Fine-root Biomass Distribution and Production Along a Barrier Island Chronosequence

MARK J. STEVENSON AND FRANK P. DAY

Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23529

ABSTRACT.—Fine roots are important 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. A sequential coring method was used to determine live fine-root biomass along a barrier island dune and swale chronosequence on the Virginia Coast Reserve–Long Term Ecological Research Site. Fine-root production and the effects of nitrogen fertilization were also examined using an in-growth core method along the chronosequence. Variation in biomass was associated with topographic position and the interaction with nitrogen and water availability along the chronosequence. The swales had significantly larger accumulations (16 to 180 g/m²) of live fine-root biomass (LFRB) than the dunes (4 to 13 g/m²). Higher LFRB was probably due to higher nitrogen levels and moister conditions in the swales. LFRB changed very little across the dune chronosequence but LFRB in the swales generally decreased from the 6-yr to the 120-yr site. However, the 6-yr swale had significantly lower biomass than the other swales. LFRB was concentrated in the upper 10-20 cm of soil in dune and swale sites across the chronosequence, with swales having proportionally more (70%) in the upper 10 cm of soil than dunes (29%). Root nitrogen concentration in LFRB was higher in the older dunes and swales. Root phosphorus concentrations increased from the 6-yr to the 120-yr dune 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 reference sites. Nitrogen fertilization also increased nitrogen concentrations in live fine roots.

INTRODUCTION

Belowground biomass and fine-root production represent a large proportion of total biomass and production in most ecosystems (Nadelhoffer and Raich, 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 analysis of functional relationships of an ecosystem.

There are 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). Production is perhaps the most difficult belowground process to study (Santantonio and Grace, 1987). The deficiencies of 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 (FRB) along a chronosequence of barrier island dunes and swales. Fine-root production was measured using an in-growth 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 Hopkinson, 1984; Howes *et al.*, 1985; Ellison *et al.*, 1986; Symbula and Day, 1988; Bertness, 1991; 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).

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 almost constantly changing in form and location due to storm activity and sea level rise. As a result, ecosystem structure and function are very dynamic. 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 primary objectives of this study were (1) to quantify 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 total nitrogen and total phosphorus content of fine roots across the chronosequence, and (4) to compare the response of fine root production to N-fertilization along the chronosequence.

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. 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 (Dueser *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 E near the ocean progressing to the older dunes and swales towards the W. 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) (Dueser *et al.*, 1976; Hayden *et al.*, 1991).

The soils on Hog Island consist of Entisols in the Newhan and Corolla series. The Newhan soils are mixed thermic Typic Udipsamments located from the lagoon to the ocean and are described as nearly level to sloping, excessively drained, sandy soils found on frontal or interior dunes. The Corolla soils are mixed thermic Aquic Udipsamments located in the swales, nearly level or gently sloping, and poorly or moderately well-drained with a seasonally high water table (Dueser *et al.*, 1976).

The island increases in age moving westward from the ocean to the lagoon. The study involved eight sites across the island. There were four dune and adjacent swales sites, 6, 24, 36 and 120 yr old. Dunes were dated from historical records consisting of aerial photo-

graphs, disturbance events such as fire and storms, and geologic markers associated with these disturbances (B. Hayden, pers. comm., Hayden *et al.*, 1991).

The dune communities were codominated by *Spartina patens* (Aiton) Muhl. and *Ammophila breviligulata* Fernald, both rhizomatous perennial grasses. Other dune species included *Panicum amarum* Ell., *Aristida tuberculosa* Nuttall and *Rumex acetosella* L. The younger (6- and 24-yr-old) swale communities were dominated by *S. patens*. The older 36- and 120-yr swales were dominated by woody thickets of *Myrica cerifera* L. (Hayden *et al.*, 1991; Conn and Day, 1993; Fahrig *et al.*, 1993). Vegetation in the swales was relatively homogeneous with high cover, whereas vegetation on the dunes was more sparse and patchy.

METHODS

Sequential core procedures.—The sequential core method was used to obtain soil samples for LFRB extractions. Ten soil cores were collected in a stratified random fashion each month (February 1991 to February 1992) from each of the dune and swale sites, except for the 6-yr-old dune and the swale communities which were sampled only four times during the study (February, May, August and November). The random samples were taken in a stratified manner from more homogeneous sections of the dune to minimize variability (*i.e.*, blowouts and other unusual features were avoided). A plunger style corer (7 cm diam by 10 cm length) was used to extract the soil cores. The soil cores were extracted in 10-cm increments down to a depth of 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 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 and rhizomes ($\leq$2 mm diam), big roots and rhizomes (>2 mm diam), dead fine roots and rhizomes and detritus (unrecognizable organic matter). 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 had 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 and internally.

