean live fine root biomass over the soil profile. Both TB and LFRB were significantly higher in the top 10 cm than in 30 or 40 cm depths (Tukey, $P < .05$) (Table 2). Forty-two percent of the total biomass measured in the cores was located in the top 10 cm. The quantities were not significantly higher in the top 10 cm (222.75 g/m^2) than the 20 cm (153.15 g/m^2) depth but there appeared to be a decrease (Table 2).

Figure 4. Monthly means of water table based on continuous well recordings. The wells were located along the chronosequence of dunes and swales. The data represent monthly annual means computed for the period February 1991 - 92.

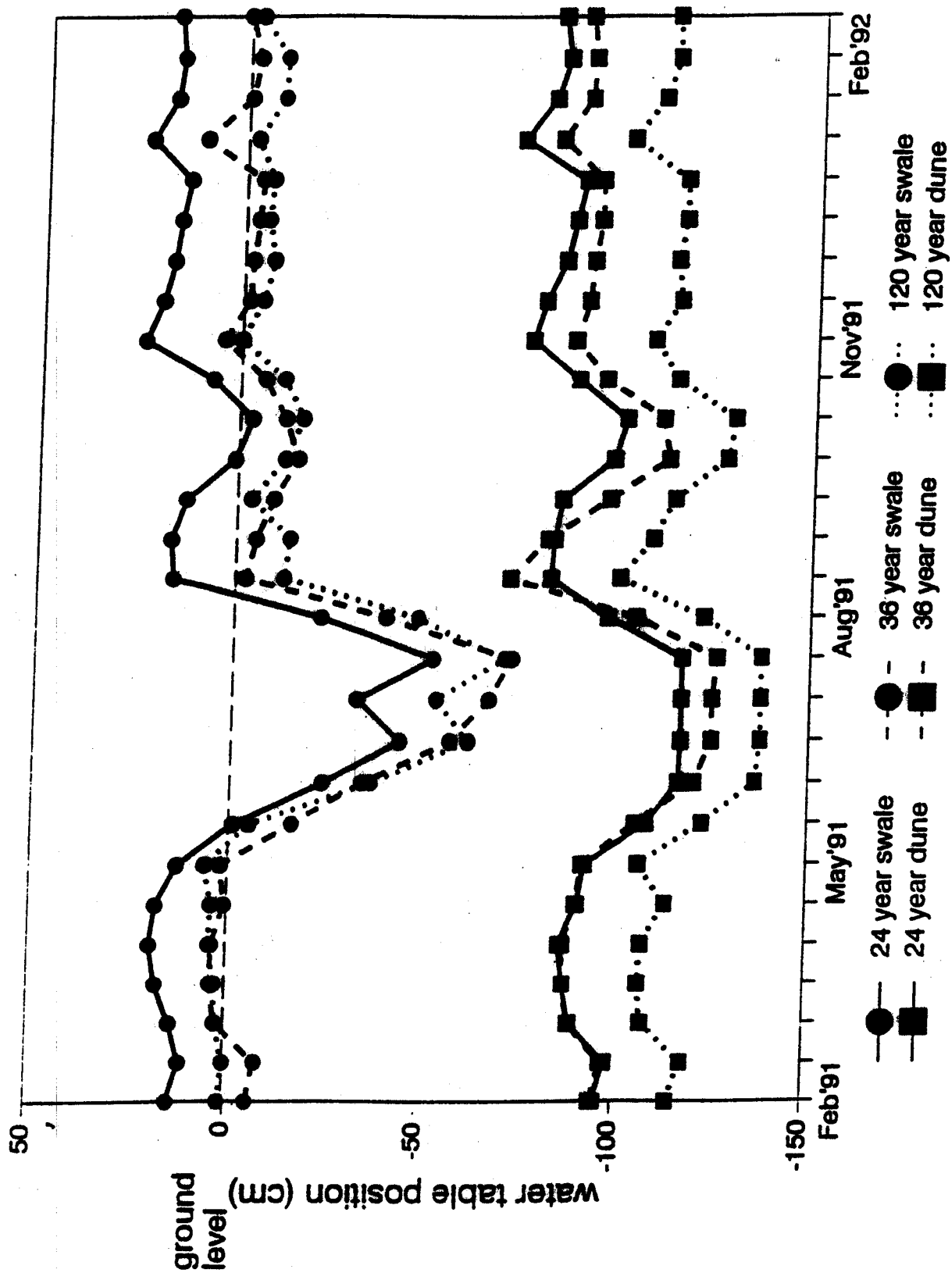


Figure 5. Annual means of organic matter (%) along the chronosequence of dunes and swales. The data represent annual means calculated for the period February 1991 - 92. Different lower case letters indicate significant differences between adjacent dunes and swales (Tukey, $P < .05$). Different upper case letters indicate significant differences among dunes or swales. Vertical bars are \pm one SE.

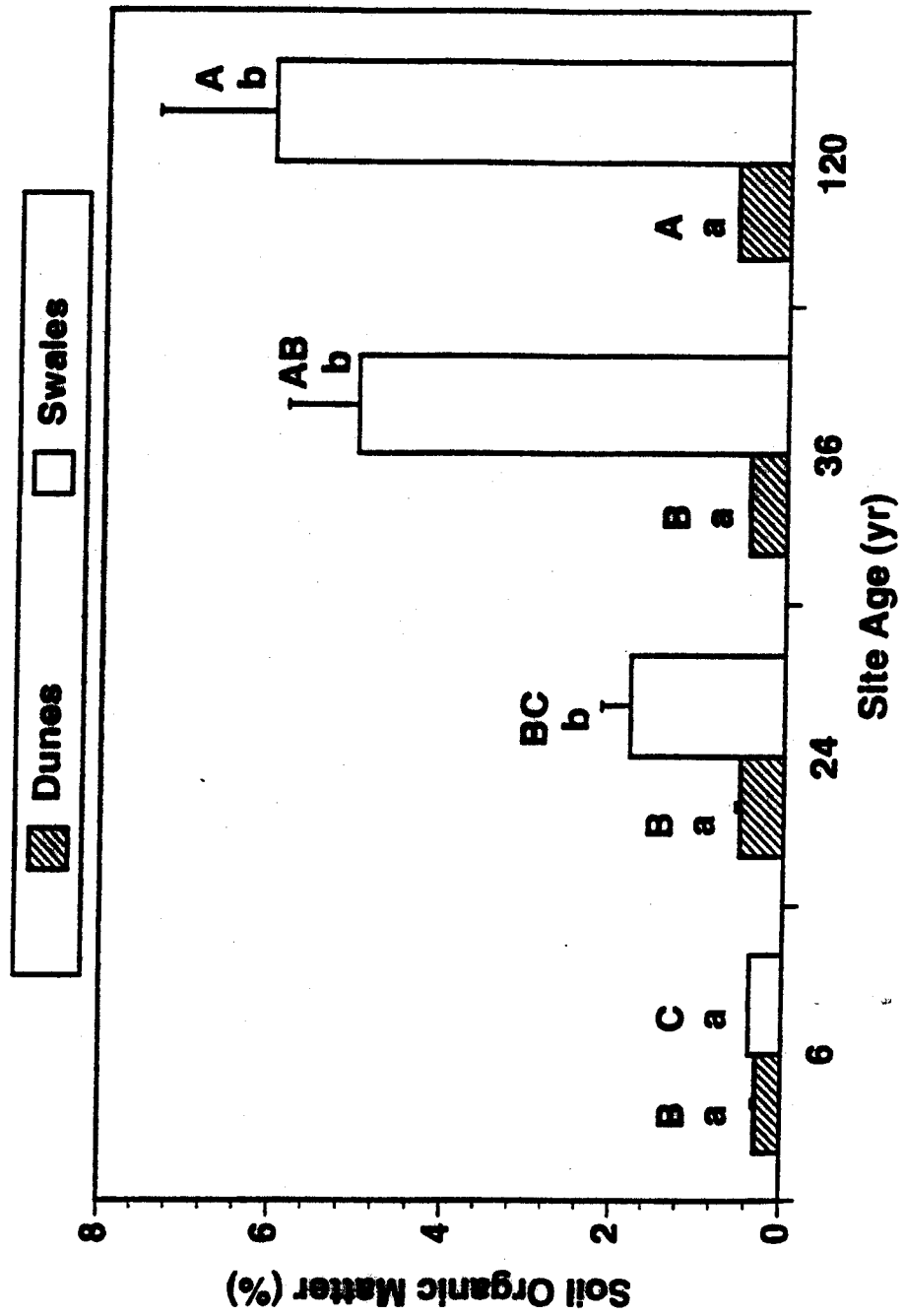


Figure 6. Annual means of ammonium and nitrite + nitrate in the soil profile along the chronosequence of dunes and swales. The data represent annual means calculated for the period February 1991 - 92. Different lower case letters indicate significant differences between adjacent dunes and swales (Tukey, $P < .05$). Different upper case letters indicate significant differences among dunes or swales. Vertical bars are \pm one SE.