After sorting, the roots were dried at 70 C for 48 h and weighed. If the fine roots (live or dead) were numerous and hard to separate from other organics in the sample, aliquots were used to break down 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 reference and N-fertilized areas. Fertilized areas were located relative to reference areas so surface run-off or ground water transport would not introduce N-fertilizer into reference areas. The 6-yr-old dune site was not used in the fertilization experiment because of spatial limitations. N fertilizer was in the form of urea as a mix of coated (70%) and uncoated (30%) granules. The fertilizer was applied every 3 mo for a total application of 60 g·N m^{-2} yr^{-1}.

Fine-root production was determined along the chronosequence of dunes in the reference and fertilized sites by an in-growth core method (Persson, 1983). Soil was extracted in February 1991 from 20, 40-cm-deep cores chosen at random from a 10 $\times$ 15 m grid with 1 m between rows at each reference and fertilized site using the corer described above. Ten cores were extracted from the 6-yr reference 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 260 days) at 10-cm increments down to a 40-cm depth using the flags as center points for coring. The extracted in-growth cores were processed in the same manner as described above. In-growth was taken as an estimate of production. It should be noted that some of the in-growth may have been the result of a wound response; thus the production values may represent overestimates.

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 (Technicon Industrial Systems, 1977). 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 (Technicon Industrial Systems, 1977). Nutrient analyses were also conducted on live fine roots obtained from the in-growth cores lumped by treatment across all depths. Note that these roots were all young roots and did not represent the normal range of mixed-aged roots.

Microenvironmental measurements.—Hydroperiod was continuously monitored by wells equipped with Stevens' model 68 Type F water level recorders. 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.

Soil cores were extracted from each dune and swale site and analyzed for NH_4 and NO_2 + NO_3 (Day, 1995). Ten-gram soil samples were extracted in 100 ml of 2 mol/liter KCl and analyzed colorimetrically on a Scientific Instruments autoanalyzer. Net nitrogen mineralization rates were quantified by soil incubations (Day, 1995). Net mineralization was calculated by subtracting mean mineral N content of nonincubated soil from mean mineral N content of soil incubated over monthly periods. Annual rates were calculated by summing incubations over a year.

Statistical analyses.—Tests for significant variation in mean LFRB among dune and swale sites were conducted using a split plot ANOVA. Site and community type (dune or swale) were main factors and depth was the split-plot factor (SAS Institute, 1985). Differences among means were analyzed using the Tukey studentized range test (alpha = 0.05). Dune age was not replicated in this study so only specific site differences can be tested. Effects of site age should only be inferred cautiously.

<center>RESULTS</center>

Microenvironmental measurements.—Annual mean soil redox potential (Eh), which measures the degree of reduction in soils, was correlated with topographic position (Table 1). The lowest readings (more reduced soils) were measured in the swales and the highest (less reduced or more oxidized soils) occurred in the dunes. The lowest annual mean for soil redox (−22 mv) was in the 24-yr swale.

Water table was lower in dunes than swales (Fig. 1). 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). Water table dropped in all sites starting in the 2nd wk in May 1991 and continued to drop till the 2nd wk 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.

TABLE 1.—Annual mean soil redox potential (mV). Different letters indicate significant differences among sites (Tukey, $P < 0.05$). One standard error in parentheses

Site	N	Eh
Dune, 6-yr	19	449 (8) b
Dune, 24-yr	76	488 (5) b
Dune, 36-yr	76	529 (5) a
Dune, 120-yr	76	541 (5) a
Swale, 6-yr	19	104 (17) d
Swale, 24-yr	38	−22 (9) e
Swale, 36-yr	38	136 (14) d
Swale, 120-yr	38	213 (16) c

Soil ammonium was significantly lower (Tukey, $P < 0.05$) in the 6-yr-old dune in comparison to all the other dunes (Table 2). The 24-, 36- and 120-yr dunes were not significantly different from one another. Soil ammonium in swales increased from the 6-yr to 120-yr site. The two younger swales had significantly lower percentages of soil ammonium (Tukey, $P < 0.05$) than the 36-yr and 120-yr swales. Nitrite + nitrate exhibited a strong pattern across the chronosequence (Table 2). The dunes and swales were significantly different from one
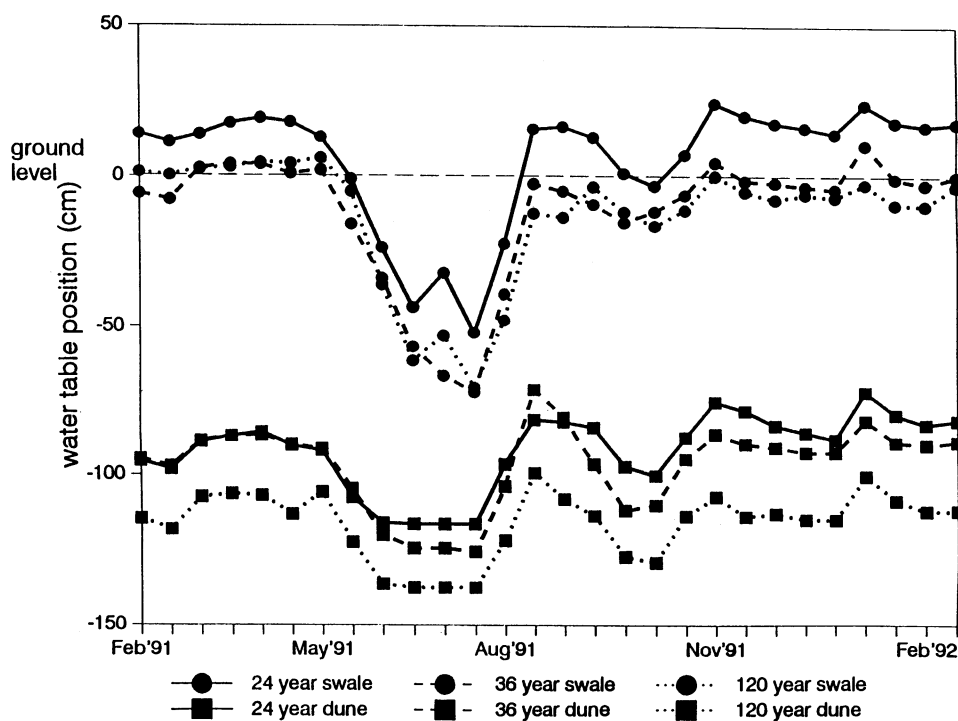

FIG. 1.—Monthly means of water table based on continuous well recordings. The wells were located along the chronosequence of dunes and swales. The data represent monthly annual means computed for the period February 1991–1992

TABLE 2.—Annual means of extractable nitrogen in the soil (mg/kg soil) and annual net nitrogen mineralization rates (g m^{-2} yr^{-1}). Different lower case letters indicate significant differences among dunes (reference sites) or swales (Tukey, P < 0.05). Different upper case letters indicate significant differences among fertilized sites on dunes (P < 0.05). One standard error in parentheses

Site		NH$_4$	NO$_2$ + NO$_3$	Annual net N-mineralization
Dune, 6-yr		0.75 (0.04) b	0.25 (0.03) bc	0.02
Dune, 24-yr	Reference	2.11 (0.17) a	0.16 (0.01) c	0.20
	Fertilized	18.98 (1.93) B	1.39 (0.15) B	1.45
Dune, 36-yr	Reference	2.54 (0.22) a	0.28 (0.01) b	0.02
	Fertilized	23.86 (2.10) B	1.68 (0.15) AB	0.87
Dune, 120-yr	Reference	2.46 (0.25) a	0.44 (0.03) a	0.19
	Fertilized	36.67 (3.81) A	2.19 (0.22) A	0.23
Swale, 6-yr		1.01 (0.09) b	0.11 (0.04) b	0.17
Swale, 24-yr		1.01 (0.08) b	0.05 (0.003) b	0.23
Swale, 36-yr		5.16 (0.56) a	0.78 (0.20) ab	0.43
Swale, 120-yr		4.75 (0.44) a	1.25 (0.33) a	1.61

another. The 6-yr swale was significantly lower in NO$_2$ + NO$_3$ (Tukey, P < 0.05) than the 120-yr swale but was not significantly different from the other swales. Annual net nitrogen mineralization also tended to be higher on the older sites, indicating greater nitrogen availability. The fertilization treatment on the dunes resulted in significantly greater NH$_4$ and NO$_2$ + NO$_3$ levels in the soil and higher annual net nitrogen mineralization rates; however, mineralization rates declined in the fertilized areas from the 24-yr to the 120-yr dune (Table 2).