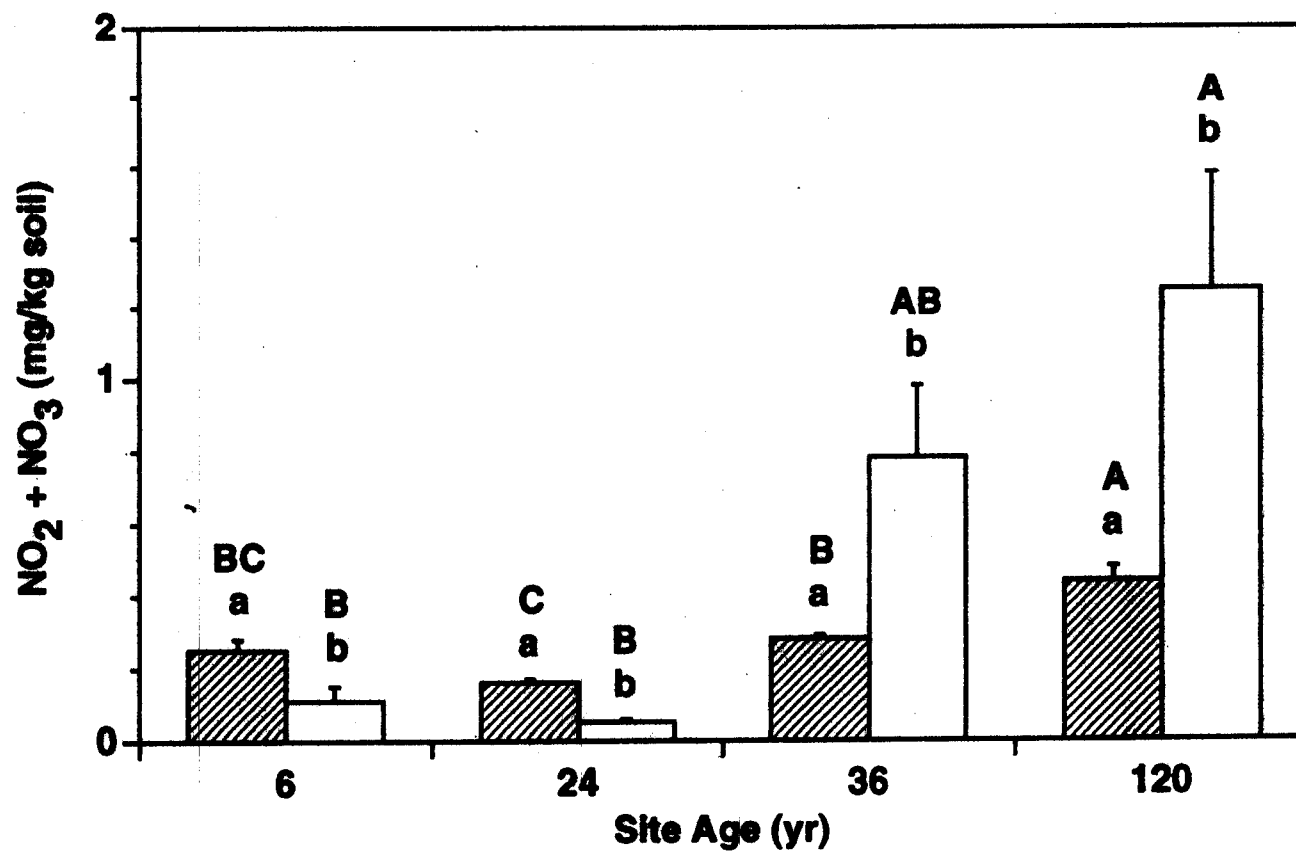
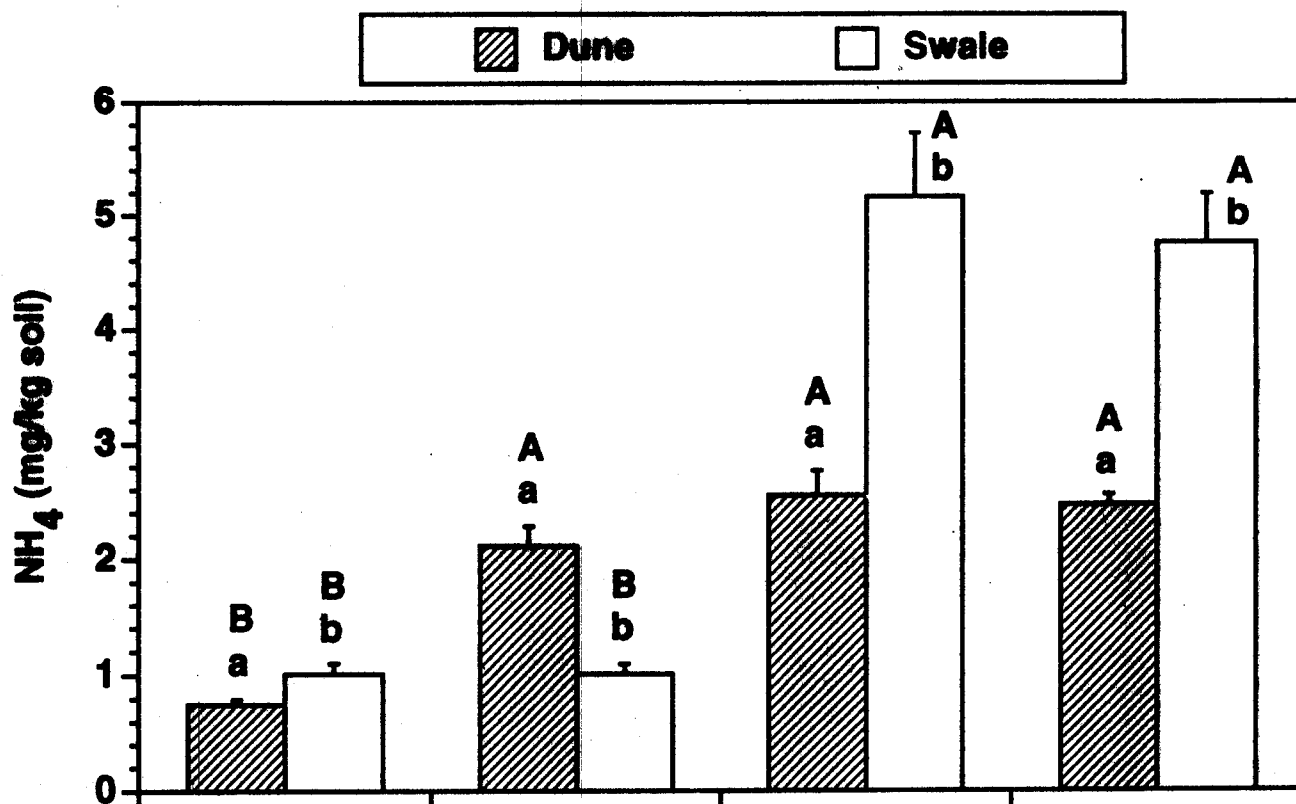


Table 1. Annual means of total biomass (live fine roots, dead fine roots and detrital material) and live fine root (≤ 2 mm diam.) biomass (g/m^2). Live fine roots and necromass (dead roots and detritus) shown as a percent of total annual mean biomass. Split-plot ANOVA determined significant differences between dune and swale sites ($P < .0001$). Different lower case letters indicate significant differences within site type (Tukey, $P < .05$). One standard error in parenthesis.

Site	Total biomass (g/m^2)	Live fine root		Percent of total biomass		Ratio
		biomass (g/m^2)	biomass (g/m^2)	Necromass	Live fine roots	
6 yr dune	95 (17) (b)	5 (2) (b)	5 (2) (b)	95	5	19:1
24 yr dune	229 (39) (a)	13 (3) (a)	13 (3) (a)	94	6	16:1
36 yr dune	116 (8) (b)	6 (1) (ab)	6 (1) (ab)	95	5	19:1
120 yr dune	64 (8) (b)	4 (1) (b)	4 (1) (b)	84	16	5:1
6 yr swale	59 (10) (c)	16 (4) (c)	16 (4) (c)	73	27	2.7:1
24 yr swale	744 (65) (b)	180 (27) (a)	180 (27) (a)	76	24	3:1
36 yr swale	929 (90) (b)	105 (10) (b)	105 (10) (b)	89	11	8:1
120 yr swale	1505 (176) (a)	122 (17) (ab)	122 (17) (ab)	92	8	11:1

Figure 7. Monthly means of total biomass (g/m^2) (live fine roots, dead fine roots and detrital material) along the chronosequence of barrier island dunes and swales. Total biomass represents all depths combined (0-40 cm). Fine roots are ≤ 2 mm diam.. Vertical bars are \pm one SE.

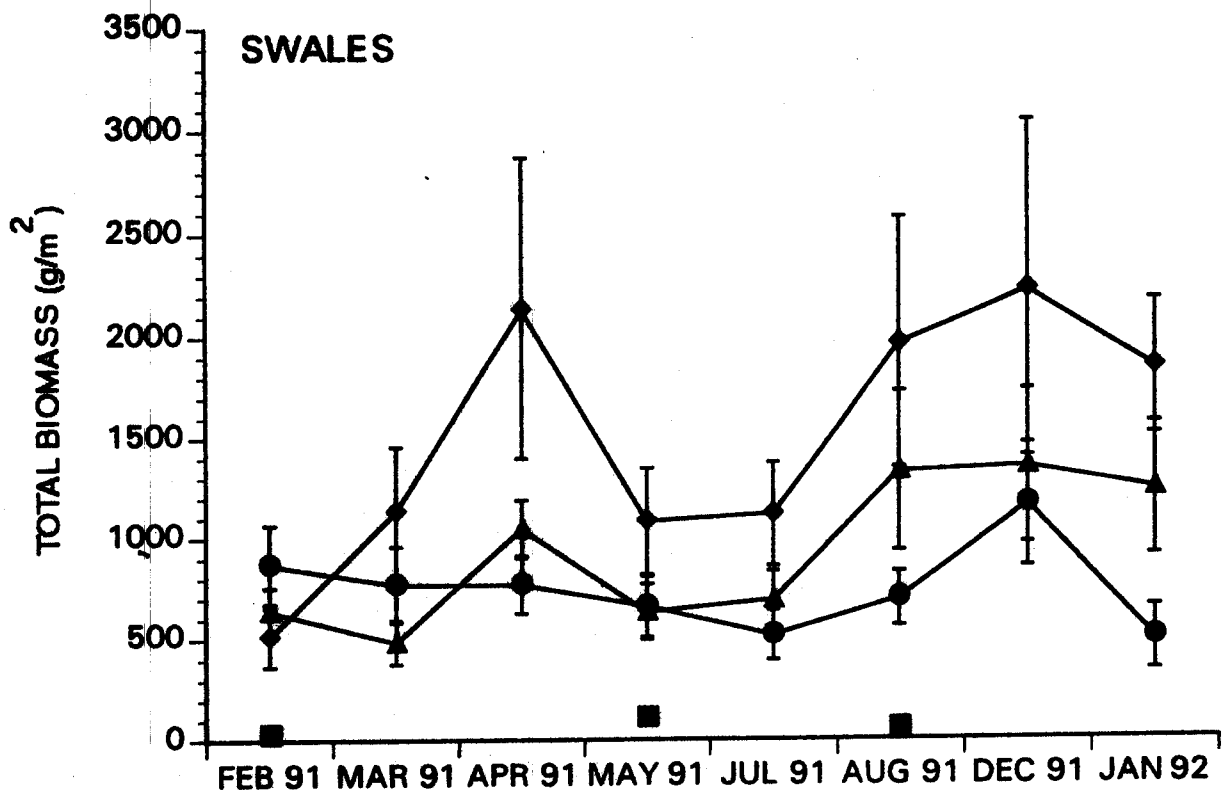
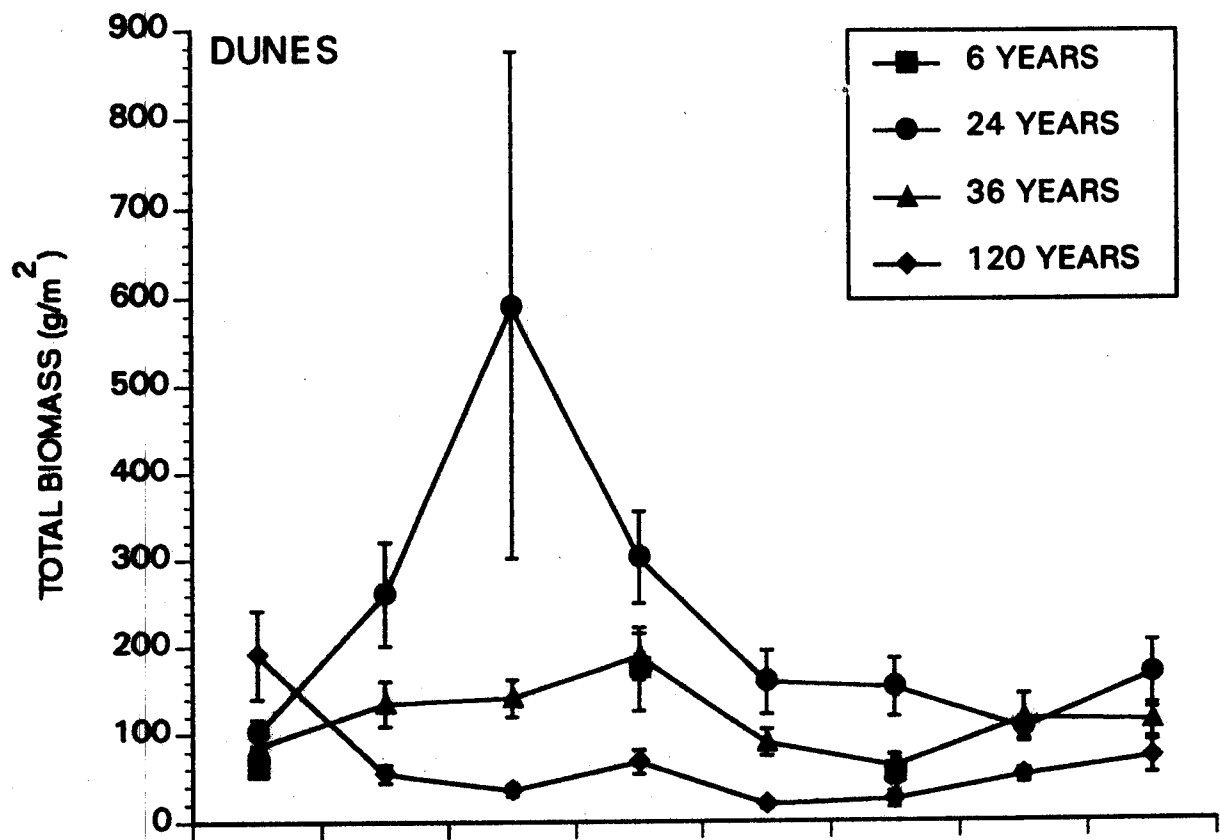


Figure 8. Monthly means of live fine root (≤ 2 mm diam.) biomass (g/m^2) along the chronosequence of dunes and swales. The live fine roots represent all depths combined (0-40 cm) for each sampling period. Vertical bars are \pm one SE.

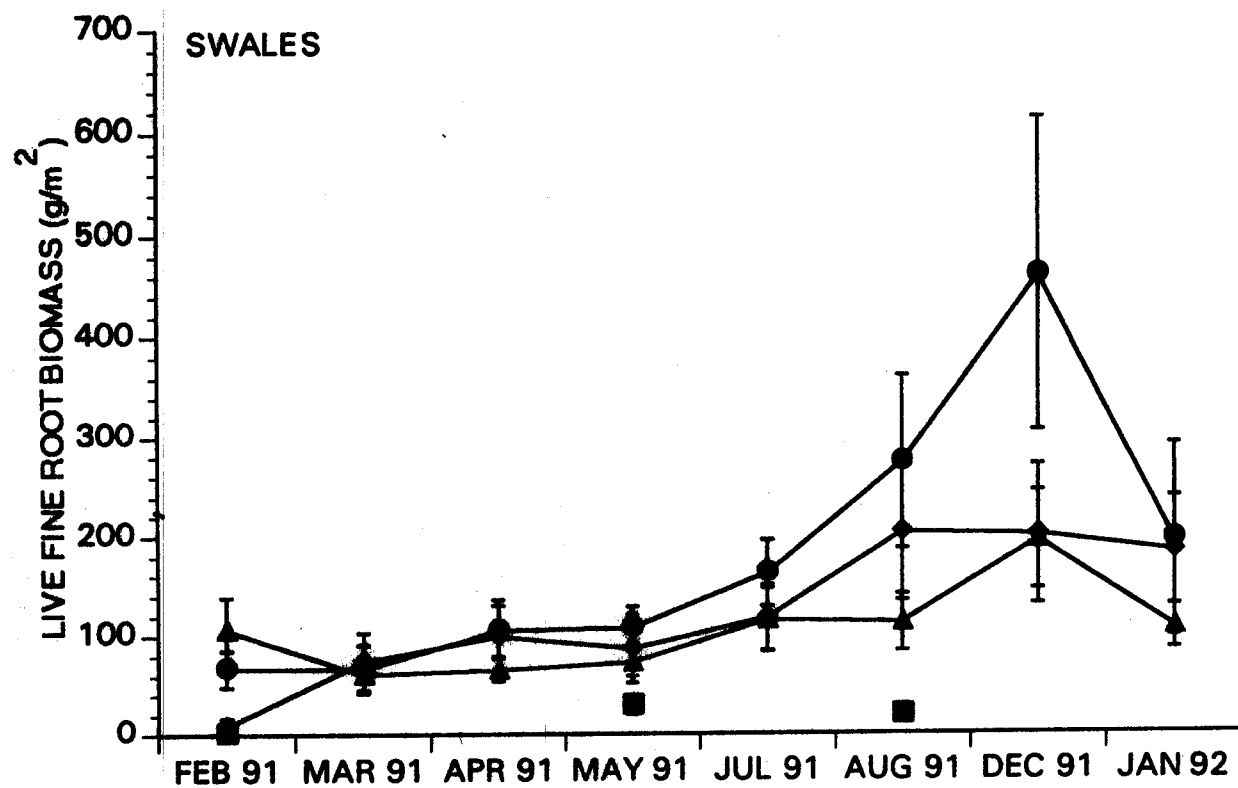
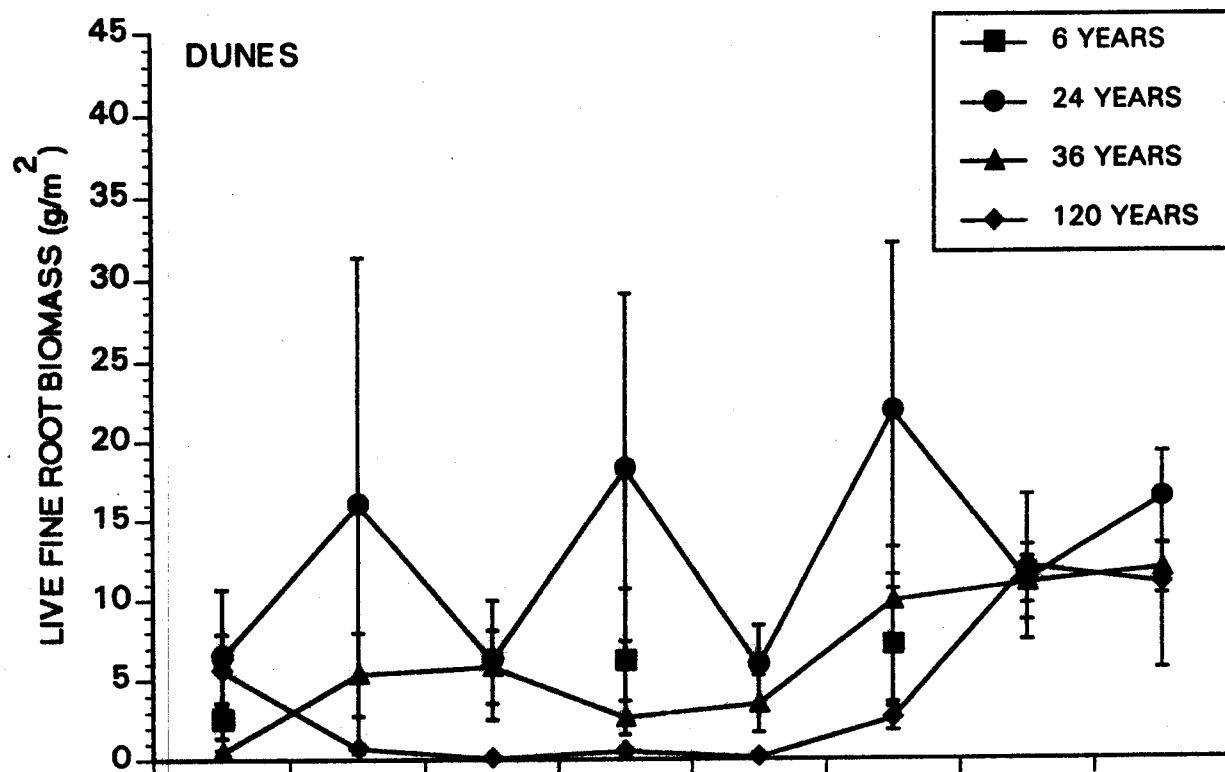