Biomass, dune sites.—The 24-yr-old dune (13.0 g/m^2) was significantly higher in LFRB (Tukey, P < 0.05) than the 6-yr (5.0 g/m^2) and the 120-yr (4.0 g/m^2) dunes, but not significantly higher than the 36-yr-old dune (6.0 g/m^2) (Table 3). Monthly mean live fine root (≤2 mm diam) biomass on all dunes was not significantly different between months

TABLE 3.—Annual means of LFRB (≤2 mm diam) (g/m^{-2}) and fine root production (g m^{-2} yr^{-1}). Production data are only available for the dunes. Different lower-case letters indicate significant differences among dunes (reference sites) or swales (Tukey, P < 0.05). Different upper-case letters indicate significant differences among reference and fertilized sites on the dunes (P < 0.05). One standard error in parentheses

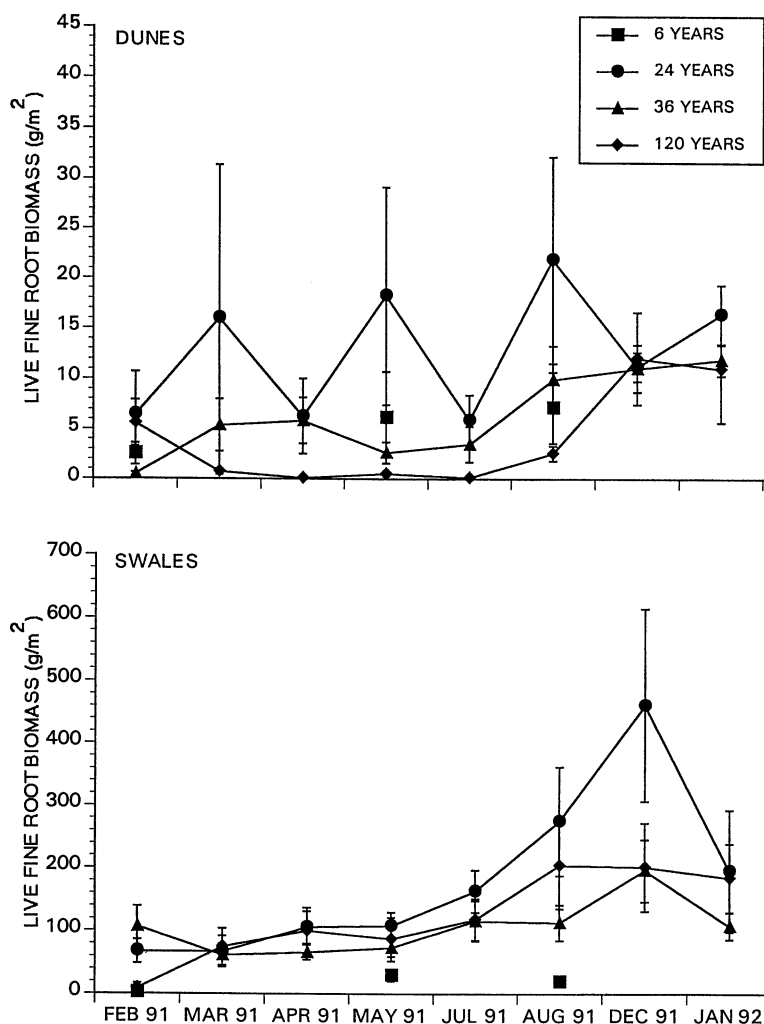| Site		Fine-root biomass	Net fine-root production
Dune, 6-yr		5 (2) b	10 (3) C
Dune, 24-yr	Reference	13 (3) a	18 (4) C
	Fertilized		44 (6) A
Dune, 36-yr	Reference	6 (1) ab	14 (2) C
	Fertilized		40 (5) AB
Dune, 120-yr	Reference	4 (1) b	17 (3) C
	Fertilized		26 (4) B
Swale, 6-yr		16 (4) c	
Swale, 24-yr		180 (27) a	
Swale, 36-yr		105 (10) b	
Swale, 120-yr		122 (17) ab	

FIG. 2.—Monthly means (g/m²) LFRB of (≤2 mm diam) (g/m²) along the chronosequence of dunes and swales. The live fine roots represent all depths combined (0–40 cm) for each sampling period. The 6-yr site was sampled Feb., May and Aug., not monthly like the other sites. Vertical bars are ± 1 SE

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 most variability. It followed a pattern of alternating highs and lows from February 1991–January 1992, but the standard error per month was so large it was hard to say if there was a significant alternating high-low pattern (Fig. 2). The 24-yr dune monthly mean LFRBs were significantly different (Tukey, $P < 0.05$) from those on the 6-yr or 120-yr-old dunes (Fig. 2).