Table 2. Annual means of total biomass (live fine roots, dead fine roots and detrital material) and live fine root (≤ 2 mm diam.) biomass (g/m^2) by depth and site type. Slit-plot ANOVA determined significant differences between sitetypes ($P < .0001$). Different lower case letters indicate significant differences in biomass distribution (Tukey, $P < .05$).

Site	Depth in cm	Total biomass		Live fine root		Annual percent per depth	
		(g/m^2)	(g/m^2)	biomass, (g/m^2)	(g/m^2)	Total biomass	Live fine roots
Dune (b)	10	222.75 (a)		12.0 (a)		42.3	38.7
	20	153.15 (ab)		9.0 (b)		29.1	29.0
	30	94.03 (bc)		7.0 (b)		17.8	22.6
	40	56.77 (c)		3.0 (b)		10.8	9.7
Swale (a)	10	2820.6 (a)		342.41 (a)		74.4	70.0
	20	398.3 (b)		74.04 (b)		10.5	15.1
	30	293.2 (b)		38.64 (b)		7.7	7.9
	40	279.9 (b)		34.37 (b)		7.4	7.0

Swale Sites. --- Percentages of live fine root biomass of total biomass decreased with increases in swale age (Table 1). The 6 yr old swale had the highest percentage of LFRB (27%) and was similar to the 24 yr swale (24%) (Table 1).

Annual mean total biomass increased with increases in swale age. The 120 yr swale was significantly higher (Tukey, $P < .05$) in annual mean total biomass than all other swales (Fig. 9). The 6 yr old swale had significantly lower annual means (TB, 59 g/m^2 and LFRB, 16 g/m^2) in comparison to all other swales (Fig. 9). This result was predicted based on its early stage of successional development. The 24 yr and 36 yr swales were not significantly different from each other and this may be due to their closeness in age.

Monthly mean total biomass showed two general peaks during the study. The two peaks were not significant in all swale communities. The 120 yr swale produced two significant peaks (Fig. 7). Monthly mean total biomass (2230 g/m^2) was significantly higher (Tukey, $P < .05$) during December 1991 in contrast to February 1991, March 1991, May 1991 and July 1991. The second peak occurred during April 1991 (2137 g/m^2) and was only significantly different from February 1991 and May 1991 (Tukey, $P < .05$) (Fig. 7). The 120 yr swale was generally significantly different from all the other swales throughout the study. There were significant differences in TB distribution by depth (Split-plot ANOVA, $P < .0001$). Seventy-four percent of swale TB was concentrated in the upper 10 cm and was significantly different (Tukey, $P < .05$) from the 20-40 cm depths (Table 2).

Only one biomass peaks was observed for monthly mean live fine root biomass. Generally, LFRB increased in swales from February 1991 to a maximum in December 1991. There were no significant differences between months during March 1991-August 1991 (Fig. 8). In contrast to TB, the highest peak occurred in the 24 yr swale and not in the 120 yr swale. The 24 yr swale's LFRB during December 1991 was significantly different from LFRB during February 1991-July 1991 (Tukey, $P < .05$) (Fig. 8). The 36 yr and 120 yr swales were not significantly different from each other during the study. The 24 yr swale produced the largest amount of annual mean LFRB (180 g/m^2) and was significantly different (Tukey, $P < .05$) from the other swales (Fig. 8). There were

significant differences in LFRB distribution by depth (Split-plot ANOVA, $P < .0001$). Seventy percent of the LFRB was concentrated in the upper 10 cm. There was a significant difference (Tukey, $P < .05$) between the upper 10 cm and the lower 20-40 cm depths (Table 2).

Dune vs. Swale.--- The dune and swale communities were determined to be significantly different for both TB and LFRB (Split-plot ANOVA, $P \leq .0001$). Swales generally produced larger quantities of annual mean live fine root biomass and total biomass than the dune communities (Fig. 9). The only sites where this pattern did not hold true was between the youngest dune and swale communities. The six yr old dune had higher total biomass than the six yr old swale (95 g/m^2 vs. 64 g/m^2 respectively). The pattern did hold for annual mean live fine root biomass. The six year swale was higher in live fine root biomass, (16 g/m^2) than the six year dune (5 g/m^2).

Annual mean total biomass increased with increased swale age, but this pattern was not observed for the dunes. Both dunes and swales showed greatest annual mean LFRB in the 24 yr sites. The biomass distributions were similar for dunes and swales (Table 2). Both had higher TB and LFRB quantities in the upper 10 cm. Swale quantities for TB (2820.6 g/m^2) and LFRB (342.41 g/m^2) in the upper 10 cm were significantly higher (Split-plot ANOVA, $P < .0001$) than the dunes (TB = 222.75 g/m^2 , LFRB = 12 g/m^2). More TB was allocated to the upper 10 cm in swales (74%) than dunes (42%).

Fine Root Production Response to N-fertilization.--- N-fertilized plots were significantly higher (Split-plot ANOVA, $P < .0001$) in NPP than the control plots (Fig. 10). Fine root production rates were not significantly different among the control sites. N-fertilized plots showed a pattern of significantly decreased production rates with increased dune age (Tukey, $P < .05$). The fertilized 24 yr dune ($44 \text{ g m}^{-2} \text{ yr}^{-1}$) was not significantly different than the 36 yr dune ($40 \text{ g m}^{-2} \text{ yr}^{-1}$) but was significantly higher than the 120 yr old dune ($26 \text{ g m}^{-2} \text{ yr}^{-1}$) (Tukey, $P < .05$) (Fig. 10). There were no significant differences in production rates by depth for the control and fertilized sites.

Figure 9. Annual means of total biomass (live fine roots, dead fine roots and detrital material) and live fine root biomass (g/m^2) for each dune and swale site. The annual means represent all depths combined (0-40 cm) and all sampling periods combined. Fine roots are ≤ 2 mm diam.. Different lower case letters indicate significant differences among dunes or swales (Tukey's studentized range test, $P < .05$). Vertical bars are \pm one SE.