There were significant differences in the distribution of annual mean LFRB over the soil profile. LFRB was significantly higher in the top 20-cm depths, in comparison to the lower

TABLE 4.—Annual means (g/m²)LFRB of (≤2 mm diam) by depth and site type. Split-plot ANOVA determined significant differences between site types (P < 0.0001). Different letters indicate significant differences between depths (Tukey, P < 0.05). One standard error in parentheses

Site	Depth in cm	Biomass (g/m²)	Annual percent per depth
Dune	10	9.0 (5) ab	29.0
	20	12.0 (3) a	38.7
	30	7.0 (3) ab	22.6
	40	3.0 (1) b	9.7
Swale	10	342.41 (45) a	70.0
	20	74.04 (20) b	15.1
	30	38.64 (6) b	7.9
	40	34.37 (6) b	7.0

40 cm (Tukey, P < 0.05) (Table 4). Thirty-nine percent of the LFRB in the cores was located in the top 20 cm.

Biomass, swale sites.—Percentages of LFRB of total biomass decreased across the swale chronosequence (Table 3). The 6-yr-old swale had the highest percentage of LFRB (27%) and was similar to the 24-yr swale (24%). The 6-yr-old swale had significantly lower annual mean LFRB (16 g/m²) in comparison to all other swales. The percentage of LFRB in TB for the 24-yr and 36-yr swales were not significantly different from each other.

Only one biomass peak was observed for monthly mean LFRB. Generally, LFRB increased in swales from February 1991 to a maximum in December 1991. There were no significant differences among months during March 1991–August 1991 (Fig. 2). The highest peak occurred in the 24-yr swale. The 24-yr swale's LFRB during December 1991 was significantly different from its LFRB during February 1991–July 1991 (Tukey, P < 0.05). The 36-yr and 120-yr swales were not significantly different from each other during the study. The 24-yr swale produced the largest annual mean LFRB (180 g/m²) and was significantly different (Tukey, P < 0.05) from the other swales.

There were significant differences in LFRB distribution by depth (Split-plot ANOVA, P < 0.0001). Seventy percent of the LFRB was concentrated in the upper 10 cm. There was a significant difference (Tukey, P < 0.05) between the upper 10 cm (342.41 g/m²) depth and the lower 20-cm, 30-cm and 40-cm depths (74.04, 38.64 and 34.37 g/m²), respectively (Table 4).

Dune vs. swale LFRB.—The dune and swale sites were determined to be significantly different for LFRB (Split-plot ANOVA, P ≤ 0.0001). Swales had higher annual mean LFRB than dunes (Table 3).

Biomass distributions were similar for dunes and swales (Table 4). Both had higher LFRB quantities in the upper 10–20 cm. Swale LFRB (342.41 g/m²) in the upper 10 cm was significantly higher (Split-plot ANOVA, P < 0.0001) than the dunes LFRB (9.0 g/m²). A higher percentage of LFRB was allocated to the upper 10 cm in swales (70%) than dunes (29%).

Fine root production response to N-fertilization.—N-fertilized plots were significantly higher (Split-plot ANOVA, P < 0.0001) in fine root production than the reference plots (Table 3). Fine root production rates were not significantly different among the reference sites. N-fertilized plots showed a pattern of significantly decreased production rates across the dune chronosequence (Tukey, P < 0.05). The fertilized 24-yr dune (44 g m⁻² yr⁻¹) was not

TABLE 5.—Total nitrogen and phosphorus in live fine roots from biomass harvest and in-growth production (% dry mass). Lumping samples resulted in inadequate replication for statistical comparisons