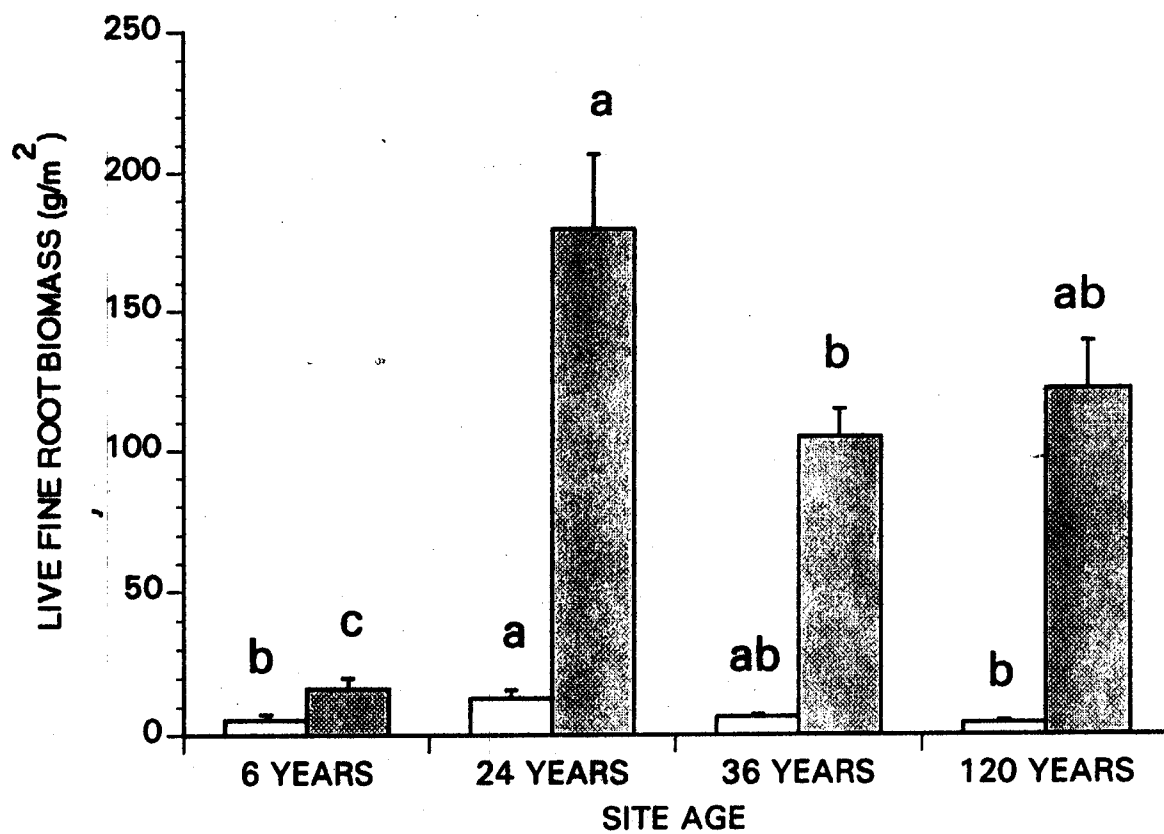
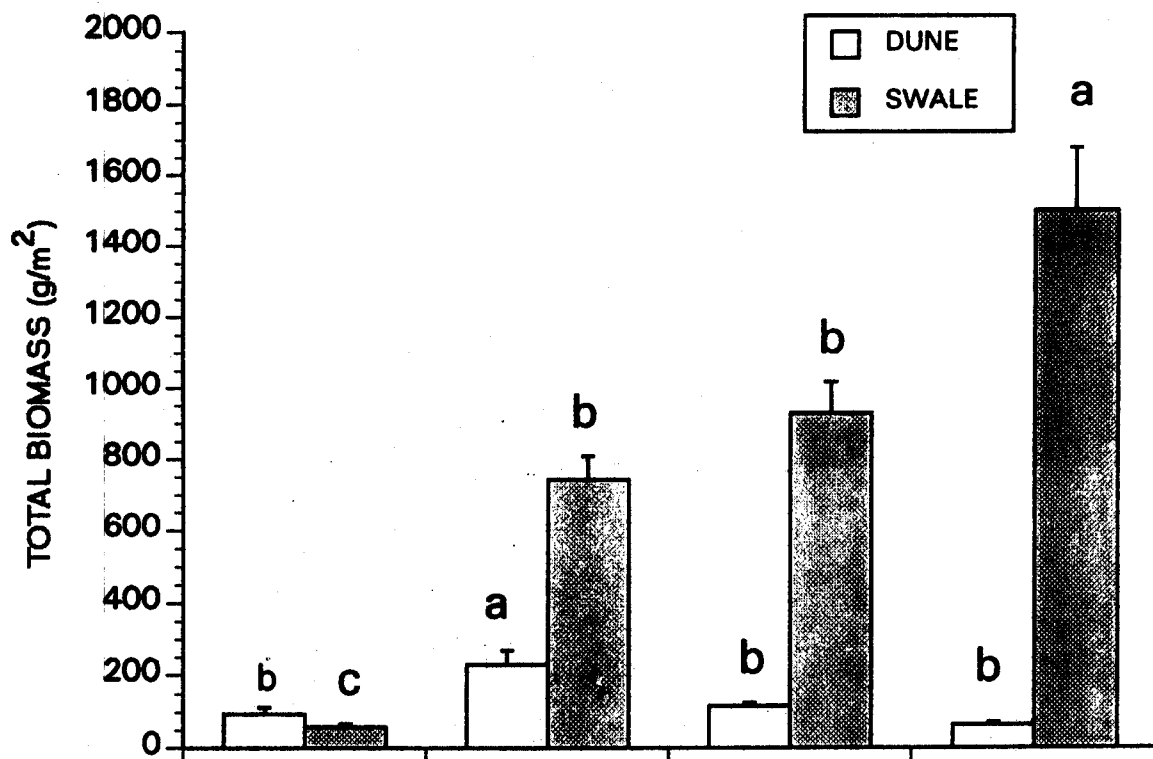


Figure 10. Annual mean production rates of live fine roots (≤ 2 mm diam.) ($\text{g m}^{-2} \text{ yr}^{-1}$) along the chronosequence of barrier island dunes. The annual means were produced over a 260 day period (February 1991-October 1991) and combine all depths. They were determined using an ingrowth production method. Different lower case letters indicate significant differences (Tukey, $P < .05$). Vertical bars are \pm one SE.

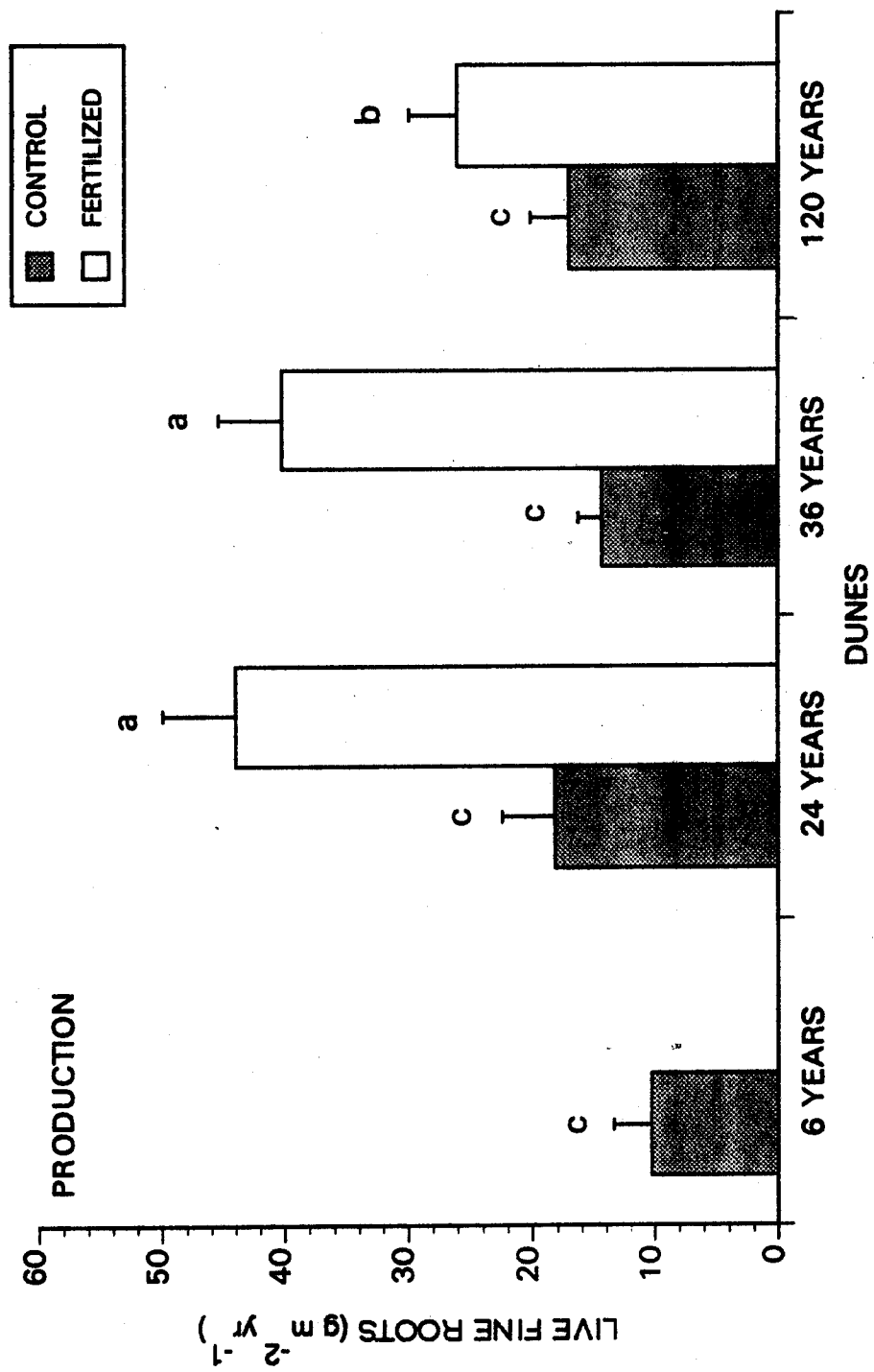


Figure 11. Total nitrogen (TKN) and total phosphorus (mg/100g) in live fine root tissue (≤ 2 mm diam.). The live fine root biomass used for the tissue analysis came from adjacent dune and swale sites along the barrier island chronosequence. The small sample size prevented adequate replicates to test for statistical differences. Vertical bars are \pm one SE.

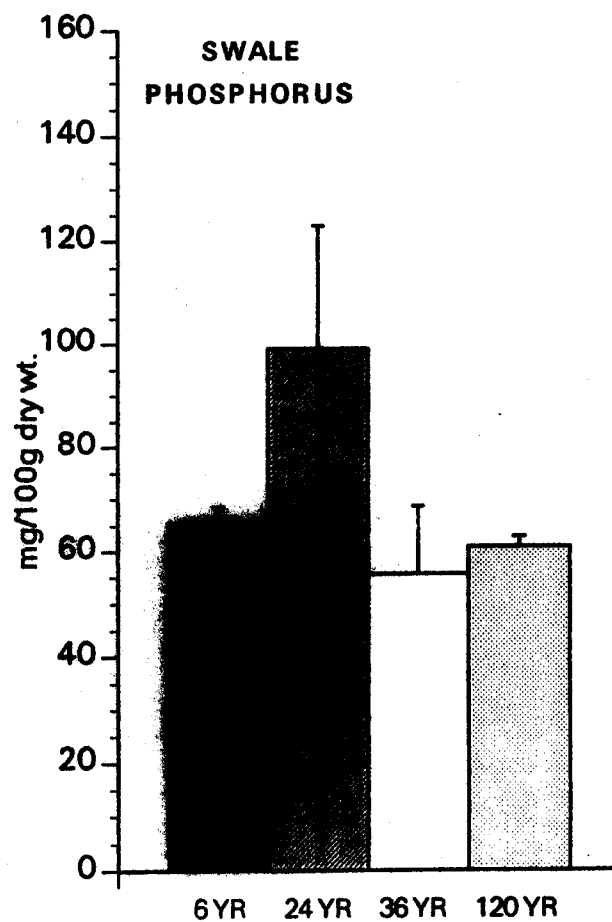
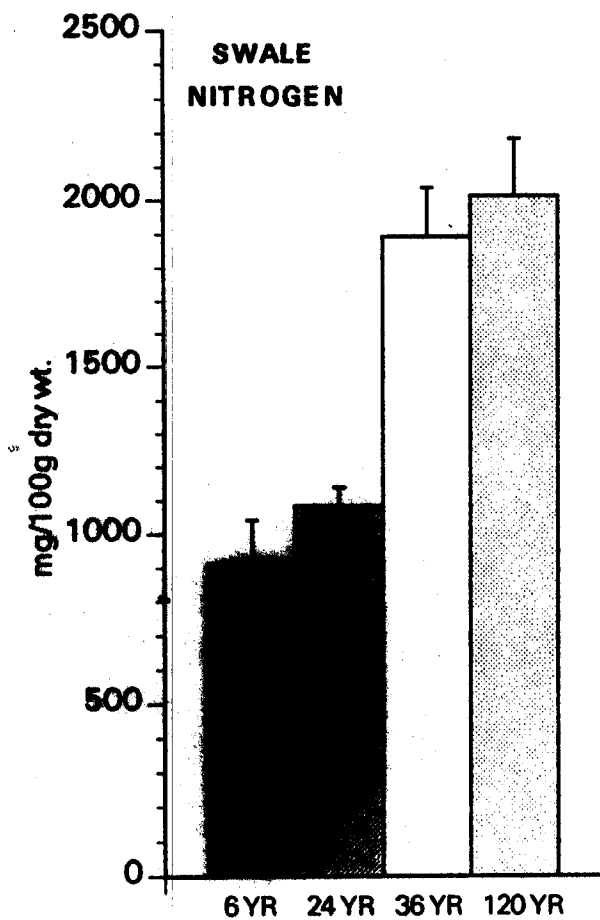
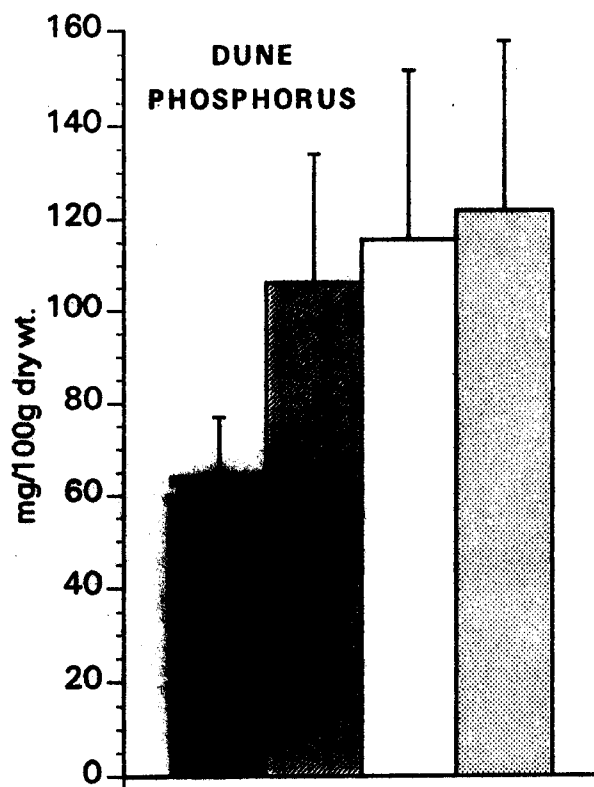
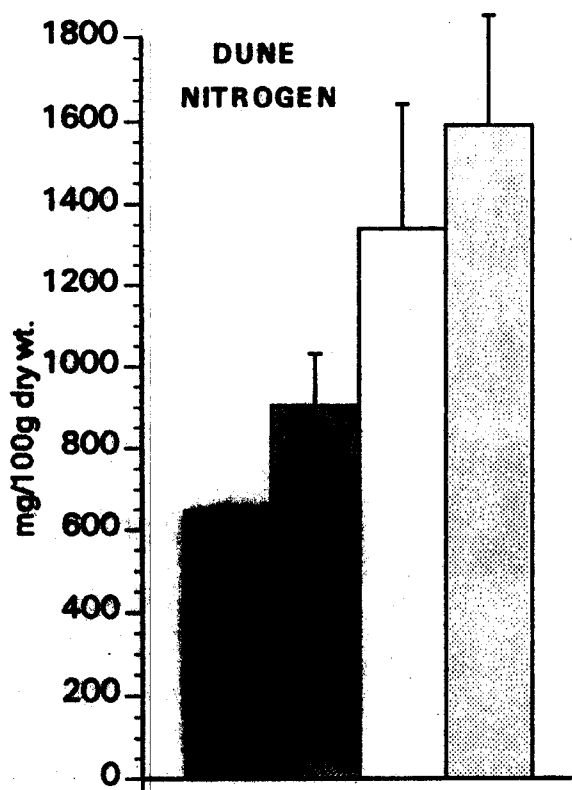
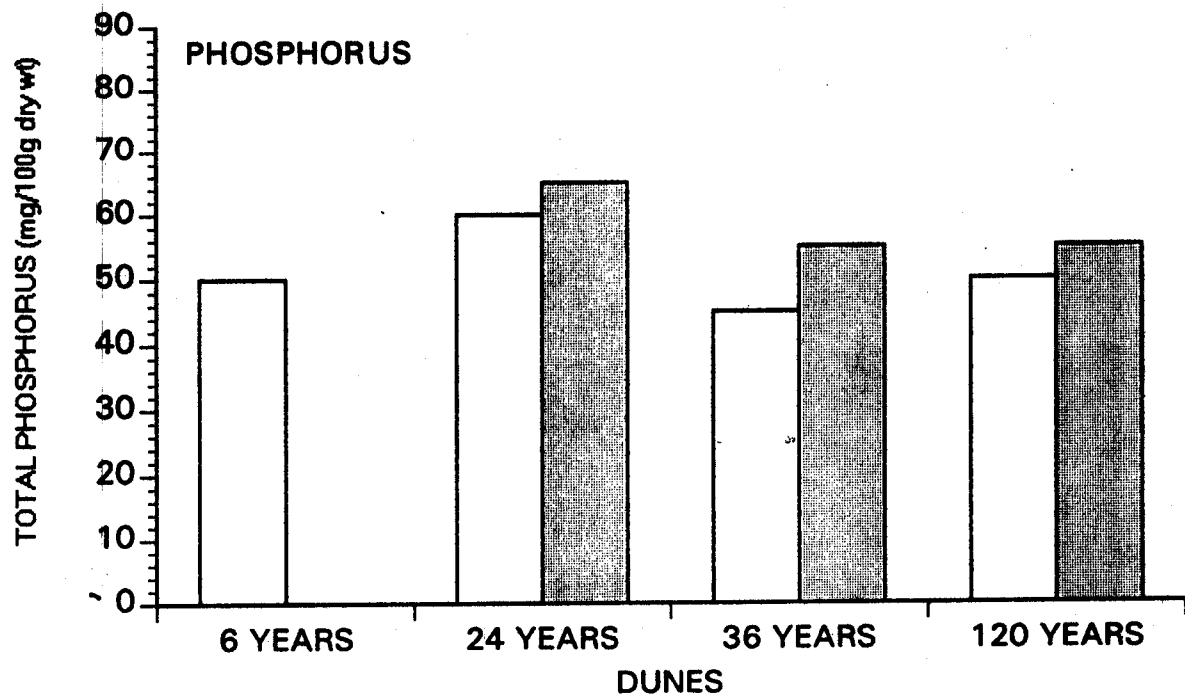
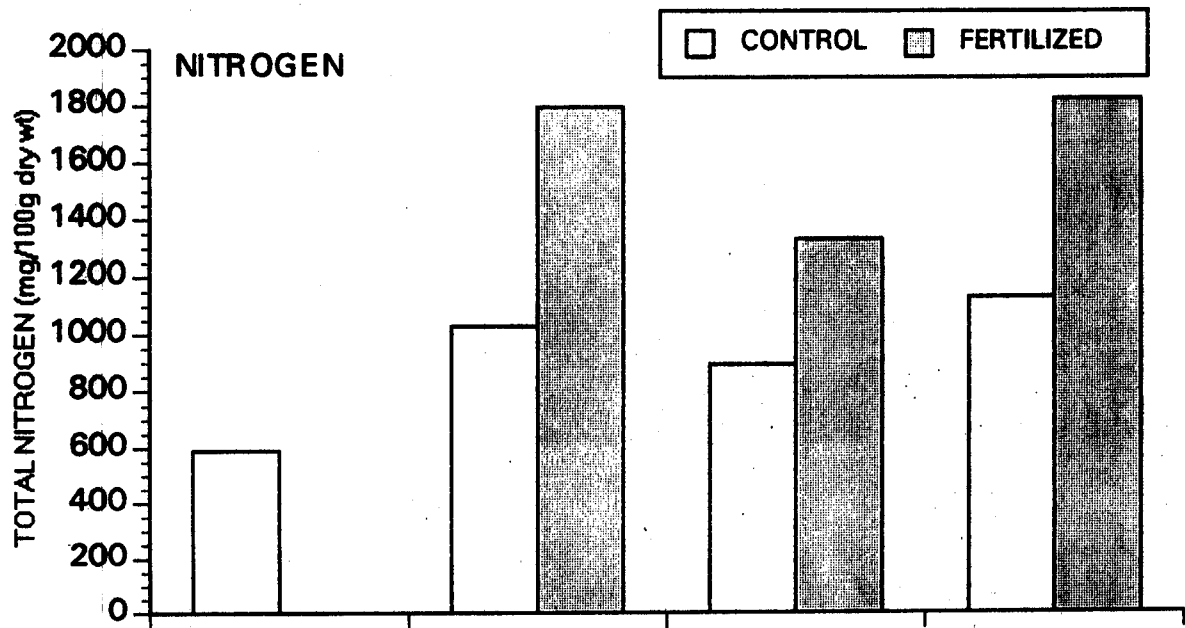