Site		Nitrogen		Phosphorus	
		Biomass	Ingrowth production	Biomass	Ingrowth production
Dune, 6-yr		0.65	0.59	0.064	0.050
Dune, 24-yr	Reference	0.90	1.03	0.105	0.060
	Fertilized		1.80		0.065
Dune, 36-yr	Reference	1.34	0.90	0.115	0.045
	Fertilized		1.33		0.055
Dune, 120-yr	Reference	1.59	1.13	0.122	0.050
	Fertilized		1.83		0.055
Swale, 6-yr		0.91		0.065	
Swale, 24-yr		1.08		0.098	
Swale, 36-yr		1.89		0.056	
Swale, 120-yr		2.01		0.061	

significantly different than the fertilized 36-yr dune (40 g m^{-2} yr^{-1}) but was significantly higher than the fertilized 120-yr-old dune (26 g m^{-2} yr^{-1}) (Tukey, P < 0.05).

Live fine root nutrient concentrations.—Mean total Kjeldahl nitrogen (TKN) in root tissues increased in concentration across the chronosequence (Table 5). Root nitrogen was higher in the swales than the dunes. Nitrogen concentrations were relatively similar between the two younger (6- and 24-yr) dunes and between the two younger swales. Similar nitrogen content was found in the two older (36- and 120-yr) dunes and in the two older swales. 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.

Similar root nutrient analyses were conducted for fine roots obtained from the production measurements, 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 (Table 5). Total phosphorus root content was similar between reference and fertilized plots along the dune chronosequence. Total phosphorus levels were dramatically lower than TKN levels.

Root nitrogen content was significantly higher in N-fertilized plots than reference plots, as expected (Table 5). The reference plots showed slightly increased root nitrogen content across the chronosequence, similar to the pattern observed in the LFRB of the biomass study. The lowest N levels were in the 6-yr dune (0.59% of mass) and the highest levels in the 120-yr dune (1.13% of mass). The fertilized plots showed a different pattern. Root nitrogen content was similar between the 24-yr (1.79% of mass) and 120-yr (1.83% of mass) dunes while the 36-yr dune had a slightly lower root nitrogen content (1.33% of mass) (Table 5). 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 are exposed to higher wind conditions and moving sand, and poorer soil development than associated swale com-

munities. 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, as low depressions along the chronosequence, collect water and sediment, create a moist soil environment and provide 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 provide a base to help explain differences between community types. In the present study, site, community type, N-availability and hydrology all interacted and influenced LFRB and production.

LFRB generally decreased across the chronosequence from the 24-yr to 120-yr sites. 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 across the chronosequence. 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* alters root morphology to survive anaerobic 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, whereas under dry conditions fewer roots and less total biomass were produced (Knapp and Seastedt, 1986; Hayes and Seastedt, 1987). In addition, water can limit nitrogen availability in the soil which can also influence root production (Kachi and Hirose, 1983; Nobel *et al.*, 1989).

Soil nitrogen levels and root nitrogen concentrations increased across the chronosequence. 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) found higher concentrations in older communities than in younger communities. In the present study similar patterns were observed. The soils on Hog Island were identified as nitrogen-limited (Hayden *et al.*, 1991). Even though net nitrogen mineralization rates increased across the chronosequence, 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 biomass. Kachi and Hirose (1983) observed plant growth in sandy soils was affected by the nutrient status of the soil environment.

Depth variations.—LFRB was concentrated in the upper 10–20 cm. Biomass concentration in the upper soil horizon did not differ between dunes and swales, but swales had proportionally more in the upper 10 cm than the dunes. Forested and marsh systems (Roman and Daiber, 1984; Schubauer and Hopkinson, 1984; Ellison *et al.*, 1986); swamp forest (Powell and Day, 1991) and tallgrass prairie (Hayes and Seastedt, 1987) exhibited similar patterns of higher concentrations of fine roots in the top 10–20 cm of the soil profile. Conn and Day (1993) similarly found higher concentrations of fine roots in the upper 10 cm of soil on Hog Island. Schubauer and Hopkinson (1984) suggested that roots are concentrated in the upper depths close to the surface because remineralization and nutrient supplies are greatest there.

Dune vs. swale.—LFRB in the dunes remained relatively unchanged across the chronosequence. Swales showed a general decrease in LFRB across the island. Greater LFRB in the swales than the dunes may be associated with the type of roots and soil environment. The roots in the dunes were generally shorter-lived perennial roots growing in a xeric soil environment. The swales contained two general types of roots in a 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 longer lived, woody *Myrica cerifera* roots (Conn and Day, 1993).

Seasonal patterns differed between the dune and swale sites in terms of LFRB. LFRB in the swale sites seemed not to respond as dramatically to periods of higher water table as did the dunes. The dune communities showed high variability through the year corresponding to the variability in the water table. 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 roots of perennials increased well after the onset of regular frosts.

Effects of fertilization.—Nitrogen additions in the form of urea fertilizer significantly increased production rates on all dunes. 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). Productivity rates were higher in the upper depths for both reference 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. Production rates in the fertilized sites for the 24-yr and 36-yr dunes were 2.5 times those observed in their reference sites in contrast to 1.5 times for the 120-yr dune. Even though nitrogen concentrations in the soil were highest on the oldest fertilized site, nitrogen availability was lowest as evidenced by nitrogen mineralization rates.

The younger reference sites were more limited in nitrogen than the older reference sites so they might be expected to have a greater response to nitrogen additions. Greater nitrogen availability in the 120-yr reference site may be influenced by *Myrica cerifera* thicket encroachment. *Myrica cerifera* has nitrogen fixing root nodules and may have contributed additional nitrogen to the soil through nitrogen-rich litterfall. The nitrogen levels in the soil on the 120-yr dune may have reached concentrations at which additional nitrogen was sequestered in organic matter or elsewhere and not mineralized and made available. Studies have shown increases in nitrogen levels can decrease the root: shoot ratio and increase allocation of nutrients to areas were supplies were lower (Lajtha and Schlesinger, 1988; Nobel *et al.,* 1989).

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. Our results suggest that fine roots play an important role in ecosystem processes, including nutrient cycling, on barrier islands.

LITERATURE CITED

ABER, J. D., J. M. MELILLO, K. J. NADELHOFFER, C. A. McCLAUGHERTY AND J. PASTOR. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia,* **66**:317–321.

BERTNESS, M. C. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology,* **72**:138–148.

BOHM, W. 1979. Methods of studying root systems. Springer-Verlag, New York, N.Y. 188 p.

BOWMAN, W. D., T. A. THEODOSE, J. C. SCHARDT AND R. T. CONANT. 1993. Constraints of nutrients availability on primary production in two alpine tundra communities. *Ecology,* **74**:2085–2097.

BURDICK, D. M. 1989. Root aerenchyma development in *Spartina patens* in response to flooding. *Am. J. Bot.,* **76**:777–780.

CONN, C. E. AND F. P. DAY. 1993. Belowground patterns on a coastal barrier island in Virginia. *Bull. Torrey Bot. Club,* **120**:121–127.

DAHLMAN, R. C. AND C. L. KUCERA. 1965. Root productivity and turnover in native prairie. *Ecology,* **46**: 84–89.

DAY, F. P. 1995. Environmental influences on belowground decomposition on a coastal barrier island determined by cotton strip assay. *Pedobiologia,* **39**:289–303.

DE LA CRUZ, A. A. AND C. T. HACKNEY. 1977. Energy value, elemental comparison and productivity of belowground biomass of a *Juncus* tidal marsh. *Ecology,* **58**:1165–1170.

DUESER, R. D., M. A. GRAHAM, G. J. HENNESSY, C. MCCAFFREY, A. W. NIEDERODA, T. W. RICE AND B. WILLIAMS. 1976. Ecosystems description: the Virginia coast reserve study. The Nature Conservancy, Arlington, Va. 568 p.

EHRENFELD, J. G. 1990. Dynamics and processes of barrier island vegetation. *Aquat. Sci.,* **2**:437–480.

ELLISON, A. M., M. D. BERTNESS AND T. MILLER. 1986. Seasonal patterns in the belowground biomass of *Spartina alterniflora* (Gramineae) across a tidal gradient. *Am. J. Bot.,* **73**:1548–1554.

FAULKNER, S. P., W. H. PATRICK AND R. P. GAMBELL. 1989. Field techniques for measuring wetland soil parameters. *Soil Sci. Soc. Am. J.,* **53**:883–890.

FAHRIG, L., B. HAYDEN AND R. DOLAN. 1993. Distribution of barrier island plants in relation to overwash disturbance: a test of life history theory. *J. Coastal Res.,* **9**:403–412.

GALLAGHER, J. L. AND F. G. PLUMLEY. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *Am. J. Bot.,* **66**:156–161.

GLEESON, S. K. AND D. TILMAN. 1990. Allocation and transient dynamics of succession on poor soils. *Ecology,* **71**:1144–1155.