Figure 12. Total nitrogen and total phosphorus (mg/100g) in live fine root tissue (≤ 2 mm diam.). The roots were from the dune ingrowth production study . The small sample size prevented adequate replicates to test for statistical differences.



Live Fine Root Nutrient Concentrations.--- Mean total Kjeldahl nitrogen (TKN) in root tissues increased in concentration with increased age for dunes and swales. Root nitrogen was higher in the swales than the dunes. Nitrogen concentrations were relatively similar between the two younger (6 yr and 24 yr) dunes and between the two younger swales. Similar nitrogen content was found between the two older (36 and 120 yr) dunes and between the two older swales (Fig. 11). Phosphorus levels in roots increased significantly from the 6 yr dune to the 24 yr dune and showed a slight but nonsignificant increase from the 24 to 120 yr dune. Phosphorus levels in the swales were similar among sites except in the 24 yr swale (99 mg/ 100 g dry wt vs. 55-66 mg/100 g dry wt) (Fig. 11).

Similar root nutrient analyses were conducted for fine roots obtained during the production study. But these analyses represent one time period and not several as was the case in the biomass study. Nutrient patterns similar to those found in the LFR from the biomass study were obtained in LFR from the production study. Total phosphorus (TP) root content was similar between control and fertilized plots along the dune chronosequence. TP levels were dramatically lower than TKN levels.

Nitrogen root content was significantly higher in N-fertilized plots than control plots, as expected. The rise in nitrogen was expected due to the application of urea fertilizer. The control plots showed slightly increased root nitrogen content as site age increased, similar to the pattern observed in the LFRB of the biomass study. The lowest N levels were in the 6 yr dune (590 mg/100 g dry wt) and the highest levels in the 120 yr dune (1130 mg/100 g dry wt). The fertilized plots showed a different pattern. Root nitrogen content was similar between the 24 yr (1795 mg/100 g dry wt) and 120 yr (1825 mg/100 g dry wt) dunes while the 36 yr dune had a slightly lower root nitrogen content (1330 mg/100 g dry wt) (Fig. 12). Significant differences among treatments could not be tested due to small sample sizes.

DISCUSSION

Patterns across the chronosequence.---Barrier islands are very dynamic landscapes with many factors influencing their structure and function. Dune formations face exposure to higher wind conditions and moving sand, and poorer soil development than associated swale communities. The dunes are rebuilt during overwash events and sediments are carried over dunes onto lower lying protected areas where sediments settle out (Ehrenfeld,

1990; Hayden et al. 1991). Swales provide these low depressions along the chronosequence, collecting water and sediment, creating a moist soil environment and providing some protection against high winds. Environmental influences help determine the zonation and composition of plant communities (Ehrenfeld, 1990). Structural and functional differences associated with topographic position and successional age provides a base to help explain differences between community types. In the present study, site age, community type, N-availability and hydrology all played an interacting role in live fine root biomass and total biomass distribution as well as production rates.

Live fine root biomass (LFRB) showed a general decrease with increased age from the 24 yr to 120 yr dunes and swales. The availability of water in dune and swale communities was probably the major factor influencing the decrease of LFRB. Water table position relative to ground level decreased for dunes and swales with increased site age. In addition, water table in the dunes was lower than in swales identifying the dunes as xeric and the swales more mesic (Fig. 3 and 4). Higher water tables in the 24 yr dune and swale likely increased available soil water and generally produced a positive influence on LFRB. *Spartina patens* roots have been shown to alter their root morphology to survive anaerobic root conditions during short term flooding events (Burdick, 1989; Pezeshki et al., 1991). Two tallgrass prairie studies showed wet and dry conditions had a dramatic effect on root dynamics. Wetter soil produced more roots and total biomass while under dry conditions, less roots and total biomass were produced (Knapp and Seastedt, 1986; Hayes and Seastedt, 1987). In addition, soil water can limit nitrogen availability in the soil solution which can also influence root production (Kachi and Hirose, 1983; Nobel et al., 1989).

Soil nitrogen levels and root nitrogen concentrations increased with increased dune and swale age. These same patterns were observed in other studies involving chronosequences (Kachi and Hirose, 1983; Rose, 1988; Gleeson and Tilman 1990). Rose (1988) and Gleeson and Tilman (1990) identified larger concentrations of root nitrogen than soil nitrogen and the concentrations were higher in older communities than younger communities. In the present study similar patterns were observed. Nitrogen concentrations were higher in the roots than the soil (Fig. 6 and 10). The soils on Hog Island were identified as nitrogen limited (Hayden et al., 1991). Even though root nitrogen

and soil nitrogen increased across the dunes indicating higher nitrogen availability these patterns were not seen in LFRB suggesting some other factor is influencing production (like water availability). Swales were areas higher in available nitrogen and water, creating an environment more conducive to producing higher fine root and biomass quantities (Fig 6 and 9). Kachi and Hirose (1983) observed plant growth in sandy soils was affected by the nutrient status of the soil environment.

Depth Variations.--- Live fine root biomass and total biomass were concentrated in the upper 10 cm depth. The higher biomass concentration in the upper soil horizon did not differ between dunes and swales. But swales were observed to have higher concentration among all the depths in contrast to the dunes (Table 2). Other studies have indicated similar results; forested and marsh systems (Schubauer and Hopkins, 1984; Roman and Daiber, 1984; Ellison et al., 1986; swamp forest (Powell and Day 1991) tall grass prairies (Hayes and Seastedt, 1987) and barrier islands (Conn and Day, 1993). They observed higher concentrations of fine roots in the top 10 cm to 20 cm of the soil profile. Conn and Day (1993) examined biomass patterns on Hog Island and obtained results similar to the present study. They identified higher concentrations of fine roots in the upper 10 cm. Schubauer and Hopkins (1984) suggested that the live material is concentrated in the upper depths close to the surface because remineralization and nutrient supplies are greatest there.

This allocation pattern may be particularly important in nutrient poor ecosystems such as barrier islands. Higher fine root concentrations can help minimize water losses from the ecosystem and improve plant competitiveness for soil nitrogen (Nobel et al., 1989; Gleeson and Tilman, 1990). Nutrient poor ecosystems have concentrations of roots in the upper horizons where nutrient availability is greatest. This increases availability of nitrogen (Fisher et al., 1987; Vogt et al., 1993) which in turn provides nutrients required for increased plant growth (Lajtha and Schlesinger, 1988; Nobel et al., 1989).

Dune vs. Swale.--- Total biomass (TB) in the dunes remained relatively unchanged across the chronosequence. Swales showed an increase in TB with increased site age. Greater TB in the swales may be associated with the type of roots and soil environment. The roots in the dunes were generally short lived perennial rhizomatous roots growing in a xeric soil environment. The swales contained two general types of roots in a more mesic (saturated soil) environment. The roots in the younger (6 and 24 yr) swales were

composed of fine rhizomatous, *Spartina patens* perennial roots but the 36 and 120 yr swales contained more long lived, woody *Myrica cerifera* roots (Conn and Day, 1993). The woody roots take longer to decompose than the herbaceous roots (Conn and Day, unpublished).