GREGORY, P. J. 1987. Root development and function, p. 147–166. *In:* P. J. Gregory, J. V. Lake and D. A. Rose (eds.). Society for Experimental Biology, Seminar Series 30. Cambridge University Press, Cambridge, Mass.

HAYDEN, B. P., R. D. DUESER, J. T. CALLAHAN AND H. H. SHUGART. 1991. Long-term research at the Virginia Coast Reserve. Modeling a highly dynamic environment. *BioScience,* **41**:310–318.

HAYES, D. C. AND T. R. SEASTEDT. 1987. Root dynamics of tallgrass prairie in wet and dry years. *Can. J. Bot.,* **65**:787–791.

HOWES, B. L., J. W. H. DACEY AND J. M. TEAL. 1985. Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology,* **66**:595–605.

KACHI, N. AND T. HIROSE. 1983. Limiting nutrients for plant growth in coastal sand dune soils. *J. Ecol.,* **71**:937–944.

KNAPP, A. K. AND T. R. SEASTEDT. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience,* **36**:662–668.

LAJTHA, K. AND W. H. SCHLESINGER. 1988. The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. *Ecology,* **69**:24–39.

LUND, Z. F., R. W. PEARSON AND G. W. BUCHANAN. 1970. An implanted soil mass technique to study herbicide effects on root growth. *Weed Sci.,* **18**:279–281.

MCCLAUGHERTY, C. A., J. D. ABER AND J. M. MELILLO. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology,* **63**:1481–1490.

NADELHOFFER, K. J. AND J. W. RAICH. 1992. Fine root production estimates and belowground carbon allocation in forested ecosystems. *Ecology,* **73**:1139–1147.

———, J. D. ABER AND J. M. MELILLO. 1985. Fine roots, net primary production and soil nitrogen availability: a new hypothesis. *Ecology,* **66**:1377–1390.

NEIL, C. 1992. Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology,* **73**:1918–1921.

NOBEL, P. S., E. QUERO AND H. LINARES. 1989. Root versus shoot biomass: responses to water, nitrogen, and phosphorus applications for *Agave lechuguilla. Bot. Gaz.,* **150**:411–416.

PERSSON, H. 1983. The distribution and productivity of fine roots in boreal forest. *Plant Soil,* **71**:87–101.

PEZESHKI, S. R., S. W. MATTHEWS AND R. D. DELAUNE. 1991. Root cortex structure and metabolic responses of *Spartina patens* to soil redox conditions. *Environ. Exp. Bot.,* **31**:91–97.

POWELL, S. W. AND F. P. DAY. 1991. Root production in four communities in the Great Dismal Swamp. *Am. J. Bot.,* **78**:288–297.

ROMAN, C. T. AND F. C. DAIBER. 1984. Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes. *Bull. Torrey Bot. Club,* **78**:288–297.

ROSE, S. L. 1988. Above and belowground community development in a marine sand dune ecosystem. *Plant Soil,* **109**:215–226.

SANTANTONIO, D. A. AND J. C. GRACE. 1987. Estimating fine root production and turnover from biomass and decomposition data: a compartment-flow model. *Can. J. For. Res.,* **17**:900–908.

SAS INSTITUTE INC. 1985. SAS user's guide: Statistics. Cary, N.C.

SCHUBAUER, J. P. AND C. S. HOPKINSON. 1984. Above and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnol. Oceanogr.,* **29**:1052–1065.

SEASTEDT, T. R. 1988. Mass nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology,* **69**:59–65.

SMITH, K. K., R. E. GOOD AND N. F. GOOD. 1979. Production dynamics for above and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine Coastal Mar. Sci.,* **9**: 189–201.

SYMBULA, M. AND F. P. DAY. 1988. Evaluation of two methods for estimating belowground production in a freshwater swamp forest. *Am. Midl. Nat.,* **74**:405–415.

TECHNICON INDUSTRIAL SYSTEMS. 1977. Individual/simultaneous determination of nitrogen and phosphorus in BD acid digests. Industrial Method No. 329-74w/B. Technicon Industrial Systems, Tarrytown, New York.

VALIELA, I., J. M. TEAL AND N. Y. PERSSON. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. *Limnol. Oceanogr.,* **21**:245–252.

WILSON, S. D. AND D. TILMAN. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology,* **74**:599–611.