In the present study total biomass (live fine roots, dead fine roots and detrital material) contained a larger percentage of necromass (dead fine roots and detritus) relative to live fine roots (Table 1). The greater buildup of necromass in swales can be explained by more saturated conditions which can inhibit decay if anaerobic conditions develop (Tucacz and Day, 1990; Powell and Day, 1991). During late fall through late winter swales had extremely high water table positions and anaerobic soils (Fig. 3 and 4). Wetter conditions reduced nitrogen availability by immobilization and denitrification (Fisher et al., 1987) as well as reduced oxygen available for microbial respiration may have contributed to lower decomposition rates (Koch et al., 1990; Tucacz and Day, 1990; Powell and Day, 1991). Decomposition rates were lower in the swales than in the dunes on Hog Island (Conn and Day, 1994, unpublished) explaining the greater accumulation of organic material in the soil profile of swale communities in contrast to dune communities (Fig. 9). The swales soils were higher in OM and provided an area for ion exchange and a larger surface area to retain nutrients in the soil (Cameron and Hayes, 1986; Haynes, 1986; Lajtha and Schlesinger, 1988; Brady, 1990). Swales contain more nitrogen and more water producing more LFRB through greater productivity and slower decay.

Seasonal patterns differed between the dune and swale communities in terms of total biomass and live fine root biomass quantities. Total biomass in the swale communities seemed to correspond to periods of higher water table. A double peak was observed for total biomass in the swale communities, one in spring and one in fall (Fig. 4 and 7). The dune communities seemed to show one spring peak (April 1991). Ellison et al. (1986) discovered, in a Rhode Island marsh, a belowground biomass peak in midsummer associated with a peak in aboveground biomass. Ellison et al. (1986) only obtained one peak but in other studies conducted in southern marshes another peak occurred in late fall after the winter dieback (Gallagher, 1983). Because of the shorter growing season in the higher latitudes a second peak may not occur (Gallagher, 1983). Ellison et al. (1986) indicated because of the shorter growing season root growth is compressed into a shorter

time period eliminating a second growth period. Monthly total biomass seemed to closely follow a moisture gradient. When the water table drops, total biomass (live fine roots, dead fine roots and detrital material) drops. In swales, a drop in water table still leaves soil moist but aerobic and these conditions could hasten decay, decreasing total biomass. A similar pattern has been observed in numerous other belowground studies, showing decreased water availability, root growth and dry wt. contributed to decreasing TB. (Dahlman and Kucera, 1965; Knapp and Seastedt, 1986; Hayes and Seastedt, 1987; Nobel et al., 1989)

Monthly LFRB increased for dune and swale communities during the study and peaked during the early winter months. In southeastern Minnesota, Wilson and Tilman (1993) demonstrated a similar pattern where biomass of perennials increased well after the onset of regular frosts. The 24 yr dune and swale generally produced the highest monthly mean LFRB throughout most of the growing season. Because live fine roots were more abundant on the 24 yr old dune and swale than the other sites, there may be a common element between them such as higher water tables. Live fine root biomass seemed to increase more at the end of summer, (July 1991) for the dunes and swales which had higher water tables. Water availability has been shown to dramatically influence root biomass alone or in combination with nitrogen (Fisher et al., 1987).

Live fine root quantities were lower in the dunes than the swales due to possibly limited available nutrients and low soil moisture. Sandy soils are typically nutrient poor due to rapid percolation and low soil OM that contribute to higher rates of potential leaching and increased losses of nutrients and water (Kachi and Hirose, 1983).

Effects of fertilization.--- Nitrogen additions in the form of urea fertilizer significantly increased production rates on all dunes (Tukey, $P < .05$). These results were expected and have been observed in other studies involving roots in dunes (Kachi and Hirose, 1983), forests (Aber et al., 1985; Nadelhoffer et al., 1985) alpine tundra (Bowman et al., 1993) and old fields (Wilson and Tilman, 1993). Higher productivity rates were observed in the upper depths for both control and fertilized sites across the chronosequence. Dahlman and Kucera (1965) observed the same pattern of lower productivity rates with increased depth in native prairies. The younger fertilized dunes, (24 yr and 36 yr) had significantly higher production rates than the 120 yr dune (Tukey, $P < .05$) (Fig. 11). The production rates in

the fertilized sites for the 24 yr and 36 yr dunes were 2.5 times those observed in their control sites in contrast to 1.5 times for the 120 yr dune. Nitrogen availability and nitrogen allocation interacting with water availability may explain the different rates.

Nutrient availability associated with community structure may explain why production responses in the younger sites were greater than older sites. The younger sites were more limited in nitrogen than the older sites so they would have a greater response to nitrogen additions. Greater nitrogen availability in the 120 yr dunes may be influenced by Myrica cerifera thicket encroachment. Myrica cerifera has nitrogen fixing nodules on its root system and through its nitrogen fixing ability may have contributed additional amounts of nitrogen to the soil environment through nitrogen rich litterfall (Conn and Day 1993). The nitrogen levels in the soil on the 120 yr dune may have reached concentrations where additional nitrogen was no longer allocated for increased root growth. Workers have shown increases in nitrogen levels can decrease the root: shoot ratio and allocate nutrients to other areas where supplies were lower (Lajtha and Klein, 1988; Nobel et al., 1989).

CONCLUSION

The present study evaluated biomass and production at a landscape level by focusing on responses of dunes and swales along a barrier island chronosequence. The study sought to identify functional responses by community type and determine if any differences were associated with site age. Nutrient availability and soil water were the two major factors influencing belowground processes. These factors were limiting on the barrier island and they seemed to help define why these communities were different in total biomass and live fine root biomass quantities.

Studies have examined the role of fine root biomass and total biomass as well as root production rates along chronosequences in forest, prairie, dune and desert ecosystems. However, few have identified the interactions taking place in dune and swale communities along a barrier island chronosequence. Fine roots play an important role in community development on barrier islands. Fine roots can influence nutrient losses from the soil environment along with regulating water loss based on their distribution in the upper depths and their concentration at those depths (Nobel et al., 1989; Gleeson and Tilman, 1990). Other studies have shown fine roots can be a large contributor to soil organic matter and

nitrogen through their decomposition (McClagherty et al., 1982; Seastedt, 1988). Fine roots are a critical component to understand in the physically dynamic barrier island systems.

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Appendix 1. Monthly mean total biomass (live fine roots, dead fine roots and detrital material) in (g/m^2) along the chronosequence of barrier island dune sites. Different lower case letters indicate significant differences (Tukey, $P < .05$). One standard error in parenthesis.

Sampling period	6 yr dune		24 yr dune		36 yr dune		120 yr dune	
	(b)		(a)		(b)		(b)	
February (ab)	60 (9)		101 (16)		86 (14)		191 (51)	
March (ab)			260 (60)		135 (26)		54 (10)	
April (a)			589 (287)		141 (21)		35 (6)	
May (ab)	174 (48)		302 (52)		189 (26)		67 (14)	
July (b)			158 (37)		89 (16)		18 (4)	
August (b)	52 (11)		152 (33)		61 (14)		23 (8)	
December (b)			104 (13)		116 (28)		50 (8)	
January (ab)			166 (38)		113 (20)		70 (19)	

Appendix 2. Monthly mean total biomass (live fine roots, dead fine roots and detrital material) in (g/m^2) along the chronosequence of barrier island swale sites. Different lower case letters indicate significant differences (Tukey, $P < .05$). One standard error in parenthesis.

Sampling period	6 yr swale (c)	24 yr swale (b)	36 yr swale (b)	120 yr swale (a)
February (d)	24 (8)	871 (196)	640 (117)	512 (147)
March (bcd)		771 (190)	484 (109)	1135 (324)
April (ab)		770 (143)	1048 (143)	2137 (736)
May (cd)	104 (25)	660 (151)	634 (139)	1085 (264)
July (bcd)		515 (123)	694 (142)	1119 (259)
August (abcd)	48 (12)	698 (136)	1333 (399)	1968 (614)
December (a)		1165 (307)	1357 (385)	2230 (819)
January (abc)		498 (159)	1244 (330)	1851 (333)

Appendix 3. Monthly means of live fine root (≤ 2 mm) biomass (g/m^2) along the chronosequence of barrier island dune sites. Different lower case letters indicate significant differences (Tukey, $P < .05$). One standard error in parenthesis.

Sampling period	6 yr dune (b)	24 yr dune (a)	36 yr dune (ab)	120 yr dune (b)
February	3 (1)	6 (4)	1 (.1)	6 (2)
March		16 (15)	5 (3)	1 (.3)
April		6 (4)	6 (2)	1 (.04)
May	6 (5)	18 (11)	3 (1)	1 (.3)
July		6 (3)	3 (2)	1 (.07)
August	7 (4)	22 (10)	10 (3)	3 (1)
December		11 (1)	11 (2)	12 (5)
Jananuary		16 (3)	12 (2)	11 (5)

Appendix 4. Monthly means of live fine root (≤ 2 mm) biomass (g/m^2) along the chronosequence of barrier island swale sites. Different lower case letters indicate significant differences (Tukey, $P < .05$). One standard error in parenthesis.

Sampling period	6 yr swale (c)	24 yr swale (a)	36 yr swale (b)	120 yr swale (ab)
February (c)	1 (.5)	67 (19)	107 (32)	9 (8)
March (bc)		67 (25)	61 (18)	74 (29)
April (bc)		105 (26)	66 (12)	100 (36)
May (bc)	29 (9)	108 (22)	73 (14)	87 (34)
July (bc)		163 (34)	116 (32)	118 (33)
August (bc)	18 (5)	275 (87)	113 (29)	204 (69)
December (a)		461 (154)	196 (50)	201 (71)
January (b)		196 (97)	108 (21)	184 (55)